University of Alberta

Spatial associations of beaver ponds and culverts in boreal headwater streams

by

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Abstract

Beavers and culverts can cause impoundments in streams and thus, influence wetland distribution. I examined change in beaver dams and beaver ponds in response to culvert presence and environmental covariates at scales of < 50m, 300m, and 1,000m using forest inventory and time-series aerial photography. Covariates were regressed using GLMs and GLMMs and the top models predicting dam occurrence were selected using AIC. Forest inventory analysis indicated beaver pond occurrence at the 300m scale was positively related to culvert presence on second-order streams. Beaver occurrence was not significantly related to culvert presence at the 1,000m scale. Proportion of inundated stream was positively related to forested area and third-order streams at 300m scale. From aerial photograph analysis, intact beaver dams at the 300m scale were positively related to culverts when beaver dams were present prior to culvert installation regardless of stream order. My results show that culverts may affect beaver activity and subsequently wetland distribution in boreal northcentral, Alberta.

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Chapter 1 Literature review

1.1 Research scope and rational: Effects of beavers and roads on wetlands

Wetlands along streams are influenced by ecosystem dynamics of the stream and the riparian zone (the land surrounding the stream). Anthropogenic and natural disturbances can affect water flow which can subsequently change how wetland ecosystems function. In my research I studied two disturbances that affect stream and terrestrial ecosystems: beavers (*Castor canadensis*) and culverts. Beavers and culverts can cause disturbances to water flow and flow volume, thus influencing wetland formation and persistence. Forest users such as forest companies, petroleum extraction businesses, peat harvesters, trappers, and recreationists are aware of the importance of water yield, water quality, and flood prevention. The presence and arrangement of beaver dams in Alberta riparian zones were hypothesized to influence the way water and vegetation respond on the landscape as well as the response of road-building endeavors. I related abundance and distribution of beaver dams and ponds in headwater systems to culvert presence, and the scale at which beaver activity may be affected by culvert presence. My study was designed to detect change in beaver dams and ponds in response to culvert presence at scales of < 50m, 300m, and 1,000m.

Beavers cause natural disturbances that create wetlands (herein, beaver ponds) and maintain riparian vegetation in stream ecosystems, by damming watercourses and felling trees. Roads and culverts/bridges (herein, stream crossings) are prevalent human disturbances that may redirect sub-surface water flow to the surface (Forman and Alexander 1998) and increase sediment release into streams (Trombulak and Frissell 2000, Lane and Sheridan 2002). Culverts alter flood regimes, lateral channel migration, and increase sedimentation (Jeglum 1975, Forman and Alexander 1998, Jones et al. 2000, Jensen et al. 2001). When water is impounded by a beaver dam or culvert, 1) riparian plants replace upland species, 2) flooded trees die and become snags, and 4) the area of open surface water increases. Riparian zone vegetation characteristics of beaver ponds created by plugged culverts or beaver dams in close proximity to culverts (< 50m) are different from beaver ponds not associated with culverts (Martell 2004). It is unknown if impoundment of water by beaver dams built near culverts affects beaver distribution and activity locally or at the scale of the stream network.

Results of my thesis could be used to improve management of road infrastructure to minimize effects on wetland distribution and wetland characteristics. This research also increases the knowledge of pattern and abundance of beaver activity in boreal headwater streams in northcentral, Alberta.

1.2 Definitions and terminology

In this thesis I use the following definitions:

Allochthonous input – matter entering a system that originates outside the system.

Beaverscape – the region of current or potential beaver impoundment, meadow, and foraging area.

Boreal forest - the boreal forest ecozone of Canada as defined in Ecoregions Working Group, (1989)

Culvert – a cylinder or box made out of metal or wood that allows water to pass under a road. In my thesis all culverts were corrugated metal cylinders averaging 0.5 to 2 metres in diameter.

Downstream – (see also upstream) Location along a stream, relative to a reference point, in the same direction of water flow.

Headwater stream(s) – low order streams, first- to third-order, that usually occur at higher elevation, have a steeper gradient, and are narrower than river systems. I refer to all first- to third-order streams as headwater or *small streams.*

Fluvial – in reference to something within or belonging to a stream, or landform originating from a stream.

Riparian zone – the "three-dimensional ecotones of interaction that include terrestrial and aquatic ecosystems, that extend down into the groundwater, up above the canopy, outward across the floodplain, up the near-slopes that drain to the water, laterally into the terrestrial ecosystem, and along the water course at a variable width" (Ilhardt et al. 2000).

River network – the entire stream and river system (see definitions)

River system – in this thesis I use the term "river system" when referring the water channel network of fourth-order streams and higher, the width of river systems is often > 20m.

Strahler stream order – Strahler (1957) stream ordering system where the streams at the origin of a watershed are assigned an order of one, or first-order. Two first-order streams join to become a second-order, two second-order streams form a third-order stream. A stream/river formed by the conjunction of a higher and a lower ordered stream, retains the higher (larger number) order. The definition of first-order stream is dependent on the spatial scale of the stream network.

Stream system - I use the term "stream system" when referring the water channel network of third-order streams and lower. Although similar to "headwater stream" (see definition), the term "stream system" does not imply the inclusion of the entire network of first- to third-order streams, but a subset.

Upstream – (see also downstream) Location along a stream, relative to a reference point, in the opposite direction of water flow.

Water channel - the area of open water in a stream or river.

Water regime – the typical period of high and low water flow for a stream or river system - may be measured on a daily to yearly basis.

Wetlands - areas inundated with water such that the soil is saturated but the surface water is seasonally or yearly (if permanent) less than 2 metres deep.

1.3 Hydrological dynamics of headwater systems

To understand the scale and magnitude of disturbance effects on stream systems, it is necessary to understand how headwater systems influence ecological function of the river continuum. Headwaters contribute 50 - 80% of the total stream length of the river network (Meyer and Wallace 2001, Gomi et al. 2002, Moore and Richardson 2003). Sub-surface water is collected in the headwaters (Nichols and Verry 2001) and thus is a water source for the downstream river system. Headwater systems are significant sources of nutrients, organic matter, and sediment for the downstream network (Gomi et al. 2002). The water regime of headwater systems influences stream morphology, nutrient transport, and vegetation composition (Townsend 2001). Amoros and Bornette (2002) defined four ways that water transports energy and matter in rivers: 1) longitudinally along the stream network, 2) laterally from upland areas to the water channel, 3) vertically from the surface of the water to the stream bottom and to the groundwater, and 4) temporally where inter-annual variation in water levels drives the exchange of organic matter and inorganic matter and shifts between metabolization and transportation of nutrients. Headwater streams are also sources of dissolved organic carbon. Naiman et al. (1987), in a study based in northern Quebec, reported that first- to third-order streams stored carbon while the carbon was metabolized in seventh- to ninth-order rivers. Disturbance events in headwater systems that affect water flow and nutrient cycling can potentially influence not only ecological processes in the headwaters, but also processes downstream.

Change in water levels, spatially and temporally (Amoros and Bornette 2002), drive many aquatic and terrestrial processes. Cordes et al. (1997) reported that large flood events were responsible for major periods of regeneration of poplar species (*Populus* spp.) in the upper and lower Red Deer River of southern Alberta. Prolonged periods of inundation (without a drawdown period) were correlated with the decline of emergent aquatic plant species (Harris and Marshall 1963). Magnitude and frequency of water level fluctuation also affect the type of river wetlands that are formed (Roulet 2000). Water levels, including periodicity, have a direct effect on soil chemistry and structure, decomposition rates, and availability of soil nutrients (Kozlowski 1997). To understand headwater and downstream ecological linkages, it is necessary to understand what factors influence the water regime of headwater systems. Beaver dams and roads are potential disturbances to the water regime of headwater systems, thus will influence headwater wetland creation and ecology.

1.4 Agents of landscape disturbance in boreal streams

1.4.1 The effects of beavers on headwater hydrology

1.4.1.1 Natural history of beavers

Beavers typically concentrate dam construction in low-order streams (Snodgrass and Meffe 1998, Suzuki and McComb 1998, Johnston and Naiman 1990*a*, McKinstry et al. 2001) where the hydrologic regime and local topography are conducive to maintenance of pond water levels, and where forage and construction material are available. Beavers will colonize high-order rivers and lakes by building lodges along the shore or banks but dam building is not common. Colonies are established family groups (4-5 beavers) consisting of one or two lodges associated with a pond created and maintained by a system of dams. Dams are built in linear succession; an initial dam is built, lowering water levels downstream and raising levels upstream. Subsequent dams are often constructed downstream. Beaver colonies will remain in an area, maintaining dams, as long as forage and construction material are available and if the colony is not predated, extirpated by disease, or trapped. When a beaver dam is abandoned, the stream will eventually either breach or flank the dam, thereby draining the pond and exposing the rich organic soil on which plant communities establish. Drained beaver ponds are commonly called "beaver meadows", as they are initially dominated by forbes, graminoides and shrub species. As colonies come and go, the main headwater channel of beaver influenced systems will often meander, both eroding and depositing sediment.

The spatial extent of beaver influence in stream systems depends on beaver density, which is affected by trapping and hunting, predation, and diseases. Humans have been, and are still, the greatest limitation to beaver distribution and abundance. Prior to the peak of the fur trade in the 1800s, the North American population of beavers was estimated to be 60,000,000 (Hill 1982). Currently, beaver populations are estimated to be 1/10 of historic levels (Hill 1982). Beaver populations in the boreal forest have been recovering since the 1900s, a time when beavers were nearly extirpated from North American (Howard and Larson 1985, Beier and Barrett 1987, Snodgrass 1997). It has not yet been shown however, if the current landscape can support historic beaver population levels.

1.4.1.2 Beavers as an agent of landscape change

Zoogeomorphological agents modify the structure of their physical environment to meet their needs (Butler 1995). Similarly, ecological engineers "build, modify, and destroy habitat in their quest for food and survival" (Rosemond and Anderson 2003). Keystone species modify the surroundings and provide conditions suitable for other organisms that otherwise would not be present (Paine 1966). Beaver are recognized as an ecological engineer (Wright et al. 2002), a zoogeomorphological agent (Naiman et al. 1994, Butler 1995) and a keystone species (Paine 1966) in river landscapes.

Beyond modifying the landscape locally, beaver dams change flood regimes, stream channel morphology, and cause vegetation change within the riparian zone (Rudemann and Schoonmaker 1938, Naiman et al. 1986, Naiman et al. 1988, Johnston and Naiman 1990*b*). Outside of wildlife biology research, beaver influences on hydrology are rarely recognized. For example, a review of fluvial geomorphology (Dollar 2000), did not mention beaver as a driver of landscape change. Wildlife and wetland literature however, support the concept of the beaver as a driver of aquatic and terrestrial processes in headwater streams (Johnston and Naiman 1987, Naiman et al. 1988, Naiman et al. 1994).

1.4.1.3 Effects of beaver on headwater systems

Naiman et al. (1986) identified seven ways that beavers change the river landscape; they: "1) modify channel geomorphology, 2) increase retention of sediment and organic matter, 3) create and maintain wetlands, 4) modify nutrient cycling and decomposition dynamics by wetting soils, by altering the hydrologic regime, and by creating anaerobic zones in soils and sediments, 5) modify the riparian zone, including the species composition and growth form of plants, their chemistry, and the quantity of allochthonous inputs, 6) influence the character of water and material transported downstream and 7) modify habitat [sic]". Gurnell (1998) summarized the hydrogeomorpological influence of dams: "1) the ponds above the dams will act to sustain low flows and to attenuate flood peaks, 2) increased complexity of the stream network and water table, and 3) increased sediment storage". When a beaver dam fails, the effects can be measured kilometres downstream of the site, resulting in a disturbance to the river system – especially if the failure of one dam causes a domino effect, where the flood wave causes dams downstream to fail (Hillman 1998). Thus, dam "blow-out" is a disturbance to the water regime that causes long lasting effects on aquatic and riparian processes.

Increased flora and fauna species richness is linked to the presence of beaver ponds and meadows in the stream system. Beaver activity affects species diversity in terrestrial and aquatic systems by introducing variation in pond age, altering stream flow rate, and changing water distribution (drying and wetting).

As beaver ponds age, new organisms colonize available habitat. A headwater system with ponds of varying age should have higher species richness. Ray et al. (2001) reported that pond age and the number of neighbouring ponds within 250m explained significant variation in macrophyte species richness of Minnesota beaver pond bogs. Snodgrass and Meffe (1998) also reported a correlation between beaver pond age and fish species richness in the Upper Coast Plain of South Carolina. Fish species richness was highest for young ponds (9-17 years) and decreased in older ponds (> 17 years). In northern Ontario however, Barnes and Mallik (2001) reported that there were no significant differences in vegetation species richness, diversity, or evenness within 40m of recent and old abandoned impoundments (n=15).

One of the mechanisms promoting increased species richness is the change in water flow caused by beaver dams; water flow rate upstream of a dam is decreased and downstream water flow rate is increased. Schlosser (1995) concluded that flora and fauna adapted to specific flow conditions around beaver dams replaced the previous community. Species diversity in catchments dominated by streams with fast moving water may increase when a mosaic of beaver ponds introduces sections of slow moving water into the landscape (Collen and Gibson 2001). Beaver dams may increase invertebrate habitat diversity in otherwise slow moving water (Clifford et al. 1993). Beaver alteration to stream flow can be advantageous or disadvantageous for certain fish species. Schlosser (1995) reported that beaver ponds acted as "reproductive sources for fish", but the adjacent stream acted as potential sinks. Metts et al. (2001) concluded that some herpetofaunal communities adapted to lentic systems benefited from beaver ponds as compared to unimpounded stream sections (n=3) in the Piedmont of South Carolina.

Beaver impoundments have a direct effect on wetland and species diversity in river landscape through changes to the water distribution. Upstream of dams, the stream channel is widened as water pools behind dams. McKinstry et al. (2001) reported that waterfowl abundance was higher in streams with beaver than without, primarily due to the increase in width of the stream.

Spatial and temporal dynamics of beaver pond creation and abandonment influence headwater species richness (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). Pollock et al. (1998) reported that plant species richness in southeast Alaska was highest at intermediate flood events or events that had high spatial variation at scales of 1 m^2 to 1,000m^2. Wright et al. (2002) proposed that beavers increased herbaceous species richness in the riparian zone by 25% because the beavers created habitat conditions not located elsewhere in the landscape. Wright et al. (2002) proposed that it is not the beaver ponds themselves that are species-rich but the collective mosaic of beaver influenced and non-influenced patches in the stream network; if beaver were to completely dominate the landscape species richness at the stream network level would decrease.

Beaver and road ecology within headwater streams can be studied at many different scales, but perceptions of relationships may change depending on the scale at which they are studied. Appropriate scale of study could be beaver dam or culvert, colony or pond, stream reach or, watershed. Levin (1992) suggested that in ecological studies, patterns must be identified before a causative mechanism can be identified and that there is no single correct scale at which to study these ecological relationships. Roads and beaver ponds are large entities that likely affect, and are affected by several different processes acting together in time and space, and different patterns of interaction can emerge at different scales.

1.4.1.4 Magnitude of beaver disturbance over time

The boreal landscape has only recently had beaver numbers in the range where disturbance effects can be measured at the landscape scale. In my study area in northcentral Alberta, beaver were nearly absent in the early 1950s but were abundant in low-order streams by the 1970s (Martell 2004). Given the long absence of beavers from headwater systems, it is unknown whether the current beaverscape is representative of what the beaverscape may have looked like when the density of beavers was higher. Litvaitis (2003) modelled the likely proportion of shrublands and early successional forest in New England under different natural disturbance regimes (beaver, windthrow, defoliating insects, pathogens and irregular fires) in a 4000 ha watershed. With the absence of the aforementioned disturbances, shrublands and early successional forest made up 2% of the watershed; however, with inclusion of modelled disturbances, 6% of the watershed was shrublands and thickets.

Beaver recolonizing abandoned beaverscapes are likely to encounter areas that have not been influenced by beaver for nearly a century. Johnston and Naiman (1990*a*) followed beaver growth trends, in Voyageurs National Park, Minnesota (=290km^2), from 1940, when beaver were nearly extirpated, to 1986 when the landscape was saturated with beaver. Johnston and Naiman (1990*a*) reported that creation of beaver modified patches (ponds) rose rapidly during the first two decades; faster than the beaver population was growing. Johnston and Naiman (1990*a*) suggested that the rate of patch formation was constrained by geomorphology and not available forage. Beaver-modified patches were visible after 46 yrs and no patches had secondary succession. Johnston and Naiman (1990*a*) did not comment on whether this was because colony-sites were never abandoned or if abandoned beavers meadows were stable over the study period.

Given that beavers have just started to influence stream systems since the 1950s throughout north America, albeit not at historical levels, beaver ponds are likely no older than 50 years in most of boreal North America; possibly beaver ponds are younger in age now than they would have been 200 yrs ago. It is difficult to determine then, the characteristics of a "natural riparian" system and therefore how to gauge the magnitude of beavers as a disturbance agent.

1.4.2 The effects of roads on headwater hydrology

Forman (2000) estimated that the area of the coterminous United States affected ecologically by roads is about 19%. Given the ubiquity of roads on the landscape and area ecologically impacted, likely few studies can claim to have a zero road effect (Forman, 2000). Roads affect several hydrological processes: 1) roads can cause subsurface water to pool at the surface and change the direction of subsurface water flow (Forman and Alexander 1998), 2) in wetland areas, roads can block surface and subsurface water flow (Megahan 1972, Wemple et al. 1996), 3) in some streams the placement of a bridge or culvert restricts the movement of the stream, and changes flow rate, 4) roads on hill slopes can concentrate water flow forming stream channels higher up the slope than before the road, thereby elongating the first-order network (Forman and Alexander 1998) and 5) surface water is carried alongside roads through ditches, forming an effective extension of the stream network (Forman and Alexander 1998, Trombulak and Frissell 2000). Trombulak and Frissell (2000) reported two ways that road effects can be persistent through time and space: 1) long-term road use can cause the soil compaction that persists long after the road is decommissioned, and 2) flows of energy downstream can also carry the effect of roads such as increased sedimentation much further than would occur in a terrestrial system. Effects of roads are also sensitive to change in precipitation. Lane and Sheridan (2002) reported that sedimentation release at stream crossings in Australia did not affect water quality (in terms of regulation thresholds). Rainfall events led to turbidity levels high enough to affect water quality for downstream sites, while upstream sites where not affected.

According to Forman and Alexander (1998) "by altering surface or subsurface flow, roads can destroy and create wetland habitat". Few studies have examined effects of culverts on surface and subsurface water movement with respect to wetland ecosystems. Jeglum (1975) reported that a road bisecting a slowly draining peatland valley in Kenogami, Ontario raised the water table 55-cm higher upslope compared to downslope. Jeglum (1975) compared the road to that of a beaver dam with regards to effect on the upstream water table. Upslope vegetation changed to a wet floating-to-spongy sphagnum-dominated mat with pools of water and beaver channels at the edges. Using aerial photography to estimate tree loss over the years following construction of the road, they reported that there was no significant tree loss upslope after 9 years, yet after 21 years, tree loss was significant. Although roads have an effect on stream dynamics by affecting water distribution and flow, effects will be related to road width, type, traffic density, network connectivity and frequency of spur roads into remote areas (Forman and Alexander 1998). Although stream crossings and beavers both affect hydrology, interactions between stream crossings and beavers have been little studied.

1.5 Beaver dam- and colony-site selection in headwater streams

Beaver habitat-selection models distinguish two types of selection: colony-site (Beier and Barrett 1987, Slough and Sadleir 1977, Howard and Larson 1985) and dam-site (McComb et al. 1990, Barnes and Mallik 1997, Jensen et al. 2001, Curtis and Jensen 2004). Most researchers consider dams-sites within 100m of a colony, to have been built and maintained by the colony (Snodgrass, 1997). Although there is some overlap in selection criteria, variables that influence dam-site and colony-site selection may differ. For a colony to establish and persist, forage must be accessible to the beavers. Dam placement however requires specific flow and topographic conditions that are not related to forage. A dam must be created prior to establishment of a colony but the number and location of dams within a colony are not necessary related to other factors dictating colony length (inundated stream) or colony area (pond size).

Biotic and abiotic variables related to beaver dam and colony site selection in the boreal forest are proportion of deciduous/hardwood trees, shrub and grass/sedge cover, watershed area, cross section, gradient, stream width, stream depth, soil moisture, culvert opening, and bank slope. In addition, variables may have interaction effects, for example Curtis and Jensen (2004) reported an interaction between deciduous trees and gradient. Table 1 in Appendix A outlines results of seven beaver habitat selection studies discussed in this section.

Most studies include at least one measure of stream size such as watershed area, stream cross section, or stream depth/width. Watershed area and stream cross section have been positively associated with dam- and colony-site selection (Howard et al. 1985, Barnes, et al. 1997), but mixed results were obtained using stream width and depth (Slough et al. 1977, Howard et al. 1985, Beier et al. 1987, Curtis et al. 2004). Overwhelmingly, gradient was negatively associated with beaver activity (Slough et al. 1977, Howard et al. 1985, Beier et al. 1987, McComb et al. 1990, Jensen et al. 2001, Curtis et al. 2004). Beavers have been shown to establish colonies along stretches of stream with deciduous tree species, particularly *Populus* spp. (Slough et al. 1977, Howard et al. 1985, McComb et al. 1990, Curtis et al. 2004). Coniferous species are frequently used as construction material for dams and lodges but none of the habitat selection studies in Appendix A reported it as a significant variable; only Howard et al. 1985 tested coniferous as a potential covariate. Barnes and Mallik (1996) reported that beavers in northern Ontario selected trees for dam construction based on size, not on species.

Habitat selection models with only vegetation variables do not adequately explain variation in beaver dam- or colony-site selection (Howard and Larson 1985, Beier and Barrett 1987, Suzuki and McComb 1998). Models based on physical variables with and without vegetation variables have explained variance in dam-site selection, colony establishment, and longevity. Despite evidence that culverts and roads affect hydrology, and that beaver frequently dam culverts, only a few studies have explicitly considered stream crossings as a determinant of beaver habitat selection.

1.5.1 Effects of stream crossings on beaver habitat selection

Beavers frequently block culverts with dams (McKinstry and Anderson 1999, Jensen et al. 2001, Curtis and Jensen 2004). Beavers may use ponds formed behind dammed culverts to establish a colony and to access forage tree species from the water's edge (Jeglum 1975). Although there may be an association between culverts and beaver, there is little research that identifies the mechanisms by which beavers respond to culverts, and how or whether culverts affect patterns of beaver activity and ecological processes. To my knowledge, only three peer reviewed papers (McComb et al. 1990, Jensen et al. 2001, Curtis and Jensen 2004), and one M.Sc. thesis (Martell 2004) examined the interaction between stream crossings and beaver.

Martell (2004) compared vegetation change up- and downstream of culverts and beaver dams. She reported that it was not possible to separate the effect of culverts on water levels as beaver almost always dammed culverts where a stream was present. However, Martell (2004) concluded that beavers were a major disturbance agent in low-order streams and documented a marked increase in beaver activity from 1951 to 2001, thereby changing the structure of entire stream reaches. Beaver activity was persistent as dams were frequently re-built over a period of 50 yrs. There was no difference in snag and stand density, or tree basal area between upstream and downstream in culverted beaver ponds. There was little difference between up- and downstream vegetation structure of a dam compared to the culvert. Sample size (n = 6) however, posed a problem in the statistical analysis. McComb et al. (1990) examined key biotic and abiotic variables related to dam-site selection in first- to third-order streams in Oregon using 14 dam sites and 41 random non-dam sites, measuring variables downstream. McComb et al. (1990) reported there was no relationship between dam-selection and distance to anthropic features - bridges, roads, and building. The authors did not separate the effect of culvert presence from other anthropic features. Curtis and Jensen (2004) and Jensen et al. (2001) investigated the relationship of culverts and beaver activity in New York State. They concluded that: 1) the probability of a plugged culvert was not related to deciduous trees near the culvert however, beaver presence near a culvert was related to deciduous trees, 2) gradient was a key variable related to beaver activity both within the culvert and near the culvert, and 3) Jensen et al. (2001) proposed that culverts, constricting water flow in lower gradient streams may present stimuli, like the sound of rushing water, which stimulate dam building. Although these two studies provided insights into beaver habitat use around culverted and non-culverted sites, there is still a gap in understanding differences in beaver activity in culverted and non-culverted streams.

If beavers respond to culvert presence as a favourable habitat condition, at which to construct dams, then the following three questions are raised: 1) Do ponds near culverts have similar characteristics similar to ponds in non-culverted areas?; 2) Are beavers drawn to a culvert and away from other areas thus changing the distribution of beaver across the landscape?; and 3) Do culverts improve sub-optimal beaver habitat? Answers to these questions will have a direct impact on policy guiding culvert installation in beaverscapes.

1.6 Modelling and monitoring stream processes

1.6.1 Mapping stream systems

One of the difficulties with detecting beaver or culvert-caused changes in wetland characteristics is determining temporal and spatial extent of the disturbance. Headwater systems make up the majority of the river network length, although their riparian zones may make up only a fraction of the total area. Additionally, small streams have narrow widths and high edge to length ratio, making them notoriously difficult to map accurately (Lehmann and Lachavanne 1997). Thus it is difficult to quantity changes over time. I will contrast two types of remotely sensed data commonly used to map headwater river ecosystems: satellite imagery and aerial photography.

