AN ABSTRACT OF THE THESIS OF

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Abstract approved:

Gordon Reeves

Since the 1964 earthquake and geologic uplift, beavers (*Castor canadensis*) have expanded their historic range from the inland (outwash plain) Copper River Delta, Alaska to the once tidally influenced areas of the outer area (uplifted marsh). The uplift presents a unique opportunity to observe beaver expansion, habitat selection and influence on hydrologic structure of a coastal wetland ecosystem after a major disturbance.

First, I examined the relationship between the sites of active beaver lodges and associated water and vegetative features (Chapter 2). I hypothesized that active lodge sites would be associated with distinct water features and woody vegetation types in each landscape. I used aerial photographic and ground survey methods to compare sightability and to determine habitat associations. I developed an *a priori* set of models to determine active beaver lodge occurrence using logistic regression with presence and absence as the response variables and water features and vegetation cover as the dependent variables. My results were similar between survey methods but differed between the two major landscape types. In the uplifted marsh, odds of an active lodge occurrance increased with the presence of former tidal sloughs and an increase in mixed shrub coverage. The odds of an active lodge occurrence increased with the presence of streams and decreased with

increasing closed cottonwood-alder-willow coverage in the outwash plain. Post earthquake uplift, beaver now exploit a unique topographic setting through the use and modification of former tidal sloughs and a transitioning mixed shrub vegetation community.

Second, I quantified the influence of beaver on the surface water of the West Copper River Delta using remote sensing (Chapter 3). Water features were documented from digitized aerial photographs from 1959, 1974, 1986, 1992/1993, and 1996. My results showed that surface water area in beaver influenced water impoundments increased from 0 to 20% from 1959 to 1996, concurrent with beaver colonization of the uplifted marsh. These results suggest that beavers may have altered the trajectory of wetland change on the West Copper River Delta by raising the water table within open water basins and flooding those areas that would have otherwise drained. Beaver may be used an effective management tool in wetland restoration where key habitat features are available.

Beaver Ecology on the West Copper River Delta, Alaska.

by
Erin E. Cooper

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APPROVED:

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Major Professor, representing Wildlife Science

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Head of the Department of Fisheries and Wildlife

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Erin E. Cooper, Author

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Chapter 1

INTRODUCTION

Beavers (*Castor canadensis*) are ecosystem engineers that can have far-reaching effects on the landscapes they inhabit (Jones et al. 1994; Naiman et al. 1988; Wright et al. 2002). Beaver habitat selection dictates the extent and locations of these effects and influences the structure and composition of the vegetative communities through dam construction, subsequent water impoundment and herbivory (Barnes and Mallik 1996; Barnes and Dibble 1988). These landscape changes may in turn provide habitat for numerous fish and wildlife species (Brown et al. 1996; Grover and Baldassarre 1995; Lang 2003; Sigourney et al. 2006).

The Copper River Delta (CRD) in south central Alaska, provides a unique opportunity to investigate expansion, habitat selection and manipulation by beaver. The CRD was uplifted 1.8-3.4 m in 1964 by a magnitude 9.2 earthquake (Reimnitz 1966), which resulted in changes in hydrology, vegetation communities and rapid succession in portions of the CRD (Boggs 2000; Potyandy et al. 1975; Thilenius 1990). The western portion of the Delta (WCRD) has two distinct landscape types, glacial outwash plain and uplifted marsh. The outwash plain is located on the upper 1/3 of the WCRD and the uplifted marsh comprises the 2/3 of the WCRD adjacent to the tidal flats (Thilenius 1990). The outwash plain had minimal effects after the uplift, but the uplifted marsh transitioned from a tidally-influenced marsh to a perched freshwater-influenced wetland

(Boggs 2000). Historically, the extent of beaver activity on the CRD was on the outwash plain (Roberds 1955). After the uplift, beavers expanded onto the uplifted marsh and exploited old tidal sloughs with woody plant establishment (Crow 1999).

Habitat selection by beaver has been widely studied across North America (Allen 1983; Beier and Barrett 1987; Boyce 1974; Dieter and McCabe 1989; Suzuki and McComb 1998). Beavers select distinct habitat variables within a landscape. Water features range from streams to lakes to rivers with an array of woody vegetation and landforms (i.e., slope, valley shape and/or stream width). However, previous beaver studies were conducted in relatively homogenous landscapes (Boyce 1974; Dieter and McCabe 1989; Johnston and Naiman 1990b; Suzuki and McComb 1998). Consequently, little is known about the variability in habitat use by beavers in more diverse settings.

The cycle of beaver dam construction and deterioration influences the amount of standing water and vegetation (Fryxell 2001; Johnston and Naiman 1990a; Wright et al. 2002). Creation of ponds through building dams can raise the water table, which can change vegetative communities (Goslee et al. 1997; Harris and Marshall 1963; Pezeshki 2001; Remillard et al. 1987). During periods of beaver occupancy, an area may be flooded by beaver impoundments, which raises the water table and saturates soils. This restricts some types of vegetation, particulary trees and shrubs (Batzli and Dawson 1997; Goslee et al. 1997; Thilenius 1990) used by beavers. The water table drops when dams deteriorate and break, lowering the water table and allowing the establishment of vegetation that favors drier conditions. This pattern of occupation and abandonment may create a mosaic of landscape vegetation types (patches) that would not exist without the presence of beavers (Grover and Baldassarre 1995; Syphard and Garcia 2001; Wright et al. 2002).

I investigated beaver expansion, habitat selection and subsequent landscape influences using two methods. First, I investigated beaver habitat selection using aerial photography and ground surveys (Chapter 2). These methods provided an opportunity to compare aerial photography to complete ground surveys. I compared locations of active lodges to satellite imagery (vegetation) and water features identified from digital orthophotos using logistic regression. I analyzed both survey methods and landscape types individually to examine differences among them.

Second, I examined beaver habitat expansion and manipulation through water impoundments (dams) using aerial photographs from 1959, 1974, 1992-93, and 1996 (Chapter 3). Water impoundments are easily recognized from aerial photographs (Johnston and Naiman 1990b) and were digitized within a Geographic Information System to quantify beaver-influenced surface water changes over time. The presence of water impoundments were then used to track beaver expansion onto the uplifted marsh.

These investigations may allow managers to understand beaver site selection and the potential impacts of beaver water impoundments on the landscape. Previous studies on succession indicate that the CRD will transition into a drier landscape comprised of a matrix of bog and forest. Beavers may respond to these changes and also affect the trajectory of succession on the CRD influencing both the landscape and the species that rely on it.

Chapter 2

Beaver Habitat Associations in Two Landscape Types of the West Copper River Delta, Alaska

Erin E. Cooper

ABSTRACT

Since the 1964 Alaska earthquake and geologic uplift, beavers (*Castor canadensis*) have expanded their range from the upper Copper River Delta (outwash plain) to the once tidally-influenced areas of the outer Delta (uplifted marsh). The hydrology and vegetation of the outwash plain remained relatively unchanged following the earthquake. In contrast, the uplifted marsh is transitioning from a tidally influenced saltwater marsh to a fresh water wetland. I hypothesized that active beaver lodge sites would be associated with distinct water features and woody vegetation types in each landscape type (outwash plain and uplifted marsh). I surveyed beaver lodges by aerial photographic and intensive ground surveys from late August to October, 2005 to determine active sites. I used digital orthophotos to identify water features and satellite imagery to quantify vegetation cover for active lodge locations and for randomly selected points. I developed models of active beaver lodge occurrence using logistic regression with presence and absence as the response variable. In the uplifted marsh, odds of active lodge sites increased with the presence of former tidal sloughs and an increase in mixed shrub coverage. The odds of active lodge occurrence increased with the presence of streams and decreased with increasing closed cottonwood-alder-willow coverage in the outwash plain. Post earthquake, beaver now exploit a unique topographic setting through modification of former tidal sloughs and a transitioning mixed shrub vegetation community.

INTRODUCTION

Habitat selection by beaver (*Castor canadensis*) has been widely studied across North America (Allen 1983; Beier and Barrett 1987; Boyce 1974; Dieter and McCabe 1989; Suzuki and McComb 1998). Although key beaver habitat features have been identified (Allen 1983), beaver occupy a wide range of habitats because of the various landscapes in which they occur (Allen 1983; Dieter and McCabe 1989; Rebertus 1986; Suzuki and McComb 1998). Water features range from streams to lakes to rivers with an array of woody vegetation and landforms (i.e., slope, valley shape and/or stream width). However, previous beaver studies were conducted in relatively homogenous landscapes (Boyce 1974; Dieter and McCabe 1989; Johnston and Naiman 1990; Suzuki and McComb 1998). Consequently, little is known about the variability in habitat use by beavers in more diverse settings.

The Copper River Delta (CRD) in south central Alaska, provides a unique opportunity to investigate habitat selection by beaver in a diverse landscape. The CRD was uplifted 1.8-3.4 m in 1964 by a magnitude 9.2 earthquake (Reimnitz 1966), which resulted in changes in hydrology, vegetation communities and rapid succession in portions of the CRD (Boggs 2000; Potyandy et al. 1975; Thilenius 1990). The western portion of the CRD (hereafter referred to as the WCRD) has two distinct landscape types, outwash plain and uplifted marsh. The outwash plain is described by Davidson (1998) as glacial and alluvial outwash plains, braided glacial rivers, freshwater streams, freshwater ponds and lakes and ponds, low terraces, sand and gravel bars that are the direct result of upland erosion. Water flow in rivers and streams is highly variable and may increase or decrease significantly in some areas depending on season and rainfall (Boggs 2000; Thilenius 1990). The outwash plain was not influenced by tidal water inundation prior to the 1964 earthquake so the vegetation communities have remained fairly constant in recent history (Boggs 2000).

The area of the WCRD closest to the ocean is the uplifted marsh. It currently consists of freshwater interbasin perched ponds, levees, tidal creeks (old tidal slough channels) and freshwater streams (Boggs 2000). The uplifted marsh was a tidally-influenced marsh prior to the 1964 uplift (Potyandy et al. 1975). After uplift, it became a perched freshwater wetland (Thilenius 1990). This area was colonized by woody vegetation following the earthquake (Crow 1971) and underwent rapid vegetation succession (Thilenius 1990, 1995). Levees previously dominated by herbacious-graminoid cover have become colonized by Sitka alder (*Alnus crispa sinuate*), willow (*Salix* spp.) and black cottonwood (*Populus balsamifera*)(Crow 1971).

The distribution of beavers on the WCRD also changed following the earthquake. Historically, beavers were primarily restricted to the outwash plain, the area furthest from the ocean (Roberds 1955). Beavers did not inhabit the outer portions of the WCRD because of tidal inundation and lack of woody vegetation (Roberds 1955). After the earthquake and uplift, beavers expanded their range into the uplifted marsh. The topography of this area is flat, with old tidal sloughs and riverbanks providing the only relief. Many of these old tidal sloughs were dammed by beavers in the mid 1980's, creating a complex of linear ponds (Crow 1999).

Beaver densities in the uplifted marsh on the WCRD are now among the highest found in North America (1.5/km^2)(Alaska Department of Fish and Game 1990; Novak

1999) and subsequently, beavers are an integral part of the ecosystem. Beaver impoundments are important nutrient storage and fish rearing areas (Bryant 1991; Lang 2003). Dusky Canada geese (*Branta canadensis occidentalis*) and various other waterfowl species use beaver impoundments during nesting and brood rearing (Tom Fondell, personal communication 2007). Still, very little is known about the ecology of beavers on the Delta. Although I believe that beavers have contributed to the overall structure of the water and vegetation on the Delta, no site-specific study has been conducted on beaver habitat selection.

My objective was to examine the relationship between habitat features and active beaver lodges on the outwash plain and the uplifted marsh of the west Copper River Delta. I hypothesized that beaver activity would be associated with patterns of vegetation and water that would vary between the two areas.

STUDY AREA

I conducted this study on the WCRD in south central Alaska (Fig. 2.1). The 121,000-ha WCRD extends from the base of the Chugach Mountains to mudflats stretching into the Gulf of Alaska. It is separated from the eastern CRD by the Copper River. The specific areas I studied were defined as uplifted marsh and glacial outwash plain by Davidson (1998). The glacial outwash plain encompasses the northern third of the WCRD, and the uplifted marsh comprises the southern two-thirds adjacent to tidal flats (Thilenius 1990).

Prior to the uplift, the uplifted marsh was intermittently flooded by high tides (Boggs 2000; Hansen 1961; Thilenius 1995). The surface substrate of this area is organic with glacial silt and inorganic substrates at a 1-m depth (Thilenius 1995). Lake and or pond depth in this area averages 0.7-1.1 m (Thilenius 1995). Larger lakes and ponds near the coast have a greater surface area of water compared to emergent vegetation than the lakes and ponds further inland (Boggs 2000; Thilenius 1990). The uplift caused extensive shifts of plant zones on the CRD. In some cases, the boundary between the tidally influenced areas and the freshwater wetlands shifted 15 km seaward. (Reimnitz 1972). Over time, salt dissipated from the uplifted marsh soils, which were then colonized by freshwater plant species intoleratant of the previously saline soils and saltwater (Crow 1971). Prior to 1964, the community types in the uplifted marsh were primarily salt tolerant sedge (*Carex spp*.) and mixed grass/forb communities (Boggs 2000). Vegetation in interlevee basins, lakes and ponds now includes sphagnum moss (*Sphagnum spp*.), bluejoint grass (*Calamagrostis canadensis*), Sitka sedge (*Carex stichensis*), yellow pond-lily (*Nuphar polysepala*), pond weed (*Potomogeten* spp.), and sweetgale (*Myrica gale*). Levees and drier areas mostly contain Sitka alder, Barclay willow (*Salix barclayi*), and Sitka willow (*Salix sitchensis*), black cottonwood and Sitka spruce (*Picea sitchensis*) (Boggs 2000; DeVelice et al. 2001).

Vegetation on the outwash plain consists of Sitka sedge, bluejoint grass, sweetgale, tall blueberry (*Vaccinium ovalifolium*), salmonberry (*Rubus spectabilis*), willow (*Salix spp*), Sitka alder, black cottonwood, Sitka spruce and western hemlock (*Tsuga heterophylla*) (Boggs 2000). Many of the lakes and ponds in the outwash plain are covered with emergent vegetation in the summer months, including pond-lily and pond weed.

Trapping has historically occurred on the WCRD and continues into present day. Currently, trapping mortalities account for an average of 60 individuals annually on the

WCRD (Alaska Department of Fish and Game 2004), much of which occurs near the highway on the outwash plain.

METHODS

Surveys

I conducted ground surveys in conjunction with aerial photographic surveys to provide data for concurrent analyses of the location of active beaver lodges. Historically, beaver surveys were conducted by low elevation aerial surveys and ground survey methods, depending on lodge visibility, costs, and accessibility (Atwater 1940; Hay 1958; Murphy and Smith 2001; Robel and Fox 1993). Ground surveys give a complete census of surveyed areas but are limited by access, which restricts the scope of inference.