1.6.1.1 Satellite imagery

LandSat imagery is frequently used to map river systems. The major limitations are the 30m spatial resolution of the sensor, and the ability of the sensor to distinguish different species of vegetation by its spectral signature. Headwater riparian zone widths are < 60m across and the stream width is often < 5m (Congalton et al. 2002, Narumalani et al. 1997). Apan et al. (2002) concluded it was difficult to separate riparian vegetation from upland vegetation based on LandSat spectral signatures, and instead relied on defined riparian widths to describe riparian vegetation - widths ranged from 50 to 200m, for low to high stream orders. Narumalani et al. (1997) classified riparian areas ranging from 30 to 53m in width (one side of the stream) using LandSat imagery represented by 1 or 2 pixels. They did not provide any assessment of accuracy for their analysis. LandSat imagery has been used with more success in larger river systems, associated wetland complexes and open surface water (Bartlett and Klemas 1977, Dottavio 1984). LandSat Thematic Mapper imagery successfully identified beaver impoundments along a 250-km^2 segment of a large river in North Carolina (Townsend et al. 1995). Classification accuracy of the LandSat imagery was improved by including a measure of proximity to preferred vegetation for potential beaver sites. Classification of riparian zones in LandSat imagery can also be improved by using scenes taken at different periods. Lunetta and Balogh (1999) stated that by overlaying leaf-on and leaf-off imagery, they could often pick out riparian vegetation more effectively as water saturated soils and surface water are more easily detected without leaf cover. Accuracy of single-date imagery was 69% while two-date was 88% for classifying wetland habitats. The narrow widths of headwater streams limit the ability of LandSat to map these systems.

1.6.1.2 Aerial photography

Most aerial photography used for vegetation inventory in Canada is available at scales of 1:15,000 or 1:40,000. Air photo interpretation is a standard method for counting beaver colonies (Dickinson 1971, Naiman et al. 1988, Broschart et al. 1989) and monitoring water levels over time (Williams and Lyon 1997).

Congalton et al. (2002) compared LandSat and air photos for mapping riparian vegetation in Oregon. Streams were buffered at widths, 0-15.25 m and 15.25-61 m, to characterize riparian and upland vegetation, respectively, using both LandSat and air photos. The resolution of the LandSat was too coarse to distinguish riparian and upland vegetation. Only 25% of the LandSat agreed with interpreted air photos in the 0-15.25 m buffer and 36% in the 15.25-61 m buffer. Schuft et al. (1999) however, had difficulty using 1:24,000 colour aerial photography to separate the riparian vegetation from upland vegetation and instead used a buffer width of 300m around the stream to define the riparian zone vegetation. Johnston and Naiman (1990*b*) also concluded it was difficult to discern the riparian zone from upland vegetation using 1:24,000 colour late May/early June aerial photographs. They also used a 300m buffer around the stream to distinguish riparian from upland vegetation. Despite some limitations, aerial photography is often used to map riparian vegetation, wetlands, and stream channels using a classification method to categorize landscape features. In the next sections I will discuss the application of existing landcover databases to identify beaver ponds.

1.6.1.3 Mapping remotely sensed data

The utility of maps developed from remotely sensed data often depends more on the classification method used than the resolution of the data from which it was interpreted (Muller 1997). Wetland inventories, such as those published by government agencies, have been shown to be useful for identifying beaver ponds. Gotie and Jenks (1982) used the New York State Freshwater Inventory with U. S. Geological Survey topographic maps to identify areas of beaver occupation. Of 337 sites identified on the wetland maps, 296 were beaver colony sites in the aerial photographs. Beaver activity would not have been the primary purpose of the New York State Freshwater Inventory, but when combined with knowledge of topographic features, and forage and construction material preferred by beavers, it accurately predicted beaver presence. Broschart et al. (1989) reported that shallow marsh and seasonally flooded meadow was a habitat indicator of beaver population trends. Both vegetation and wetland inventories frequently use these categories without necessarily recognizing them as beaver-created features. Broschart et al. (1989) proposed that shallow marshes represented new flooding, and thus, an expanding beaver population. Seasonally flooded meadows had lower water levels, suggesting a decreasing beaver population that is not maintaining dams.

Availability of some habitat types may be systematically underrepresented in some mapped products. Often first-order streams are not mapped accurately or not mapped at all (Snodgrass 1997, Johnston and Naiman 1990*b*, Meyer and Wallace 2001) or they are simplified, underestimating their sinuosity (McCleary et al. 2002). If potential beaver habitat is identified using existing available mapped streams, low-order streams could be underrepresented and therefore such maps cannot inform beaver management policy.

1.6.3 Quantifying change and its drivers in stream systems

Controlled, replicated experiments are difficult to conduct over a large spatial extent. In landscape studies of road effects on wetlands, road presence is "controlled" using spatial and temporal variability. For example, identifying wetlands near a road and those away from a road uses spatial variability, and comparing wetlands before and after presence of a road using time-series data aerial photography uses temporal variability. Research in landscape change has taken advantage of remote sensing technology by using coarse images derived from satellite sensors and aerial photography flown at high and low scale. However, detecting change from one time step to another is usually quantified by analysis of degree of overlap between interpreted maps, or proportional change of landscape components within a defined study area. Detecting drivers of change in stream systems has relied on correlational studies between pre- and post-change landscapes, and a measure of the influential agents on the landscape. Some difficulties associated with such studies are the ability to predict the change taking place, pseudoreplication of observations, and testing alternative hypothesis for mechanisms of change

The effect of a disturbance event within the river system is not always predictable. For example, the response of subsurface water flow to a road varies depending on precipitation, antecedent moisture and flow direction resulting in the wetting up of some areas and drying of others.

River systems are inextricably linked along the river continuum – what happens upstream is likely to affect what happens downstream. Experimental units along the same stretch of stream may not be independent and as such pseudoreplication may be unavoidable. Blocking the treatment into a factorial treatment in an ANOVA style statistical test, can statistically account for pseudodoreplication. However, an ANOVA is only appropriate if the response variable is normally distributed or can be transformed into a normal distribution. Generalized linear models, or GLMs, allow for the modelling of non-Gaussian distributions, and mixed models within GLM (GLMM) allow for nesting or blocking random variables. The mixed model tries to capture variance in the response variable for those experimental units that occur in blocked random effects. Some studies may benefit from such statistical methods when pseudoreplication is an issue.

Traditional hypothesis-testing usually tests a model against a null model or constant mean. Such hypothesis testing in river studies is common. Johnson (1999) recommended exploring alternatives to this approach, as "the null hypothesis about the properties of a population is almost always known *a priori* to be false". Anderson et al. (2000) also discourage the use of the null model hypothesis testing, as it is "an artefact of the statistical test". These authors recommend the use of information-theoretic methods that have several *a priori* models tested at the same time. Each hypothesis can be ranked according to its weight of evidence against all other proposed models.

1.7 Overview of thesis chapters

Beaver activity increases species richness in headwater systems and alters stream channel morphology. Channel morphology can be modified up- and downstream of the immediate beaver pond through alteration of water flow, sediment deposition and translocation, and nutrient inputs. Culverts themselves also affect sedimentation patterns, flood regime, and stream channel migration. Beaver, possibly due to constriction of the stream channel or sound cues, frequently dam culverts. Although dams and culverts may influence ecological processes, beaver behaviour may change with culvert presence. If culvert presence affects beaver activity, it is unknown at what scale this interaction occurs.

In chapters two and three I examined the relationship between beaver activity and culverts. In chapter two I used coarse resolution data to develop surrogate measures of beaver pond occurrence and the lengths of inundated streams. I documented the distribution of beaver ponds in the study area. In that chapter, I had three research objectives: 1) establish the degree of utility of vegetation inventory for quantifying beaver influence on the landscape, 2) describe location and abundance of both beaver activity and stream crossings as distributed within the river network, and 3) describe the relationship of both beaver presence and proportion of inundated stream in culverted and non-culverted streams in headwater systems, at two scales 300m and 1,000m from culverts and associated landscape variables. In chapter three I used aerial photography from 1976-78 to 1999-2001 to measure beaver activity using abundance of intact and breached dams, inundated stream length and pond area. I related beaver activity to culvert presence within headwater streams. In this chapter my objective was to describe change in beaver activity over a 24-26 year period (1976-78 to 1999-2000) at three spatial scales: 1) **third-order watershed** using a sub-sample of selected streams 2) **stream** 300m up- and downstream of culverted streams in a paired control treatment and 3) **site** 5m and 50m up- and downstream from culverts. As indices of beaver activity, I used abundance of dams (intact and breached), and length of stream inundated by a beaver ponds and beaver pond size.

1.8 Literature cited

Amoros, C., Bornette, G. 2002. Connectivity and Biocomplexity in Waterbodies of Riverine Floodplains. Freshwater Biology 47:761-776.

Anderson, D.R., Burnham, K.P. Thompson, W. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.

Apan, A., Raine, S.R., Paterson, M.S. 2002. Mapping and analysis of changes in the riparian landscape structure of the Lockyer Valley catchment, Queensland Australia. Landscape and Urban Planning Journal 59:43-47.

Barnes, D.M., Mallik, A.U. 1996. Use of woody plants in construction of beaver dams in northern Ontario. Canadian Journal of Zoology 74:1781-1786.

Barnes, D.M., Mallik, A.U. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. Journal of Wildlife Management 61:1371-1377.

Bartlett, D.S., Klemas, V. 1977. Variability of wetland reflectance and its effect on automatic categorization of satellite imagery. Photogrammetric Engineering and Remote Sensing 43: 742-42.

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

Broschart, M.R., Johnston, C.A., Naiman, R.J. 1989. Predicting beaver colony density in boreal landscapes. Journal of Wildlife Management 53:929-934.

Butler, D.R. 1995. Zoogeomorphology: animals as geomorphic agents. Cambridge University Press, New York , New York, USA.

Clifford H.F., Wiley G.M., Casey R.J. 1993. Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. Canadian Journal of Zoology 71:1439-1447.

Collen, P., Gibson, R.J. 2001. The general ecology of beavers (Castor Spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. Reviews in Fish Biology and Fisheries 10:439-461.

Congalton, R.G., Birch, K., Jones, R., Schriever, J. 2002. Evaluating remotely sensed techniques for mapping riparian vegetation. Computers and Electronics in Agriculture 37:113-126.

Cordes, L.D., Hughes, M.R., Getty, M. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. Journal of Biogeography 24:675-695.

Curtis, P.D., Jensen, P.G. 2004. Habitat features affecting beaver occupancy along roadsides in New York state. Journal of Wildlife Management 68:278-287.

Dickinson, N.R. 1971. Aerial photography as an aid in beaver management. New York Fish and Game Journal 18:57-61.

Dollar, E.S.J. 2000. Fluvial geomorphology. Progress in Physical Geography 24:385-406.

Dottavio, C.L. 1984. Potential benefits of new satellite sensors to wetland mapping. Photogrammetric Engineering and Remote Sensing 50:599-606.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Ecological Land Classification Series No. 23. Ottawa, Ont., Sustainable Development Branch, Conservation and Protection, Environment Canada.

Forman, R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14:31-35.

Forman, R.T.T., Alexander, L.E. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-231.

Gomi, T., Sidle, R.C., Richardson, J.S. 2002. Understanding processes and downstream linkages of headwater systems. Bioscience 52:905-916.

Gotie, R., Jenks, D. 1982. Assessment of the use of wetland inventory maps for determining potential beaver habitat. New York Fish and Game Journal 31:55-62.

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

Harris, S.W., Marshall, W.H. 1963. Ecology of water-level manipulations on a northern march. Ecology 44:331-334.

Hill, E. P. 1982. Beaver. Pages 256-281 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America. Johns Hopkins Univ. Press, Baltimore, MD.

Hillman, G.R. 1998. Flood wave attenuation by a wetland following a beaver dam failure on a second order boreal stream. Wetlands 18:21-34.

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

Ilhardt, B.L., Verry, E.S., and Palik, B.J. 2000. Defining riparian areas. Pages 23-42 *in* Ilhardt, B.L., Verry, E.S., Palik, B.J. editors. Riparian management in forests of the continental eastern United States. Lewis Publishers, New York, New York, USA.

Jeglum J.K. 1975. Vegetation-habitat Changes Caused by Damming a Peatland Drainageway in Northern Ontario. Canadian Field-Naturalist 89:400-412

Jensen, P.G., Curtis, P.D., Lehnert, M.E., Hamelin, D.L. 2001. Habitat and structural factors influencing beaver interference with highway culverts. Wildlife Society Bulletin 29:654-664.

Johnson, D.H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763-772.

Johnston, C.A., Naiman, R.J. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1:47-57.

Johnston, C.A., Naiman, R.J. 1990. Aquatic patch creation in relation to beaver population trends. Ecology 71:1617-1621.

-----. 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5-19.

Jones, J.A., Swanson, F.J., Wemple, B.C. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14:76-85.

Kozlowski, T.T. 1997. Responses of woody plants to flooding and salinity. Tree Physiology Monograph 1:1-17.

Lane, P.N.J., Sheridan, G.J. 2002. Impact of an unsealed forest road stream crossing: water quality and sediment sources. Hydrological Processes 16:2599-2612.

Lehmann, A., Lachavanne, J.B. 1997. Geographic information systems and remote sensing in aquatic botany. Aquatic Botany 58:195-207.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Litvaitis, J.A. 2003. Are pre-Columbian conditions relevant baselines for managed forests in the northeastern United States? Forest Ecology and Management 185:113-126.

Lunetta, R.S., Balogh, M.E. 1999. Application of multi-temporal Landsat 5 TM imagery for wetland identification. Photogrammetric Engineering and Remote Sensing 65:1303-1310.

Martell, K.A. 2004. Patterns of riparian disturbance in Alberta's boreal mixedwood forest: beavers, roads and buffers. Thesis. University of Alberta, Edmonton, Alberta, Canada.

McCleary, R., Weik, C., and Blackburn, J. 2002. Comparison between field surveyed and GIS derived descriptors of small streams within the west-central foothills of Alberta. Foothills Model Forest, Alberta, Canada.

McComb, W.C., Sedell, J.R., Buchholz, T.D. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50:273-281.

McKinstry, M.C., Caffrey, P., Anderson, S.H. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American water resources association 37:1571-1577.

McKinstry M.C, Anderson S.H. 1999. Attitudes of private- and public-land managers in Wyoming, USA, toward beaver. Environmental Management 23:95-101.

Megahan, W.F.1. 1972. Subsurface flow interception by a logging road in mountains of central Idaho. Pages 350-356 *in* Proceedings of a national symposium of watersheds in transition. American Water Resources Association, Bethesda, Maryland, USA.

Metts, B.S., Lanham, J., Drew, Russell, K.R. 2001. Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the Upper Piedmont of South Carolina. The American Midland Naturalist 145:54-65.

Meyer, J.L. and J.B. Wallace. 2001. Lost linkages and lotic ecology: rediscovering small streams. Pages 295-317 *in* M. Press, N. Huntly and S. Levin editors. Ecology: Achievement and Challenge. Blackwell Science, Oxford, UK.

Moore, D.R., Richardson, J.S. 2003. Progress towards understanding the structure, function, and ecological significance of small stream channels and their riparian zones. Canadian Journal of Forest Resources 33:1349-1351.

Muller, E. 1997. Mapping riparian vegetation along rivers: old concepts and new methods. Aquatic Botany 58:411-437.

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

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

Naiman, R.J., Melillo, J.M., Lock, M.A. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68:1139-1156.

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

Narumalani, S., Zhou, Y., Jensen, J.R. 1997. Application of remote sensing and geographic information systems to the delineation and analysis of riparian buffer zones. Aquatic Botany 58:393-409.

Nichols, D.S., Verry, E.S. 2001. Stream Flow and Ground Water Recharge From Small Forested Watersheds in North Central Minnesota. Journal of Hydrology 245:89-103.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

Pollock MM, Naiman RJ, Hanley TA. 1998. Plant species richness in riparian wetlands- a test of biodiversity theory. Ecology 79:94-105.

Ray, A.M., Rebertus, A.J., Ray, H.L. 2001. Macrophyte succession in Minnesota beaver ponds. Canadian Journal of Botany 79:487-499.

Rosemond, A.D., Anderson, C.B. 2003. Engineering role models: do non-human species have the answers? Ecological Engineering 20:379-387.

Roulet, N.T. 2000. Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: prospects and significance for Canada. Wetlands 20:605-615.

Rudemann, R., Schoonmaker, W.J. 1938. Beaver dams as geologic agents. Science 88:523-525.

Schlosser, I.J. 1995. Dispersal, boundary processes, and tropic-level interactions in streams adjacent to beaver ponds. Ecology 76:908-925.

Schlosser, I.J., Kallemeyn, L.W. 2000. Spatial variation in dish assemblages across a beaver-influenced successional landscape. Ecology 81:1371-1382.

Schuft, M.J., Moser, T.J., Wigington, P.J., Stevens, D.L., Mcallister, L.S., Chapman, S.S., Ernst, T.L. 1999. Development of landscape metrics for characterizing riparian-stream networks. Photogrammetric Engineering and Remote Sensing 65:1157-1167.

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

Snodgrass, J.W. 1997. Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North America landscape. Journal of Applied Ecology 34:1043-1056.

Snodgrass, J.W., Meffe, G.K. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928-942.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys Union 38:913-920.

Suzuki, N., McComb, W.C. 1998. Habitat Classification Models for Beaver (*Castor canadensis*) in the Streams of the Central Oregon Coast Range. Northwest Science 72:102-110.

Townsend, P.A. 2001. Relationships between vegetation patterns and hydroperiod on the Roanoke River floodplain, North Carolina. Plant Ecology 156:43-58.

Townsend, P.A., Walsh S.J., and Butler D.R. 1995. Beaver pond identification through a satellite-based ecological habitat classification. Pages 102-111 in ACSM/ASPRS Annual Convention and Exposition. Technical Papers Volume 2.

Trombulak, S.C., Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

Wemple, B.C., Jones, J.A., Grant, G.E. 1996. Channel network extension by logging roads in two basins, western Cascades, Oregon. Water Resources Bulletin 32:1195-1207.

Williams, D.C., Lyon, J.G. 1997. Historical aerial photographs and a geographic information system (GIS) to determine effects of long-term water level fluctuations on wetlands along the St. Marys River, Michigan, USA. Aquatic Botany 58:363-378.

Wright, J.P., Jones, C.G., Flecker, A.S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96-101.

Chapter 2 Effects of culvert proximity on beaver pond distribution in boreal headwater streams

2.1 Introduction

Wetlands are important components of stream systems. Wetlands provide several ecological services, which rely on functional wetland processes. Wetland processes are influenced by the dynamics of the stream and the riparian zone. Anthropogenic and natural disturbances on river and riparian ecosystems can affect hydrology, which can drive wetland structure and function. Culverts and beavers are potential disturbances to hydrology.

In boreal forests, beavers (*Castor canadensis*) create and maintain riparian vegetation and wetlands (herein, beaver ponds) by altering the aquatic landscape via damming activity thereby causing water impoundment, and the terrestrial landscape, by foraging for food and construction material. Road development, an alteration of the terrestrial landscape, is directly linked to changes in subsurface flow (Trombulak and Frissell 2000), pooling of subsurface water (Forman and Alexander 1998) and increased sediment release into streams (Trombulak and Frissell 2000, Lane and Sheridan 2002). At stream crossings, culverts alter flood regimes, affect lateral channel migration, and increase sedimentation (Jeglum 1975, Forman and Alexander 1998, Jones et al. 2000, Jensen et al. 2001). Beavers frequently block culverts with dam structures (McKinstry and Anderson 1999, Jensen et al. 2001, Curtis and Jensen 2004) but effects on the distribution and characteristics of beaver ponds due to culvert-beaver interactions have not been investigated.

Spatial and temporal dynamics of beaver pond creation and abandonment influence headwater species richness (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). Wright et al. (2002) proposed that is not the beaver ponds themselves that are species-rich but the collective mosaic of beaver influenced and non-influenced patches in the stream network; if beaver were to completely dominate the landscape species richness at the stream network level would decrease.

Beaver activity in northern regions of the boreal forest is increasing, as is extension of the road network. However, there is a dearth of scientific knowledge about the degree of beaver influence and habitat use of beaver in boreal Canada post 1980s. Beavers have been rapidly re-colonizing boreal streams but the extent of the distribution has not been monitored. Culverts may affect beaver dam placement (Jensen et al. 2001 and Curtis and Jensen 2004) and thus, where beavers establish colonies. Culverts may influence overall beaver occurrence in a stretch of stream and the degree to which beaver influence a stretch of stream. By incorporating culvert presence on river systems into beaver habitat selection models, we will be better able to understand how beaver are responding to their environment and effects of future culvert installation or removal. I had three objectives: 1) establish the degree of utility of AVI for measuring beaver influence on the landscape, 2) describe location and abundance of both beaver activity and stream crossings as distributed within the river network, and 3) describe the relationship of both beaver presence and proportion of inundated stream in culverted and non-culverted streams in headwater systems, at two scales, 300m and 1,000m, from culverts and associated landscape variables.

2.2 Study area

The study area (Figure 2.1) is located in north-central Alberta (-115.30 E, 54.61 N to –109.94 E, 57.74 N) in the Mid-Boreal Uplands and Wabasca Lowlands ecoregions of the Boreal Plains Ecozone (Ecoregions Working Group 1989), approximately 60,000-km^2. The forested landscape is dominated by trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) and to a lesser degree balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*). Wetlands in the riparian zones largely develop on fluvial wetlands on postglacial tills. The riparian zone (vegetation along streams and lakes) is dominated by trembling aspen, green alder (*Alnus crispa*), river alder (*Alnus tenuifolia*), and willow (*Salix spp.*). The flat lowlands contain bogs and fens dominated by tamarack (*Larix laricina*) and black spruce (*Picea mariana*). Mean summer and winter temperatures are 13.7 and -11.9 °C, respectively (Beckingham and Archibald 1996). Mean summer and winter precipitation is 238 and 63 mm, respectively. The topography of the Mid-Boreal Uplands ecoregion is characterized as undulating to flat lowlands and rolling uplands. Elevation range is 400 to 800m ASL (Ecoregions Working Group 1989). The predominate parent materials are loamy to clay-textured glacial till, lacustrine deposits, and inclusions of coarse, fluvioglacial deposits (Ecoregions Working Group 1989). Wabasca lowland is low-relief and poorly drained, and organic soil covers about 50% of the area. The dominant soils in the Mid-Boreal Uplands and Wabasca lowland are Organic, Grey Luvisols, Brunisols, and Gleysols. (Beckingham and Archibald 1996).

Petroleum, natural gas and mineral extraction and forest harvesting have been underway in the area since the mid-20th century. An extensive road network, which includes two highways and several secondary roads connecting industrial activity and communities, has expanded since the early 1970s (Schneider 2002), and consequently there has been an increase in stream crossings.

2.3 Materials and methods

Data overview

I used six digital data sources in this study, including: 1) the *Alberta Vegetation Inventory (AVI)* - a 1:20,000 scale vegetation inventory used primarily for forestry inventory in Alberta. 2) A *Digital Elevation Model (DEM)* - a Digital Elevation Model (DEM) for the study area was created from the 1:50,000 Canadian Digital Elevation Data (CDED). The CDED was resampled from a resolution of 18 x 18 m pixel to a 100 x 100m pixel resolution. 3) *Land use disposition database* – database maintained by Sustainable Resources Development, Government of Alberta that contains the ownership of land disposition licenses, these are when land use permit took effect (herein, Start date). 4) *Road network* – all roads, highways and roads used by industry in the study area prior to 2000. 5) *Small-scale orthorectified photography* - black and white 1:40,000 to 1:60,000 aerial photography that was orthorectified, herein orthophotography stored in a UTM projection (Zone 12), Nad27 datum. 6) *Stream network* – 1:50,000 stream network with flow direction (including through lakes).

2.3.1 Data preparation

2.3.1.1 Response variables

I derived two response variables for 300 and 1,000m stream segments: 1) BP - presence of at least one beaver pond within the segment, and 2) IS – proportion of inundated stream. IS was calculated as the proportion of stream segment that intersected beaver pond(s). I used seasonally flooded, non-permanent water bodies delineated in the AVI overlaid beaver ponds and the stream network to calculate the proportion of stream inundated by beaver ponds.

2.3.1.2 Covariates

Categorical covariates used were culvert presence (CP), stream order (SO), stream flow direction (SD), AVI year (AY), and road age (RA). Continuous covariates used were deciduous (DC) and coniferous (CN) forest composition, stream gradient (GD), easting (X) and northing (Y). (Table 2.1)

The intersection of the road and stream network identified bridges and culverts (herein referred to as stream crossings). Culvert presence (CP) was verified using orthophoto coverage. Where orthophoto coverage did not exist, I assumed that stream crossings on first- to third-order streams were culverts. I observed very few bridges on first- to third-order streams. Flow direction (SD) was identified using the stream network. Stream order (SO) was calculated by assigning a Strahler order to each stream segment (Strahler 1957). All four vegetation covariates, DC, CN, FA, and HB were derived from the AVI. The AVI was classified into deciduous and coniferous forest stands based on species composition. A stand was classified as deciduous forest cover if it was > 50% trembling aspen, balsam poplar, and paper birch. A stand was classified as coniferous forest cover if it was > 50% white spruce, balsam fir and alpine fir (*Abies lasiocarpa*). If a stand had a greater proportion of leading coniferous species than deciduous, the stand was classified as coniferous. I did not include pine species (*Pinus* spp.) a dry site upland genus or black spruce, associated with bogs, in proportion of coniferous forest. Pines were rare to accidental components of the conifer component so were not considered relevant influences. Variables DC and CN were used as a surrogate measure for the dominant riparian vegetation type. I estimated total forest cover, FA by summing DC and CN. Each stream segment was assessed for proportion of DC and CN outside a 100m beaver foraging zone to a distance of 100m (Figure 2.3). The beaver forage zone is about 100m from the water's edge (Howard and Larson 1985, Johnston and Naiman 1987). The beaver forage zone was excluded to minimize inclusion of vegetation communities potentially affected by impounded water (open water and snags), and beavers foraging for food and construction material. Estimated proportion of deciduous and coniferous forest was assumed to be correlated with available forage within the beaver forage zone before beaver influence. I combined area burned and harvested since 1970 within 200m of the stream network to form the covariate HB; a control for potential absence of historically treed landscape and effect of fire on beaver colonies. Gradient (GD) was calculated for up- and downstream segments using a triangulated irregular network (TIN), based on the DEM, within 2 kilometres or a 20 pixel distance of the segment. To control for temporal variation in precipitation, I included the year the inventory aerial photography was flown (AY). Road age (RA), was used as a surrogate for culvert age, non-culverted sites were assigned RA = 0. RA was estimated using the Land Use Disposition "start date" attribute minus AY to estimate the age of the culvert when the map was interpreted. I included the easting (X) and northing (Y) coordinate (in metres) to control for spatial variation in precipitation.