Aerial Photographic Survey

Aerial photography is used to cover large areas that may be difficult to access on the ground and has been used to census various wildlife species (Dolbeer et al. 1997; Hiby et al. 1988; Sidle et al. 2001), but not specifically for beavers. Beaver cache piles (floating woody mats located in water near lodges) are commonly used by wildlife biologists to identify active beaver colonies (lodges) and to quantify population size (Hay 1958; Payne 1981; Swenson et al. 1983). Generally, caches are too small to be reliably identified on high altitude aerial photographs. Previous beaver studies have, therefore, used aerial surveys with on-board observers to identify cache piles (Hay 1958; Payne 1981; Swenson et al. 1983). However, because of the increased resolution of digital photography and the relatively large size of cache piles on the CRD (5-9 m^2, personal observation), I opted to use this method to locate and enumerate active lodges.

I conducted aerial photography in a systematic fashion. Flight lines were created in a Geographic Information System (GIS) starting at a random ground location. Thirty six systematic (700-m spacing) flight lines were delineated running east to west, which allowed the flights to be conducted in 3 days and provided adequate coverage of the ground area. Flights were conducted in a Cessna 206 at approximately 160 kph with a vertically-mounted Kodak™ DCS Pro 14N digital camera with a Garmin™ Global Positioning System (GPS) V attachment. During the flight, flight lines were transferred to the TRACKER ANALYST™ program, while a technician monitored the camera operation via computer. Test flights at various focal lengths and altitudes were determined the largest ground area that could be covered under camera and lodge identification constraints (pixel size/area). A final combination of a 80-mm focal length at a height of 1,219 m provided the maximum coverage (approximately 350 x 500 m, which varies slightly by photograph) while maintaining sufficient resolution to identify lodge and cache pile structures (Figure 2.2). The minimum time between photos was 8 seconds because of camera buffer limitations. This limitation resulted in a systematically spaced set of photos across each flightline. The resulting photographs covered approximately 50-60% of the WCRD.

Post flight, each photograph was converted to a joint photographic experts group (jpeg) file with an associated GIS georeference file from a GPS center point to determine the area coverage of the photographs and to assist in lodge location placement in subsequent GIS coverages. All photographs were visually inspected for accuracy of placement using georeferenced digital orthophotos. I created a GIS coverage using the estimated size and individual photograph center points. This GIS coverage provided georeferenced spatial information for each photograph.

Two observers independently recorded active lodge locations from all digital aerial photographs. I expected some observer error, therefore, 2 observers were used to increase the chance of locating active lodges. These observers had no prior knowledge of the location or likelihood of location of active lodges on the WCRD. Active lodge locations were identified by mud on lodges and a large cache pile in the water nearby. In some locations, brush piles were observed but no lodge could be identified from the photograph. These brush piles were not considered active lodge locations for my analyses. Active lodge locations identified by each observer were then compared. Any active lodge identified by an observer was included in the sample for the aerial photographic survey. I pooled active lodge locations between observers for the total number and locations of active lodges observed. Active lodge locations identified from aerial digital photographs were digitized into a separate GIS using US Forest Service georeferenced orthophotos as a reference and base map. Lodge locations were placed ≤ 2 m of actual locations from photographs.

Ground Survey

We conducted ground surveys from late August through September 2005, when beavers were building winter cache piles and activity was high (Hay 1958). Rivers across the WCRD were selected as start points for surveys. Search areas were: Eyak River, Ibek River, Scott River, Alaganik Slough, Pete Dahl Slough, Gus Stevens Slough, the Copper

River Highway, Eighteen Mile Stream System, and Wrong-way Stream. Water features on the outwash plain were further apart and more widely dispersed than on the uplifted marsh. This scarcity of water features resulted in a smaller proportion of outwash plain area surveyed. Active beaver colonies were identified by a combination of scent mounds, mud slides, fresh mud on lodges, new cache piles and recent cutting activity (Robel and Fox 1993). We searched areas on foot, and in canoe and airboat (large rivers only). We surveyed entire old tidal slough systems in the uplifted marsh area by canoe from the tidally influenced mouth to the point where the width of open water was <2 m. During ground surveys, we visually inspected ponds adjacent to tidal sloughs. This method resulted in a complete census of surveyed areas. We recorded locations for active and inactive lodges on a handheld GPS unit. Search areas covered on the ground were then digitized in a GIS.

Sightability

I compared active lodge sites identified from aerial photographs to active lodge sites surveyed from the ground to determine the accuracy of active lodge site locations determined from the digital aerial photographs. Overlap of the 2 survey methods was delineated in a GIS. I compared the active lodges located within the overlap areas for both survey methods to ascertain sightability (accuracy) of the aerial surveys. Sightability was determined as the number of active lodges observed in the aerial surveys divided by the total lodges observed within each landscape type. Sightability may differ in areas with dense tree cover where lodges were not visible from the air. Sightability may also be influenced by vegetation, therefore I considered surveys with error > 20% as possibly biased due to vegetation. I selected a threshold of sightability >80% between survey methods for both landscape types that would allow analysis of only the aerial survey data and a sightability ≤80% would dictate that I analyze both survey methods separately.

Habitat Measures

The US Forest Service developed a GIS coverage that defined both the uplifted marsh and the outwash plain (Davidson 1998). I modified Forest Service GIS coverages for the uplifted marsh (19,960 ha) and outwash plain (16,859 ha) for this study to include lake and rivers located within and adjacent to the original Forest Service coverages (Figure 2.1). A separate set of random locations was created within a GIS for each survey method and landscape type (aerial uplifted, aerial outwash, ground uplifted, ground outwash) for comparison to active lodge locations.

I used circular plots with a radius of 30-m and 100-m to characterize core area and home ranges (Figure 2.3) around the active lodge and random locations to determine if active lodges differentially associated with habitat variables at the 2 scales. Core areas are defined as those areas most heavily used within a home range (Wheatley 1997b) and were determined to be approximately 0.94 ha during the fall in Manitoba (Wheatley 1997a). Beaver may travel 30-100 m inland to food resources from associated water systems (Novak 1999). Thus, I considered core areas with 30-m radius for analysis of active lodge and random site characteristics and buffered each location by 30 m to produce 0.28-ha circular plots. Wheatley (1997a) stated that beaver in Manitoba have fall home ranges averaging 3 ha so I buffered beaver lodges and random sites by a 100-m radius to produce 3.14-ha circular plots equivalent to fall home range sizes.

Water and woody vegetation have been identified as important habitat resources for beavers (Allen 1983; Johnston and Naiman 1990; Novak 1999). Additionally, herbaceous and emergent aquatic vegetation are important summer food sources for beaver (Allen 1983). Allen (1983) stated that water should always be included in beaver habitat models considering that active lodges are constructed on or adjacent to a water body. Habitat selection may also be scale dependent, thus the scale at which habitat variables are measured should reflect possible biological constraints (ie., home range or core area of use) (Wiens 1989). I identified 4 water categories, 3 woody vegetation categories, 2 additional food variables and 2 different scales that may be important predictors of active lodge locations (Table 2.1).

Select vegetation communities and water categories on the WCRD were measured from satellite imagery and digital orthophotos. Water categories (sloughs, streams rivers, lakes or ponds) were identified in digital orthophotos and were recorded as either present or absent within the 30-m and 100-m radius plots. A vegetation analysis of the CRD was completed in 1994 using Satellite Pour l'Observation de la Terre (SPOT) imagery (Kempka et al. 1994). I used the resulting GIS vegetation coverage map for these analyses. Vegetation variables selected from the total possible variables (14) within the satellite imagery were closed cottonwood-alder-willow, mixed shrubs, and sweet gale. Other summer food habitat variables of interest were aquatic emergent and herbaceous-sedge communities. Vegetation classes developed, digitally mapped and ground proofed by Kempka et al. (1994) were used for the vegetation analysis in this study (Table 2.1). Although satellite imagery was taken in 1989, the vegetation variables of interest are still current and have not transitioned into different cover and vegetation classes as defined by

Kempka et al. (1994) (Table 2.1)(Dean Davidson, USFS, personal communication 2006). I recorded habitat data from the satellite coverage associated with each point for each 30 m and 100 m plot size. The resulting vegetation data from the satellite coverage was quantified as the proportion of the total area of the plot covered by each vegetation type within the plot.

Table 2.1. Descriptions of vegetation and water variables derived from GIS grid coverage (Kempka et al 1995) and digital orthophotos for use in beaver habitat analyses.

Description	Species[a]	Shrub cover[b]	Variable
Proportion of Mixed Shrubs within a 30-m and 100-m radius circular plot .	Mixed woody shrubs and trees- Contains <40% of any one species.	≥25%	MIXED SHRUBS_{30} $\text{MIXED SHRUBS}_{100}$
Proportion of *Myrica gale* within a 30-m and 100-m radius circular plot.	*Myrica Gale*	≥40%	MYRICA_{30} MYRICA_{100}
Proportion of closed cottonwood-alder-willow within a 30-m and 100-m radius circular plot.	*Alnus crispa sinuate* *Salix spp.* *Populus balsamifera,*	≥60%	ALDER/WILLOW_{30} $\text{ALDER/WILLOW}_{100}$
Proportion of Emergent vegetation within a 30-m and 100-m radius circular plot.	*Nuphar polysepalum* *Menyanthes trifoliate* *Hipparus spp.* *Equisetum spp.*	<25%	EMERGENT_{30} EMERGENT_{100}
Proportion of Herbacious-Sedge-Gramanoid within a 30-m and 100-m radius circular plot.	*Carex spp.* *Eleocharis spp.* *Cicuta douglasii* *Calmagrostic canadensis* *Angelica spp.* *Equisetum spp.* *Epilobium spp.* *Potentilla spp.* *Achillea borealis*	<25%	HERB_{30} HERB_{100}
Tidal slough, presence or absence		n/a	SLOUGH
Stream with mean annual flow ≤3.39 m^3/s, presence or absence		n/a	STREAM
River with mean annual flow >3.39 m^3/s, presence or absence		n/a	RIVER
Lakes and ponds, presence or absence		n/a	LAKE

a. Major species within grid cell.
b. Grid cell coverage

Four categories of water (old tidal slough, river, stream and lake) were identified using the digital orthophotos (Table 2.1). Although water cover types are present in the satellite imagery, narrow linear water features used by beavers are not well represented at the 20-m grid scale of this GIS coverage. Old tidal sloughs are those features that had at one time been tidally influenced prior to the 1964 earthquake and post earthquake are only minimally tidally influenced. Consequently, most of the old tidal sloughs are located in the uplifted marsh. These sloughs are much narrower than the adjacent main waterways, which allows for these features to be dammed by beavers. Rivers and streams were separated based on flow measured as the mean annual cubic m per second (m^3/s)(Blanchett 1983). I used a stream system with both high and low flow sections (Wrong-way stream system) as a model to calculate the mean m^3/s for streams and rivers. The waterway was considered a stream if dams could exist (mean annual flow ≤ 3.39 m^3/s) and a river where water flow was too high for dams to exist (mean annual flow >3.39 m^3/s). This definition was then applied to all streams and rivers within the study area. All streams were located in the outwash plain. Rivers were then all other flowing waterways, some of which had tidal influence as much as 9.5 km upstream from the river mouth. Water filled basins >0.5 ha were considered lakes. Areas along streams and tidal sloughs where beavers created ponded water were still considered as streams and tidal sloughs. Water variables were considered as either present or absent for every active lodge and random point. The categorical water variable was considered present if the active lodge or random location was either adjacent to (within 3-m) or within the water feature, otherwise the variable was considered absent.

Statistical Methods

I developed resource selection models (Manly et al. 2002) for active beaver lodges for both ground and aerial survey methods. Activity was a binary response; 1 for an active lodge site and 0 for a random inactive site. I used logistic regression as an analysis method for this retrospective habitat selection study. The best approximating model for the odds of beaver active lodge occurrence for each survey method was selected from an *a priori* list of candidate models (Anderson and Burnham 2002). My results of logistic modeling refer to the odds of occurrence of an active beaver lodge.

The set of *a priori* models were developed describing beaver active lodge site selection criteria based on biological information and our own experience in the study area. To account for possible multicollinearity, I examined pairwise correlations among variables. Any set of correlated variables (>0.07) would be represented in the models by only one of the correlated variables. Models were developed for each landscape type from 4 water categorical variables and 5 continuous vegetation variables at 2 scales. Two suites of models were developed, 1 for each landscape type (Outwash Plain and Uplifted Marsh), and were identical for each survey method.

I ranked categories of resources in importance to predicting active lodges. For this analysis, I used the following criteria for developing models as hypotheses. First, water features (SLOUGH, LAKE, RIVER AND STREAM) were ranked as the top active lodge predictor, followed by woody vegetation (ALDER/WILLOW$_{30,100}$, MIXED SHRUBS$_{30, 100}$, and MYRICA$_{30, 100}$) and then additional food sources (EMERGENT$_{30, 100}$ and HERB$_{30, 100}$) (Table 2.1). Thus, I included water variables as the first set of variables, then a second set of woody vegetation variables was added to the first set and finally, additional possible food sources were added if sample sizes allowed.

Anderson and Burnham (2002) suggest that a quadratic rather than a linear relationship may best represent a biologically significant relationship for some habitat variables. Based on field observations, I hypothesized that a specific value for vegetation characteristics may be optimum for active lodge site selection and values below or above this would produce a lower odds ratio of an active lodge site. Therefore, I developed models with a squared term for all woody vegetation variables in addition to linear woody vegetation relationships when sample sizes allowed. I used an information theoretic approach to rank my *a priori* candidate models for each survey and landscape type. I used an Aikaike's Information Criterion adjusted for small sample size bias (AICc) in my model selection analysis (Burnham and Anderson 2002: 98-148). Models for survey types by landscape type were identical. The number of models for each landscape type was restricted by the smallest sample size for either the ground or aerial photographic surveys to allow for greater accuracy of AICc values (Burnham and Anderson 2002:149-205). A total of 75 models were selected for the uplifted marsh while 16 models were selected for the outwash plain. I compared these models using the procedure GENMOD in SAS software v. 9.1. (Copyright, SAS Institute Inc.. SAS and all other SAS Institute Inc. product or service names are registered trademarks of SAS Institute Inc., Cary, NC, USA). The model with the minimum AICc value was selected as the best approximating model for the analysis. All models with a ΔAICc value <2 were considered as competing models (Burnham and Anderson 2002: 131).

RESULTS

We conducted ground searches in late August and September 2005. Ground surveys covered 5,842 ha (30%) in the uplifted marsh and 1,287 ha (8%) in the outwash plain (Figure 2.4 a). During ground surveys a total of 89 active lodges were located in the uplifted marsh and 17 were located in the outwash plain (Figure 2.4 c).

Aerial photographs were taken on 3, 16 and 25 October 2005. The flights produced a complete set of systematic samples for the uplifted marsh and outwash plain. Aerial photographs covered 57% of the total area for each landscape type, 11,239 ha in the uplifted marsh and 9,660 ha in the outwash plain (Figure 2.4 b). A total of 109 active lodges were identified in the uplifted marsh and 29 in the outwash plain (Figure 2.4 c).

I used complete ground surveys to asses the accuracy of aerial photographic surveys where the two survey methods overlapped. Of the lodges that I identified for both surveys, 35 out of 45 lodges (78%) were identified using aerial photographs in the uplifted marsh and 5 out of 9 (56%) in the outwash plain. Thus, I conducted habitat analysis for both survey methods in both landscape types. The two survey methods overlapped 3,321 ha (16%) in the uplifted marsh and 760 ha (5%) in the outwash plain.