2.3.2 Objective 1: Utility of vegetation inventory for measuring beaver influence

I verified culverted and non-culverted sites where orthophotography was available. I considered beaver ponds detected in the AVI to have been classified correctly if impounded water upstream of an intact or breached dam was visible in the orthophoto. The pond's high-water mark, indicated by the presence of exposed soils, gramminoid/sedge/forb cover or surface water, was used as the beaver pond boundary. Exposed soils and herbaceous vegetation cover are evidence that an area was periodically inundated. I considered ponds separated by a 100m section of unimpounded stream to be distinct (Snodgrass 1997). The size distribution of "seasonally flooded land" polygons indicated that the minimum mapping unit (MMU) was approximately 0.05-ha. The minimum size of digitized beaver pond was 50 x 20m. as beaver ponds below this size were difficult to identify in the orthophoto. I used a confusion matrix (Jensen 1996) to measure producer accuracy, user accuracy, kappa statistic and overall accuracy, for presence of beaver ponds up- and downstream of culverted and non-culvert sites for 300 and 1,000m segments.

2.3.3 Objective 2: Culvert and beaver distribution with the river network

I estimated the total stream length (inundated and non-inundated) and proportion of inundated stream, by stream order, within first- to eighth-order streams. I predicted the distribution of inundated stream would be disproportionately skewed to low-order streams. If road development was random, the expected distribution of stream crossings along first to eighth order streams should follow the same distribution as stream order. Similarly, if beaver impounded streams randomly, the distribution of inundated streams should be similar to the distribution of the stream network by order. I compared the proportion of inundated stream and stream crossings to the proportion total stream by stream order. Differences between estimated proportions were subjective as no statistical test was conducted to test for significance.

2.3.4 Objective 3: Modelling beaver activity at the 300 and 1000m scale

I measured beaver activity on first- to third-order streams (Strahler 1957) by the presence of beaver ponds and length of inundated stream. Beaver activity was measured at two spatial scales: 300 and 1,000m, up- and downstream from culverted or non-culverted sites. At the 300m scale, I selected 281 culverted sites (1st order = 181, 2nd order = 63 and 3rd order = 37). At the 1,000m scale I selected 74 culverted sites (1st order = 41, 2nd order = 20 and 3rd order = 13). I randomly selected an equal number of non-culverted control sites within first- to third-order streams that were within 3km of the road network, to minimize variability in stream and landscape characteristics. I considered the stream sections up- and downstream of the culvert and control sites as independent experimental units; at the 300m scale n = 1124 and 1,000m scale n = 296. The sample size difference between two scales was due to site selection restrictions; fewer sites at the 1,000m scale met my selection criteria. At the 300m scale, all culverted and control sites were required to be at least 600m from the nearest culvert or bridge, and at the 1,000m scale, sites were at least 2,000m away. Within the 300m and 1000m culvert and control stream segments, stream order did not change nor have another stream entering the channel. Within each 300 and 1,000m stream segment I used existing spatial databases to quantify variables known to influence beaver habitat selection (Table 2.1) I evaluated 13 alternate *a priori* regression models (Table 2.2) for beaver pond presence and proportion of inundated stream. Seven models were from published literature and six were synthesized from qualitative literature and knowledge of study area conditions. Published models were modified in order to use variables from available inventory data and other digital data. Discrepancies existed as landcover attributes and scale differed or because studies used field data whereas I used only remotely sensed data. Appendix A lists the original model variables and my substitutions.

All statistical analyses were conducted using the software package R, Ver. 1.8.1 (R Core Development Team 2005). Prior to inclusion of variables in the regression models, I examined all candidate variables for correlation using Spearman's rho (r) statistic, a rank-based measure of association. I considered a value of r = 0.70 between two variables to indicate a high correlation. If two variables had a correlation of r = 0.70 or greater, the variable that I considered to be less important, biologically or intuitively, was removed. Proportion of deciduous forest and total forest area were correlated at the 300m reach scales (r = 0.90) and 1,000m reach scale (r = 0.88). I kept both covariates in the global model but did not allow them to enter into the submodels together. No other variables were highly correlated at either scale. The distribution of the covariates did not differ between culvert and control site at the 300m scale (Table 2.3) or 1,000m scale (Table 2.4).

I tested *a priori* hypotheses about beaver pond presence and inundated stream using 13 candidate regression models (Table 2.2). I made three predictions:

1) Beaver pond presence and proportion of inundated stream would be positively related to culvert presence,
2) Streams upstream of a culvert would have higher incidence of beaver pond presence and a greater proportion of inundated stream length than non-culverted controls, and
3) culverts would be a significant explanatory variable for beaver pond presence and inundated stream close to the crossing (300m) and a non-significant explanatory variable over longer distances (1,000m) as the influence of the culvert waned.

I regressed proportion of inundated stream and beaver pond presence for each of the 13 candidate models at the 300m and 1,000m scale using a Generalized Linear Model (GLM). I used binomial errors and logit link for modeling the response variable beaver pond presence and normal error and identity link, for proportion of inundated stream. I used an information-theoretic approach to select the best approximating model(s) from 15 candidate models: 13 *a priori* models, one global model, and a null model (Burnham and Anderson 2002). Models were grouped into three classes: 1) culvert influenced, 2) physical (abiotic variables), and 3) vegetation (biotic). I used Akaike Information Criterion (AIC), corrected for small sample sizes (AIC_c) when the ratio of sample size (n) and the number of parameters (K) was less than forty for the global model. The global model had 17 parameters, thus required a minimum sample size of n = 680. AIC was used at the 300m scale (n = 1124) and AIC_c at the 1,000m scale (n = 296). Following the recommendation of Burnham and Anderson (2002), if the AIC difference between the top ranked model and a lower ranked model was less than 2.00, both were considered among the "best approximating" models. In addition, I used Akaike weights (w_i) as "the weight of evidence" (Burnham and Anderson 2002) to assess how likely the best approximating model (lowest AIC score) is also the top model given the alternative candidate models.

To assess logistic model goodness-of-fit I used the Receiver Operator Characteristic (ROC) curve and related sensitivity and specificity plots (Swets 1988, Hosmer and Lemeshow 2000, Pearce and Ferrier 2000). The ROC curve "plots the probability of detecting true signal (sensitivity) and false signal (1-specificity) for an entire range of possible cutpoints [the probability above which observations are considered to show an effect]" (Hosmer and Lemeshow 2000). Sensitivity is defined as the proportion of observations that have a correctly identified true response. Specificity is the proportion of observations that have identified true non-responses. The area under the ROC curve (AUC) "provides a measure of the model's ability to discriminate between those subjects who experience the outcome of interest versus those who do not" (Hosmer and Lemeshow 2000). When AUC = 0.50 it is considered to be no better than flipping a coin, $0.7 \leq \text{AUC} < 0.8$ is acceptable discrimination and, $\text{AUC} \geq 0.80$ is excellent discrimination (Hosmer and Lemeshow 2000:162). I estimated the confidence intervals for coefficients using a multivariate analogue of the Wald test (Hosmer and Lemeshow 2000). I calculated the odds ratio for beaver pond presence (Hosmer and Lemeshow 2000) to assess magnitude of effect for significant variables.

I assessed the linear regression global model for independence and homoscedascity, normality of the residuals and influential observations. I visually examined plots of the Pearson and deviance residuals versus fitted values, and dependent and independent variables to test for independence and homoscedascity. To assess normality of the residuals, I used normal probability plots (Q-Q plots) with the Pearson residual. For the best approximating model, I tested for significance of the slope coefficients, using methods outlined in Steel and Torrie (1980:323). I calculated predicted, fitted response and respective confidence intervals using methods described in Johnson and Wichern (1992).

For both logistic and linear regression models I estimated the variance explained by the top best-approximating models using log-likelihood of the best-approximating model and the null model (Hosmer and Lemeshow 2000) as given by Equation 1. L_p is the log-likelihood of the less parsimonious model and L_o is the log-likelihood of the more parsimonious model (in this study I used the null model).

Equation 1 $$R_L^2 = 1 - L_p/L_o$$

To detect influential observations, I examined the diagonal elements of the hat matrix for leverage values (h), as a regression diagnostic test to see if any observations in the global model predicted response values that were larger than other observation with similar covariates (McCullagh and Nelder 1983:220). For both logistic and linear regression, the average value of h_i is p/N, where p is the number of parameters and N the number of observations. Hoaglin and Welsch (1978) recommended using $h_i > 2p/N$ as a threshold to indicate influential points. I examined general trends of covariate mean values for observations > and ≤ than the threshold.

2.4 Results

2.4.1 Utility of vegetation inventory for measuring beaver influence

I verified beaver ponds for 422 of 1124 (37.5%) of the 300m segments and 102 of 296 (34.5%) of the 1,000m stream segments for a total of 358.5km of first to third order streams. Of these sites, 266 were stream crossings and 258 were non-stream crossings. Results of the confusion matrix showed the user's and producer's accuracy for inundated streams were 0.71 and 0.91 respectively (Table 2.5). The overall accuracy was 94.4% and the kappa statistic was 0.64. I conclude that AVI seasonally flooded lands are good surrogates for beaver ponds.

I validated 70% of all stream crossings and 72% of all non-culvert random sites against orthophotography. Visual inspection of the orthophotography confirmed that all first- to third-order stream crossings were culverted and that bridges have rarely been constructed on these crossings in the study region.

2.4.2 Culvert and beaver distribution with the river network

Table 2.6 shows the distribution of stream crossings, stream network and inundated streams by stream order for streams within 3-km of the road network. First-order streams account for 47.8% of the total stream network but contain 56.9% of the stream crossings. Overall, lower order streams (1^{st}-3^{nd} order) had higher stream crossing density than expected (89.0%) and in high-order (4^{th} – 8^{th} order) the number of stream crossings were less than expected (11.0%).

Inundated streams also appear to be distributed non-randomly. Inundated streams were less abundant in first-order streams than expected (35.9%) and more abundant than expected in second- and third-order streams (34.0% and 22.2%). Overall, proportion of inundated streams was greater in first- to third-order streams (3.9%) than fourth- to eighth-order streams (1.2%).

2.4.3 Modelling beaver activity at the 300 and 1000m scale

Table 2.7 shows the distribution of beaver ponds and proportion of inundated stream by order, culvert and control sites, and up-downstream direction At the 300m scale, 13.0% (146/1124) segments and at the 1,000m scale, 26.4% (78/296) segments had a minimum of one beaver pond present. For those segments with a beaver pond present, 58% (SE 32.9%) of the 300m segments and 31% (SE 24.7%) of 1,000m segments were inundated.

2.4.3.1 Beaver pond presence

Stream-reach 300m scale

Road 3 was the best-approximating model of beaver pond presence in 300m segments (Table 2.8). The weight of evidence supporting *Road 3* was approximately nine times greater than that of *Phys and Veg 4* which included only physical and vegetation variables. Compared to *Road 3*, all other models had a ΔAIC score > 2.00, indicating that these models are likely not candidates for best-approximating model. Gradient and coniferous forest were negatively related to beaver occurrence ($p < 0.05$). Deciduous forest and culvert presence x second order stream interaction, relative to first-order streams, were positively related ($p < 0.05$) to beaver occurrence (Table 2.9). Culverts, through an interaction with second-order streams, were an important variable explaining beaver pond presence within 300m of a culvert.

Using *Road 3,* I calculated the odds ratio for beaver pond presence (95% CI) in culverted and non-culverted streams for a range of proportion of deciduous forest (0.00 to 0.80) and gradient (0.01 to 7%). For a 0.2 increase in proportion of deciduous forest, the odds of a dam being present increased by 1.29 times (95% CI 1.14,1.45) (Table 2.10). In Table 2.11 I calculated the odds ratio of beaver occurrence in culverted and non-culverted streams over a range of gradient values (0.5 to 7.0%) within each stream order. In first- and third-order streams the odds ratio decreased by more than half when gradient was 3%. Beaver ponds were positively related to culvert presence in second-order streams (OR = 1.52, 1.11, 2.08 95% CI) through the interaction between culverts and stream order. Figure 2.4 shows the interaction between stream order and culvert presence for probability of beaver pond occurrence for upstream segments for parameter values GD = 3.00, HB = 0.10, DC = 0.30 and CN = 0.10.

Stream-reach 1,000m scale

The best-approximating model at the 1,000m scale was *Phys and Veg 4* (Table 2.12) but three other models *Phys and Veg 2*, *Phys and Veg 3* and *Road 3* also were nearly as good (ΔAIC < 2.00). The weight of evidence for *Phys and Veg 4* and *Phys and Veg 2* were similar. The only differences in variables included in the top two models was the inclusion of stream order in *Phys and Veg 4*. The third model, *Phys and Veg 3* included an interaction effect between stream order and gradient. Significant variables in *Phys and Veg 4* were gradient, deciduous forest and second-order streams (Table 2.13). The odds ratio for change in proportion of deciduous of 0.2 was 1.49 (1.19,1.85 95% CI) (Table 2.14).

Beaver are much more likely to occur on second-order streams than third- or first-order streams. The odds ratio for beaver pond occurrence on second-order streams compared to third-order was 1.71 (0.93,3.14 95% CI) and between second- and first-order streams the odds ratio was 1.87 (1.02, 3.43).

Model diagnostics for pond occurrence at 300m and 1,000m scale

The global model showed that in both 300 and 1,000m scale global models, covariate values for stream gradient and proportion of deciduous forest were positively associated with high leverage values while proportion of coniferous forest was negatively associated. For the 300m segments, high leverage values were associated with greater proportion of harvested and burned (Table 2.15). For the 1,000m segments, high leverage values were associated with sites that had culverts present (Table 2.16). High leverage values indicate that these covariates may be influencing the model outcome.

For 300m segments, sensitivity and specificity plots for *Road 3* with a probability of beaver pond presence greater than 0.12, the proportion of correctly identified reaches and incorrectly identified reaches was 0.64 (Figure 2.5*a*). In *Phys and Veg 4*, for a probability of beaver pond presence greater than 0.25, the proportion of correctly identified reaches at the 1,000m scale was 0.63 and incorrectly identified reaches was 0.61 (Figure 2.6*a*). Both *Road 3* (300m reach scale), *Phys and Veg 4* (1,000m reach scale) showed moderate discrimination. The area under the ROC curve for these models was 0.69 (Figure 2.5*b*) and 0.68 (Figure 2.6*b*) respectively, indicating that the models had moderate ability to predict beaver pond presence. The models explained little deviance, 6.6% and 6.2% respectively

2.4.3.2 Proportion of inundated stream

Stream-reach 300m scale

The best approximating model explaining proportion of inundated stream was *Phys and Veg 1* (Table 2.17). *Phys and Veg 4* also had strong empirical support (Δ AIC$_c$ < 2.0). The weight of evidence for *Phys and Veg 1* was 1.2 times greater than *Phys and Veg 4*. Both models included stream order, and gradient as a variable. A vegetation variable was present in both models, although in *Phys and Veg 1* it was proportion of forest area and in *Phys and Veg 4* it was proportion of deciduous forest. Proportion forested area (FA) and stream order (SO), were significantly positively related to proportion of inundated stream ($\alpha = 0.05$) (Table 2.18). Proportion of inundated stream differed significantly over first-, second- and third-order streams over a range of change in proportion of forested area (0.00 to 1.0). The greatest difference however, occurred within third-order streams (Figure 2.7). Significant differences in proportion of inundated stream occurred between first- and second-order streams with 0.5% to 5% gradient and proportion of inundated stream was significantly greater in third-order streams (Figure 2.8). Variance explained by *Phys and Veg 1* as compared to the Null model was 16.4%.

Stream-reach 1,000m scale

The best-approximating model for proportion of inundated stream for 1,000m stream segments was the *Null* model followed by *Phys and Veg 2* (Table 2.19). The weight of evidence for selecting the *Null* model was 1.64 greater than *Phys and Veg 2.* The remaining 12 models had Δ AIC$_c$ was greater than 2 indicating that these models are likely not better than the *Null* model.

Model diagnostics for inundated stream at 300m and 1,000m scale

Regression diagnostics for the GLM (Gaussian link) regression global model for 300m segments indicated that at both the 300m and 1,000m scale, proportion of coniferous forest was greater for observations associated with high leverage values (Table 2.20 and Table 2.21). I did not eliminate any sample sites from the analysis even though some were related to high leverage values. The normal probability plot (Q-Q plot) for 300 and 1,000m stream segments, showed that the residuals had a normal distribution for mid-range values for proportion of inundated stream (Figure 2.9 and Figure 2.10). However, deviance residuals did not follow a normal distribution in the tails. An arcsine transformation as recommend by Zar (1999) did not improve the fit of the residuals towards a normal distribution. This indicates that the assumption of normality in the distribution of error (residuals) was violated. I considered the deviation from a normal distribution, for the global model, to be moderate and carried forward with the analysis.

Observed proportion of inundated stream and deviance residuals for *Phys and Veg 1* were positively correlated at the 300m scale (Figure 2.11). Visually it appeared that the variance of the residuals was homeoscedastic and was not evenly distributed about zero. Within the lower end of proportion of inundated stream the model was under-fitted; for the upper end the model was over-fitted. I did not examine deviance residuals for the top model at the 1,000m as it was the null model.

2.5 Discussion

2.5.1 Utility of vegetation inventory for measuring beaver influence

Mapped beaver ponds occurred most frequently on low-order streams and were rare on high-order streams. Other researchers have also shown that beaver ponds occur within first- to third-order streams in boreal streams (Naiman et al. 1986, Johnston and Naiman 1990, McKinstry et al. 2001). Producer's accuracy indicated that inundated streams present in the AVI were nearly always present in the orthophoto but the user's accuracy, which was slightly lower indicated that inundated streams which occurred in the orthophoto were not necessarily present in the AVI. I concluded that mapped seasonally flooded streams in the Alberta Vegetation Inventory (AVI) to be a reasonable measure of beaver activity in the stream network.

Beaver ponds classified as "seasonally flooded land" in forestry inventories have not been used to describe beaver distribution in other study regions in Canada. However, in Voyageurs National Park, Minnesota, Broschart et al. (1989) found that shallow marsh and seasonally flooded meadow were habitat indicators of beaver population trends. Broschart et al. (1989) proposed that shallow marshes represented new flooding, and thus, an expanding beaver population. Seasonally flooded meadows had lower water levels suggesting a decreasing beaver population that is not maintaining dams. The AVI classification made no distinction between "seasonally flooded land" and "shallow marsh". In my study "seasonally flooded meadows" represented both active and abandoned beaver ponds or in other words present and past beaver activity.

2.5.2 Culvert and beaver distribution with the river network

Culverts occurred at a higher frequency than expected in first-order order streams. This is an indication that there may be a preference towards building culverts in lower order streams rather than higher order. Beavers however, created ponds more frequently than expected in second- and third-order streams. One objective of my research was to determine if culvert position influenced beaver pond position in the stream network. This overview analysis did not separate beaver ponds located within 300m to 1,000m (proposed "culvert effect zone") of culverted and non-culverted streams. However, if beaver do select culverted streams over non-culverted streams, beaver activity could be skewed towards first-order steams that are within the culvert-effect zone.

Analysis of existing AVI over a broad area agreed with published data that beaver activity is concentrated in first- to third-order streams. I estimated, conservatively, approximately 4.0% (based on AVI) of headwater streams are influenced by beaver dams and ponds. Compared to finding of other similar studies, my estimate of beaver influenced streams using AVI is low. Other studies have shown beavers can inundate 20% - 75% of headwater stream length. In a study by Johnston and Naiman (1990), beavers had impounded an average 55% of first- to fourth-order streams. Naiman and Melillo (1984) found that beaver influenced up to 20-40% of second-order streams in the sub-arctic region of the Precambrian shield, northern Quebec. Barnes and Mallik (1997) found that active beaver dams were distributed over 75% of a 228 km^2 headwater watershed. McKinstry and Anderson (1999) estimated between 42% and 48% of streams in Wyoming are influenced by beavers.

I have proposed three possible explanations for my low estimate of beaver-influenced streams in my study area as compared to other regions. First, ponds may be too small to be detected in the orthophotography or AVI thus my estimates of inundated stream were conservative. Second, if my depiction of current beaver activity in headwater streams is accurate then perhaps beaver not have yet saturated the study area. Third, antecedent precipitation could have influenced the amount of impounded water present in the aerial photography. However, seasonally flooded land classification in the AVI is not influenced by within-season fluctuation of the water table.

2.5.3 Modelling beaver activity at the 300 and 1000m scale

2.5.3.1 Beaver pond presence

Stream-reach 300m and 1,000m scale

Within 300m of culverts, I found that beaver occurrence was negatively related to culverts, except on second-order streams, where it was positively related. At a distance of 1,000m there appeared to be little culvert effect on beaver activity. It is possible that a culvert effect existed but cannot be statistically detected because beaver activity is more variable over longer distances. It is possible that there was variation in other characteristics associated with culverts, related to beaver activity, which could have affected beaver activity but were not measured. Such examples are stream substrate or bank slope (McComb et al. 1990), which I could not assess using aerial photography or AVI.

I found that gradient was negatively related to beaver pond occurrence at the 300m and 1,000m scale. It is well documented that beaver tend to build ponds in low-order, low gradient streams. Studies have shown beaver dams and colonies are associated with gradients below 4% (Slough and Sadleir 1977, McComb et al. 1990, Curtis and Jensen 2004).

My results indicate that culverts may increase beaver pond occurrence in second-order streams. However, the magnitude of this influence is relatively low as compared to other variables such as gradient and proportion of deciduous forest. For example it is hypothetically possible that gradient and proportion of deciduous forest could offset effect of culvert presence on beaver pond presence. I postulated earlier in this study that culvert position in the watershed could influence beaver pond distribution in the stream network. This was primarily driven by the frequency that culverts occurred in first-order streams. Given that culvert influence is likely greater in second-order streams it is unlikely the beaver pond distribution would change unless culvert distribution also shifted towards occurrence in second-order streams.

2.5.3.2 Proportion of inundated stream

Stream-reach 300m and 1,000m scale

Using only sites that had beaver occupancy, rather than the entire sample, proportion of inundated stream is comparable to what has been reported in other regions. At the 300m scale the average proportion of inundated stream was 0.58 and at the 1,000m scale the average proportion of inundated stream was 0.31. At 1,000m, my models had very low weight of evidence for length of inundated stream. The use of proportion of inundated stream as a metric of beaver presence in a system was used to measure degree of beaver influence within the stream. A direct correlation does not necessarily exist between presence of a dam (i.e. presence of a pond) and degree to which the pond extends along the stream network. Finer topographic features of the stream could influence length of stream inundation. Possibly length of inundated stream over a distance of 1,000m is dependent on finer scale topographic features rather than available forage, gradient or stream order. It is also possible that beyond 300m some beaver colonies may maintain smaller or larger systems of ponds along a stretch of stream quite randomly with little environmental influence. However it is interesting that models with culvert presence did not have a strong weight of evidence at the 300m or 1,000m scale. It would seem that once beavers are established in a stream system the culvert does not play a significant role in determining how long (or large) beaver ponds can become. There are several reasons however, to report length of inundated stream as a metric for beaver influence in the stream network. Beaver influence the input of organic debris into a stream system (Naiman et al. 1994, Naiman et al. 1999). It is reasonable to propose then that the longer the length of inundated stream, the higher the degree of input of organic debris into the system.

2.5.3.3 Culvert-effect zone

I concluded from my analysis that there may be a "culvert-effect" zone similar to the "road-effect" zone coined by Forman (2000). I suggest that the "culvert-effect" zone may be about 300m for beaver pond presence. Stream direction relationship was a very weak covariate and thus I also propose that the culvert-effect zone extends up- and downstream of the culvert. In the field however, I frequently observed beaver dams more often upstream of culverts. Based on my field observations an up-downstream difference may exist but at a scale smaller than that measured in this study. Differences between impoundment rates up- and downstream of a culvert have not been reported for other studies however several mechanisms have been postulated for why up/downstream differences may occur. One mechanism postulated is the narrowing of the stream channel by a culvert which causes the stream to riffle, an audible sound, triggering the beaver to dam the culvert (Jensen et al. 2001). Riffling can occur up- or downstream of a culvert. A culvert and roadbed may also act as the terminus of a beaver pond (like a dike) or the initiation of a pond (partially built dam). Culverts and roadbeds themselves may cause water to pool upstream (Forman and Alexander 1998), attracting beaver to the open water (Jeglum 1975).