The association of active beaver lodges with water features varied between areas. All active lodges in the outwash plain and uplifted marsh for both survey methods were associated with (within 3 m) 1 of the 4 water variables (Figure 2.5) On the uplifted marsh, active lodges were found almost exclusively on sloughs, which represented about 40% of all the water types in that landscape (Figure 2.5 a, b). This pattern was consistent between the aerial and ground surveys.

I found active lodge sites in the outwash plain in all of the water features that occurred in this area and lodges were more evenly distributed among water features than in the uplifted marsh (Fig. 2.5 c, d). Active lodges were most frequently associated with streams and lakes (Figure 2.5 c, d). Proportionally (i.e., the proportion of lodges relative to the availability of a given water feature), lodges were located on streams more than rivers or lakes in both surveys. Lakes were used more than they were available in the aerial survey (Figure 2.5 c) but not in the ground survey (Figure 2.5 d). Rivers were used less proportionally in both surveys, although the differences are more pronounced for the aerial surveys.

Active lodge and vegetation coverage varied between landscape types (Figure 2.6). All woody vegetation types were associated with active lodges. Vegetation availability and use differed between survey types in the outwash plain but not in the uplifted marsh. In the uplifted marsh, vegetation use was greater than availability for both survey types (Figure 2.6 a, b). On the outwash plain ground survey, vegetation use was proportional to availability for all vegetation types (Figure 2.6 c). This contrasted with the outwash plain aerial survey where vegetation use was less than availability for most vegetation types (Figure 2.6 d).

I identified 3 competing models for the uplifted marsh aerial survey analysis. All competing models included SLOUGH and $MIXEDSHRUB_{100}$. The best approximating model produced in the AIC_C analysis contains the explanatory variables SLOUGH and $MIXEDSHRUB_{100}$ (Table 2.2). There were no competing models for the ground survey uplifted marsh analysis; the best approximating model included SLOUGH,

$MIXEDSHRUB_{30}$ and $MIXEDSHRUB_{30}^2$. I found no correlation between explanatory variables within this analysis.

Table 2.2. Rankings of *a priori* models used to relate active beaver lodge occurrence to habitat variables in uplifted marsh and outwash plain by survey method on the west Copper River Delta, Alaska.

Model	AIC_c	ΔAIC_c
Uplifted Marsh		
Aerial Survey		
SLOUGH + MIXED SHRUBS$_{100}$	-43.94	0.00
SLOUGH + MIXED SHRUBS$_{100}$ + MIXED SHRUBS$_{100}^2$	-43.86	0.08
SLOUGH + MIXED SHRUBS$_{100}$ + HERB$_{100}$	-43.51	0.43
Ground Survey		
SLOUGH + MIXED SHRUBS$_{30}$ + MIXED SHRUBS$_{30}^2$	51.98	0.00
Outwash Plain		
Aerial Survey		
STREAM + ALDER/WILLOW$_{30}$	44.21	0.00
Ground Survey		
STREAM + ALDER/WILLOW$_{30}$	15.66	0.00
STREAM + ALDER/WILLOW$_{100}$	17.57	1.90

The best approximating model for the outwash plain aerial survey analysis included STREAM and ALDER/WILLOW$_{30}$ (Table 2.2); there were no competing models. There were two competing models for the outwash plain ground survey analysis that include STREAM and ALDER/WILLOW$_{30}$ and STREAM and ALDER/WILLOW$_{100}$.

In the uplifted marsh aerial survey model, the odds of finding an active lodge increase with the presence of SLOUGH and increasing MIXEDSHRUB$_{100}$ cover (Table 2.3, Figure 2.7 a). In the uplifted marsh ground survey model, the odds of finding an active lodge increase with the presence of SLOUGH and has a quadratic relationship with increasing MIXEDSHRUB$_{30}$ and MIXEDSHRUB$_{30}^{2}$ (Table 2.3, Figure 2.7 b). In the outwash plain aerial survey model, the odds of finding an active lodge increase with the presence of STREAM and a decrease in ALDER/WILLOW$_{30}$ cover (Table 2.3, Figure 2.7 c). In the outwash plain ground survey model, the odds of finding an active lodge increase with the presence of STREAM and a decrease in ALDER/WILLOW$_{30}$ cover (Table 2.3 and figure 2.7 d).

Table 2.3. Coefficients in AICc-selected best approximating models fitted by logistic regression. Parameter estimates and confidence intervals (CI) are in log odds ratios.

Parameter	Estimate	S.E.	95% CI
Uplifted Marsh			
Aerial Survey			
SLOUGH	8.07	1.34	5.96 to 11.46
MIXED $SHRUBS_{100}$	12.24	5.04	3.06 to 23.19
Ground Survey			
SLOUGH	4.17	0.61	3.09 to 5.04
MIXED $SHRUBS_{30}$	-5.56	5.08	-16.00 to 4.06
MIXED $SHRUBS_{30}^{2}$	23.09	12.38	-0.05 to 48.74
Outwash Plain			
Aerial Survey			
STREAM	4.04	1.47	1.76 to 7.84
ALDER/$WILLOW_{30}$	-5.10	2.67	-11.60 to -0.89
Ground Survey			
STREAM	1.80	0.96	0.03 to 3.94
ALDER/$WILLOW_{30}$	-7.21	3.49	-15.51 to -1.52

DISCUSSION

I documented beaver resource selection in 2 landscape types on the WCRD using 2 survey methods. Active lodge site selection differed between the 2 landscape types but was consistent between survey methods.

Active beaver lodges were associated with distinct water features and woody vegetation types on both the uplifted marsh and outwash plain of the WCRD. Models that best fit the data were consistent between the two survey methods for each landscape type, although the scale of plots differed in the uplifted marsh analysis. Old tidal sloughs and mixed shrub cover were represented in both models for the uplifted marsh while streams and closed cottonwood/alder/willow (alder-willow) were represented in both models for the outwash plain. Thus, active beaver lodge sites are associated with specific habitat conditions depending on landscape type.

Active lodge sites had distinct relationships with vegetation and water variables. Overall, vegetative features closer to the lodge (i.e., 30 m) better predicted the presence of active lodges than did those further away (i.e., 100 m), except for the aerial survey in the uplifted marsh. The reasons for this are not immediately obvious. It could be that requirements near the lodge are more consistent or stringent than those required for the home range. The smaller plot size may also represent a greater proportion of vegetation directly associated with active lodges (i.e., slough levees). In the uplifted marsh, woody vegetation is located near slough levees and is often replaced by herbaceous vegetation as distance from the slough levee increases (moving towards lake basins). A smaller plot size may contain woody vegetation more regularly than a larger plot size, which may include both the slough levees and the pond basins.

Although vegetation variables are present in my models, their influence is not as strong as the associated water feature. Previous studies have investigated both physical and vegetative features of active lodge sites, but physical features (i.e., gradient, depth and width) are more commonly the best predictor of beaver activity and site selection (Beier and Barrett 1987; Howard and Larson 1985; Slough and Sadleir 1977; Suzuki and McComb 1998).

In the outwash plain, I found active beaver lodges associated with streams and closed cottonwood-alder-willow stands. Beavers are commonly associated with streams (Boyce 1974; Howard and Larson 1985; Suzuki and McComb 1998). Optimum stream gradient for beaver activity is <3% (Muller-Schwarze and Sun 2003; Suzuki and McComb 1998); stream gradients >15% have little value as beaver habitat (Allen 1983). The gradient on the outwash plain, which I assume reflects the gradient of streams and rivers, averages 1.6% from the tidal flats to 12 km inland and increases to an average of 7.5% beyond 12 km to the extent of the outwash plain (Thilenius 1990). This increase in land gradient in the outwash plain likely explains the absence of beaver activity in the upper most areas (>12-km) of the outwash plain where I documented 1 active beaver lodge with either or both survey methods.

Tree canopy closure of 40-60% is an indicator of optimum beaver food availability (Allen 1983). Canopy closure >60% may restrict beaver movement and increase the likelihood of cut trees hanging up in adjacent trees (Allen 1983). Areas delineated as closed cottonwood-alder-willow vegetation in the satellite imagery of the WCRD have cover of >60% (Kempka et al. 1994). Closure of the canopy in cottonwood-alder-willow stands may explain the odds of active lodges decreasing when this vegetation community increases. Herbaceous vegetation is an important food component in the summer months (Jenkins 1979), and an open canopy may also allow for greater coverage of herbaceous vegetation. Availability of herbaceous vegetation was greater than all other vegetation types and may be present in adequate amounts around most lodges. Although the herbaceous/graminoid vegetation type was not in the best approximating models, smaller patches and a thicker understory of this vegetation type may exist within open canopy vegetation types (Boggs 2000). Previous studies have also found negative association between beaver sites (dams and lodges) and shrub cover, although this has been attributed to beaver herbivory and dam building (Rebertus 1986; Suzuki and McComb 1998). Beavers may influence the density and species composition of woody vegetation in areas they inhabit by cutting select trees and shrub species for food and dams (Barnes and Dibble 1988). Although it may be argued that beaver have influenced those areas around their lodge by removing closed cottonwood-alder-willow, it is unlikely that this phenomenon is reflected in the satellite vegetation coverage which was produced 12 years previous to this study (Kempka et al. 1994).

Streams appear to be the preferred water feature in the outwash plain. Although active lodges were found in lakes, streams may be more ideal habitat due to the ability to dam water and thus control water depth. Relatively few lakes and ponds were visited in the ground survey, which accounts for the low numbers of this water feature represented in this analysis. Although lakes received little use in the uplifted marsh there is a shift to the use of lakes in the outwash plain. Water depth may influence site selection for each landscape type (Beier and Barrett 1987; Slough and Sadleir 1977); lake depth in the outwash plain may be greater on average than lake depth in the uplifted marsh allowing for year-round access to food caches in the outwash plain.

In the uplifted marsh, active beaver lodges were associated with old tidal sloughs and mixed shrub cover for both survey methods. The presence of old tidal sloughs on the WCRD has allowed beavers to colonize areas where ponds were too shallow to sustain beaver populations. Aerial survey results suggest a relationship of active lodge sites with mixed shrub communities at the 100-m scale, while ground survey results suggest a relationship with mixed shrubs at the 30-m scale. Aerial survey active lodges are more evenly detected and dispersed across the uplifted marsh as opposed to ground surveys, which were conducted in contiguous areas. Ground surveys could have resulted in identifying active lodges with similar habitat requirements due to closer spacing as opposed to aerial surveys, which were more widely dispersed across the landscape requiring a larger scale to explain the variability among active lodges.

In the presence of woody vegetation, beavers may colonize riverbanks (Dieter and McCabe 1989). Although beaver lodges are present on tidal rivers in the uplifted marsh, old tidal sloughs were the preferred water feature by beaver in this landscape type. Old tidal sloughs may be preferred to rivers because of access to food provided by the damming of these sloughs. Rivers in the WCRD also have wide banks and steep cutoffs, which could restrict beaver access to woody vegetation. The increased width of rivers could also expose beavers to a greater risk of predation (Robel et al. 1993).

Old tidal sloughs appear to have a gradient of woody vegetation. In most areas of the WCRD, a shorter mixed shrub vegetation cover replaces the closed cottonwood-alder-willow cover along the old tidal slough levees. This change is abrupt and can be seen from a distance on the ground (personal observation 2005). Closed cottonwood-alder-willow occur in areas closest to the mouths of sloughs where they meet the main river channel. As the distance to the slough mouth increases, the water table frequently rises because of beaver dams, and changes in vegetation coincide with changes in the water table (Boggs 2000). When the water table is closer to the top of the levee, the closed cottonwood-alder-willow cover diminishes rapidly. Beavers may select areas of use that have deeper water (Beier and Barrett 1987). Therefore, a preference for a mixed shrub vegetation type may actually represent a preference for greater water depth.

Woody and herbaceous vegetation was not uniformly distributed on the WCRD. Closed-cottonwood-alder-willow increased and herbaceous cover decreased on a gradient from west to east. Although beavers use a variety of deciduous woody vegetation (Jenkins 1979), and occupied sites were associated with a range of woody vegetation in the WCRD, the mixed shrub vegetation may be the best predictor of active lodge locations due to its persistence across the WCRD. Herbaceous vegetation is fairly prevalent on both landscape types and active lodge site selection may not depend on this vegetation type because of its abundance.

It is likely that beaver will continue to select different water features and vegetation in the 2 basic landscape types of the WCRD due to available resources. Water features on the WCRD vary greatly between landscape types. Old tidal sloughs are present only in the uplifted marsh and those areas of the outwash plain directly adjacent to the uplifted marsh. Beavers likely will continue to select for this resource as long as woody vegetation exists among them. Currently, various vegetation types exist on the CRD (Boggs 2000), but over time succession on slough levees and ponds that increases woody vegetation may influence beaver site selection. Streams associated with closed cottonwood-alder-willow in the outwash plain may be the best predictor of future beaver habitat because succession-driven vegetation encroachment may decrease the occurrence of lakes and ponds over time (Boggs 2000; DeVelice et al. 2001). Since the uplift, woody vegetation has established in areas of the uplifted marsh previously dominated by sedge communities (Boggs 2000; Thilenius 1990). Various studies on the WCRD predict that lakes and ponds will diminish and eventually disappear in some areas due to succession-driven bog development, which results in *sphagnum* filling lake and pond basins (Boggs 2000). Ultimately, woody vegetation and *sphagnum* may dominate the uplifted marsh with few lakes and ponds (Boggs 2000; DeVelice et al. 2001). How the vegetative community further develops may depend on the presence and activity level of beavers. Patterns of succession may be influenced by beavers, although it is not entirely clear what this influence may be on the WCRD. Managers on the CRD have speculated that beaver water impoundments may have long-term effects on succession (DeVelice et al 2001). The ability to identify beaver habitat by landscape type may then foster future development of succession models that account for beaver activity.

A further understanding of beaver habitat occupancy, dispersal and patterns of use may assist in understanding this species and its interactions with the environment on the CRD. While the beaver associations with woody vegetation types and water sources is not new information, the differences in habitat selection between landscape types on the WCRD identifies distinct features within each landscape that beavers are currently exploiting. These distinct features may then be used to infer landscape-wide potential beaver habitat using remote sensing data on the WCRD.

MANAGEMENT IMPLICATIONS

It appears that ground surveys may be the best method to determine active lodge habitat associations on the WCRD. While high resolution aerial photograph models and ground survey models produce similar results, sightability may become increasingly problematic over time if woody vegetation becomes more prevalent on the WCRD. Although models from satellite imagery and aerial photography are more coarse, they can be used at a much wider scale.

Remote sensing may be also be a cost-effective tool to monitor beaver habitat associations over time. This method may not be useful where site specific measurements, not easily determined from remote sensing (i.e., tree heights, diameters, or bank slope), are strongly associated with lodge location. Much is already known about beaver habitat selection. Applying *a priori* knowledge to coarse-scale models may be a useful indicator of landscape-wide habitat selection.