My study only allowed me to establish correlations between beaver pond occurrence and inundated streams around culverts. Beaver management was prevalent in the study area but as my sites did not have a ground-truthing component I could not measure human management of beaver activity around culverts. Additionally, no records of beaver management were available for specific culvert locations or for the study area. Likely, management of beaver activity by dam removal and beaver trapping was an unmeasured but confounding variable in the study. An active trapping program has been in place in the study area for over a decade. Third-order streams are larger in water volume and in width, likely posing a greater threat to roadbed integrity if impounded; where beavers threaten roadbed integrity, beaver presence is controlled through lethal trapping and dam removal. Beaver management in third-order streams may explain the lower frequency of beaver occurrence in third-order streams in my study area. This does however, conflict with the greater proportion of inundated stream in third-order streams.

2.6 Conclusions

In my study area beavers created ponds in first to third-order streams more often than expected given the distribution of stream order within the entire network. Culvert presence was a more important landscape feature at the 300m scale than 1,000m scale for determining beaver occurrence. Beaver occurrence within 300m of a culvert was related to stream order and gradient; beaver occurrence was lower in first- and third-order streams and higher in second-order streams. Overall however, there was a negative relationship between culverts and beaver occurrence at the 300m scale. Proportion of inundated stream measured at the 300m scale was strongly related to physical and vegetation features, gradient, deciduous forest and stream order but not presence of culverts. At 1,000m there was no relationship between measured habitat variables and proportion of inundated stream. Likely, proportion of inundated stream is related to dam number, not beaver presence, which could indicate presence of one or several dams. For a large beaver colony to become established and persist, other habitat needs must be met such as dam construction material, forage species, and adequate water flow. Studies have reported that variables related to beaver-colony site selection are proportion of deciduous forest, stream gradient, and stream size.

Management of beaver populations in the study area confounds biological expression of beaver response to culverts. Where beaver dams flood roadbeds (or present a risk of flooding), beaver populations are managed by trapping and dam removal. Intensity of management depends on intensities of beaver damage and where the greatest damage occurs, specific types of streams of a certain gradient, size, and culvert configuration may require different intensity and methods of beaver management. Trapping and shooting may be disproportionately more common near roadsides because human access is easier for beaver colonies proximal to the stream crossing. In areas where road access is currently being developed, planners should install oversized and grated culverts or bridge structures that are less easily blocked by beavers. This will be especially important where habitat conditions favour beaver activity, such as low gradients and high proportions of deciduous vegetation. Results of this research could be applied at a coarse scale to predict where desirable beaver activity (for wetland habitat creation), and where undesirable beaver activity (property damage), may be most likely.

2.7 Literature cited

Beckingham, J. D. and Archibald, J. H. Field guide to ecosites of northern Alberta. 1996. Edmonton, Alberta, Nat. Resour. Can.,Can. For. Serv., Northwest Reg., North. For. Cent. Spec. Rep. 5.

Barnes, D.M., Mallik, A.U. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. Journal of Wildlife Management 61:1371-1377.

Broschart, M.R., Johnston, C.A., Naiman, R.J. 1989. Predicting beaver colony density in boreal landscapes. Journal of Wildlife Management 53:929-934.

Burnham, K.P., Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York , New York, USA.

Curtis, P.D., Jensen, P.G. 2004. Habitat features affecting beaver occupancy along roadsides in New York state. Journal of Wildlife Management 68:278-287.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Ecological Land Classification Series No. 23. Ottawa, Ont., Sustainable Development Branch, Conservation and Protection, Environment Canada.

Ferone, J.M., Devito, K.J. 2004. Shallow groundwater-surface water interactions in pond-peatland complexes along a Boreal Plains topographic gradient. Journal of Hydrology 292:75-95.

Forman, R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14:31-35.

Forman, R.T.T., Alexander, L.E. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-231.

Hoaglin, D.C., Welsch, R.E., 1978. Hat matrix in regression and anova. American statistician 32:17-22.

Hosmer, D.W., Lemeshow, S. 2000. Applied logistic regression. Second Edition. John Wiley & Sons, Inc., USA

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

Jeglum J.K. 1975. Vegetation-habitat Changes Caused by Damming a Peatland Drainageway in Northern Ontario. Canadian Field-Naturalist 89:400-412

Jensen, J.R. 1996. Introductory digital image processing: a remote sensing perspective. Prentice Hall, Upper Saddle River, New Jersey, USA.

Jensen, P.G., Curtis, P.D., Lehnert, M.E., Hamelin, D.L. 2001. Habitat and structural factors influencing beaver interference with highway culverts. Wildlife Society Bulletin 29:654-664.

Johnston, C.A., Naiman, R.J. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1:47-57.

Johnson, R.A., Wichern, D.W. 1992. Multivariate linear regression models *in* Applied multivariate statistical analysis. Third edition. Prentice-Hall Inc., Englewood Cliffs, New Jersey.

Johnston, C.A., Naiman, R.J. 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5-19.

Jones, J.A., Swanson, F.J., Wemple, B.C. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14:76-85.

Lane, P.N.J., Sheridan, G.J. 2002. Impact of an unsealed forest road stream crossing: water quality and sediment sources. Hydrological Processes 16:2599-2612.

McComb, W.C., Sedell, J.R., Buchholz, T.D. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50:273-281.

McCullagh, P., Nelder, J.A.. 1983. Generalized linear models. University Press, Cambridge, UK.

McKinstry, M.C., Caffrey, P., Anderson, S.H. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American water resources association 37:1571-1577.

McKinstry M.C, Anderson S.H. 1999. Attitudes of private- and public-land managers in Wyoming, USA, toward beaver. Environmental Management 23:95-101

Naiman, R.J., Melillo, J.M. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia (Berlin) 62:150-155.

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

Pearce, J., Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225-245.

R: A Language and Environment for Statistical Computing. R Development Core Team. 2005. Vienna, Austria, R Foundation for Statistical Computing.

Schlosser, I.J., Kallemeyn, L.W. 2000. Spatial variation in dish assemblages across a beaver-influenced successional landscape. Ecology 81:1371-1382.

Schneider, R.R. 2002. Alternative futures: Alberta's boreal forest at the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta

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

Snodgrass, J.W. 1997. Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North America landscape. 34:1043-1056.

Snodgrass, J.W., Meffe, G.K. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928-942.

Steel, R.G.D., Torrie, J.H. 1980. Principles and procedures of statisitcs: a biometrical approach. McGraw-Hill, Inc., USA.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys Union 38:913-920.

Swets, J.A. 1988. Measuring the Accuracy of Diagnostic Systems. Science 240:1285-1293.

Trombulak, S.C., Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

Wright, J.P., Jones, C.G., Flecker, A.S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96-101.

Zar, J.H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Inc., USA.

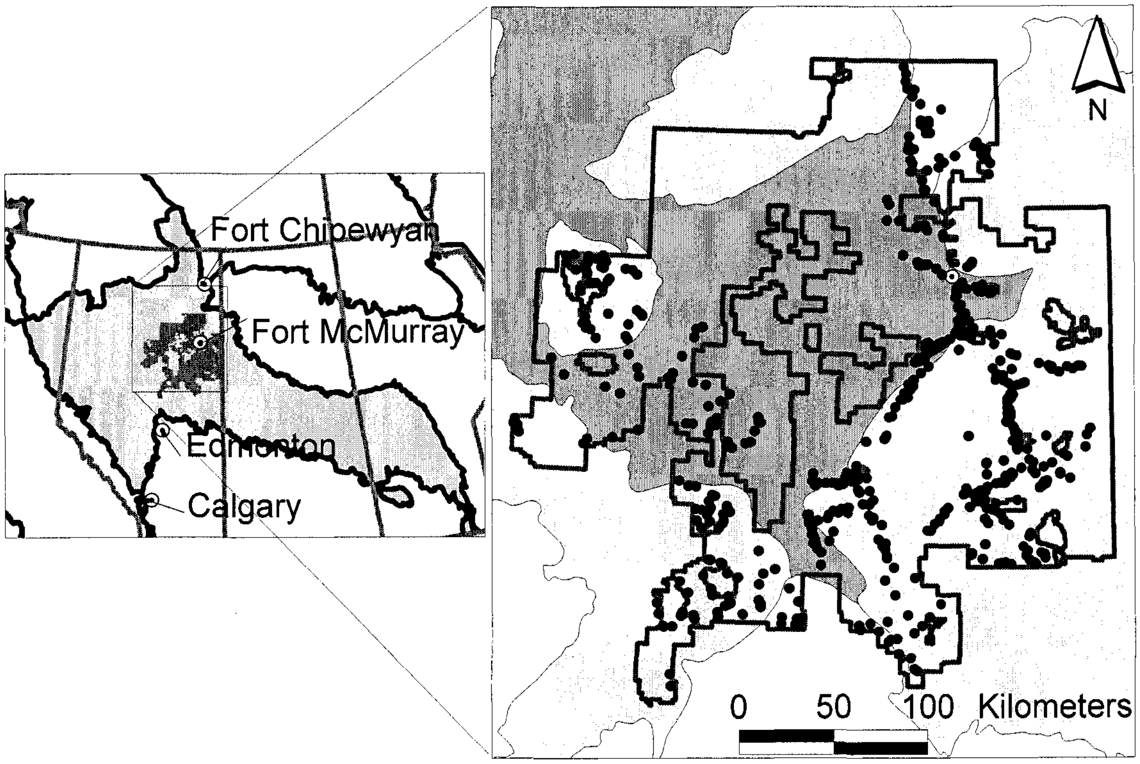


Figure 2.1 The study area (dark grey) within the Boreal Plain Ecozone (light grey) (left) and the study within the Wabasca Lowlands (dark grey) and Mid-boreal Uplands (light grey) ecoregions (right). Black dots represent both culvert and non-culvert locations (n = 1124).

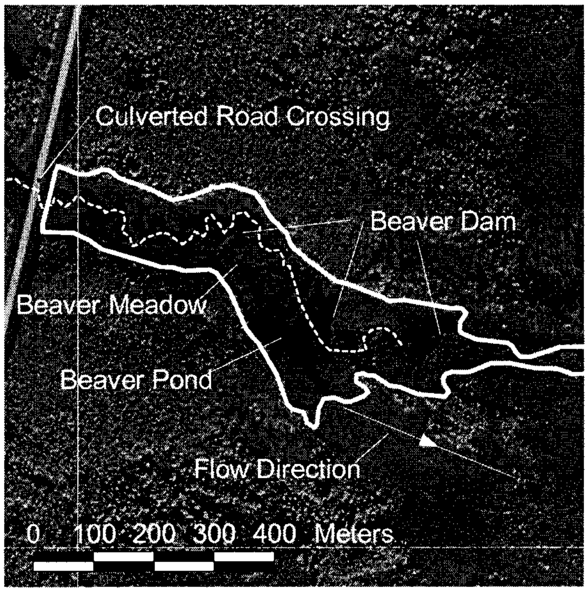


Figure 2.2 Aerial photography showing seasonally flooded, non-permanent water bodies in the Alberta Vegetation Inventory (solid white line) and presence of beaver pond, meadow and dams downstream of a culvert on a third-order stream (dashed white line).

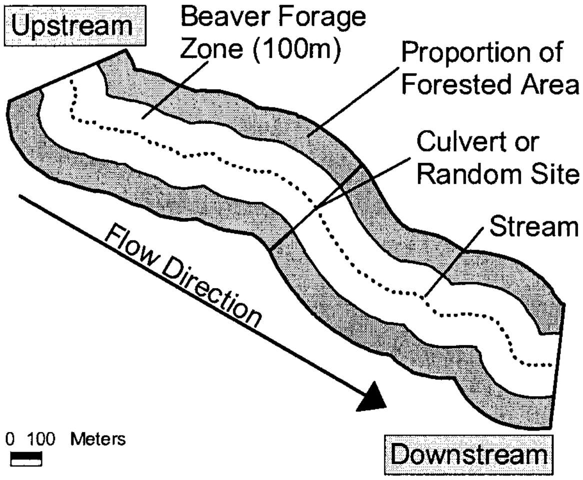


Figure 2.3 Culverted stream showing up- and downstream 1,000m stream segments buffered 100m from the 100m beaver forage zone.

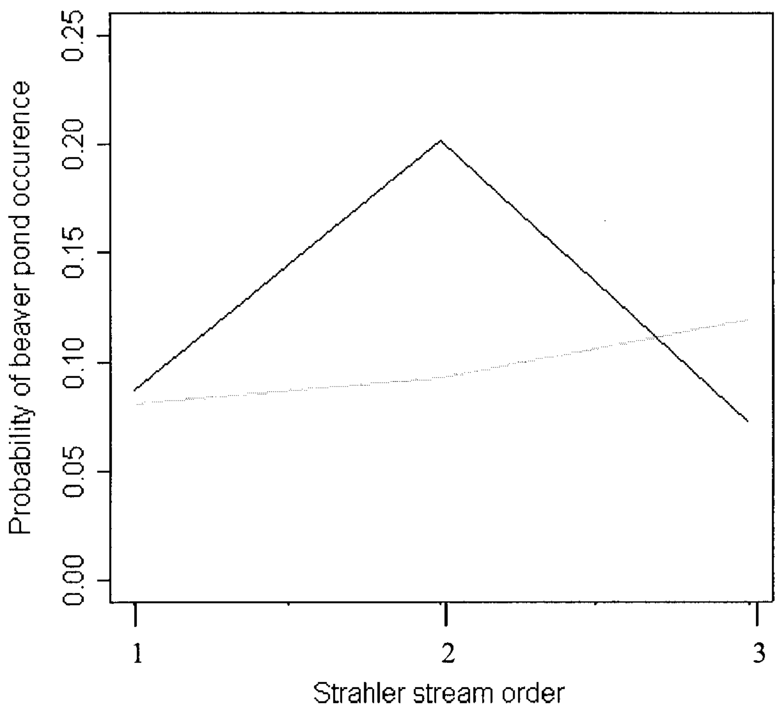


Figure 2.4 Probability of beaver pond occurrence 300m of a culvert or control site for top candidate model "Road 3" (SD + CP + GD + SO + HB + DC +CN + GDxCP + SOxCP) for first-, second- and third-order streams with (black line) and without culverts (grey line). Covariate in the model were set at GD = 3.00, HB = 0.10, DC = 0.30 and CN = 0.10.

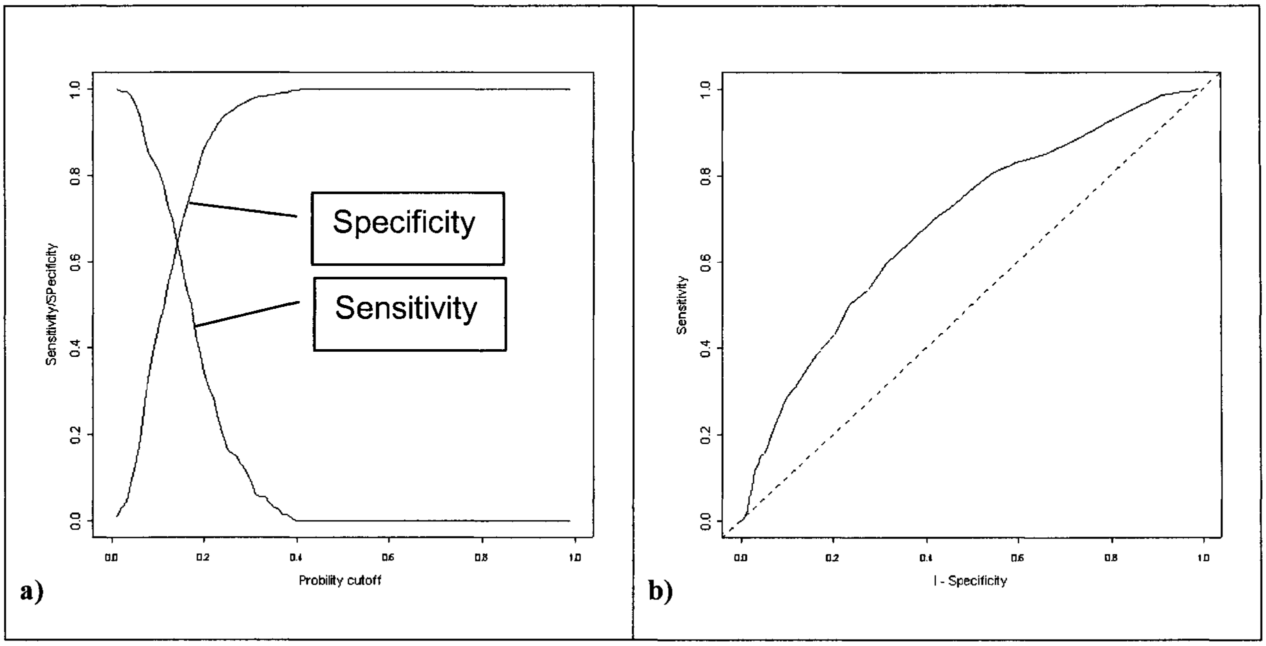


Figure 2.5 Plot of a) sensitivity and specificity versus cutpoints of 0.01 increments and b) the ROC curve (sensitivity versus 1-specificity) for all possible cutpoints (0.01 increments) in the logistic regression model *Road 3* explaining influence of biotic and abiotic attributes on occurrence of beaver pond presence within a 300m reach of stream of a culvert or random point (n = 1124). Using a cutoff of 0.12, the specificity is 0.64 and the sensitivity is 0.64. The area under the ROC curve is approximately 0.69.

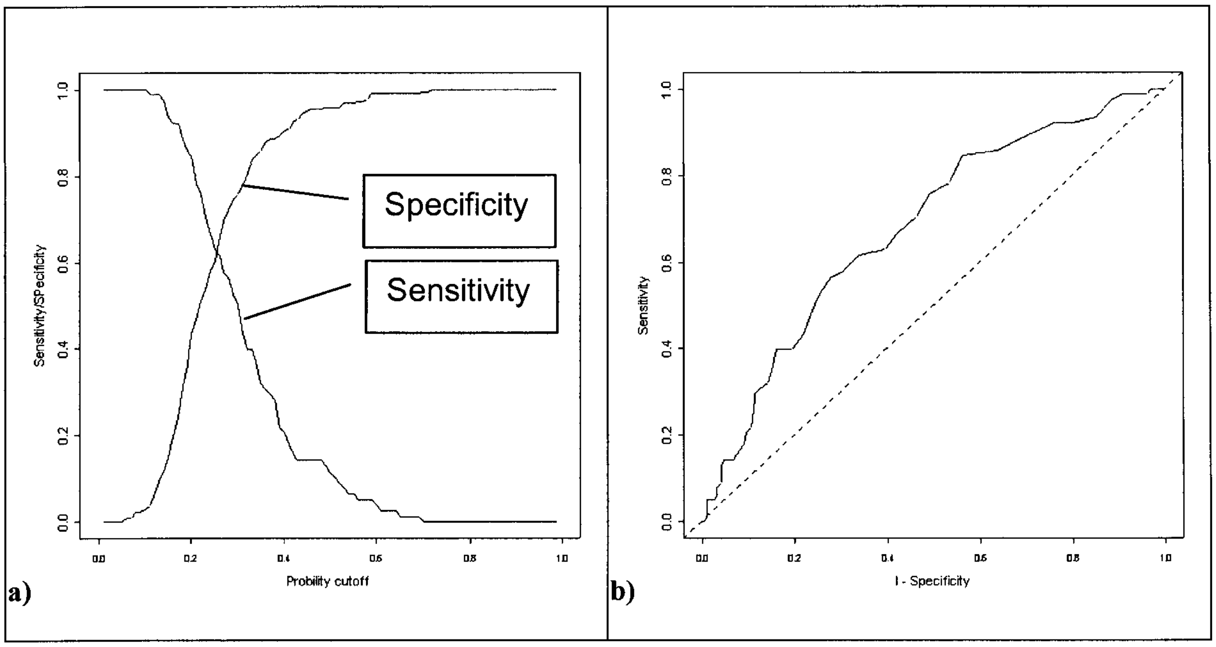


Figure 2.6 Plot of a) sensitivity and specificity versus cutpoints of 0.01 increments and b) the ROC curve (sensitivity versus 1-specificity) for all possible cutpoints (0.01 increments) in the logistic regression model *Phys and Veg 4* explaining influence of biotic and abiotic attributes on occurrence of beaver pond presence within a 1,000m reach of stream of a culvert or random point (n = 296). Using a cutoff of 0.25 the specificity is 0.63 and the sensitivity is 0.61. The area under the ROC curve is approximately 0.68.

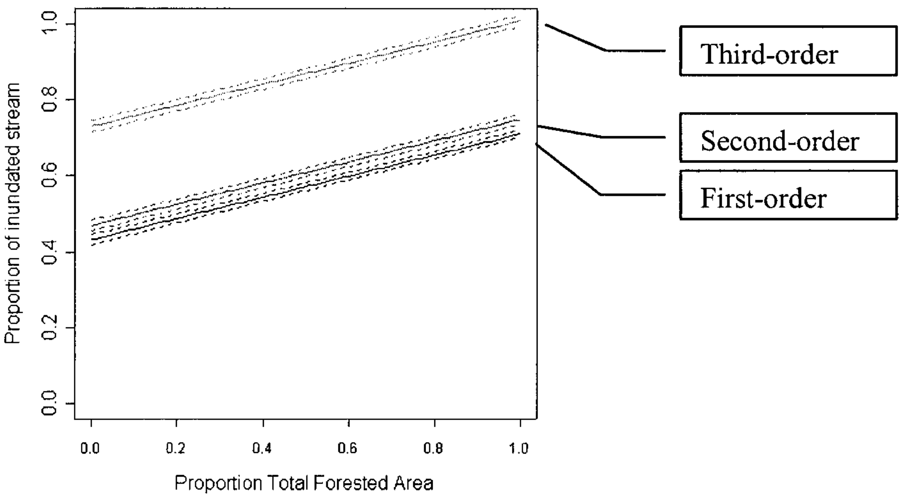


Figure 2.7 Predicted proportion of inundated stream within 300m on first-, second- and third-order stream segments as a function of proportion of deciduous forest given the stream gradient is 2.0%, with 95% confidence intervals (dotted lines).

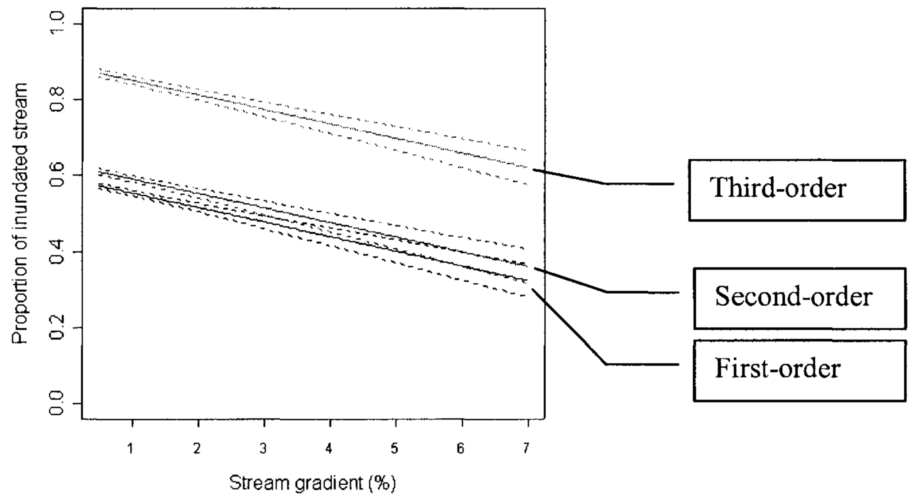
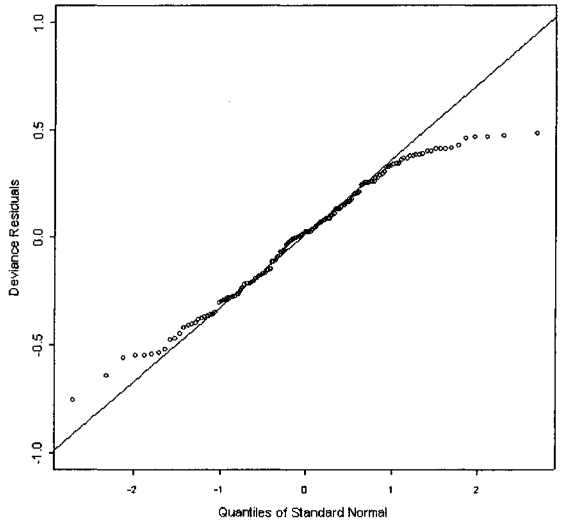
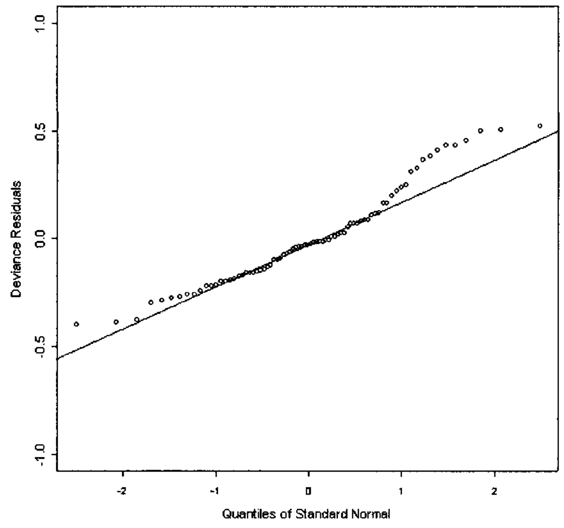


Figure 2.8 Predicted proportion of inundated stream within 300m on first-, second- and third-order stream segments as a function of stream gradient given proportion of deciduous forest is 0.3, with 95% confidence intervals (dotted lines).



(a)

Figure 2.9 Normal probability plot of deviance residuals for inundated stream length for the global model – 300m scale (n = 146).