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FIGURES

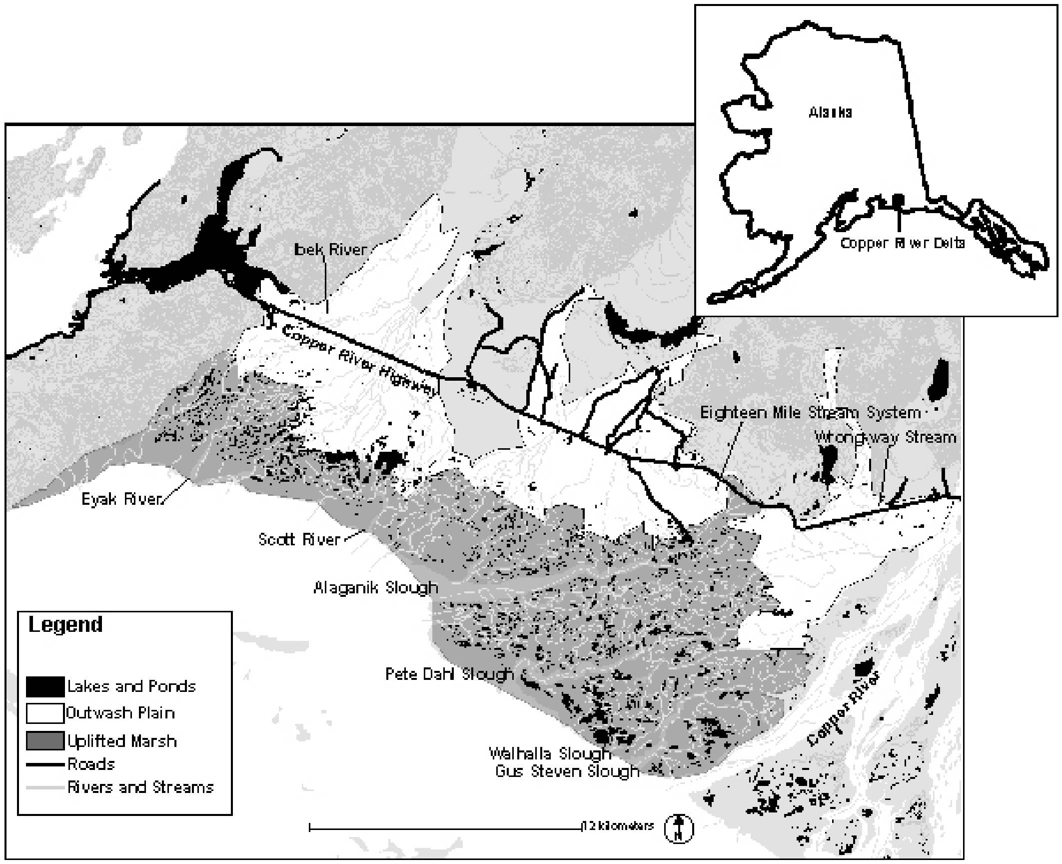

Figure 2.1. The study area on the west Copper River Delta in south central Alaska.

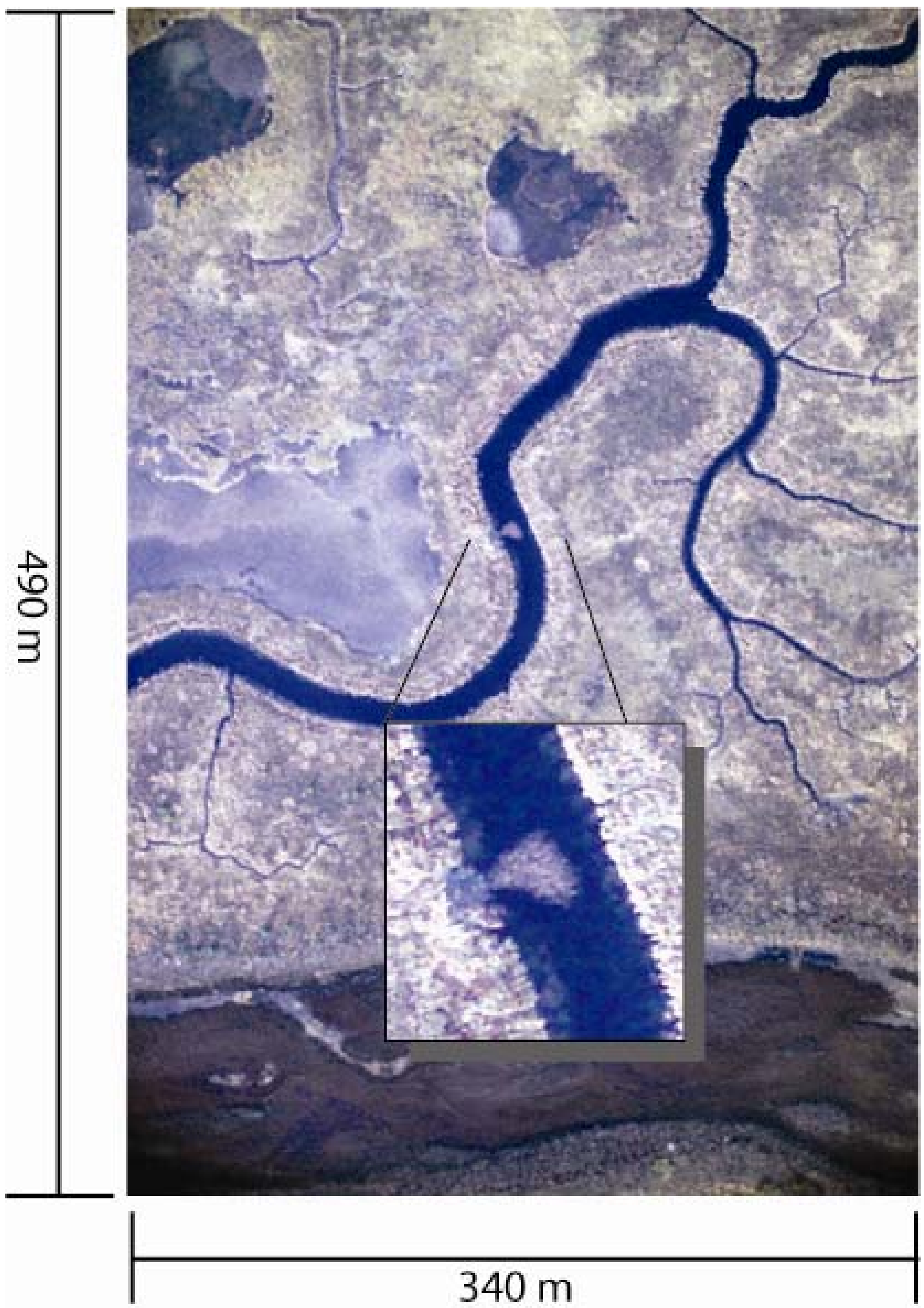

Figure 2.2. An example of an aerial photograph used to identify active beaver lodges with robust cache piles on the western Copper River Delta, Alaska.

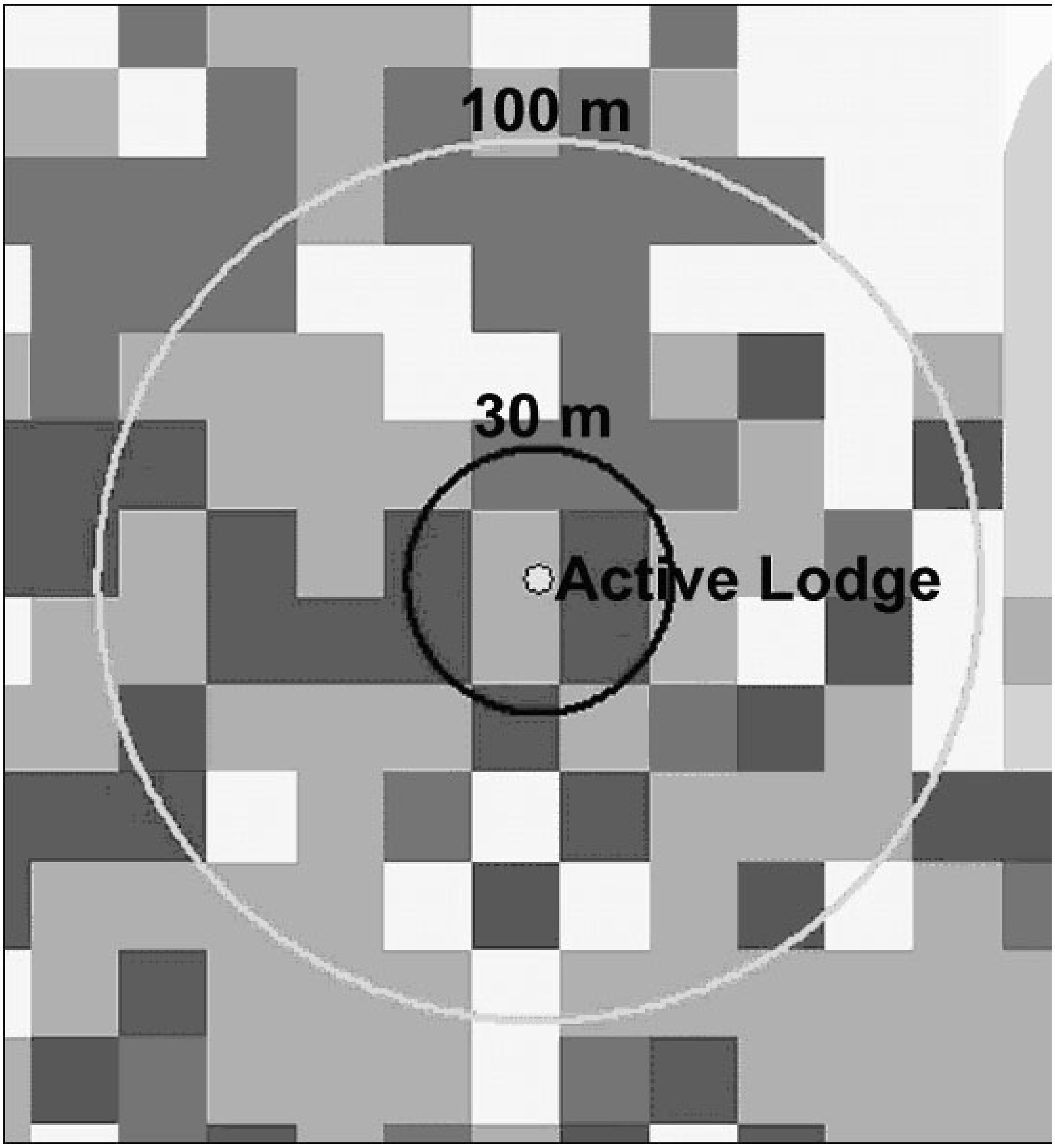

Figure 2.3. An example showing the location of an active beaver lodge on the west Copper River Delta, Alaska with 30-m and 100-m vegetation plots from the satellite imagery.

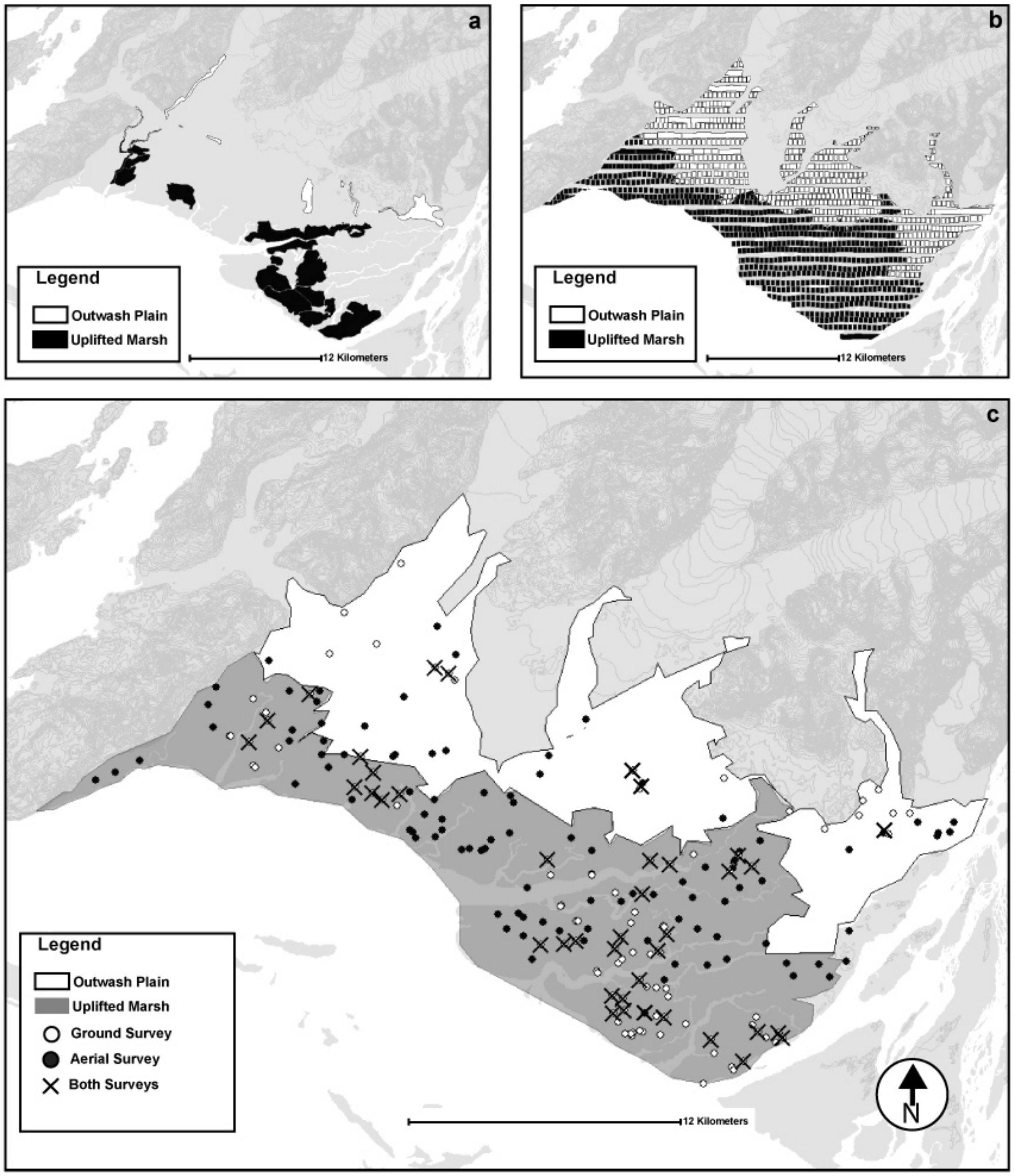

Figure 2.4. Survey coverage for the ground (a) and aerial (b) survey areas in the uplifted marsh and outwash plain, August-October 2005, and active lodge locations on the west Copper River Delta, Alaska for aerial and ground surveys (c) August-October 2005.