(a)

Figure 2.10 Normal probability plot of deviance residuals for inundated stream length for the global model – 1,000m scale (n = 78).

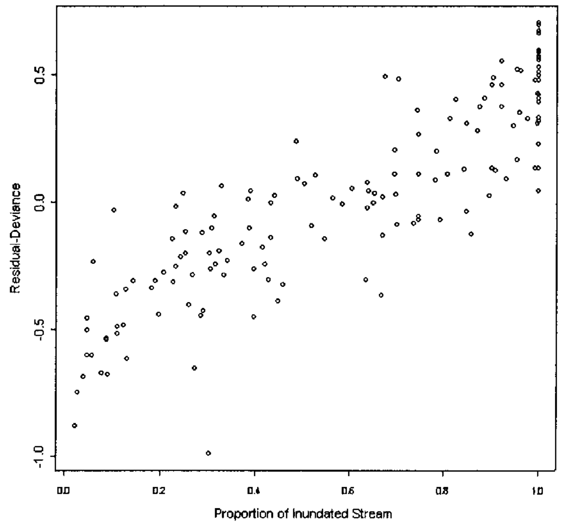


Figure 2.11 Plot of observed proportion of inundated stream with residual deviance from the model Phys & Veg 1 (n = 146).

Table 2.1 Covariates included in logistic and linear regression models of beaver pond presence and length of inundated stream.

Covariate	Unit	Code	Description
Stream Order		SO	Strahler stream order with three levels 1, 2 and 3
Stream direction		SD	Flow direction of the stream. Upstream (SD = 1) or downstream (SD = 0)
Culvert Presence		CP	Code indicated if the point is a random point along a stream (CP = 0) or a culverted stream crossing (CP = 1)
Road age		RA	Year that the stream crossing was reported to have been constructed. Random point events have an age of zero years
Harvested or burned forest	%	HB	Proportion of harvested and burned areas within 200m of the stream network
Proportion of deciduous forest	%	DC	Proportion of young and old deciduous forest outside the forage zone
Proportion of coniferous forest	%	CN	Proportion of young and old coniferous forest outside the forage zone
Proportion of forested area	%	FA	Proportion of young and old coniferous and deciduous tree species outside the forage zone
Gradient	%	GD	Average stream gradient of the 300m or 1,000m reach.
AVI year		AY	Effective date of the Alberta vegetation Inventory date.
X-coordinate	m	X	Easting of the UTM coordinate system, NAD27 Zone 12
Y-coordiante	m	Y	Northing of the UTM coordinate system, NAD27 Zone 12

Table 2.2 Candidate logistic and linear regression models explaining influence of biotic and abiotic habitat attributes on presence of beaver ponds and length of inundated stream.

Category	Model Name	Model	Source
Global	Global	SD + SO+ CP + RA + HB + DC + CN + GD + AY + X + Y + FA + SOxGD + GDxCP + FAxGD	Global
Physical	Phys 1	SD + GD	
	Phys 2	SD + AY + X + Y	
Vegetation	Veg 1	SD + HB + DC + CN	
Physical & Vegetation	Phys &Veg 1	SD + SO + FA + GD	Barnes and Mallik, 1997
	Phys &Veg 2	SD + DC + GD	McComb, Sedell and Buchholz, 1990a
	Phys &Veg 3	SD + DC + GD + SO + SOxGD	McComb, Sedell and Buchholz, 1990b
	Phys &Veg 4	SD + SO + GD + DC	Slough and Sadleir, 1977
	Phys &Veg 5	SD + SO + GD + CN	Howard and Larson, 1985
Road	Road 1	SD + CP + GD + SO + GDxCP + SOxCP	
	Road 2	SD + CP + RA	
	Road 3	SD + CP + GD + SO + GDxCP + SOxCP + HB + DC + CN	
	Road 4	SD + GD + CP	Jensen, Curtis, Lehnert and Hamelin, 2001
	Road 5	SD + FA + SO + GD + CP + FAxGD	Curtis and Jensen, 2004

Table 2.3 Habitat covariates at 300m scale stratified by present/not present for first to third order stream of 1124 stream segments 300m up- and downstream of a culvert or non-culverted site (standard deviation is shown in brackets).

	Culvert Present by Stream Order			Controls by Stream Order		
Variable	1	2	3	1	2	3
Road Age (RA)	17.7 (12.5)	17.0 (10.2)	21.2 (11.7)	-	-	-
Harvested or burned forest (HB)	0.08 (0.19)	0.04 (0.14)	0.1 (0.23)	0.09 (0.22)	0.06 (0.19)	0.02 (0.07)
Proportion of deciduous forest (DC)	0.29 (0.29)	0.34 (0.30)	0.3 (0.31)	0.27 (0.30)	0.3 (0.32)	0.23 (0.30)
Proportion of coniferous forest (CN)	0.09 (0.18)	0.07 (0.14)	0.06 (0.11)	0.07 (0.16)	0.05 (0.12)	0.09 (0.19)
Proportion of forested area (FA)	0.38 (0.33)	0.4 (0.32)	0.35 (0.33)	0.35 (0.34)	0.35 (0.35)	0.32 (0.36)
Gradient (GD)	2.11 (1.68)	1.73 (1.44)	2.52 (2.20)	1.90 (1.94)	1.74 (1.56)	2.13 (2.04)
AVI year (AY)	1994.6 (2.6)	1994.1 (2.1)	1995.3 (2.6)	1994.5 (2.3)	1994.8 (2.4)	1995.1 (2.4)

Table 2.4 Habitat covariates at 1000m scale stratified by present/not present for first to third order stream of 296 stream segments 1,000m up- and downstream of a culvert or non-culverted site (standard deviation is shown in brackets).

	Culvert Present by Stream Order			Controls by Stream Order		
Variable	1	2	3	1	2	3
Road Age (RA)	-16.9 (11.1)	-17.6 (9.4)	-20.5 (11.2)	-	-	-
Harvested or burned forest (HB)	0.06 (0.16)	0.04 (0.15)	0.08 (0.20)	0.09 (0.21)	0.09 (0.23)	0.01 (0.02)
Proportion of deciduous forest (DC)	0.26 (0.25)	0.32 (0.30)	0.37 (0.33)	0.22 (0.23)	0.37 (0.33)	0.27 (0.29)
Proportion of coniferous forest (CN)	0.12 (0.23)	0.06 (0.07)	0.04 (0.05)	0.08 (0.14)	0.07 (0.13)	0.12 (0.18)
Proportion of forested area (FA)	0.37 (0.31)	0.37 (0.32)	0.4 (0.35)	0.30 (0.28)	0.44 (0.36)	0.39 (0.37)
Gradient (GD)	1.86 (1.14)	1.65 (1.07)	2.79 (2.30)	1.32 (0.95)	1.88 (1.87)	1.72 (1.15)
AVI year (AY)	1994.5 (1.8)	1994.1 (1.5)	1994.2 (2.5)	1994.3 (1.7)	1995.3 (2.7)	1994.5 (2.3)

Table 2.5 Confusion matrix for total length of inundated stream classified using Alberta Vegetation Inventory (AVI) versus interpreted orthophotography from the same year. Overall accuracy = 94.4%, Kappa statistic = 0.63.

Downstream		Orthophotos		Row Total	Producer's Accuracy
		Not Inundated	Inundated		
AVI	Not Inundated	299.95	16.07	316.02	0.95
	Inundated	3.90	38.55	42.45	0.91
Column Total		303.85	54.62	358.47	
User's Accuracy		0.99	0.71		

Table 2.6 Proportion of total and percentage length of stream (km), length (km) and total stream length, inundated stream and number of road crossings, stratified by Strahler stream order.

Strahler Order	Stream length (km)	Stream length / total stream (%)	Inundated stream length (km)	Inundated stream length (%)	Inundated stream / total stream length (%)	Stream crossings (count)	Distribution of stream crossings (%)	Stream crossing density (stream crossings/km total stream)
1	2199	47.8	55	2.5	35.9	560	56.9	0.25
2	843	18.3	52	6.1	34.0	214	21.8	0.25
3	542	11.8	34	6.3	22.2	102	10.4	0.19
subtotal or average (1st to 3rd order)	3584	77.9	141	3.9	92.2	876	89.0	0.70
4	485	10.5	7	1.5	4.6	64	6.5	0.13
5	208	4.5	1	0.4	0.7	28	2.9	0.13
6	208	4.5	4	1.7	2.6	14	1.4	0.07
7	32	0.7	0	0.0	0.0	1	0.1	0.03
8	87	1.9	0	0.0	0.0	1	0.1	0.01
subtotal or average (4th to 8th order)	1020	22.2	12	1.2	7.8	108	11.0	0.38
Total	4604	100	153	3.3	100	984	100	0.21

Table 2.7 Cross-classification table of beaver occurrence and average proportion of inundated stream within 300 and 1,000m by stream direction and culvert presence stratified by stream order (std. dev. = standard deviation).

Scale	Direction	Site type	Beaver pond presence			Average proportion of inundated stream (std.dev.) for sites with a pond		
			Stream Order			Stream Order		
			1	2	3	1	2	3
300 (n=1124)	Up	Culvert	13	13	3	0.53 (0.11)	0.72 (0.06)	0.77 (0.03)
		Control	24	8	2	0.61 (0.12)	0.68 (0.10)	0.78 (0.08)
	Down	Culvert	17	14	2	0.37 (0.10)	0.55 (0.10)	0.53 (0.22)
		Control	26	13	5	0.61 (0.10)	0.35 (0.07)	0.99 (0.00)
			1	2	3	1	2	3
1,000 (n=296)	Up	Culvert	5	10	2	0.40 (0.10)	0.26 (0.03)	0.40 (0.05)
		Control	10	4	5	0.33 (0.07)	0.31 (0.05)	0.61 (0.24)
	Down	Culvert	8	9	2	0.27 (0.06)	0.27 (0.02)	0.33 (0.06)
		Control	13	7	3	0.03 (0.08)	0.34 (0.10)	0.09 (0.00)

Table 2.8 Logistic regression models explaining influence of biotic and abiotic attributes on occurrence of beaver pond presence within 300m from a culvert or random point (n = 1124). Model rankings were based on Akaike's Information Criterion (AIC) and Akaike weight of evidence (w_i), K is the number of model parameters. The model highlighted in grey has substantial empirical support with a change in AIC less than 2.00 as compared to the best approximating model (ΔAIC = 0).

Model	K	AIC	ΔAIC	w_i
Road 3	12	835.21	0.00	0.85
Phys & Veg 4	6	839.72	4.50	0.09
Global	17	842.78	7.57	0.02
Phys & Veg 2	4	842.91	7.69	0.02
Phys & Veg 3	8	842.93	7.72	0.02
Road 5	8	847.27	12.05	0.00
Phys & Veg 5	6	849.94	14.72	0.00
Phys & Veg 1	6	850.11	14.90	0.00
Road 1	9	853.75	18.54	0.00
Veg 1	5	856.93	21.72	0.00
Road 4	4	858.79	23.58	0.00
Phys 1	3	859.63	24.41	0.00
Null	1	870.14	34.93	0.00
Road 2	4	871.22	36.01	0.00
Phys 2	5	874.34	39.13	0.00

Table 2.9 Parameter estimates with standard error, and univariate Wald test statistics for the best approximating model for beaver pond presence at 300m including *Road 3*. (AIC = 835.21, null deviance: 868.14 on 1123 degrees of freedom; residual deviance: 811.21 on 1112 degrees of freedom).

	Parameter Estimate	Std. Error	Z value	Pr (> |z|)
(intercept)	-1.513	0.237	-6.382	0.000
SD	-0.148	0.182	-0.811	0.418
CP	-0.652	0.348	-1.875	0.061
GD	-0.316	0.103	-3.064	0.002
HB	-0.091	0.601	-0.151	0.880
DC	1.254	0.309	4.058	0.000
CN	-1.887	0.852	-2.215	0.027
SO_2	0.153	0.289	0.531	0.596
SO_3	0.432	0.352	1.228	0.220
CP x GD	0.084	0.148	0.565	0.572
CP x SO_2	0.819	0.413	1.985	0.047
CP x SO_3	-0.639	0.617	-1.036	0.300

Table 2.10 Estimated odds ratios and 95% confidence intervals for beaver occurrence, for difference in proportion of deciduous habitat, in 300m reach using *Road 3*.

Change in proportion of deciduous forest	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
odds ratio	1.13	1.29	1.46	1.65	1.87	2.12	2.41	2.73	3.09	3.51
95% CI	1.07, 1.20	1.14, 1.45	1.21, 1.75	1.30, 2.10	1.38, 2.53	1.48, 3.05	1.57, 3.68	1.68, 4.43	1.79, 5.33	1.91, 6.42

Table 2.11 Estimated odds ratios and 95% confidence intervals for beaver occurrence with culvert present/absent on first- to third-order streams, controlling for gradient (%) in 300m reach using *Road 3*.

Gradient (%)	Stream Order	0.5	1.0	2.0	3.0	4.0	5.0	6.0	7.0
OR	1	0.54	0.57	0.62	0.67	0.73	0.79	0.86	0.93
95% CI		0.30,1.00	0.34,0.96	0.46,0.82	0.48,0.93	0.42,1.26	0.39,1.6	0.38,1.97	0.37,2.38
OR	2	1.23	1.28	1.40	1.52	1.65	1.79	1.95	2.12
95% CI		0.60,2.54	0.66,2.49	0.83,2.35	1.11,2.08	1.26,2.16	1.10,2.94	1.03,3.71	0.99,4.55
OR	3	0.29	0.30	0.33	0.35	0.38	0.42	0.45	0.49
95% CI		0.09,0.93	0.10,0.93	0.12,0.91	0.14,0.88	0.18,0.84	0.22,0.78	0.30,0.68	0.39,0.63

Table 2.12 Logistic regression models explaining influence of biotic and abiotic attributes on occurrence of beaver pond presence within 1000m from a culvert or random point (n = 296), K is the number of model parameters. Model rankings were based on Akaike's Information Criterion (AIC_c) and Akaike weight of evidence (w_i). Models highlighted in grey have substantial empirical support with a change in AIC_c less than 2.00 as compared to the best approximating model ($\Delta AIC_c = 0$).

Model	K	AIC_c	ΔAIC_c	w_i
Phys & Veg 4	6	332.33	0.00	0.29
Phys & Veg 2	4	332.36	0.03	0.29
Phys & Veg 3	8	332.59	0.26	0.26
Road 3	12	334.08	1.75	0.12
Veg 1	5	337.82	5.49	0.02
Phys & Veg 1	6	339.14	6.81	0.01
Global	17	341.94	9.61	0.00
Road 5	8	342.74	10.41	0.00
Road 1	9	343.40	11.06	0.00
Null	1	343.42	11.09	0.00
Phys & Veg 5	6	344.19	11.86	0.00
Phys 1	3	346.09	13.76	0.00
Road 4	4	347.69	15.36	0.00
Phys 2	5	348.00	15.67	0.00
Road 2	4	348.09	15.76	0.00

Table 2.13 Parameter estimates with standard error and univariate Wald test statistics for the best approximating model for beaver pond presence at 1000m including *Phys and Veg 4.* (AIC =332.33, null deviance: 341.41 on 295 degrees of freedom; residual deviance: 320.11 on 290 degrees of freedom).

	Parameter Estimate	Std. Error	z value	Pr (> |z|)
(intercept)	-1.201	0.293	-4.096	0.000
SD	-0.241	0.275	-0.878	0.380
SO_2	0.624	0.310	2.010	0.044
SO_3	0.088	0.393	0.224	0.823
GD	-0.301	0.128	-2.350	0.019
DC	1.980	0.558	3.546	0.000

Table 2.14 Estimated odds ratios and 95% confidence intervals for beaver occurrence for difference in proportion of deciduous habitat at 1,000m reach using *Phys and Veg 4.*

Change in proportion of deciduous forest	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
odds ratio	1.22	1.49	1.81	2.21	2.69	3.28	4.00	4.87	5.94	7.24
95% CI	1.09,1.36	1.19,1.85	1.30,2.52	1.43,3.42	1.56,4.65	1.70,6.33	1.86,8.60	2.03,11.70	2.22,15.91	2.42,21.64

Table 2.15 Mean covariate values for observations associated with low and high leverage observations ($h_i = 0.03$) where $h_i > 2p/N$ where p is the number of parameters and N is the number of observations for 300m stream segments for the global model beaver pond presence (n = 1124).

Variable	$h_i > 0.03$	$h_i < 0.03$
Number of observations	86	1038
Beaver pond present	9.3%	13.29%
Stream order	2.09	1.44
Proportion with culverts	46.51%	50.29%
Gradient	3.52%	1.86%
Proportion of deciduous forest	0.4962	0.2728
Proportion of coniferous forest	0.0299	0.0796
Proportion of harvested and burned	0.1457	0.0599

Table 2.16 Mean covariate values for observations associated with low and high leverage observations ($h_i = 0.03$) where $h_i > 2p/N$ where p is the number of parameters and N is the number of observations for 1,000m stream segments for the global model for logistic regression estimating beaver pond presence (n = 296).

Variable	$h_i > 0.03$	$h_i < 0.03$
Number of observations	15	281
Beaver pond present	26.7%	26.3%
Stream order	2.4	1.58
Proportion with culverts	66.7%	49.1%
Gradient	5.63%	1.55%
Proportion of deciduous forest	0.7125	0.2586
Proportion of coniferous forest	0.0191	0.0872
Proportion of harvested and burned	0.0487	0.0643

Table 2.17 Linear regression models explaining influence of biotic and abiotic attributes on proportion of inundated stream within 300m from a culvert or random point (n = 146). Model rankings were based on Akaike's Information Criterion (AIC_c) and Akaike weight of evidence (w_i), K is the number of model parameters. Models highlighted in grey have substantial empirical support with a change in AIC_c less than 2.00 as compared to the best approximating model ($\Delta AIC_c = 0$).

Model	K	AIC_c	ΔAIC_c	w_i
Phys & Veg 1	6	77.09	0.00	0.41
Phys & Veg 4	6	77.43	0.34	0.34
Road 5	8	80.10	3.01	0.09
Road 3	12	80.57	3.48	0.07
Phys & Veg 3	8	80.93	3.84	0.06
Road 1	9	83.94	6.85	0.01
Phys & Veg 2	4	85.94	8.85	0.00
Veg 1	5	87.39	10.30	0.00
Phys & Veg 5	6	88.43	11.34	0.00
Phys 2	5	88.75	11.66	0.00
Global	17	90.73	13.64	0.00
Phys 1	3	91.35	14.26	0.00
Road 2	4	91.57	14.48	0.00
Road 4	4	91.60	14.51	0.00
Null	1	92.93	15.84	0.00

Table 2.18 Parameter estimates with standard error and univariate Wald test statistics for the best approximating model for proportion of inundated stream at a 300m scale, *Phys and Veg 1* model. ($AIC_c = 77.09$, null deviance: 15.716 on 145 degrees of freedom; residual deviance: 13.114 on 140 degrees of freedom).

	Parameter Estimate	Std. Error	Z value	Pr (> |z|)
(intercept)	0.409	0.061	6.665	0.000
SD	0.100	0.051	1.956	0.052
GD	-0.038	0.042	-0.919	0.360
FA	0.278	0.082	3.401	0.001
SO_2	0.037	0.056	0.663	0.508
SO_3	0.297	0.082	3.641	0.000

Table 2.19 Linear regression models explaining influence of biotic and abiotic attributes on length of inundated stream 1,000m from a culvert or random point (n = 78). Model rankings were based on Akaike's Information Criterion (AIC$_c$) and Akaike weight of evidence (w_i), K is the number of model parameters. Models highlighted in grey have substantial empirical support with a change in AIC$_c$ less than 2.00 as compared to the best approximating model (ΔAIC$_c$ = 0).

Model	K	AIC$_c$	ΔAIC$_c$	w_i
Null	1	6.38	0.00	0.41
Phys & Veg 2	4	7.38	1.00	0.25
Veg 1	5	9.53	3.16	0.08
Phys 1	3	9.58	3.20	0.08
Phys 2	5	10.33	3.95	0.06
Road 4	4	11.31	4.93	0.03
Phys & Veg 4	6	11.66	5.28	0.03
Phys & Veg 1	6	11.81	5.43	0.03
Road 2	4	12.06	5.68	0.02
Phys & Veg 3	8	15.42	9.04	0.00
Road 5	8	15.98	9.61	0.00
Phys & Veg 5	6	16.06	9.69	0.00
Road 1	9	20.29	13.92	0.00
Road 3	12	22.71	16.34	0.00
Global	17	33.44	27.06	0.00

Table 2.20 Mean covariate values for observations associated with low and high leverage observations (h_i) where $h_i > 2p/N$ where p is the number of parameters and N is the number of observations for 300m stream segments for the global model for linear regression estimating proportion of inundated stream (n = 146).

Variable	$h_i > 0.23$	$h_i < 0.23$
Number of observations	21	125
Beaver pond present	0.4611	0.6037
Stream order	1.71	1.55
Proportion with culverts	52.4%	40.8%
Gradient	1.84	1.47
Proportion of deciduous forest	0.3473	0.3643
Proportion of coniferous forest	0.0954	0.0308
Proportion of harvested and burned	0.0622	0.0430

Table 2.21 Mean covariate values for observations associated with low and high leverage observations (h_i) where $h_i > 2p/N$ where p is the number of parameters and N is the number of observations for 1,000m stream segments for the global model for linear regression estimating proportion of inundated stream (n = 78).

Variable	$h_i > 0.44$	$h_i < 0.44$
Number of observations	15	63
Beaver pond present	0.4495	0.2737
Stream order	1.73	1.68
Proportion with culverts	40.0%	47.6%
Gradient	2.06	1.54
Proportion of deciduous forest	0.3990	0.3580
Proportion of coniferous forest	0.0871	0.0585
Proportion of harvested and burned	0.0363	0.0332

Chapter 3 Effect of culverts on beaver activity in headwater streams from in northcentral Alberta, 1976 to 2001

3.1 Introduction

Beaver ponds are important habitat areas for many species and are critical for obligate wetland species. Presence of beavers in headwater streams increases the overall species diversity of the stream and riparian areas, and resistance to disturbances (Schlosser and Kallemeyn 2000) by creating a mosaic of habitat patches (Johnston and Naiman 1990*a*). Riparian habitat heterogeneity created by beaver has been linked to herbaceous species richness at the watershed scale (Wright et al. 2002). Roads influence wetland development by altering hydrology (Trombulak and Frissell 2000). Roads redirect water towards stream channels through alteration of subwater and stream channel flow (Forman and Alexander 1998, Trombulak and Frissell 2000). Culverts installed at stream crossings can alter channel movement, water flow, and increase sedimentation into the stream channel (Forman and Alexander 1998, Jones et al. 2000).

Change in water flow caused by beaver dams affects species richness; water flow rate upstream of a dam is decreased and downstream water flow rate is increased. Species diversity in catchments dominated by streams with fast moving water may increase when a mosaic of dams and associated ponds introduces sections of slow moving water into the landscape (Collen and Gibson 2001). Schlosser (1995) concluded that flora and fauna adapted to specific flow conditions around beaver dams replaced the previous community. Spatial and temporal dynamics of beaver pond creation and abandonment influence headwater species richness (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). Wright et al. (2002) proposed that it is not the beaver ponds themselves that are species-rich but the collective mosaic of beaver influenced and non-influenced patches in the stream network; if beaver were to completely dominate the landscape, species richness at the stream network level would decrease. Beaver impoundments have a direct effect on wetland and species diversity in streams through changes to the distribution of water. Upstream of a dam, the stream channel is widened as water pools behind the dam. McKinstry et al. (2001) reported that waterfowl abundance was higher in streams with beaver than without, primarily due to the increase in stream width.

Beavers frequently block culverts with dams (McKinstry and Anderson 1999, Jensen et al. 2001, Curtis and Jensen 2004). Beavers may use ponds formed behind dammed culverts to establish a colony and to access forage tree species from the water's edge (Jeglum 1975). Several dams and ponds may form within an established beaver colony. Dams are built in linear succession; an initial dam is built, lowering water levels downstream and raising levels upstream. Subsequent dams are often constructed downstream. A beaver colony will remain in an area, maintaining dams, as long as forage and construction material are available and if the colony is not predated, extirpated by disease, or trapped. When a beaver dam is abandoned, the stream will eventually either breach or flank the dam, thereby draining the pond and exposing the rich organic soil on which plant communities establish. It is possible that culverts may alter behaviour of beavers with respect to dam construction and maintenance.

Although there may be an association between culverts and beaver, there is little research that identifies the mechanisms by which beavers respond to culverts, and how or whether culverts affect patterns of beaver activity and ecological processes. If culverts alter beaver activity and distribution within small order streams, there could be a change in wetland characteristics, abundance and distribution within the stream network.

My research objectives were to describe change in beaver activity over a 24-26 year period (1976-78 to 1999-2000) at three spatial scales: 1) **third-order stream network** within selected streams 2) **stream** 300m up- and downstream of culverted streams in a paired control treatment and 3) **site** 5 and 50m up- and downstream from culverts. My study design related culvert presence/absence, environmental variables and pre-culvert dams (intact and breached) to model post-culvert intact and breached dams. I used length of inundated stream and pond area to measure the magnitude of influence of beaver within a stream with respect to culverts and environmental variables. I used intact and breached dam abundance (count) as a measure of active beaver activity and abandonment (respectively) in a stretch of stream. Vegetation metrics were used as independent covariates to describe site variability. I predicted that beaver activity would be more influenced by culverts at the site and stream scales than at the watershed scale.