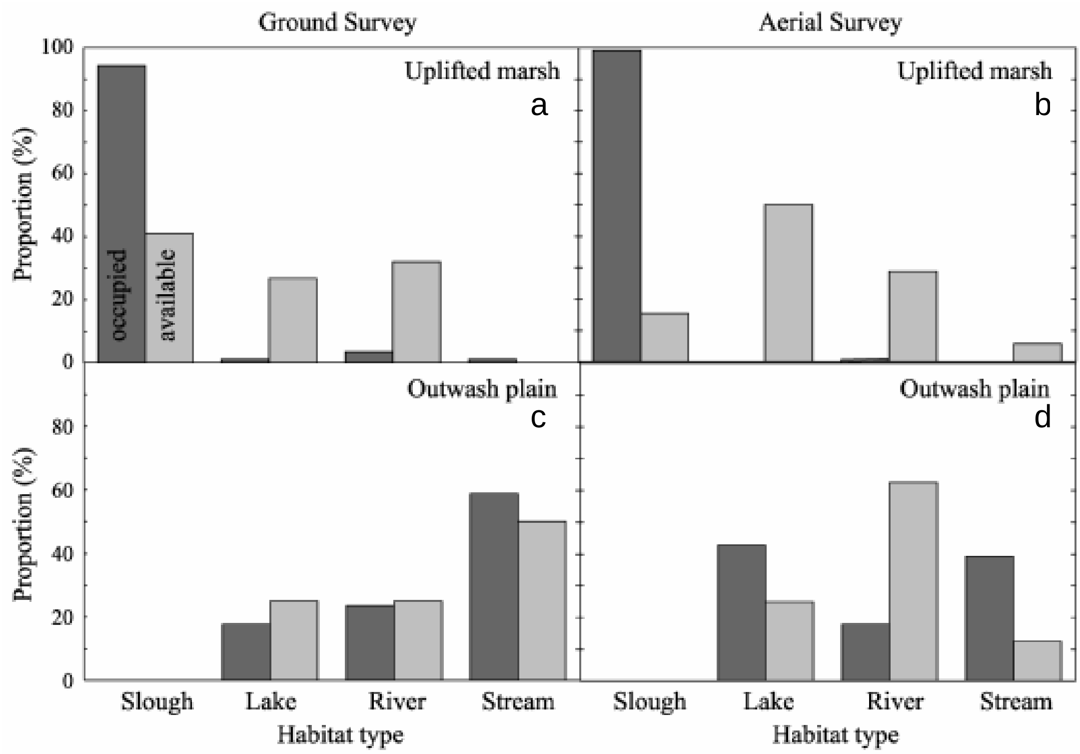

Figure 2.5. Percent of water features occupied by beaver (active lodge) and available (random points) as determined by aerial and ground surveys by landscape type of the west Copper River Delta, Alaska, August-October 2005.

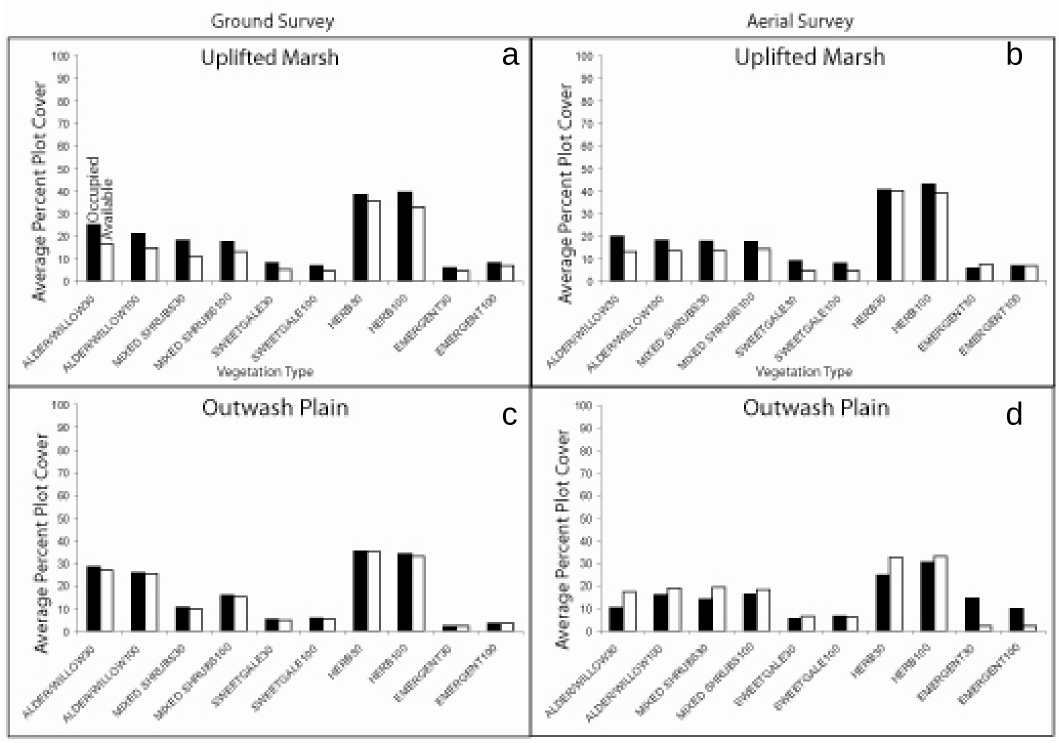

Figure 2.6. Percent of vegetation types at occupied beaver (active lodge) and available (random points) as determined by aerial and ground surveys by landscape type of the west Copper River Delta, Alaska, August-October 2005. Vegetation types that were significant in the best approximating model ($p < 0.06$) for each analysis are indicated with an asterisk.

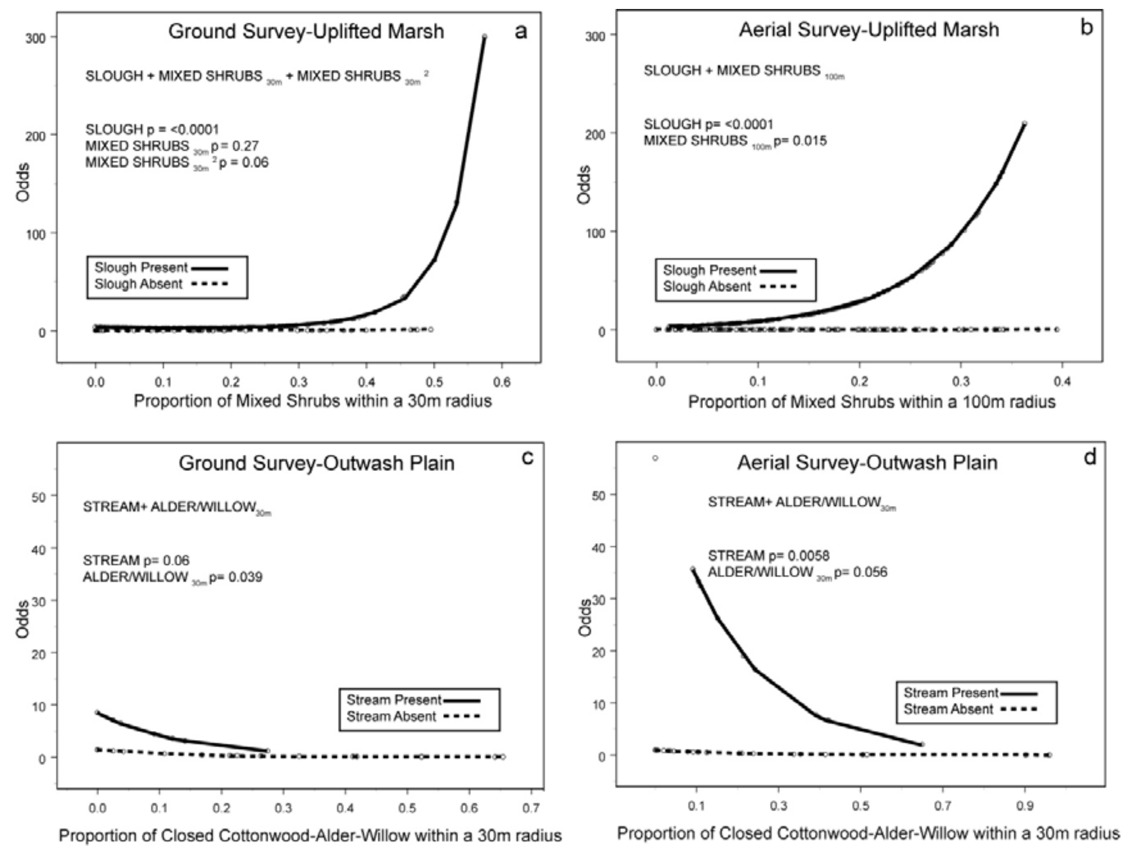

Figure 2.7. Odds for finding an active beaver lodge versus a random point for the aerial and ground surveys by landscape type on the west Copper River Delta, Alaska. The best approximating model and associated p values are listed within each plot.

Chapter 3

Beaver Influence on Surface Water Changes Over Time on the West Copper River Delta, Alaska.

Erin E. Cooper

ABSTRACT

Since the 1964 Alaska earthquake and geologic uplift, beavers (*Castor canadensis*) have expanded their historic range from the inland Copper River Delta (outwash plain) to the once tidally-influenced areas of the outer Delta (uplifted marsh). The uplift presented a unique opportunity to observe how beaver influenced the transitioning hydrologic structure of a coastal wetland ecosystem after a major disturbance. Here, I quantified the influence of beaver on the surface waters of the West Copper River Delta using remote sensing. Water features were documented from digitized aerial photographs from 1959, 1974, 1986, 1992-1993, and 1996. Surface water area in beaver-influenced water impoundments increased from 0-20% of total surface water area from 1959-1996, concurrent with beaver colonization of the uplifted marsh. These results suggest that beavers altered the trajectory of wetland change on the West Copper River Delta by raising the water table within open water basins and flooding areas that would have otherwise drained.

INTRODUCTION

Beavers (*Castor canadensis*) can have substantial impacts on the landscape that they inhabit (Barnes and Dibble 1988; Grover and Baldassarre 1995; Johnston and Naiman 1990; Naiman et al. 1994; Wright et al. 2002). They can influence the structure and composition of the vegetative community through cutting for food and dam construction (Barnes and Mallik 1996; Barnes and Dibble 1988). Dams built by beaver change flowing water to standing water and ponds in areas that were previously drained, which can alter nutrient flow (Bryant 1991) and provide habitat for a variety of fish and wildlife (Grover and Baldassarre 1995; Lang 2003; Sigourney et al. 2006).

The cycle of beaver dam construction and deterioration influences the amount of standing water and vegetation within associated systems (Fryxell 2001; Johnston and Naiman 1990; Wright et al. 2002). Creation of ponds through building dams can raise the water table, which can change vegetative communities (Goslee et al. 1997; Harris and Marshall 1963; Pezeshki 2001; Remillard et al. 1987). During periods of beaver occupancy, an area may be flooded by beaver impoundments, raising the water table and saturating soils. This will restrict some types of vegetation, particulary trees and shrubs (Batzli and Dawson 1997; Goslee et al. 1997; Thilenius 1990) used by beavers. The water table drops when dams deteriorate and break, allowing the establishment of vegetation that favors drier conditions. This pattern of occupation and abandonment may create a mosaic of landscape vegetation types (patches) that would not exist without the presence of beavers (Grover and Baldassarre 1995; Syphard and Garcia 2001; Wright et al. 2002). The western portion of the Copper River Delta (WCRD) in south central Alaska has some of the highest density of beavers (1.5/km^2) in North America (Alaska Department of Fish and Game 1990). Prior to 1964, beaver distribution was restricted to the portion of the WCRD closest to the mountains, and furthest from the ocean, (Roberds 1955). This area, classified as glacial outwash plain (Davidson 1998), is comprised of braided glacial rivers, and clear water rivers, streams, small lakes, and ponds. Vegetation includes shrubland and wooded areas with some less common open *sphagnum* spp. dominated areas (Boggs 2000). Beaver are abundant and play an important ecological role, providing habitat for various fish (Lang 2003) and wildlife (Tom Fondell personal communication 2007), and sites of nutrient storage and processing (Bryant 1991; Lang 2003).

The portion of the WCRD closest to the ocean, which was a tidally-influenced sedge marsh, was historically unsuitable for beavers (Roberds 1955). However, a 9.2 moment magnitude earthquake raised this area 1.8-3.4 m above the mean high tide line (Reimnitz 1966). As a result, this area, called the uplifted marsh (Davidson 1998) changed from a tidally influenced sedge marsh into a drier freshwater system of perched ponds, levees, and old tidal sloughs (Thilenius 1990). Vegetation underwent rapid succession from 1964 to the early 1980s (Thelinius 1990). These changes were more favorable to beavers and resulted in beavers moving relatively quickly onto the uplifted marsh following the earthquake (Crow 1999).

This landscape variation and recent history of colonization of beavers on the uplifted marsh of the WCRD present a unique opportunity to examine the pattern of colonization and to quantify the effect of beavers. The specific purpose of this study was to quantify the amount of water impounded by beavers on the uplifted marsh and glacial outwash plain of the WCRD at selected times before and after the 1964 earthquake. I do this by examining aerial photos from selected years.

STUDY AREA

The Copper River Delta (CRD), located on south-central Alaska's gulf coast, is the largest contiguous wetland on the Pacific Coast of North America: 283,000 ha and 75 km long. The study area is located on the WCRD (Figure 3.1). The WCRD encompasses approximately 121,000-ha from the base of the Chugach Mountains to mudflats stretching into the Gulf of Alaska (Figure 3.1). The WCRD is separated from the eastern CRD by the Copper River. A glacial outwash plain encompasses the northern 1/3 of the WCRD and an uplifted marsh comprises the southern 2/3 (Thilenius 1990). A new marsh exists on the coastal edges of the uplifted marsh (Davidson 1998). The specific areas investigated during this study encompassed the WCRD areas defined as uplifted marsh and outwash plain by Davidson (1998).

Many saturated areas have a sphagnum cover on both the uplifted marsh and outwash plain. Herbaceous vegetation on the WCRD is comprised of sedge meadows, grass/forb meadows and aquatic emergent and submergent vegetation on ponds. Woody vegetation of sweetgale (*Myrica gale*) and Sitka alder (*Alnus crispa sinuata*) shrublands, perist on the levees and outwash plains. Black cottonwood (*Populus balsamifera trichocarpa*) woodland and Sitka spruce (*Picea sitchensis*) forests are present on the outwash plain.

The uplifted marsh is categorized as that area which currently consists of freshwater interbasin perched ponds, levees, tidal creeks (old tidal slough channels), freshwater streams, and sea cliffs (Boggs 2000). Prior to the uplift, the marsh was intermittently flooded by extremely high tides (Boggs 2000; Hansen 1961; Thilenius 1990). The surface substrate of this area is organic with glacial silt and inorganic substrates at 1 m depth (Thilenius 1995). Lake and pond depth in this area averages 0.7-1.1 m (Thilenius 1990). Over time, salt dissipated from the uplifted marsh soils, which were then colonized by freshwater plant species (*Sphagnum, Salix, Alnus, Picea*) that were previously unable to tolerate the intermittent influence of saltwater and salty soils (Crow 1971). The uplift caused extensive shifts of plant zones on the CRD (Boggs 2000; DeVelice et al. 2001; Thilenius 1990). In some cases a shift in saltwater-influenced areas have a difference of 15 km from the pre-earthquake locations of the boundary between saltwater and freshwater (Reimnitz 1972).

The outwash plain was described by Davidson (1998) as glacial and alluvial outwash plains, braided glacial rivers, freshwater streams, freshwater ponds and lakes, low terraces, sand and gravel bars that were the direct result of upland erosion. Water flow in rivers and streams is highly variable and may increase or decrease significantly in some areas depending on season and rainfall (Boggs 2000; Thilenius 1990). The outwash plain was not influenced by tidal water inundation prior to the earthquake, therefore vegetation community types have remained fairly constant since the uplift (Boggs 2000).

Trapping has historically occurred on the WCRD and continues into present day. Currently, trapping mortalities account for an average of 60 individuals annually on the WCRD (Alaska Department of Fish and Game 2004), much of which occurs near the highway on the outwash plain.

METHODS

I developed a classification system and digital outlines for discrete surface water areas in the uplifted marsh and outwash plain to determine total area (ha) influenced by beaver. Photographs have been used to determine changes in surface water influenced by beavers (Johnston and Naiman 1990). Aerial photography exists for the entire coverage of the WCRD for the years of 1959, 1974, 1986, 1992-1993 and 1996 (Table 3.1 and Figure 3.2). Photographs for a given year were taken between the months of May to September, except for the 1992-1993, when they were taken in two separate years because of logistic contraints. The 1996 aerial photographs were digitized and georeferenced by the U.S. Forest Service in 1997, which resulted in a set of digital georeferenced orthophotos. I digitized and georeferenced aerial photographs using ERDAS IMAGINE™. Scale variations due to paper stretch or tilt in near-vertical aerial photographs were corrected during the digitizing process. I used the digital orthophotos generated by the U.S. Forest Service in 1997 as a reference source for georefencing. Root mean square (RMS) errors did not exceed 5 m RMS error for any aerial photo. After photographs were georeferenced, they were compared in a Geographic Information System (GIS) to the 1996 orthophotos for spatial accuracy.

Table 3.1. The year, date, and type of the aerial photographs of the west Copper River Delta, Alaska used in this study.

Photo Year	Date	Type
1959	5/59	Black and White
1974	6/74, 7/74, 9/74	True Color
1986	7/86	Color Infrared
1992-1993	8/92, 7/93	True Color
1996	7/96	Black and White converted Color Infrared

Surface water area of specific water features in the uplifted marsh and outwash plain were then interpreted from the set of georeferenced aerial photographs. To avoid the time and effort involved in analyzing 100% of the study area, I randomly sampled 20 percent of each landscape type. I determined that 48, 100-ha plots and 36, 100-ha plots would cover 20% of the respective landscape types of uplifted marsh and outwash plain. I created random plots by first generating random points in a GIS, these points were then placed in the uplifted marsh (48) and the outwash plain (37). I used these random points as center points for 564-m radius circular plots. Water features were then identified, categorized and delineated within each plot.

Water features are easily recognized in aerial photographs. Furthermore, beaver impounded water can be identified through the presence of dams. I identified all water features within each plot for each year of aerial photographs. Water features smaller than 0.01 ha were excluded from analysis. Many linear water features (streams and sloughs) also exist on the WCRD. Linear water features with a width < 2 m could not be identified on all photos and were also excluded from analysis. Each water feature type was categorized as fresh, fresh beaver influenced, brackish, turbid or tidal (Table 3.2). Analysis did not include tidal areas or turbid river water because of major daily and seasonal fluctuations. Some lakes contained both fresh water and turbid water influenced by adjacent rivers. I could not separate turbid water, which in some cases only included parts of the water body. Therefore, lakes with turbid water were included in the analysis and categorized as fresh water. Brackish water, which resulted from tidal influence, was only present in the 1959 photographs (Potyandy et al. 1975) and is used for comparison purposes. It appears that the 1959 photos were taken at high tide because of the absence of water in tidal sloughs. In cases where beaver influenced water connected to pre-existing lakes, the previous photo year water level (without beaver influence) was determined as fresh water and any additional water was then determined as beaver influenced.

Table 3.2. Water feature types used in surface water analysis.

Water Feature Type	**Description**	**Associated Sources**
Fresh	Fed by either rainwater and or runoff. Does not include glacially influenced water (see turbid).	Lakes, Streams and Old Tidal Sloughs (sloughs)
Beaver Influenced	Fresh water that has been impounded by beaver dams.	Lakes, Streams and Old tidal sloughs (sloughs)
Brackish	Fresh water intermittently influence by tidal flooding.	Lakes
Turbid	Water with apparent turbidity most likely from glacial runoff.	Rivers and Lakes
Tidal	Areas of tidally influenced water	Rivers (near the mouth)

Water features were further categorized by source as lake (ponds and lakes), stream, old tidal slough (slough) or river. Ponds and lakes are hereafter referred to as lake/lakes for the purposes of this study. Old tidal sloughs (sloughs) are pre-earthquake tidally-influenced waterways < 30 m with no glacial runoff influence. Rivers and streams were separated based on flow measured as the mean annual cubic meter per second (m^3/s)(Blanchett 1983). A water source was considered a stream where dams could exist (mean annual flow $\leq 3.4\ m^3/s$) and a river where water flow was too high for dams to exist (mean annual flow $> 3.4\ m^3/s$). All streams were located in the outwash plain with none in the uplifted marsh. All river water was categorized as either turbid or tidal due to glacial sediments and/or tidal influence at the mouth.

Patterns of beaver colonization may be both temporal and spatial (Fustec et al. 2001). The number of plots with any beaver-influenced water was calculated for each photo year to determine the temporal pattern of dispersal for the uplifted marsh and outwash plain. Spatial patterns of dispersal were determined within the uplifted marsh by the distance of the center of the plot to the tidal edge along the uplifted marsh. Plots closest to the tidal edge are furthest from the outwash plain. Distance from the tidal edge was determined from the plot center point within a GIS and was used as an indicator of dispersal. I considered the outwash plain as the source population for the uplifted marsh colonization. Thus, plots that are closest to the tidal edge were then the furthest from this source population.

A GIS was used to quantify total surface water area for each plot and landscape type, which were additionally categorized by type and source (Figure 3.3). Individual lakes and sloughs were not tracked through time. Surface water data was then extracted from the GIS for analysis. Precipitation data (National Oceanic and Atmospheric Administration weather station) collected at the Cordova Airport (in the center of the study area) were examined for three months prior to the photograph date to assess the possible influence of high precipitation on increases in surface water.

RESULTS

The pattern of changes in the number of plots with beaver-influenced water varied between the outwash plain and the uplifted marsh on the WCRD (Figure 3.4). The number of plots with beaver-influenced water increased over time in the uplifted marsh increased over time. (Figure 3.4). The greatest increase occurred between 1974 and 1992 with only a small increase after 1992. The pattern on the outwash plain was fairly stable over time (Figure 3.4).

Colonization by beaver of the uplifted marsh proceeded from the area adjacent to the outwash plain to the tidal edge of the marsh (Figure 3.5 a). The only plot occupied in the uplifted marsh in 1974 was adjacent to the outwash plain (plot furthest from the coast). By 1986, beaver occupied plots in all distance categories, but plots <2,000 m from the coast were still <50% occupied (Figure 3.5 a). In 1992, almost all plots (45) in the uplifted marsh had some degree of beaver occupancy regardless of distance from coast with two additional plots occupied by 1996 (47).

Beaver activity on the different parts of the outwash plain was relatively stable through the study period (Figure 3.5 b). Within each distance category, the number of occupied plots varied little over time.

Patterns of changes in the surface area of water associated with beavers differed between the uplifted marsh and the outwash plain. Fresh surface water area in the uplifted marsh increased from 1959-1996 (Figure 3.6 a). In 1959, all surface water in the plots was brackish. The change from a tidally-influenced marsh to an uplifted perched wetland is evident in 1974 with the absence of brackish water and a large increase in fresh surface water area. Surface water area in plots from 1974-1996 in the uplifted marsh and outwash plain was entirely fresh (lakes, sloughs and streams). Total fresh surface water area increased in the uplifted marsh by 25% from 1974-1996, which translates into a change in the average plot surface water area from 13% of total plot area (1974) to 17% (1996). Beaver-influenced water in the uplifted marsh increased from <1% of surface water area in 1974 to 20% of surface water area in 1996 (Figure 3.6 a). Beaver-influence water increased from 0%-3% of total plot area from 1959-1996 in the uplifted marsh.

There did not appear to be a distinct trend in the increase or decrease of surface water area in the outwash plain (Figure 3.6b). The area of surface water remained relatively stable over time in the outwash plain. Total surface water area was within a range of 7-10% of total plot area for all years. Beaver-influenced water ranged from 0.6-1% of total plot area in the outwash plain.

I quantified surface water in the uplifted marsh and outwash for all sources (lakes, sloughs and streams) (Figure 3.7). Lakes were the major contributor of surface water for all years on both the uplifted marsh (80-100%) and outwash plain (87-91%)(Table 3.3). In the uplifted marsh, surface water in sloughs increased over time from 0-19% of the total fresh surface water (Figure 3.7 a), much of which was in beaver impoundments (91-100% of total beaver influenced water for all years) (Table 3.3). In the outwash plain, a majority of the year to year variability in surface water comes from lakes (Figure 3.7 b). Streams in the outwash plain only comprised 9-20% (Figure 3.7 b) of total surface water but contributed 70-90% of beaver influenced water for all years (Table 3.3).

Table 3.3. Percent of beaver influenced surface water area within each water feature by landscape type.

	Photo Year				
Landscape Type	**1959**	**1974**	**1986**	**1992-93**	**1996**
Uplifted Marsh					
Slough	0	100	97	91	92
Lake	0	0	3	9	8
Stream	0	0	0	0	0
Outwash Plain					
Slough	0	3	13	6	13
Lake	30	7	0	15	9
Stream	70	90	87	79	78

Although I did not perform a statistical analysis on these data because of the lack of independence between photo year and precipitation amounts, it appears that photo years with high levels of precipitation did not correspond with greater area of surface water. Precipitation trends did not appear to influence surface water area by year (Figure 3.8). The 1996 photos have the lowest precipitation amounts three months prior to the photo date (Figure 3.8) but surface area of water in 1996 was the highest for both the uplifted marsh and outwash plain (Figure 3.7). Alternately, 1986 had higher precipitation than 1996 but the surface water area was lower in 1986 than in 1996.

DISCUSSION

Beaver colonization in the uplifted marsh of WCRD did not occur immediately after the earthquake in 1964 but lagged by approximately 20 years. The time lag between the uplift and beaver occupancy may be an indicator of the time required for the establishment of woody vegetation, with which beaver numbers are associated with on the WCRD (Cooper 2007). Beaver expansion occurred rapidly after 1986, with beavers moving into previously unoccupied areas. This expansion slowed by 1996, with a reduced rate of new occupancy. Surface water increases between 1974 and 1996 were fairly similar among the years considered in this study. Although beaver had expanded into a majority of habitat by 1992, water levels continued to increase, which suggests that dam building continued in the remaining unoccupied suitable habitats. Although I did not look past 1996, it may be the case that beaver had reached a point where all available habitat was occupied in the uplifted marsh by that time.

Beaver-influenced surface water area on the outwash plain was more uniform over the study period compared to the increase on the uplifted marsh. In contrast, beaver plot occupancy was relatively constant over time in the outwash plain. Although some sites with high quality habitat may not be abandoned, other sites may go through intermittent occupancy depending on the quality of the habitat (Howard and Larson 1985). Beavers inhabited the outwash plain prior to the uplift (Roberds 1955). Beavers may occupy and abandon sites repeatedly in areas where they have a long term presence (Fryxell 2001). During periods of abandonment, dams are not maintained and may breach releasing the water held behind them. Concurrently, new dams may be constructed at new occupied sites. The result is that there may be variation at the site scale but the large landscape pattern is more stable. The even distribution of beaver influenced plots and surface water on the outwash plain over the study period appears to be indicative of this type of sustained landscape occupancy.

Overall surface water fluctuated over time in the outwash plain, specifically in lakes. Potyandy et al. (1975) observed that glacial streams and rivers may influence surface water areas in some lakes and ponds on the WCRD. Since turbid and fresh water was combined in lakes, the fluctuations in fresh surface water over time may have resulted from the intermittent influence of glacial rivers and streams.

Beaver range expansion commonly occurs through the dispersal of 2-year-old juveniles that move from areas with established territories to unoccupied habitat (Bergrund and Miller 1977; Bradt 1938; Fustec et al. 2001), Patterns of dispersal may not be regular and beavers may travel further than the nearest available habitat when dispersing (Harris 1991). The outwash plain was the likely source population for the expansion of beavers into the uplifted marsh. Beaver expansion into the uplifted marsh occurred initially in plots closest to the outwash plain. Dispersing beavers also select for areas of abundant food resources, which may be higher than previous lodge locations (Harris 1991). Beavers may have abandoned some areas in the outwash plain to colonize the newly developing uplifted marsh.

Changes in beaver site occupancy on the WCRD may be influenced by wildlife predation and trapping. Wolves (*Canis lupis*), coyotes (*Canis latrans*) and brown bears (*Ursus arctos*) are all known predators of beaver (Engelhart and Muller-Schwarze 1995) and are common residents of the CRD (Campbell 1990; Carnes 2004; Miller 2004). Not much is known about the influence these predators have on the population of beavers on the CRD. Many old lodges on the WCRD show signs of predator disturbance in the form of large holes in the sides and tops. This disturbance is most likely due to brown bears, which have been observed destroying lodges on the WCRD (Sean Meade personal communication 2005). Beavers are a common food source for wolves on the CRD (Carnes 2004), although wolves are currently rare on the WCRD. Trapping has occurred on the CRD through much of its history (Roberds 1955). Although the number of beavers currently trapped on the WCRD is small, this activity may still influence occupancy of plots if whole families are trapped out of a lodge.

Expansion of beavers onto the uplifted marsh was facilitated, in part, by the geomorphic setting of the uplifted marsh. The types, size, distribution, and abundance of geomorphic features of a landscape influences habitat suitability for beavers (Johnston and Naiman 1987), particularly with regards to their ability to build dams (Suzuki and McComb 1998). The size and shape of (Howard and Larson 1985; Suzuki and McComb

1998) and the flow amount (Naiman et al. 1986) in a channel influence the potential for beavers to successfully construct dams. Former tidal sloughs appear to have been favorable for dam construction (Cooper 2007). The features were also widely distributed across the uplifted marsh and provide a template for beaver colonization.

Although I did not track individual sloughs and lakes through time it appears that some lakes within the uplifted marsh increased in size after beaver occupancy of adjacent sloughs while other lakes continued to diminish in surface area. This could be due to hydrologic connection between some lake basins and sloughs that were not readily apparent in the aerial photographs.

Beaver influence the composition of vegetation in areas they inhabit by flooding areas (Grover and Baldassarre 1995; Wright et al. 2002), cutting woody vegetation (Barnes and Dibble 1988; Pastor and Naiman 1992) and subsequent dam loss (Wright et al. 2002). The current patterns of succession on the uplifted marsh suggest that ponds may eventually fill with sphagnum and levees will transition to a spruce dominant vegetation type (Boggs 2000). During periods of beaver occupancy an area may be flooded by beaver impoundments. These impoundments may reduce woody vegetation (alder, cottonwood and spruce) that rely on aerated soils (Batzli and Dawson 1997; Boggs 2000; Mitchell and Niering 1993; Thilenius 1990). Bog development through sphagnum growth resulting in pond size reduction may be reduced through increase of open water (Rochefort 2000). Beaver herbivory may also influence succession and woody vegetation composition through the removal of select species within woody vegetation communities (Barnes and Dibble 1988). Dam failure and subsequent water loss may also create unique vegetation communities within a landscape (Wright et al. 2002). Consequently, a pattern of occupation and abandonment may create a mosaic of vegetation types (patches) across the landscape that would not exist without the presence of beavers (Grover and Baldassarre 1995; Syphard and Garcia 2001; Wright et al. 2002).