3.2 Study area

The study area (Figure 2.1) is located in north-central Alberta (-115.30 E, 54.61 N to – 109.94 E, 57.74 N) in the Mid-Boreal Uplands and Wabasca Lowlands ecoregions of the Boreal Plains Ecozone (Ecoregions Working Group 1989), approximately 60,000-km^2. The forested landscape is dominated by trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) and to a lesser degree balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*). Wetlands in the riparian zones largely develop on fluvial wetlands on postglacial tills. The riparian zone (vegetation along streams and lakes) is dominated by trembling aspen, green alder (*Alnus crispa*), river alder (*Alnus tenuifolia*), and willow (*Salix spp.*). The flat lowlands contain bogs and fens dominated by tamarack (*Larix laricina*) and black spruce (*Picea mariana*). Mean summer and winter temperatures are 13.7 and -11.9 °C, respectively (Beckingham and Archibald 1996). Mean summer and winter precipitation is 238 and 63 mm, respectively. The topography of the Mid-Boreal Uplands ecoregion is characterized as undulating to flat lowlands and rolling uplands. Elevation range is 400 to 800m ASL (Ecoregions Working Group 1989). The predominate parent materials are loamy to clay-textured glacial till, lacustrine deposits, and inclusions of coarse, fluvioglacial deposits (Ecoregions Working Group 1989). Wabasca lowland is low-relief and poorly drained, and organic soil covers about 50% of the area. The dominant soils in the Mid-Boreal Uplands and Wabasca lowland are Organic, Grey Luvisols, Brunisols, and Gleysols. (Beckingham and Archibald 1996).

Petroleum, natural gas and mineral extraction and forest harvesting have been underway in the area since the mid-20th century. An extensive road network, which includes two highways and several secondary roads connecting industrial activity and communities, has expanded since the early 1970s (Schneider 2002), and consequently there has been an increase in stream crossings.

3.3 Materials and methods

Data overview

I used six digital data sources in this study, including: 1) the *Alberta Vegetation Inventory (AVI)* - a 1:20,000 scale vegetation inventory used primarily for forestry inventory in Alberta. 2)

A *Digital Elevation Model (DEM)* - a Digital Elevation Model (DEM) for the study area was created from the 1:50,000 Canadian Digital Elevation Data (CDED). The CDED was resampled from a resolution of 18 x 18 m pixel to a 100 x 100m pixel resolution. 3) *Land use disposition database* – database maintained by Sustainable Resources Development, Government of Alberta that contains the ownership of land disposition licenses, these are when land use permit took effect (herein, Start date). 4) *Road network* – all roads, highways and roads used by industry in the study area prior to 2000. 5) *Small-scale orthorectified photography* - black and white 1:40,000 to 1:60,000 aerial photography that was orthorectified, herein orthophotography stored in a UTM projection (Zone 12), Nad27 datum. 6) *Stream network* – 1:50,000 stream network with flow direction (including through lakes).

ArcView 3.2 (ESRI ArcView 3.2) was used for digitizing and visualization of data layers. ArcInfo 8.3 (ESRI Arc 8.3) was used for spatial analyses. The study area has low relief and as such, georectification (as opposed to orthorectification) is an appropriate method to reduce distortion in aerial photography (Welch and Jordan 1996). I used georectified 1,15,000 aerial photography to digitize the stream and beaver activity (Carstensen and Campbell 1991, Barrette et al. 2000).

Watershed selection

Literature review and results of Chapter 2 indicated that beavers predominately dam third-order streams and lower (Johnston and Naiman 1990*b*, Snodgrass and Meffe 1998, Suzuki and McComb 1998, McKinstry et al. 2001). The Strahler stream ordering system (Strahler 1957) was used to define third-order watersheds (Figure 3.2) in the study area using the stream network data. A total of 1166 third-order watersheds were identified (Figure 3.3). I selected a balanced sample of twenty third-order watersheds from this population using selection criteria listed in Table 3.1 and an algorithm created by Cumming (2003). Data from the AVI were used to remove watersheds with less than 9.5% deciduous forest prior to the selection process. Proportion burned, logged, and deciduous forest were estimated from the AVI within a 750m buffer around the stream network for each watershed, eliminating a center ring of 250m (diameter). The ring was used to minimize the influence of beaver ponds and foraging on the estimate of available deciduous forest.

Ten watersheds were selected along a low road density gradient (less than 0.2 stream crossings per km of stream) and ten watersheds were balanced along a high road density gradient (greater than 0.2 stream crossings per km of stream) using the road network database. A Kolmogorov-Smirnov test was used to ensure that the selected watersheds were representative of the third-order watershed population with respect to the selection criteria. After assessing stream crossings in the field, I added one extra third-order watershed (with high stream crossing density) to increase my sample size of culverted stream crossings. Due to time constraints, I reduced the scope of my research from comparing watersheds with low and high density stream crossings to streams and watersheds associated with culverts; 14 of 21 watersheds met this criterion. Culverted and non-culverted sites used in this study were sampled from the 14 selected watersheds.

3.3.1 Data preparation

3.3.1.1 Response Variables

Aerial photography was from years 1976-1978 and years 1999-2001, herein referred to as pre-culvert and post-culvert, respectively. Pre-culvert aerial photography was black and white and post-culvert photography was either true colour or colour infrared. The scale of aerial photography for both periods was 1:15,000. Pre-culvert aerial photographs were mostly from early summer months June-July while post-culvert photographs were taken in early spring April – May. All aerial photography was digitally scanned at an initial resolution of 1200 pixels per inch (ppi) using an Afga Duoscan desktop scanner. The digital images were then converted to raster images (herein, image(s)). All images were resampled from 1200 ppi to 800 ppi in ArcInfo to save storage space using the resample function available in ArcInfo GRID.

Each image was georectified using a minimum of six control points taken from orthorectified basemaps. The images were georectified in ArcInfo Grid (warp function), specifying a second order polynomial transformation with a nearest neighbour resampling algorithm. Control points were adjusted and/or more points added until the root mean square error was less than 4.0m. All photo interpreted features were digitized at mapping scales of 1:1,000 and 1:1,875. Concurrent with digitizing, a hardcopy of the 1:15,000 digital aerial photos were viewed through an 8x single optic lens on a light-table, to confirm identification of features interpreted in the digital image.

Prior to identification of stream crossing structures, beaver dams, and impounded water, I made three reconnaissance survey trips to the study area; one on the ground and two by helicopter. The purpose of these trips was to train my eye to recognize beaver ponds and dams, and vegetation structure (grass, shrub, coniferous, deciduous and mixed stands) within riparian areas of third-order watersheds (Figure 3.4). I used 2001 and 2002 colour, 1:15,000 aerial photos and observed dam, pond, and stream crossing structures in the photo and on the ground. There was no quantitative validation of aerial photography interpretation of landscape features for these visits. Culverted stream crossings were easily differentiated from bridges both in helicopter surveys and in the aerial photography.

I delineated the stream network in the pre- and post-culvert aerial photography 1,000m up- and downstream of all identified culverts, bridges, and seismic lines with no crossing structure for each chronosequence. The stream network was delineated in both sequences as some locations had significant change in the stream network. This was especially true where beaver activity was present. I estimated stream crossing (culverts and bridges) density of first- to third-order streams within watersheds using the intersection of the digital road and stream networks. Only stream crossings constructed prior to 1994 were included in the stream crossing density for each watershed.

Dams: intact and breached

At each site, for both time periods, I digitized all intact and breached dams, observed along the stream. Figure 3.5 shows an example of a culverted stream crossing in year 1999 with beavers dams and impounded water both up and downstream of the culvert and no culvert and no beaver activity in 1978. Distinction between breached and intact dams was subjective. A dam was interpreted as intact (active) if it 1) impounded water, and 2) appeared as a continuous line, without a gap, across the length of the stream. A dam was considered breached it if had a visible gap, greater than 1mm, on the aerial photography at a scale of 1:1,185 (approximately 2 metres ground length). Breached dams were easily identified if the stream meandered around the dam or broke through it. At times, breached dams were also found to impound some water, due to a poorly drained pond. There was no minimum mapping length for dams.

Ponds and inundated stream length

I delineated all ponds along the stream network that contained surface water, moist soil devoid of vegetation or ice/snow cover that were longer than 10 metres along the stream network (minimum mapping unit) and wider than the "normal stream width". Ice and snow was still visible on the stream (April & May) in some photographs. Where there was overlap between photographs taken in snow cover and green-up conditions, green-up conditions were used. In the few photographs where snow-covered frozen ponds occurred, they were easily identified as the surrounding riparian vegetation was always snow-free. The boundary of the snow pack and riparian vegetation was used as the pond boundary. If recently flooded living riparian vegetation or older snags obscured the surface water below over an area larger than 15 x 15 m (0.0225 ha), the vegetation was treated as an island. Ponds were intersected with the digitized stream network to calculate total length of inundated stream.

Ground-truthing aerial photography interpretation

I assessed the accuracy of post-culvert (1999-2001) aerial photography interpretation of intact and breached beaver dams in culverted streams against field observations for 2003. A 2 to 4 year discrepancy existed between the aerial photography and field observations. Dams that were intact in the aerial photography were often found to be breached on the ground, but still impounded water. To account for conversion of intact dams to breached dams and vice versa, I combined intact and breached dams for my assessment of aerial photography interpretation. At each site, in the field and with aerial photography, dam presence (intact and/or breached) and stream impoundment, were assessed for presence/absence, within 5 and 50m of the rights-of-way on both sides of the culvert, starting at the inlet for upstream and outlet for downstream. Impoundments were counted as present in both the field and the aerial photography if the length of inundated stream was longer than 10. I used a confusion matrix (Jensen, 1996) to assess classification accuracy of 50m up- and downstream of a culvert (see Chapter 2). No accuracy assessment was conducted for estimated length of inundated stream or pond area.

3.3.1.2 Covariates

The AVI was classified into deciduous and coniferous forest stands based on species composition. A stand was classified as DC if it was > 50% trembling aspen, balsam poplar, or paper birch. A stand was classified as CN if it was > 50% white spruce, balsam fir or alpine fir (*Abies lasiocarpa*). I did not include pine species (*Pinus* spp.; a dry site upland species) or black spruce (associated with bogs) in calculating the proportion of coniferous forest. Variables DC and CN were used as a surrogate measure for the dominant riparian vegetation type. Each stream segment was assessed for proportion of DC and CN outside a 100m beaver foraging zone to a distance of 100m (Figure 3.6). The beaver forage zone is about 100m from the water's edge (Howard and Larson 1985, Johnston and Naiman 1987). The beaver forage zone was excluded to minimize inclusion of vegetation communities potentially affected by impounded water (open water and snags), and beavers foraging for food and construction material. Estimated proportion of deciduous and coniferous forest was assumed to be correlated with available forage within the beaver forage zone before beaver influence. Gradient (GD) was calculated for up- and downstream segments using a triangulated irregular network (TIN), based on the DEM, within 2 km or a 20 pixel distance of the segment.

3.4.3 Objective 1: Beaver activity at the watershed scale

At the watershed scale I compared general changes in beaver activity and stream crossing frequency over time. I identified a total of 14 non-culverted crossings (seismic lines and roads that abutted a stream), 71 culverts, and 5 bridges, collectively referred to as "sites", within 14 of 21 watersheds (Figure 3.1*b*). I estimated beaver activity (number of intact and breached dams, pond area and length of inundated stream), 1,000m up- and downstream of non-culverted and culvert stream crossings in pre- and post-culvert periods.

I compared beaver activity change in pre-culvert and post-culvert periods at the watershed scale. I summarized beaver activity by Strahler stream order within all selected stream segments for: 1) total length of stream, 2) inundated stream, 3) number of intact dams, 4) number of breached dams, 5) number of culverted stream crossings, and 6) number of unculverted stream abutments. I tested whether breached and intact dams, culverts and, unculverted abutments occurred in proportion to the distribution of first- to third-order streams using Neu et al. (1974) ($\alpha = 0.05$).

3.4.4 Objective 2: Beaver activity at the stream scale

I selected 31 sites that had no culvert in 1976 but had a culvert by 1999. Culvert presence was verified using aerial photography (Figure 3.1*c*). All sites were at least 1200m downstream and 600m upstream from another culvert or bridge prior to 1999 - 2001 photos. This distance was use to minimize effects of other culverts on my sample. I used a split-plot study design, where a culvert (treatment) was paired with a control located 600m upstream of the culvert. Beaver activity was measured 300m up- and downstream of the culvert and control (Figure 3.7). For each aerial photograph chronosequence at each culverted and control location, I counted the number of intact and breached dams, measured the length of impounded stream, and total area of impounded surface water, 300m up- and downstream. Several covariates were assessed within each 300m segment to reflect biotic and abiotic habitat characteristic known to influence beaver activity (Table 3.2). I tested the hypothesis that beaver activity 300m in combined up- and downstream of culverted locations is significantly different from downstream controls.

I developed *a priori* candidate regression models to explain variation for four measures of beaver activity: 1) intact dams (Table 3.3), 2) breached dams (Table 3.4), 3) inundated streams (Table 3.5) and 4) pond area (Table 3.6) as observed in 1999 to 2001 aerial photography for streams culverted after 1976-1978. Generalized linear mixed models (GLMM) with negative binomial error (Otter Research glmmADMB) was used to model intact and breached dams, and a GLMM for Gaussian data (Lindsey GLMM) was used for length of inundated stream and pond area. For both negative binomial and linear GLMMs, I used paired control and treatment sites as the random effect. Akaiki's Information Criterion (AIC) score was used to select the top candidate model from a set of *a priori* models (Burnham and Anderson 2002). I used Akaike Information Criterion (AIC) corrected for small sample sizes (AIC_c) when the ratio of sample size (n) and the number of parameters (K) was less than 40 (Burnham and Anderson 2002). Prior to model selection, I examined all candidate variables for correlation using Spearman's rho (r) statistic, a rank-based measure of association. Several of the variables used to model beaver activity had an $r > 0.70$. ISr, (post-culvert length of inundated stream) was correlated to Pr (post-culvert total pond area). Similarly ISo (pre-culvert length of inundated stream), Po (pre-culvert total pond area) and DIo (pre-culvert total intact dams) were correlated. These variables, however, did not occur together in any of the *a priori* models. All statistical analyses were conducted in R, Ver. 1.8.1 (R Core Development Team 2005).

3.4.5 Objective 3: Beaver activity at the site scale

From June to October 2003, I assessed up- and downstream beaver dam and impoundment presence for all accessible culverted stream crossings (herein, field-sites) within the selected watersheds (Figure 3.1*d*). One culvert that was just outside a watershed boundary was added to the sample set to increase the total number of culverts sampled. Selection criteria required all sites to have water present in the stream channel 50m up- and downstream of the site. I tested the hypothesis that dam presence would be more frequent upstream of a dam compared to downstream.

I assessed presence/absence of beaver dams (combining intact and breached dams) within 5 and 50m of a culvert. I tested the hypothesis that the presence of beaver activity occurred 1) upstream, 2) downstream and 3) both up- and downstream at an expected ratio of 1:1:1 respectively using a Chi-square goodness of fit test ($\alpha = 0.05$) (Zar 1999).

3.4 Results

3.4.1 Ground-truthing aerial photography interpretation

Overall accuracy of beaver dams interpreted from aerial photography was 38.5% for downstream sites (Table 3.7) and 82.1% for upstream sites (Table 3.8). User and producer accuracy for beaver presence downstream of a culvert were both 0.00. User and producer accuracy for beaver presence upstream of a culvert was 0.45 and 0.83, respectively. The Kappa statistic for the confusion matrix was 0.23 for downstream sites and 0.36 for upstream sites.

3.4.2 Beaver activity at the watershed scale

A total of 152 km and 153 km of stream was delineated for pre-culvert and post-culvert sites (Table 3.9). The discrepancy between the chronosequences for total stream length was due to changes in stream course and increased sinuosity of the stream channels, primarily due to beaver dams. In the pre-culvert period, intact dams, breached dams, and lengths of inundated streams were found less often than expected within first order streams and more often than expected in third. Post-culvert patterns were similar but intact dams in third-order streams occurred as expected. In the pre-culvert period, culverts were found more than expected in first order streams, and less than expected in second order streams.

A visual comparison of the results in Table 3.9 indicated that the distribution of intact and breached dams in first- to third-order streams remained constant between the two periods. Both total dam density and proportion of inundated stream doubled over the study period. In the pre-culvert period, intact dam density was approximately 0.70 dams per km of stream (106 dams / 152km), while the post-culvert density increased to 1.13 dams per km of stream (172 dams / 153km). The combined density of intact and breached dams in the pre-culvert era was 1.15, and post-culvert was 2.17 dams per km of stream. The percentage of the headwater stream network inundated by beaver ponds in the pre- and post-culvert period was 13.2% (20/152) and 20.3% (31/153), respectively. The number of culvert crossings within the 14 watersheds increased 3.38 times (71/21), and culverts in second order stream increased 9.0 times (18/2).

3.4.3 Beaver activity at the stream scale

Total number of beaver dams, intact and breached, within each site (pre- and post-culvert) used in the stream scale analysis are shown in Table 3.10. Total intact dams in pre- and post-culvert period were 25 and 31, respectively. Total breached dams in pre- and post-culvert period were 10 and 42, respectively. In the pre-culvert period, the maximum number of intact dams in a site was four and breached dams it was three. In the post-culvert period, the maximum was seven and six respectively.

3.4.3.1 Intact dams

The best approximating model explaining variance in intact beaver dams was *Culvert and pre- culvert beaver activity* DIr = DIo + CP + DIo x CP (Table 3.11) ($w_i = 0.48$). The second best approximating model was *Culvert* ($\Delta AIC_c = 0.91; w_i = 0.31$). For all other models $\Delta AIC_c > 2.0$. For the model *Culvert and Pre-culvert beaver activity*, pre-culvert beaver dam count without the culvert interaction effect was not significant (DIo = 0.091, p-value = 0.728) (Table 3.12). Interestingly, the number of intact dams before, in the pre-culvert period had significant positive influence on the number of dams present when a culvert was present (Table 3.12). Culvert presence, however, had a negative relationship with the number of intact beaver dams when no intact dam was present in the pre-culvert period (Table 3.12, Figure 3.8). Culverted sites had a significantly lower number of beaver dams given a pre-culvert dam count of 0 or 1. Culvert presence was significantly related to an increase in the number of post-culvert beaver dams when pre-culvert dam count was > 1. Predicted beaver dam count value for culverted streams with > 1 pre-culvert dam was larger than I observed in the field. For example, four pre-culvert intact dams predicted about ten post-culvert dams, given culvert presence, in my model. The largest number of intact dams that I observed within a site was seven (Table 3.10).

3.4.3.2 Breached Dams

The best approximating model explaining variance in the number of breached beaver dams was *Pre-culvert Beaver Activity* DBr = GD + DC + CN + DBo (Table 3.11). The weight of evidence for this model was 0.23. Proportion of coniferous vegetation was a significant variable in the model (CN = -5.143, p-value = 0.050) (Table 3.13). Four other models also were good candidates for best approximating model, with a change in AICc score less than 2.0. Of these models the most parsimonious was "Vegetation".

3.4.3.3 Inundated streams

The best approximating model explaining variance in length of inundated stream was *Post-culvert beaver activity – intact dams* DIr (Table 3.11). The weight of evidence for this model was 1.0. Post-culvert intact beaver dams, was a significant variable (DIr = 33.972, p-value < 0.0000).

3.4.3.4 Pond area

The best approximating model explaining variance in pond area was *Post-culvert Inundated Stream* Pr=ISr (Table 3.11). The weight of evidence for this model was very strong (w_i = 1.0). Post-culvert length of inundated stream was a significant variable in the model (ISr = 18.961, p-value < 0.000). This indicated that, for an increase of 1m in inundated stream, pond area increased by 18m^2.

3.4.4 Beaver activity at the site scale

Beaver dam occurrence within 5m of a culvert occurred as would be expected if dams were equally distributed. Occurrence of beaver dams within 50m of a culvert was significantly different from the expected distribution of 1:1:1 (Table 3.14). Beaver dams downstream of a culvert were rare when no beaver dam occurred upstream.

3.5 Discussion

3.5.1 Ground-truthing aerial photography interpretation

Overall my results comparing aerial photography interpretation and ground-truthing indicated that either 1) beaver dams were not accurately detected in the aerial photography or 2) the gap between the year of the field work, 2003, and the aerial photography, 1999-2001, was sufficient to allow for change in beaver activity around the culverts sampled in the field. I believe the 2-4 year gap between the field and aerial photography did not allow for accurate ground truthing of beaver dams interpreted from the aerial photography. Beaver dams, lodges and ponds are conspicuous features along streams and can be easily identified in 1:15,000 aerial photography. Despite the low accuracy aerial photography interpretation, I was confident that for the year of the photo I correctly identified beaver dams and ponds.

3.5.2 Beaver activity at the watershed scale

Estimated dam density in my study for intact dams, and combined intact and breached dams was well below what has been published in the literature. Naiman et al. (1986) reported that dam density on the sub-arctic region of the Precambrian shield, northern Quebec, averaged 10.6 dams/km of stream. In northern Minnesota, dam density averaged 2.5 dams/km of stream (Naiman et al. 1988). Length of inundated stream classed is also well below what has been published in the literature. Johnston and Naiman (1990*b*) reported that between first- and fourth-order streams studied within this system, beaver impounded, on average, 55% of the stream network, and first- and second-order streams contained 80.3% of the total stream network. Naiman and Melillo (1984) observed that beaver influenced 20-40% of second-order streams. The proportion of inundated stream in my study area is low compared to what has been reported in the literature. It is possible that beaver in my study area have not yet saturated the landscape. Beaver populations may have a higher mortality rate in my study areas, keeping the populations levels low. Habitat available in my study may not be able to sustain high beaver population levels or habitat in the past may have been overused by beavers and is now fallow. The latter is not as likely as beaver activity was still relatively low in 1976, indicating that beaver are still expanding their range. In the same study area, Martell (2004) found that little to no beaver activity existed in the early 1950s. A detailed study on the potential carrying capacity of the river system for beaver colonies would confirm my hypothesis.

3.5.3 Beaver activity at the stream scale

For intact dams, the top model had an interaction effect between culvert presence and the number of pre-culvert intact dams. If the pre-culvert intact dam count was greater than one, there was a positive relationship between culverts and intact beaver dams. Thus, the negative relationship of a culvert to beaver presence may be attenuated if there is historic presence of beavers. This is a very interesting result as it may mean that the culvert/beaver relationship can change depending on the history of beaver activity at the site, regardless of other environmental and physical characteristics known to be important beaver habitat variables. Presence of beaver dams prior to the culvert is an indication that there is already a well-established beaver colony and not likely to be abandoned quickly or if abandoned would likely be easily re-colonized.

In the study area culverts are actively managed to control beaver activity through trapping and dam removal. This could lead to a negative relationship between culvert presence and intact beaver dams. However, it does not explain why historic presence of beaver dams results in a positive relationship with post-culvert intact dams. It is possible that beaver colony persistence over time is more likely when the colony is present (as indicated by intact dams) before a culvert is installed; colonies can be maintained regardless of trapping effort over time as the colony infrastructure is already in place (established lodge, series of dams etc). Boyce (1981) found that in Chena River (Fairbanks), Alaska, dispersing juveniles had higher survivorship when high quality colony sites were available to them as a result of the previous adult beaver occupants being trapped out. Martell (2004) reported repeated dam-site colonization after abandonment over a period of 50 yrs. If a section of stream around a culvert does not have a historical beaver colony but is suitable beaver habitat, dispersing individuals will likely be trapped or dams removed before a significant amount of water can be impounded.

Over the period of my study, the number of intact dams increased slightly but the number of breached dams increased by a factor of 4. The rapid “growth” in abandoned dams over a period of 22-24 years indicated that there might be a high rate of colony abandonment, relative to colonization, as dams were not maintained. Over the study period, many of these dams could have been breached then repaired and breached again. It is also difficult to ascertain which of the breached dams were only temporarily breached. It was surprising that the weight of evidence for models containing a culvert treatment was not as high for breached dams as it was for intact dams. In fact, for post-culvert breached dams, only one of the top models included pre-culvert intact and breached dams interaction with culvert presence. This indicated that culverts likely are not related to colony abandonment, or the conversion of intact dams to breached dams. I did not however explicitly test this hypothesis. Effect of culverts on intact to breached dam ratios and abundance would be an interesting area for future research to monitor effects of culverts and controls on stream systems with varying levels of beaver activity.

Coniferous vegetation appeared to be a significant covariate negatively related to breached beaver dams. Likely my results show that areas high in coniferous forest do not attract beaver and thus do not have breached dams. Few studies have used hardwoods or coniferous trees as a covariate when modelling beaver dam-sites selection or colony establishment, if they did it was not a significant predictor of beaver activity (Howard and Larson 1985). Most studies conclude that proportion of deciduous forest in the riparian zone is positively related to beaver activity (Slough and Sadleir 1977, Howard and Larson 1985, McComb et al. 1990, Curtis and Jensen 2004).

The post-culvert abundance of beaver dams was the most important predictor of inundated stream length. Those models that included the presence of a culvert were not top candidate models. I did not find any peer reviewed studies relating beaver colony size or length of inundated stream to habitat variables. Fine-scale features of the stream such as bank slope or stream incision could explain length of inundated stream (McComb et al. 1990). However I did not measure these features in the field and it is was not possible to measure these features in the aerial photography.

Models containing culvert presence were not good candidates for explaining pond area. Likely, pond area is controlled by local topography such as bank slope and stream sinuosity.