Beavers may also channel between lakes and dammed sloughs (Muller-Schwarze and Sun 2003). This activity not only connects the two water bodies but may also influence surface water area in the future if sloughs are abandoned and subsequent dam failure results in the draining of both sloughs and adjacent lakes. In recent years this phenomena has occurred in slough and lake systems within the uplifted marsh (personal observation 2005). Consequently, beaver-created channels may have far reaching effects on surface water area in the future.

The CRD has experienced periodic earthquakes historically. This process may occur cyclically approximately every 600 years (Reimnitz 1972), punctuated by each uplift event and followed by eventual succession, beaver colonization and subsidence. Uplift events occur in discrete windows of time often lasting just a few minutes (Reimnitz 1972). After the uplift, vegetative succession occurred relatively rapidly and is expected to continue until subsidence occurs (Boggs 2000; DeVelice et al. 2001). Beavers then exploited the vegetative succession by colonizing these new areas of hardwood trees and shrubs subsequently influencing the distribution and abundance of vegetation.

MANAGEMENT IMPLICATIONS

Coastal and interior wetlands in Alaska are currently diminishing possibly due to warming and drying weather trends (Klein et al. 2005; Riordan 2005). On the WCRD however, beavers appear to have increased surface water over time, essentially reversing drying trends. Beaver colonization may be a possible tool to manage wetland reductions in suitable habitat.

Beaver influences on surface water and subsequent vegetation succession may in turn have far reaching consequences for other species. Changes in vegetation through succession have previously been investigated on the CRD, although beaver influences were not included in the analysis (DeVelice et al. 2001). Understanding the potential impacts of beaver on surface water and vegetation succession may assist in refining past work. Beavers influence succession and fish and wildlife of occupied areas.

Although beaver may increase the total amount of surface water area present, the type of water bodies resulting from beaver activity may be quite different from what occurred before beaver colonization. In the case of the WCRD, although overall surface water area in sloughs and lakes increased over time, some lakes did diminish in size. Increases in surface water area due to beaver activity may be beneficial to some species (Brown et al. 1996; Grover and Baldassarre 1995). Dusky Canada geese (*Branta canadensis occidentalis*) and other waterfowl species for instance are commonly associated with beaver-influenced sloughs but waterbird species such as red-throated loons (*Gavia stellata*), horned grebes (*Podiceps auritus*), arctic terns (*Sterna paradisaea*), Aleutian terns (*Sterna aleutica*), red-necked phalaropes (*Phalaropus lobatus*) and short-billed dowitchers (*Limnodromus griseus*) and are not commonly seen in beaver-influenced sloughs (USFS unpublished data 2006). Thus, an increase in surface water may not benefit all species depending on what types of water bodies form.

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FIGURES

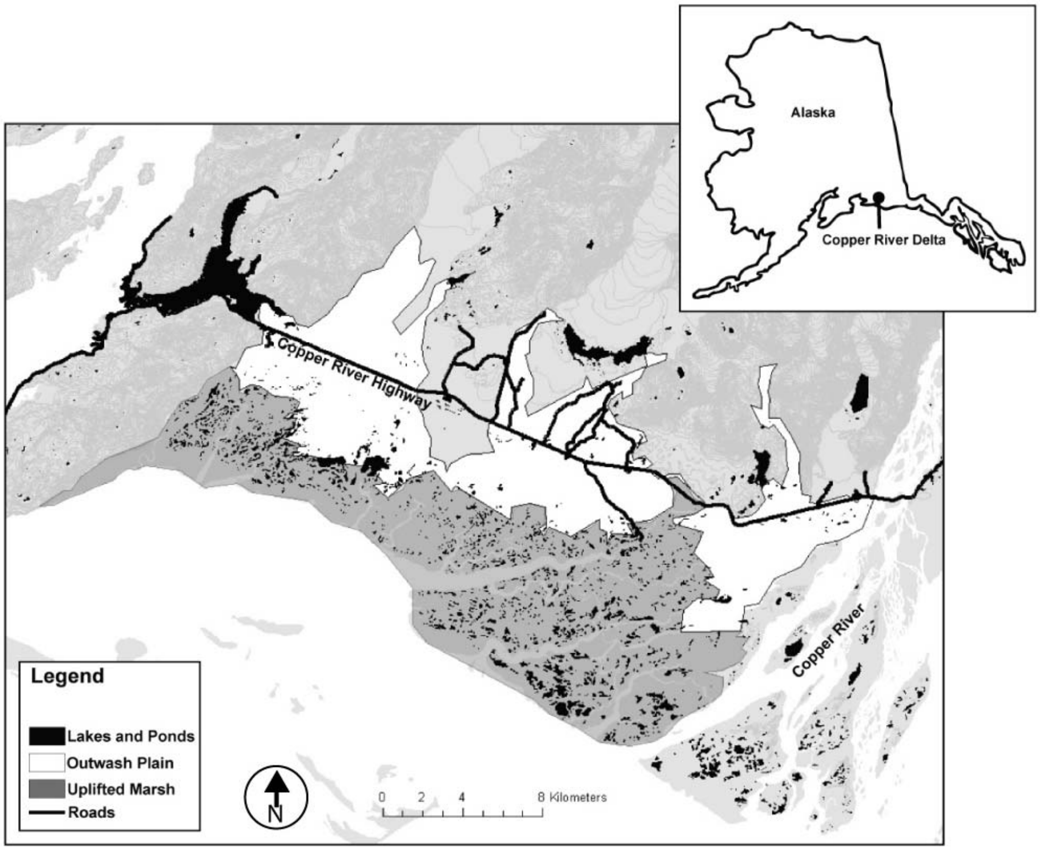
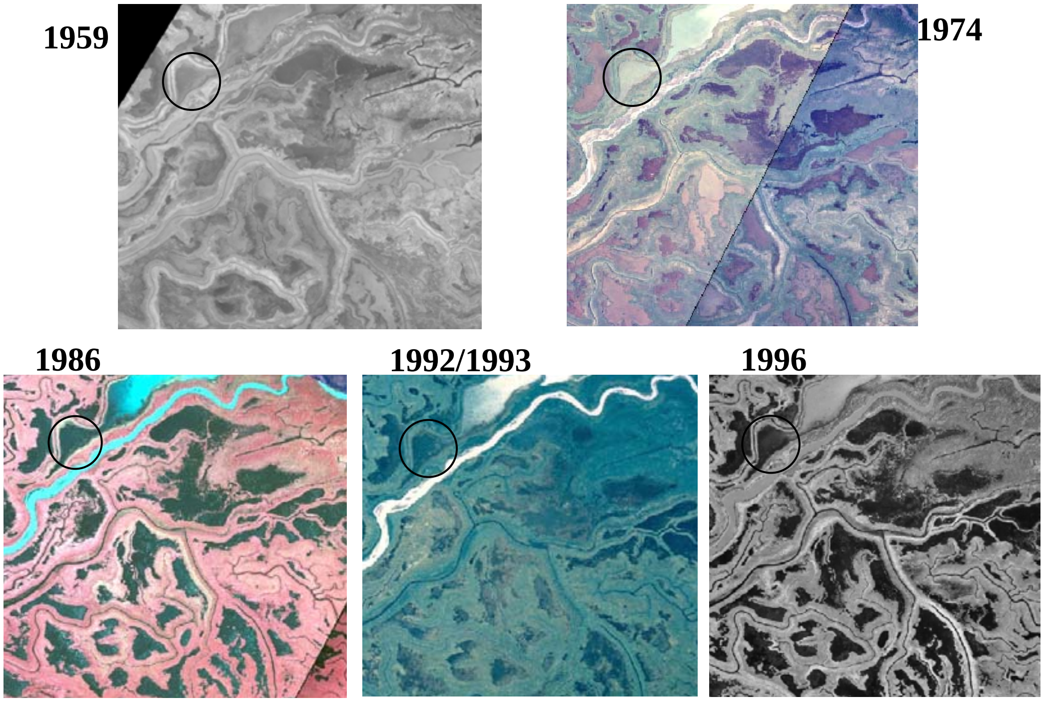


Figure 3.1. The study area on the west Copper River Delta in south central Alaska.



1959 1974

1986 1992/1993 1996

Figure 3.2 An example of photographs showing changes in water features related to beaver activity on the west Copper River Delta, Alaska.. The black circle in each photograph references the same area for each year.

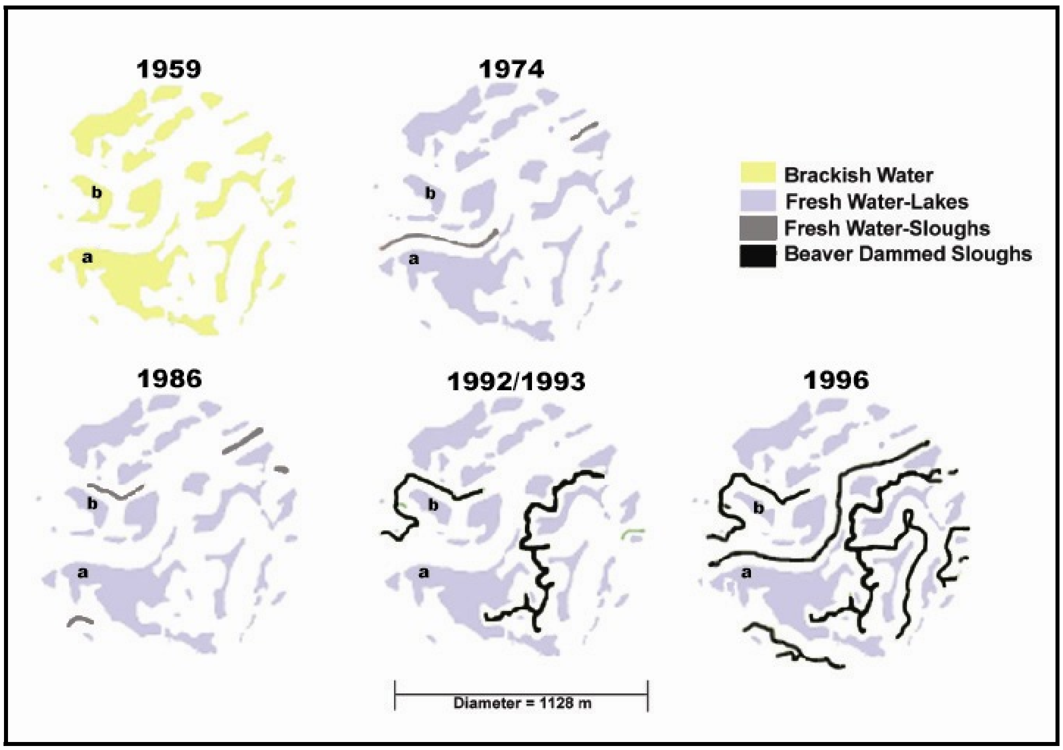


Figure 3.3 A 100-ha plot over time in the uplifted marsh on the west Copper River Delta, Alaska. Surface water is defined by water feature type for each photo year. Surface water increases in some lakes over time (a) and decreases in others (b).

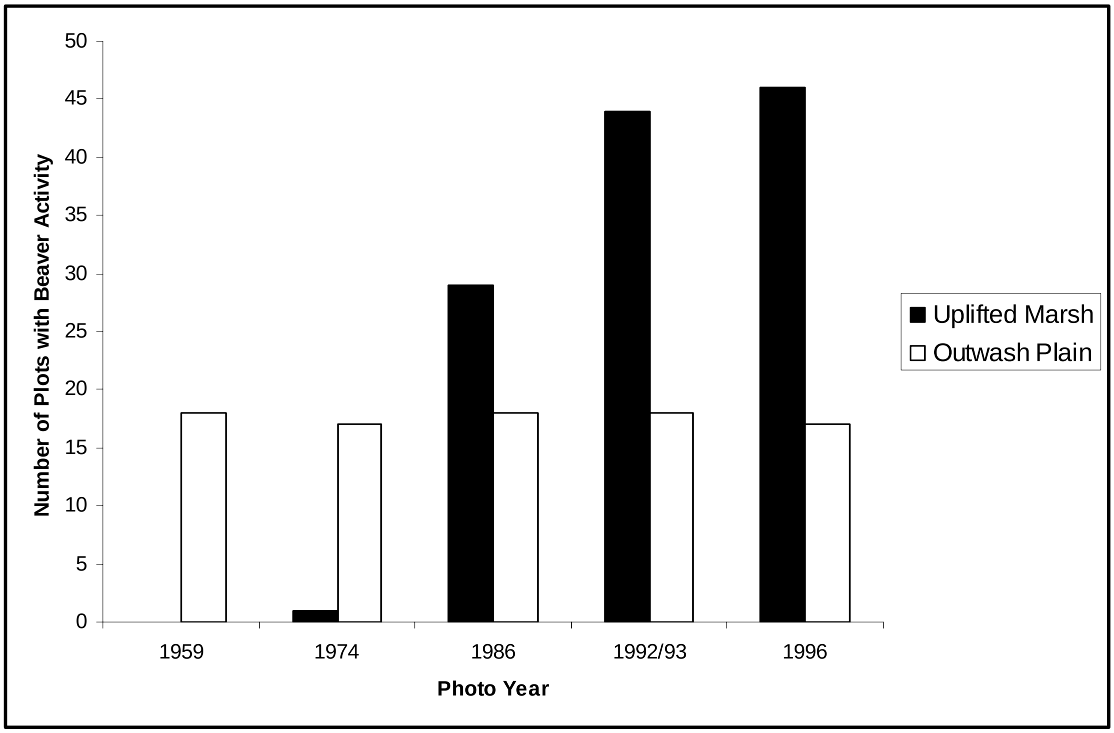


Figure 3.4. Number of plots with beaver influenced fresh water on the west Copper River Delta for each year of photographs analyzed.