3.5.4 Beaver activity at the site scale

Percentage of stream sections with a beaver dam (intact or breached) within 50m up- and downstream of a culvert (as measured on the ground) was 36.7% (18/49) which is similar to percentage of unculverted stream sections at the 300m scale with dam presence (intact and breached) as measured in aerial photography, 38.7% (12/31). However, on the ground, at the 50m scale, dams upstream of a culvert occurred more frequently than expected.

The paired occurrence of beaver dams within 50m up- and downstream of a culverts and rare downstream-only occurrence of beaver dams suggests that the downstream dams are built *after* the upstream dam. It is difficult, however to state whether this was due to the culvert itself or modification of the stream that may be caused by the culvert. Jensen et al. (2001) found that beaver frequently dammed inside culverts but did not test whether there was an up-downstream relationship. Although plugging of culverts did occur in my study, it was more common to see a dam outside the culvert within 5 to 50m.

My study only allowed me to establish correlations between beaver pond occurrence and inundated stream around culverts. Analysis using time-series aerial photography within 1 to 2 years pre- and post-culvert, could be used to test the direction of dam succession (up-versus downstream establishment of a dam). Another approach would be a controlled study on the ground where an area is monitored for beaver activity before and after culvert installation. A larger sample size and inclusion of other possible explanatory variables, such as bank height, erosion, culvert condition, culvert size, culvert age, and history of beaver activity, would be required to fully address the mechanisms that may cause beaver to dam up-or downstream of a culvert.

Beaver management was prevalent in the study area but as my sites did not have a ground-truthing component I could not measure human management of beaver activity around culverts. Additionally, no records of beaver management were available for specific culvert locations or for the study area. Likely, management of beaver activity by dam removal and beaver trapping was an unmeasured but confounding variable in the study. An active trapping program has been in place in the study area for over a decade. Intensity of beaver management at culverts could affect my results. Management of beaver activity would likely result in an underestimation of the frequency beaver dams near culverts.

3.6 Conclusions

Within third-order watersheds, total beaver dam count and inundated stream, doubled from 1976 to 2001. Concurrently, the number of culverts in the study area tripled. Despite the increase in beaver activity, dam density, and proportion of influenced stream (inundated stream) is far below what has been reported in the literature for the boreal forest. Possibly, the beaver population in my study area is still expanding, and has yet to occupy all available habitat.

In my analysis I found that intact beaver dams were negatively related to the presence of culverts unless intact beaver dams were present historically; in which case the culvert actually was positively related to intact beaver dam count. While culverts do appear to affect beaver activity within 300m, I did not detect that culverts influence beaver activity at the 1,000m scale. Given that culvert density was about 1 culvert for every 2-km of stream, it is unlikely that culverts would affect beaver activity at the level of a third-order watershed. However if the "culvert effect zone" for beaver is about 300m, areas with high culvert density may have a watershed-wide negative influence on beaver activity and subsequently wetland distribution.

Although I quantified changes in beaver pond area and inundated stream, I did not classify wetlands according to wetland type. Wetland processes are related to water levels and species assemblages. Wetland processes would likely be affected by culvert and beaver alteration of hydrology at a scale that cannot be detected using aerial photography. To understand changes in wetland processes, future research should include a component of wetland classification.

3.6 Literature cited

Barrette, J., August, P., Golet, F. 2000. Accuracy assessment of wetland boundary delineation using aerial photography and digital orthophotography. Photogrammetric Engineering and Remote Sensing 66:409-416.

Beckingham, J. D. and Archibald, J. H. Field guide to ecosites of northern Alberta. 1996. Edmonton, Alberta, Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent. Spec. Rep. 5.

Boyce, M.S. 1981. Beaver life-history responses to exploitation. Journal of Applied Ecology 18:749-753.

Burnham, K.P., Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York , New York, USA.

Carstensen, L.W.Jr., Campbell, J.B. 1991. Desktop scanning for cartographic digitization and spatial analysis. Photogrammetric Engineering and Remote Sensing 57:1437-1446.

Cumming, S. G. 2003. Balanced designs for multiple GLMs. unpublished software

Curtis, P.D., Jensen, P.G. 2004. Habitat features affecting beaver occupancy along roadsides in New York state. Journal of Wildlife Management 68:278-287.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Ecological Land Classification Series No. 23. Ottawa, Ont., Sustainable Development Branch, Conservation and Protection, Environment Canada.

Environmental Systems Research Institute, Inc (ESRI). ArcView GIS 3.2.

Environmental Systems Research Institute, Inc (ESRI). ARCINFO 8.3.

R: A Language and Environment for Statistical Computing. R Development Core Team. 2005. Vienna, Austria, R Foundation for Statistical Computing.

Ferone, J.M., Devito, K.J. 2004. Shallow groundwater-surface water interactions in pond-peatland complexes along a Boreal Plains topographic gradient. Journal of Hydrology 292:75-95.

Forman, R.T.T., Alexander, L.E. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-231.

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

Jensen, J.R. 1996. Introductory digital image processing: a remote sensing perspective. Prentice Hall, Upper Saddle River, New Jersey, USA.

Jensen, P.G., Curtis, P.D., Lehnert, M.E., Hamelin, D.L. 2001. Habitat and structural factors influencing beaver interference with highway culverts. Wildlife Society Bulletin 29:654-664.

Johnston, C.A., Naiman, R.J. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1:47-57.

Johnston, C.A., Naiman, R.J. 1990. Aquatic patch creation in relation to beaver population trends. Ecology 71:1617-1621.

-----. 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5-19.

Jones, J.A., Swanson, F.J., Wemple, B.C. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14:76-85.

Lindsey, J.K. GLMM. Non-normal repeated measurements models *in* R – Repeated Package for R1.6.0 - R1.9.1. http://popgen.unimaas.nl/=jlindsey/rcode.html. Accessed Nov. 23, 2005.

Martell, K.A. 2004. Patterns of riparian disturbance in Alberta's boreal mixedwood forest: beavers, roads and buffers. Thesis. University of Alberta, Edmonton, Alberta, Canada.

McComb, W.C., Sedell, J.R., Buchholz, T.D. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50:273-281.

McKinstry, M.C., Caffrey, P., Anderson, S.H. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American water resources association 37:1571-1577.

Naiman, R.J., Melillo, J.M. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia (Berlin) 62:150-155.

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

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

Neu, C.W., Byers, C.R., Peek, J.M. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541-545.

Otter Research Ltd. glmmADMB. Mixed models for overdispersed and zero-inflated count data in R. http://otter-rsch.com/admbre/examples/glmmadmb/glmmADMB.html. Accessed Nov. 23, 2005

R: A Language and Environment for Statistical Computing. R Development Core Team. 2005. Vienna, Austria, R Foundation for Statistical Computing.

Schlosser, I.J., Kallemeyn, L.W., 2000. Spatial variation in dish assemblages across a beaver-influenced successional landscape. Ecology 81:1371-1382.

Schneider, R.R. 2002. Alternative futures: Alberta's boreal forest at the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta

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

Snodgrass, J.W., Meffe, G.K. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928-942.

Strahler, A.N., 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys Union 38:913-920.

Suzuki, N., Mccomb, W.C. 1998. Habitat Classification Models for Beaver (*Castor canadensis*) in the Streams of the Central Oregon Coast Range. Northwest Science 72:102-110.

Trombulak, S.C., Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

Welch, R., Jordan, T. 1996. Using scanned air photographs *in* S. Morain and S.L. Baros, editors. Raster imagery in geographic information systems. Onward Press.

Wright, J.P., Jones, C.G., Flecker, A.S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96-101.

Zar, J.H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Inc., USA

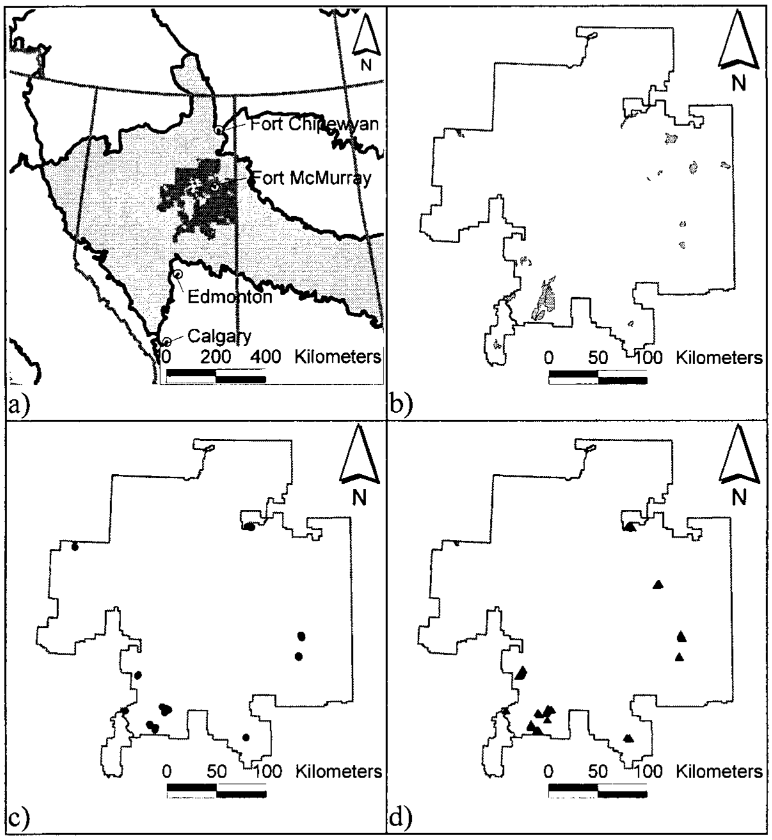


Figure 3.1 Map of study area in north-central Alberta, Canada showing locations of a) the study area within Alberta, b) 14 sampled watersheds, b) thirty-nine stream-reaches and c) forty-nine field-sites. Note that point location in panels a,b, and c are overlapping.

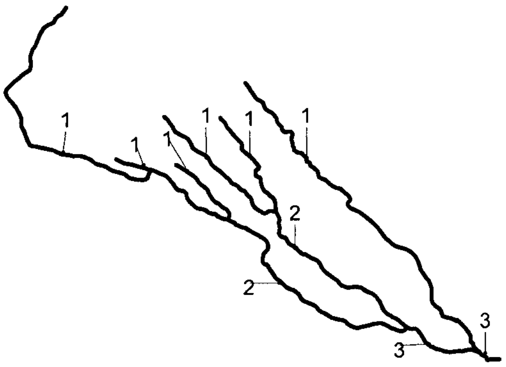


Figure 3.2 Strahler stream ordering system using an example of a third-order stream system within northcentral Alberta.

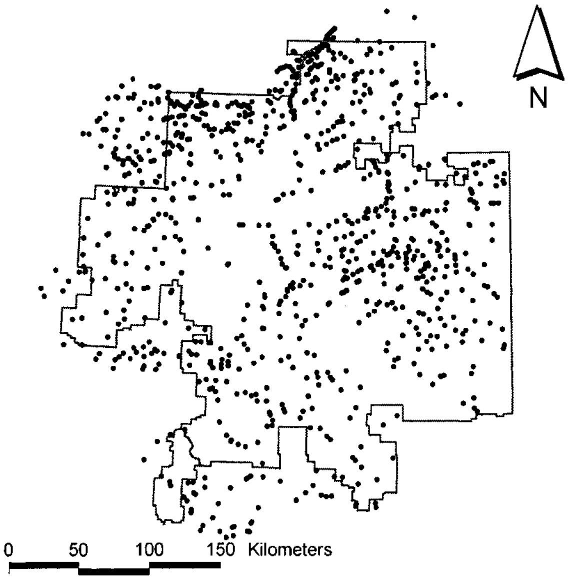


Figure 3.3 Third-order watershed outlets (dots) in the study area, northcentral Alberta (n = 1166).

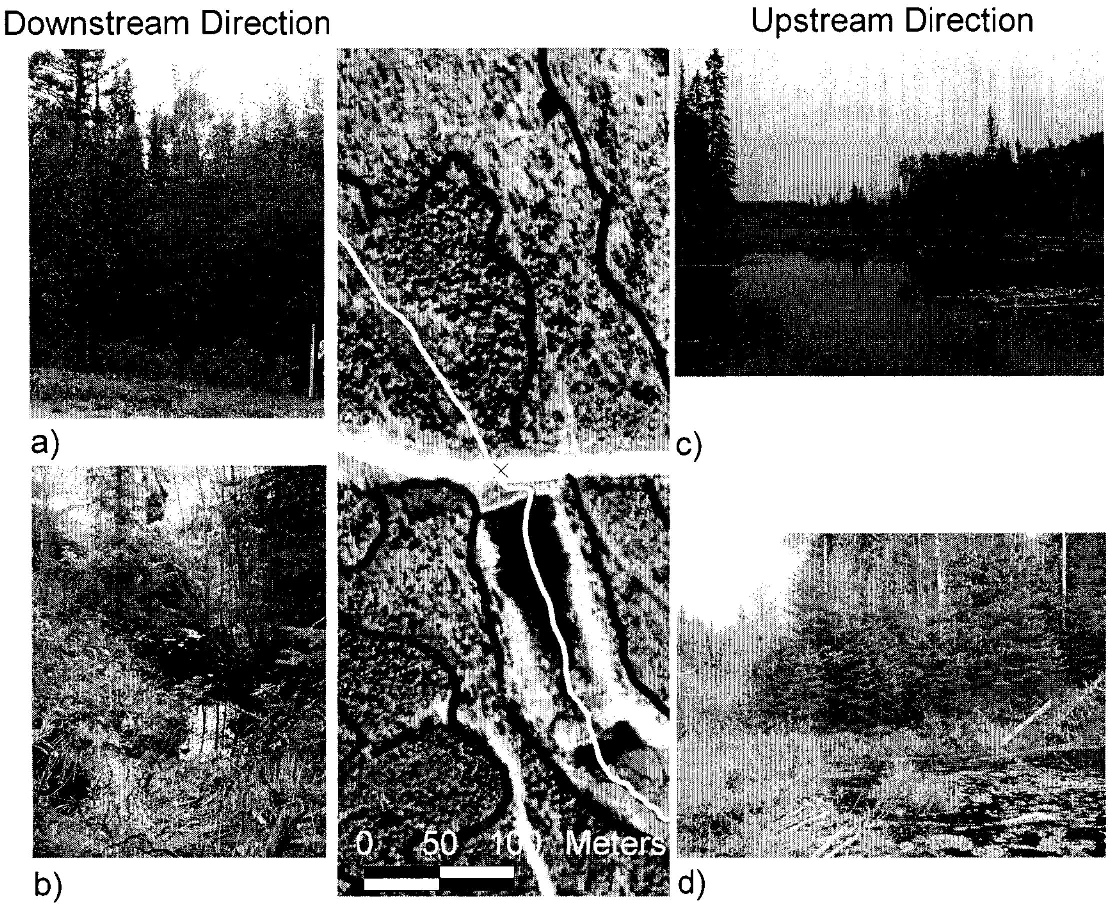


Figure 3.4 Example of a site assessed in the field for beaver activity within a 1999 aerial photo of a field-site. Photographs were taken in 2003 showing the downstream view (a and b) and upstream view (c and d) from the culvert.

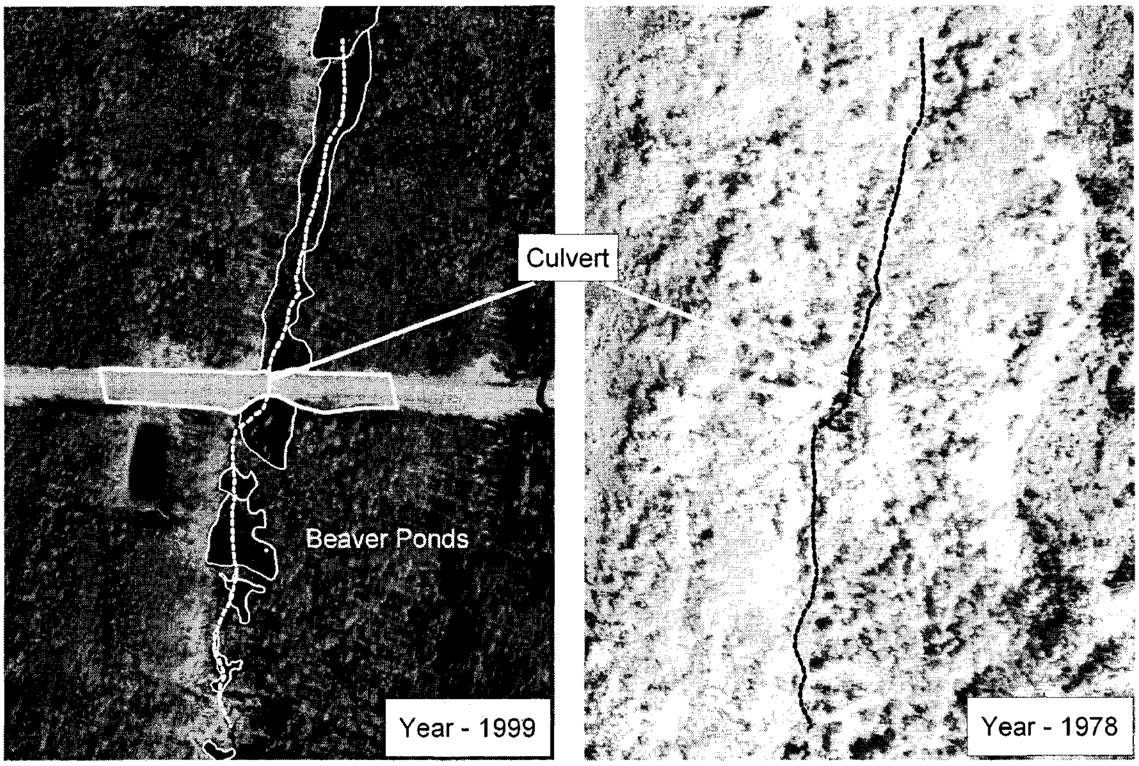


Figure 3.5 Example of changes in beaver activity pre-culvert (1978) and post-culvert (1999). The dashed line is the stream network. Areas outlined in a thin white line in the 1999 photo are beaver ponds, the thick white line is the road right-of-way.

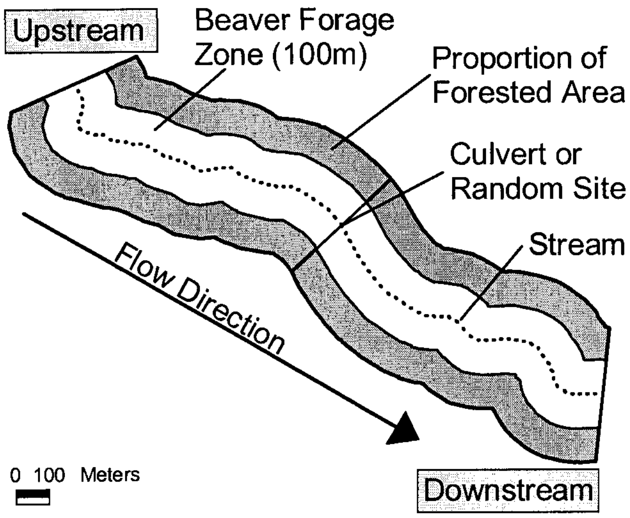


Figure 3.6 Culverted crossing with up- and downstream 1,000m stream segments buffered 100m from the 100m beaver forage zone

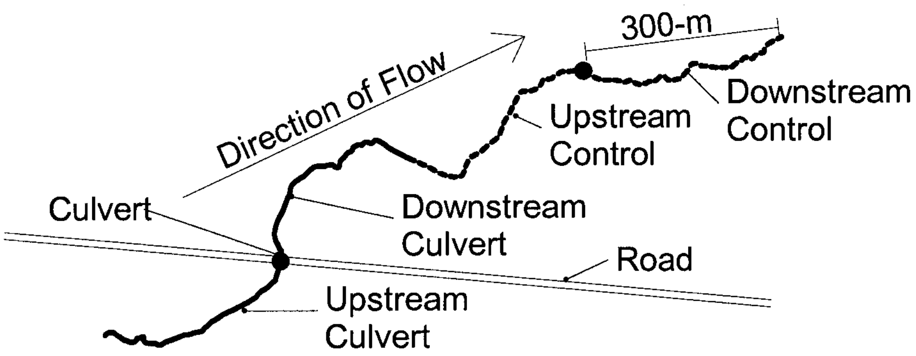


Figure 3.7 Stream scale study design – beaver activity was measured 300m up/downstream of a culvert (treatment) and paired with an up/downstream control 600m downstream of the culvert.

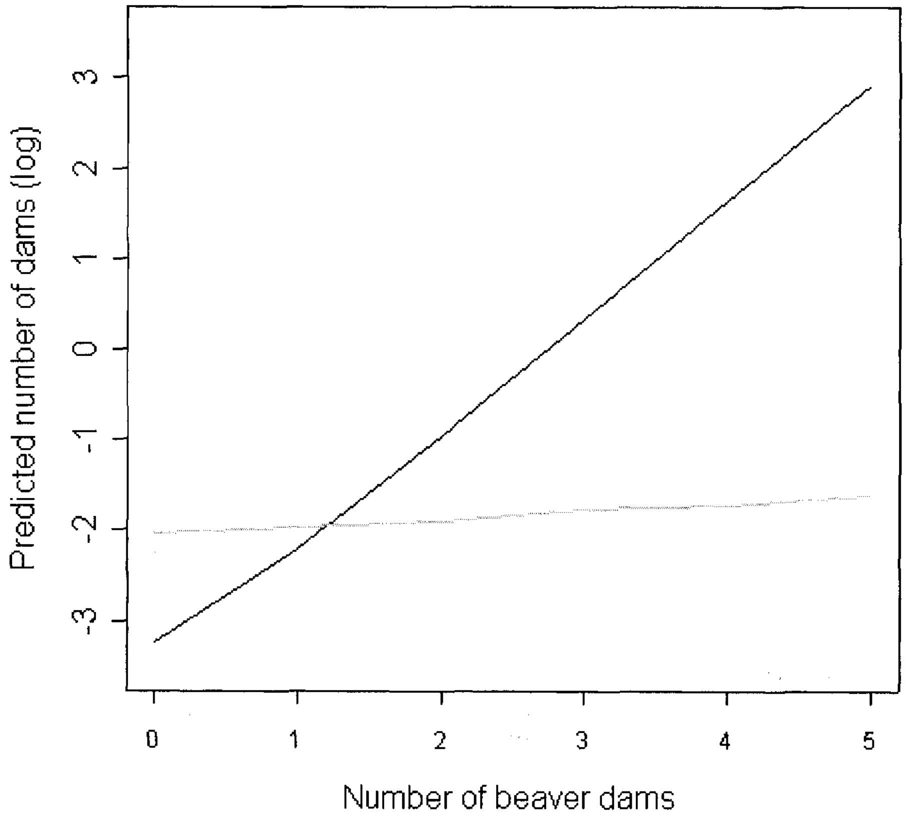


Figure 3.8 Predicted intact beaver dam count for top candidate model (DIr = DIo + CP + DIo x CP) over a range of intact dams in 1976-78 (DIo) for culvert presence (black line) and absence (grey line).

Table 3.1 Selection criteria for choosing a balanced and representative sample of twenty, third-order watersheds from the population of third-order watersheds in the study area (n = 1166).

Code	Description	Used to select balanced sample unit?	Remain in the population if violated?
Water	Area of watershed covered by permanent watersbodies is less than 25%	no	no
B_H	Area burned or harvested since 1970is less than 30% of watershed	no	yes
Wetland	Area of watershed with wetland (muskeg and marsh) is less than 25%	no	yes
Length	Total length of stream segments by order is greater than 1 km	no	yes
Photos	Aerial Photography is available for entire watershed for two periods, 1976-78 and 1999-2001 at a scale of 1:15,000.	no	yes
Dec	Area of watershed a distance of 250m away from the stream to a distance of 750m greater than 9.5% deciduous forest	yes	no
Rdx	Low is less than 0.2 stream crossings per km of stream and high is greater than 0.2	yes	yes
Area	Area of the watershed (stream network buffered by 750m)	yes	yes
Northing	7 digit coordinate value of the watershed outlet in the UTM zone 12 Nad27 coordinate system, in the north-south direction	yes	yes
Easting	6 digit coordinate value of the watershed outlet in the UTM zone 12 Nad27 coordinate system, in the east-west direction	yes	yes

Table 3.2 Covariates measured in 300m stream reaches (note that not every covariate is used within each group of candidate models).

Code	Units	Description
GD	% slope	Average percent slope of 300m stream segment using the surrounding 2 km landscape (see methods)
DC	proportion	Proportion of deciduous forest outside the forage zone
CN	proportion	Proportion of coniferous forest outside the forage zone
CP	0 or 1	Presence of a culvert across stream in 1999 to 2001 aerial photography. 1 = present 0 = control, no culvert
DIr	count	Number of intact beaver dams within 300m of culvert or control in 1999 to 2001 aerial photography
DIo	count	Number of intact beaver dams within 300m of culvert or control in 1976 to 1978 aerial photography
DBr	count	Number of breached beaver dams within 300m of culvert or control in 1999 to 2001 aerial photography
DBo	count	Number of breached beaver dams within 300m of culvert or control in 1976 to 1978 aerial photography
ISr	m	Total length of inundated stream within 300m of culvert or control in 1999 to 2001 aerial photography
ISo	m	Total length of inundated stream within 300m of culvert or control in 1976 to 1978 aerial photography
Pr	m^2	Total pond area within 300m of culvert or control in 1999 to 2001 aerial photography
Po	m^2	Total pond area within 300m of culvert or control in 1976 to 1978 aerial photography

Table 3.3 Candidate models for influence of culvert treatment on number of intact beaver ponds 300m up- and downstream of a culvert and paired control

Category	Model
Null	DIr = (intercept)
Global	DIr = GD + DC + CN + DIo + CP + DIo x CP
Culvert	DIr = GD + DC + CN + CP
	DIr = CP
Vegetation	DIr = GD + DC + CN
Pre-culvert beaver activity	DIr = GD + DC + CN + DIo
	DIr = DIo
Culvert and pre-culvert beaver activity	DIr = DIo + CP + DIo x CP

Table 3.4 Candidate models for influence of culvert treatment on number of breached beaver dams 300m up and downstream of a culvert and paired control

Category	Model
Null	DBr = (intercept)
Culvert	DBr = GD + DC + CN + CP
	DBr = CP
Vegetation	DBr = GD + DC + CN
Pre-culvert beaver activity	DBr = GD + DC + CN + DIo + DBo
	DBr = GD + DC + CN + DBo
	DBr = DIo + DBo
	DBr = DBo
Culvert and pre-culvert beaver activity	DBr = GD + DC + CN + DBo + DBo x CP
	DBr = DIo + DBo +DIo x CP + DBo x CP
	DBr = DBo + CP + DBo x CP

Table 3.5 Candidate models for influence of culvert treatment on length of inundated stream 300m up- and downstream of a culvert and paired control

Category	Model
Null	ISr = (intercept)
Culvert	ISr = GD + DC + CN + CP
	ISr = CP
Vegetation and Gradient	ISr = GD + DC + CN
Pre-culvert inundated stream	ISr = GD + DC + CN + ISo
	ISr = ISo
Pre-culvert beaver dams (intact or breached)	ISr = DIo
	ISr = DIr
Culvert and pre-culvert inundated stream	ISr = GD + DC + CN + ISo + CP + ISo x CP
	ISr = ISo + CP + ISo x CP

Table 3.6 Candidate models for influence of culvert treatment on pond area 300m up- and downstream of a culvert and paired control

Category	Model
Null	Pr = (intercept)
Culvert	Pr = GD + DC + CN + CP
Culvert	Pr = CP
Vegetation and Gradient	Pr = GD + DC + CN
Pre-culvert pond area	Pr = GD + DC + CN + Po
	Pr = Po
Pre-culvert beaver dams (intact or breached) and inundated stream	Pr = DIo
	Pr = DIr
	Pr = ISr
Culvert and pre-culvert pond area	Pr = GD + DC + CN + Po + CP + Po x CP
	Pr = Po + CP + Po x CP

Table 3.7 Confusion matrix for beaver dam presence/absence within 50m downstream of a culvert using field observations (training data) versus interpreted aerial photography from 1999 to 2001 (classified data). Overall accuracy = 38.5%, Kappa statistic = 0.23.

Downstream		Field Observations		Row Total	Producer's Accuracy
		not present	present		
Aerial Photography	not present	30	8	38	0.79
	present	1	0	1	0.00
Column Total		31	8	39	
User's Accuracy		0.97	0.00		

Table 3.8 Confusion matrix for beaver dam presence/absence within 50m upstream of a culvert using field observations (training data) versus interpreted aerial photography from 1999 to 2001 (classified data). Overall accuracy = 82.1%, Kappa statistic = 0.36.

Upstream		Field Observations		Row Total	Producer's Accuracy
		not present	present		
Aerial Photography	not present	27	6	33	0.82
	present	1	5	6	0.83
Column Total		28	11	39	
User's Accuracy		0.96	0.45		

Table 3.9 Total length of stream and inundated stream and number of intact and breached dams, culverted and unculverted stream crossings by Strahler order for years 1976-79 (pre-culvert) and years 1999-2001 (post-culvert) for the delineated stream network within the study area (=152 km of first to third-order streams). Proportion of total is bolded in brackets. (-) indicated use was significantly less than expected, (+) indicated use was significantly more than expected (Neu et al. 1974).

		Stream Length (km)	Dams Intact	Dam Breached	Inundated Stream Length (km)	Number of Culverted Stream Crossings	Number of Unculverted Streams *
Pre-culvert	1	79 **(0.521)**	29 **(0.274) (-)**	9 **(0.132) (-)**	4 **(0.209)**	16 **(0.762) (+)**	18 **(0.563)**
	2	46 **(0.305)**	32 **(0.302)**	20 **(0.294)**	5 **(0.250)**	2 **(0.095) (-)**	11 **(0.344)**
	3	26 **(0.174)**	45 **(0.425) (+)**	39 **(0.574) (+)**	11 **(0.541)**	3 **(0.143)**	3 **(0.094)**
	Total	152	106	68	20	21	32
Post-culvert	1	78 **(0.513)**	66 **(0.384) (-)**	41 **(0.256) (-)**	10 **(0.318)**	44 **(0.620)**	33 **(0.550)**
	2	47 **(0.308)**	66 **(0.384)**	56 **(0.350)**	9 **(0.289)**	18 **(0.254)**	22 **(0.367)**
	3	27 **(0.179)**	40 **(0.233)**	63 **(0.394) (+)**	12 **(0.394)**	9 **(0.127)**	5 **(0.083) (-)**
	Total	153	172	160	31	71	60

*unculverted Streams – These are streams that had a road or seismic line abutting the stream but which were not culverted. However, many pre-culvert "non-culverted streams" are "culverted stream crossings" in the post-culvert period.

Table 3.10 Total number of culverted and control sites (n=62) which had 0 to 7 intact or breached dams in 1999-2001 and 1967-78 in the study area.

	1999-2001		1976-78	
Number of Dams	Intact Dams	Breached Dams	Intact Dams	Breached Dams
0	48	44	52	56
1	7	8	3	3
2	3	4	1	2
3	2	2	4	1
4	0	1	2	0
5	1	2	0	0
6	0	1	0	0
7	1	0	0	0
Total Number of Dams	31	42	25	10

Table 3.11 Ranked candidate models for 1999-2001 1) Intact Dams, 2) Breached Dams, 3) Proportion of Inundated Stream and 4) Pond Area using Akaike's Information Criterion corrected for small sample size (AICc) n = 31. Only models that had ΔAICc < 2.00 as are shown.

Response	Model	K	AIC_c	ΔAIC_c	w_i^d
1) Number of Intact Dams	DIo + CP + DIo x CP	4	146.08	0.00	0.48
	CP	2	146.99	0.91	0.31
2) Number of Breached Dams	GD + DC + CN + DBo	5	166.93	0.00	0.23
	GD + DC + CN + DIo + DBo	6	167.20	0.27	0.21
	GD + DC + CN	4	167.39	0.46	0.19
	GD + DC + CN + DIo x CP + DBo x CP	7	167.80	0.87	0.15
3) Proportion of Inundated Streams	DIr	2	1353.78	0.00	1.00
4) Pond Area	ISr	2	2021.37	0.00	1.00

Table 3.12 Univariate Wald test statistic results for the best approximating model (DIr = DIo + CP + DIo x CP) for count of intact beaver dams

	Estimate	Std. Error	Z value	Pr (> |z|)
(intercept)	-2.067	0.574	-3.598	0.001
DIo	0.091	0.259	0.349	0.728
CP	-1.472	0.519	-2.838	0.006
DIo x CP	1.202	0.519	2.318	0.023

Table 3.13 Univariate Wald test statistic results for the best approximating model (DBr = GD + DC +CN + DBo) for count of breached beaver dams

	Estimate	Std. Error	Z value	Pr (> |z|)
(intercept)	-2.195	0.565	-3.882	0.000
GD	0.188	0.376	0.500	0.618
DC	1.201	0.786	1.527	0.130
CN	-5.143	2.585	-1.990	0.050
DBo	0.608	0.330	1.839	0.069

Table 3.14 Results of Chi-square goodness of fit test comparing observed (field data) to expected dam presence within 5m or 50m of a culvert where expected is 1:1:1 upstream, downstream and both up-downstream (expected values are in brackets). $\chi^2_{c(0.05,2)} = 5.99$.

Distance from culvert	Upstream Only	Downstream Only	Up- and Downstream	χ^2	p-value
5 m	5 (3)	1 (3)	3 (3)	2.67	0.2636
50m	7 (6)	1 (6)	10 (6)	7.00	0.0302

Chapter 4 Management of beavers as an agent of disturbance in low-order streams

4.1 Interaction of beavers and culverts on wetlands: A synopsis of vegetation inventory and time-series studies

Results of my research show that beaver activity as measured by dam abundance, pond area and length of inundated stream, has doubled from 1976 to 1999 in low-order streams. In the early 1950's beaver activity was almost non-existent in the study area (Martell 2004). I concluded that mapped seasonally flooded streams in the Alberta Vegetation Inventory (AVI) are reasonable indicators of beaver activity in the stream network. Analysis of existing AVI over a broad area agreed with published data that beaver activity is concentrated in first- to third-order streams. I estimated, conservatively, approximately 4.0% (based on AVI in chapter 2 of this thesis) to 20.4% (based on aerial photography in chapter 3 of this thesis) of headwater streams are influenced by beaver activity - likely this amount is closer to 20%. Other studies have shown beavers can inundate 20% - 75% of headwater stream length. In another study by Johnston and Naiman (1990), beavers had impounded, on average, 55% of the stream network of first- to fourth-order streams. Naiman and Melillo (1984) found that beaver influenced up to 20-40% of second-order streams in the sub-arctic region of the Precambrian shield, northern Quebec. Barnes and Mallik (1997) found that active beaver dams were distributed over 75% of a 228 km^2 headwater watershed. McKinstry and Anderson (1999) estimated between 42% and 48% of streams in Wyoming are influenced by beavers.

My study did not detect a statistical difference in measured covariates for culverted and non-culverted sites, indicating that the sites were not biased with respect to the covariates. Beaver occupancy of streams around culverts however, was dependent on scale. Percentage of stream sections with a beaver dam (intact or breached) within 50m up- and downstream of a culvert (as measured on the ground) was 36.7% (18/49) which is similar to the percentage of unculverted stream sections at the 300m scale with dam presence (intact and breached) as measured in aerial photography, 38.7% (12/31). However on the ground, at the 50m scale, dams upstream of a culvert occurred more frequently than expected. A direction effect up- and downstream of a culvert was not detected at the 300m or 1,000m scale using forest inventory or aerial photography. Within 300m of culverts, I found dam abundance, inundated stream length and pond area to be negatively related to culvert presence as compared to sites without culverts. At a distance of 1,000m there appeared to be no culvert effect on beaver activity. It is possible that a culvert effect exists but cannot be statistically detected because beaver activity is more variable over longer distances. It is possible that there was variation in other characteristics associated with culverts, related to beaver activity, which could have affected beaver activity but were not measured. Such examples are stream substrate or bank slope (McComb et al. 1990), which I could not assess using aerial photography or AVI.

My study did not include measurement of management activity at the culvert crossings. At several sites however, there were active lethal trapping programs, dam deconstruction, beaver stop control devices and mesh screens over culverts. In some locations beaver were able to establish very large ponds upstream of a culvert with apparently little consequence for road integrity. Other factors likely to explain differences in management activities are frequency of road use and road ownership. To accommodate the heavier traffic volumes and loads of forestry roads, provincial law requires forestry roads to meet higher standards of roadbed load capacity than those used by the petroleum industry. Thus, the forest industry may be more likely to engage in an active beaver-trapping program to reduce potential of road damage caused by impounded water. At sites managed for beaver activity, it is possible that beavers were not able to establish, colonize or adequately maintain dams around culverts but management was not heavy enough to prevent beavers from repeatedly damming culverts and creating small ponds. I have concluded that culverts do affect beaver activity at a local scale (< 300m) which may have implications for wetland distribution in low-order streams, especially given the road density of northern remote areas is likely to increase in the next 20 yrs. It is not possible however to disentangle the beavers biological response to culverts and human management of beavers in this study.

4.2 A world with beavers: A case for disturbance based forest management

Beaver activity shapes headwater river systems, creating "a complex pattern that may involve the formation of emergent marshes, bogs, and forested wetlands, which appear to persist in a somewhat stable condition for centuries." (Naiman et al. 1988). In low-order streams, flora and fauna colonizing beaver dams meadows and ponds result in an overall increase in species diversity (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000, Wright et al. 2002) and increases ecosystem resilience to disturbance. Beavers diversify stream structure and may increase ecosystem resilience to other types of disturbance (Butler, 1995, Naiman and Rogers, 1997). Lundberg and Moberg (2003) defined ecosystem resilience as the "buffer capacity and opportunity for reorganization that provide ecological memory". If ecosystem resilience is a management goal, management of beaver activity should seek to maintain a range of beaver activity similar to that of a system with unmanaged beaver populations. A precedent has been set by the adoption of a natural disturbance regime based on fire dynamics to dictate forest harvesting patterns and extent by the forest industry (Hunter 1993). Beaver disturbance dynamics in headwater river systems of the boreal forest should be included in natural disturbance regime studies.

Currently, policy related to forest practices in riparian zones relies on stream classification and not what the stream may look like in the future. Foresters are informed of harvesting practices allowed in riparian zones using four stream classes: large permanent, small permanent, intermittent, and ephemeral streams. First- to third-order streams in my study area were categorized as ephemeral and intermittent, with a small number of third-order streams that were classified as small permanent. Logging in ephemeral streams is permitted up to the high water mark; in intermittent streams logging is also permitted up to the high-water mark but with the retention of a brush buffer along the channel. In small permanent streams, no harvesting is allowed within 30m of the high-water mark, with some exceptions, harvest may take place within the 30m but no machinery may operate within 20m. Currently riparian buffers policy does not take into consideration disturbance agents that may alter stream width and flow rate.

In my study, beaver impoundments widened the stream between 5 and 100m metres - extending the riparian zone well beyond the recommended treed buffer for small permanent streams. Intermittent and ephemeral streams have no treed riparian buffer. In addition, it is difficult to anticipate the potential effects of beaver in low-order streams as low-order stream are often poorly mapped; even though they make up between 70-90% of the total stream length of most drainage systems. Because wetlands along ephemeral and intermittent streams don't have protection, they may become the most scarce wetland type in the boreal forest under logging conditions as permitted now. It is also possible for streams to transition from ephemeral to intermittent. I have observed several cases where ephemeral streams became intermittent streams after beaver raised water levels and reduced canopy cover. If effects from forestry activity on stream ecosystem function are dependent on stream type, as is implied in buffer strip guidelines, planning appropriate buffer strips will not be possible for streams that transition from one classification to another. Inclusion of current and future beaver influence in low-order streams need to be addressed in forest management policy to minimize cumulative impacts of beaver and forestry activity on the river system. However, it is expected that beaver activity around culverts and bridges will continue to be managed, despite what forestry practices may be adopted to incorporate beaver dynamics; this may have an effect on beaver populations and activity.

4.2.1 Study design for quantifying effects of landscape disturbances

Jones et al. (2000) proposed a site selection process based on stratification of river systems for the detection of culvert effects on debris flow. This model can be adapted for studying effects of culverts on beaver activity. The original method proposed by Jones et al. (2000) was as follows:

"1) landscape stratification of inherent stream network susceptibility to floods or debris flows, 2) overlay road and stream networks and creation of areas with various densities of road-stream crossings, emphasizing mid-slope road-stream crossings, and 3) designations of expected high- and low-impact segments based on numbers of upstream road-stream crossings where sampling of selected biological variables would be conducted."

Adapting the method proposed by Jones et al. (2000) for effects of culverts on beaver activity is straightforward: 1) identify third-order watersheds within the river system as lower order streams susceptible to beaver disturbance and hydrological alteration by culverts, 2) calculate culvert crossing density within third-order watersheds, and 3) select watersheds with no to low density of crossings and those with the highest densities, while keeping other landscape variables constant. This method controls for interaction between culverts and the stream system at multiple spatial scales.

4.3 Effects of beaver management on wetlands and river systems

Beavers are managed in areas where road integrity is threatened, or land development/use is impeded by beaver activity. Beavers are also recognized for their beneficial effects and ecological services. In series of interviews conducted by McKinstry and Anderson (1999), farmers reported that beaver ponds could be used as a water source for livestock. In the same study however, McKinstry and Anderson (1999) noted farmers considered beavers a nuisance when beaver dams blocked irrigation ditches and culverts. Strategies can be integrated into beaver management programmes to increase the likelihood that beavers will persist in those systems and, at the same time minimizing damage to roads caused by beaver impoundments.

Beaver management involves trapping, removal of dams and/or lodges, and inundation prevention with beaver excluders. Beaver management strategies often do not consider effects of wetlands and obligate wetland species. For example, Fort McMurray Today – Kevin Wilson (no date)" reported Alberta Transportation removed 12 dams, from streams flowing through culverts and bridges over a 170km section of highway; dams were removed in the Fall to minimize disturbance of fish habitat. Studies have shown that beaver dams and ponds provide specific habitat conditions for fish that would otherwise not be present in the system (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). Removal of beaver from existing habitat has consequences for beaver population dynamics. Boyce (1981) found that in Chena River (Fairbanks), Alaska, dispersing juveniles had higher survivorship when high quality sites were available to them due to the previous adult beaver occupants being trapped out. Removal of debris dams can increase sedimentation downstream (Bilby and Likens 1980), so removal of beaver dams is expected to have similar results. Given that beavers are a major disturbance agent of stream systems, there is a potential for changes in stream ecosystem function and processes when beaver activity is managed. Management techniques can be used that allow beavers to persist in river systems while minimizing human/beaver conflicts. In the next section I discuss viable alternatives to trapping and dam removal.

4.4 Beaver management techniques

A common method of beaver management is trapping and dam removal. Viable alternatives however, are habitat modification and alteration of culvert structure. Beavers select areas abundant with deciduous vegetation for forage and building dams (Slough et al. 1977, Howard et al. 1985, McComb et al. 1990). Curtis and Jensen (2004) recommended maintaining open areas along highway corridors to discourage beaver colonization in proximity to culverts. Curtis and Jensen (2004) did not provide an estimate of how much tree cover should be removed nor over what spatial area. In a way, reduction of tree cover is applied indirectly through reduction of vegetation in the road right-of-way. Effectiveness of vegetation removal within the right-of-way as a deterrent of beaver activity has not been reported in the literature. Likely, vegetation removal is not a deterrent as I observed several instances of beaver damming culverts when the right-of-way was cleared of treed vegetation. In this case beavers transported, via the stream, dam construction material from treed sites further up- or downstream. Vegetation management should be applied with caution as reduction of deciduous tree cover over a large area may have an effect on stream bank stability, organic inputs, and temperature regulation.

Modification of culverts is commonly used to deter beavers from damming them (Partington 2002) or less commonly, by shunting water through the dam to reduce water level changes upstream (Roblee 1982). A report by Partington (2002) discussed the installation of the "Beaver Stop" device and evaluation of its effectiveness. The "Beaver Stop" is a mesh screen that extends out horizontally from the culvert up to 3 m. An alternative design to the "Beaver Stop" is a simple mesh screen covering the culvert. Although the screen prevents beaver from building inside the culvert, which is more difficult to access and thus more costly, the beaver can effectively dam outside of the screen. Partington (2002) reported that the screen method could at times help the beavers establish a dam, presumably by providing the foundation. Partington (2002) reported that one year following the installation of a Beaver Stop device on a 600mm corrugated-steel culvert, which had been actively dammed by beaver, beavers attempted to dam the Beaver Stop but did not successfully block water flow. Roblee (1982) reported that corrugated plastic drainage tubing was an effective control for water levels in 9 out of 11 beaver dammed sites. Using this method, dams are not destroyed as the tube is installed underwater, through the dam, allowing water to silently move across without alerting the beaver. However, Roblee (1982) reported that the tubing was more costly than a yearly trapping program (2.17 vs 1.76 person days per year). Although, in areas where beavers were trapped out and the dam destroyed, 41% of the sites had beaver reoccurrences within three years thereby requiring repeated trapping.

Another management option is to install culverts that are much larger than would be required by stream crossing regulations. Jensen et al. (2001) concluded that low gradient streams required a larger culvert to prevent beaver from plugging the culvert and suggested installing oversized culverts, dependent on stream gradient. This may have side benefits to ease of fish passage through culverts. Jensen et al. (2001) also recommended against installing two or more smaller size culverts together, as beaver easily dam small culverts. Techniques exist to manage beaver activity around stream crossings that can maintain wetlands; maintaining, in turn, stream resilience and critical wildlife areas.

4.6 Recommendations for future research on beaver activity and culverts

Based on my thesis results, and other work done in the area of disturbance regimes, beaver and road ecology, I have several recommendations for future management policy at stream crossings:

- Consider the extension of the no-logging zone buffer zone on ephemeral and intermittent streams that have or may have beavers.
- Include beaver disturbance dynamics in headwater river systems of the boreal forest in natural disturbance regime studies.
- Verify mapping accuracy of low-order streams when assessing an area of potential beaver activity.

Suggestions for future research that would continue or extend my research, while informing the above policy recommendations, are:

- Scale up results of this research conducted at the stream reach level ≤ 1,000m to other third-order watersheds to assess: 1) potential effects of current and future culvert installations, and 2) model accuracy through aerial photography interpretation and monitoring programs.
- Include a measure of road characteristics including road owner/maintenance (forestry, petroleum or public sector) to assess effects on beaver activity.
- Assessment of beaver control devices, trapping, dam/lodge and hunting pressures on beaver activity in the stream network.
- Relate culvert and stream parameters, such as culvert size, and stream volume/flow to beaver activity within the stream system 1,000m up- and downstream of the culvert.
- Compare beaver activity and hydrological change up- and downstream of culverts and beaver dams.
- In future studies control for, or apply known levels of beaver population management.

4.7 Literature cited

Barnes, D.M., Mallik, A.U. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. Journal of Wildlife Management 61:1371-1377.

Bilby, R.E., Likens G.E. 1980. Importance of organic debris jams in the structure and function of stream ecosystems. Ecology 61:1107-1113.

Boyce, M.S. 1981. Beaver life-history responses to exploitation. Journal of Applied Ecology 18:749-753.

Butler, D.R. 1995. Zoogeomorphology: animals as geomorphic agents. Cambridge University Press, New York , New York, USA.

Curtis, P.D., Jensen, P.G. 2004. Habitat features affecting beaver occupancy along roadsides in New York state. Journal of Wildlife Management 68:278-287.

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

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65:115-120.

Jensen, P.G., Curtis, P.D., Lehnert, M.E., Hamelin, D.L. 2001. Habitat and structural factors influencing beaver interference with highway culverts. Wildlife Society Bulletin 29:654-664.

Johnston, C.A., Naiman, R.J. 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5-19.

Lundberg, J., Moberg, F. 2003. Mobile link organisms and rcosystem functioning: implications for ecosystem resilience and management. Ecosystems 6:87-98.

Martell, K.A. 2004. Patterns of riparian disturbance in Alberta's boreal mixedwood forest: beavers, roads and buffers. Thesis. University of Alberta, Edmonton, Alberta, Canada. 185 pp.

McComb, W.C., Sedell, J.R., Buchholz, T.D. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50:273-281.

McKinstry M.C, Anderson S.H. 1999. Attitudes of private- and public-land managers in Wyoming, USA, toward beaver. Environmental Management 23:95-101.

McKinstry, M.C., Caffrey, P. Anderson, S.H., 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American Water Resources Association 37:1571-1577.

Naiman, R.J., Melillo, J.M. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia (Berlin) 62:150-155.

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

Naiman, R.J., Rogers, K.H. 1997. Large animals and system-level characteristics in river corridors. BioScience 47:521-529.

Partington M. 2002. Preventing beaver dams from blocking culverts. Advantage Forest Engineering Research Institute of Canada FERIC 3(54).

Schlosser, I.J., Kallemeyn, L.W. 2000. Spatial variation in dish assemblages across a beaver-influenced successional landscape. Ecology 81:1371-1382.

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

Snodgrass, J.W., Meffe, G.K. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928-942.

Roblee, K.J. 1982. Use of corrugated plastic drainage tubing for controlling water levels at nuisance beaver sites. New York Fish and Game Journal 31:63-80.

Wilson, K. Trapper concerned as beaver dams moved from near roadway. Fort McMurray Today (date unknown).

Wright, J.P., Jones, C.G., Flecker, A.S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96-101

Appendix A- Beaver habitat models

Summary of seven beaver habitat selection studies showing positive (+) and negative (-) correlation between the response variable and covariate, as reported in the study. Some covariates were generalized to allow cross-study comparisons.

Corresponding variable used in my study na = not applicable to my study				SO	SO	DC	GD	DC	SO	SO	na	CP	DC*GD	na	na	1-FA	FA	1-FA	CN	na
Authors	Study Area	River System	Response	Watershed Area	Cross Section	Deciduous Veg	Gradient	Shrub	Stream width	Stream depth	Soil Moisture	Culvert Opening	Dec. Veg.* Gradient	Bank Slope	Valley floor width	Grass/sedge cover	Total Canopy	Open - no treed vegetation	Coniferous Vegetation	Cropland
(Barnes and Mallik, 1997)	Chapleau Crown Game Preserve	One watershed 228-km^2	active abandoned and no-dam	+	+															
(Curtis and Jensen, 2004)	Northern and southern New York	Areas with culverts	Any sign of beaver activity, past or current			+	-			-		+	+			-		-		
(Howard and Larson, 1985)	Massachusetts		Colony density and longevity	+		+	-		+		-								-	-
(Jensen et al. 2001)	Northern and southern New York	Areas with culverts	Beaver presence in culverts				-				-									
(McComb et al. 1990)	Oregon	Third-order basin	dams			+	-							-			+	+		
(Slough and Sadleir, 1977)	Northern interior of BC		No.Colony sites per stream sec.			+	-	+	-											
(Beier and Barrett, 1987)	Sierra Nevada, California		Active colony, abandoned, present/past usage, no activity				-		+	+										