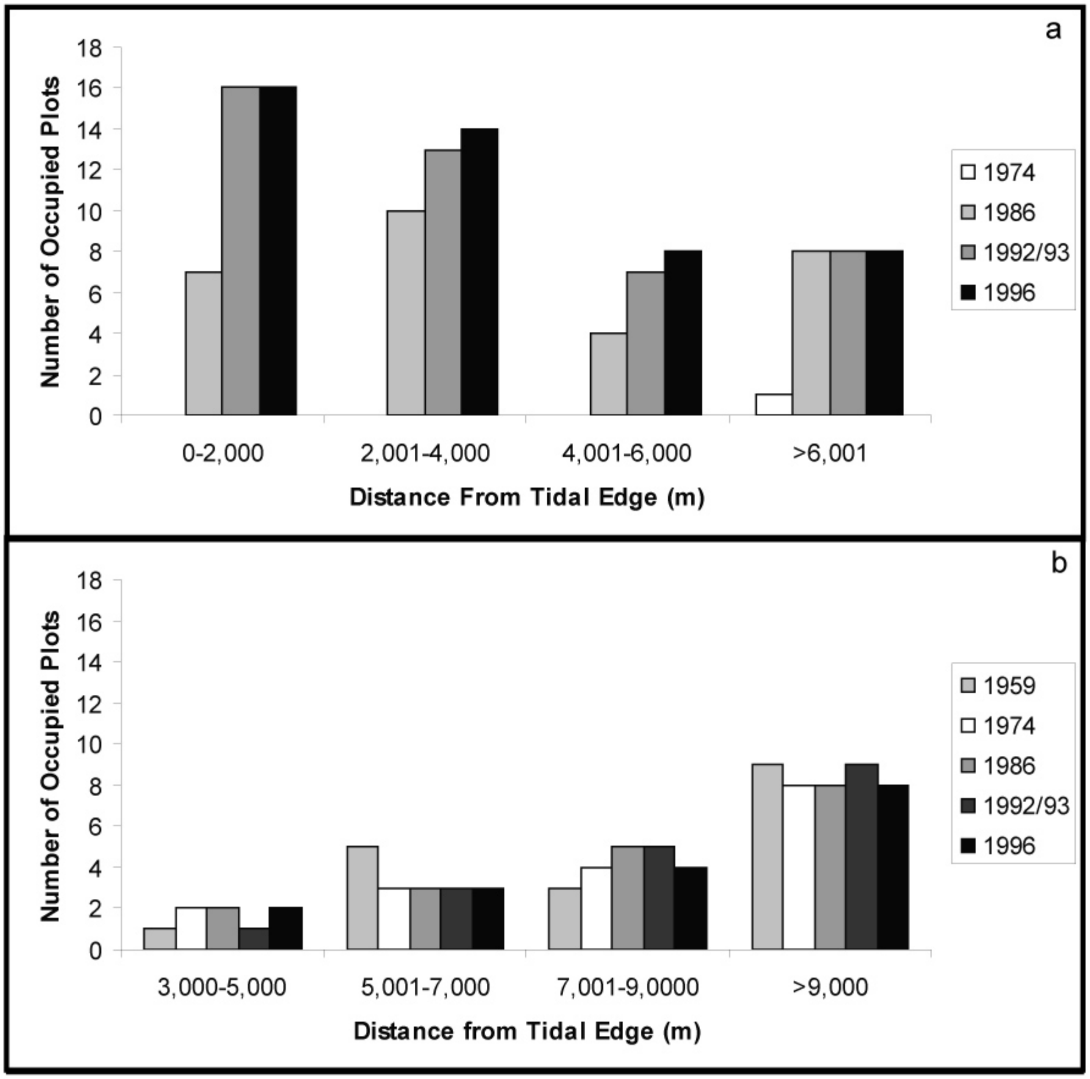


Figure 3.5. Plots with beaver activity present (dams) compared to the distance from the coast in meters for each photo year for both the uplifted marsh (a) and outwash plain (b) on the west Copper River Delta, Alaska.

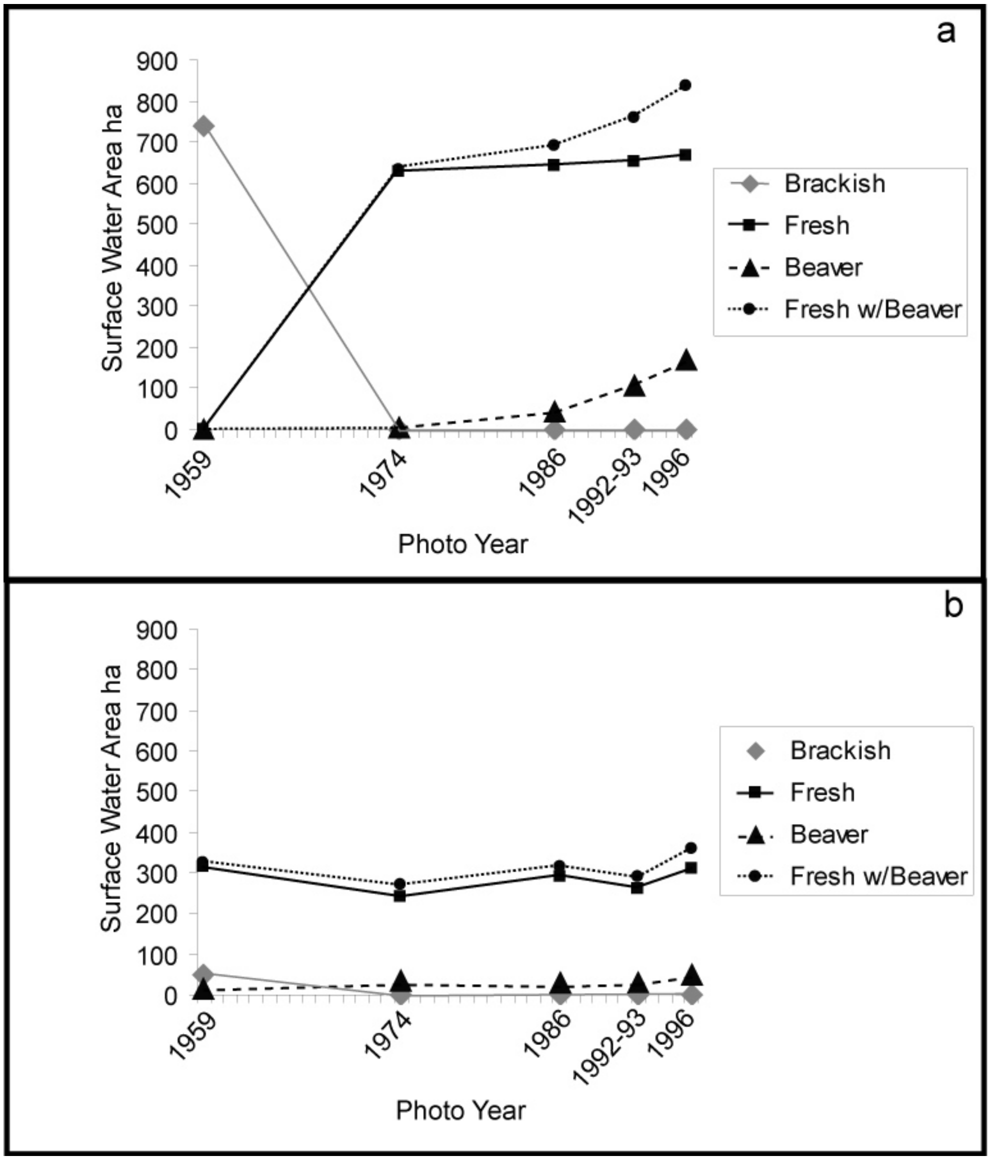


Figure 3.6. Surface water area of (ha) associated with beaver influence on the uplifted marsh (a) and outwash plain (b) of the west Copper River Delta, Alaska. Fresh water and beaver influenced water are shown separately and combined (Fresh w/Beaver).

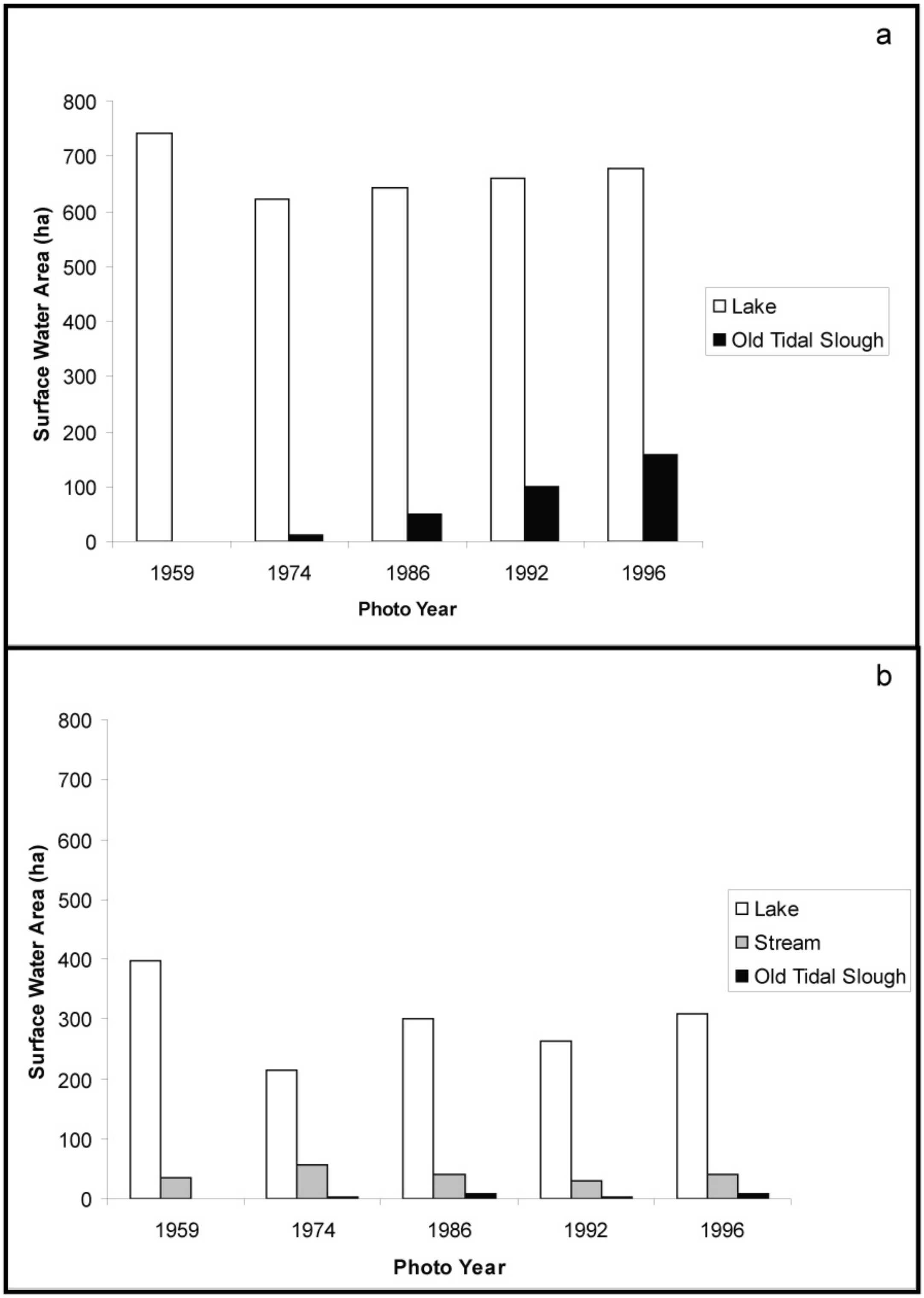


Figure 3.7. Surface water area (ha) by source and year on the uplifted marsh (a) and outwash plain (b) on the west Copper River Delta, Alaska

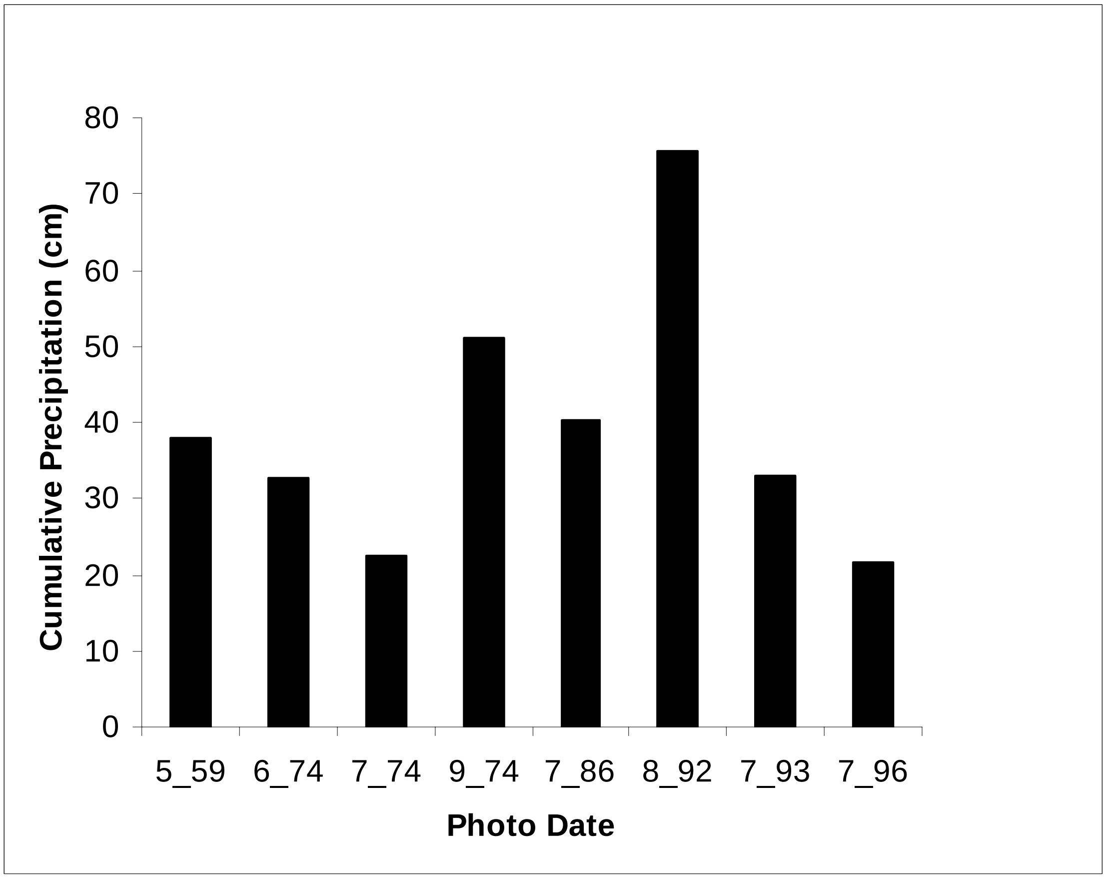


Figure 3.8. Cumulative precipitation on the west Copper River Delta, Alaska for the three months prior to the photo date.

Chapter 4

SUMMARY AND CONCLUSIONS

Beaver habitat selection on the western Copper River Delta (WCRD) differs between landscape types. Beavers are opportunistic and exploit available water and woody vegetation on a landscape. On the WCRD, beavers colonized newly formed areas and appear to respond to differences in landscape type through habitat selection at specific scales. Best approximating models for both survey methods were similar within each landscape type. In the uplifted marsh, active beaver lodges are associated with old tidal sloughs and increasing mixed shrub cover. In the outwash plain active beaver lodges are associated with streams and decreasing closed cottonwood-alder-willow cover.

While vegetation variables are present in my models, their influence is not as strong as the associated water feature. Both water and woody vegetation variables were identified in all best approximating models. Although previous studies have investigated both physical and vegetative features of active lodge sites, physical features (i.e., gradient, depth and width) are more commonly the best predictor of beaver activity and site selection (Beier and Barrett 1987; Howard and Larson 1985; Slough and Sadleir 1977).

In the uplifted marsh, active beaver lodges were associated with old tidal sloughs and mixed shrub cover for both survey methods. The presence of old tidal sloughs on the WCRD has allowed beavers to colonize areas where ponds were too shallow to sustain beaver populations. Aerial survey results suggest a relationship of active lodge sites with mixed shrub communities at the 100-m scale, while ground survey results suggest a relationship with mixed shrubs at the 30-m scale. Active beaver lodges were not located in lakes and ponds on the uplifted marsh. Lakes and ponds are somewhat shallow on the uplifted and marsh and may not be adequate habitat because of beaver lodge water depth constraints (Beier and Barrett 1987; Slough and Sadleir 1977).

In the outwash plain, I found active beaver lodges associated with streams and decreasing closed cottonwood-alder-willow stands at the 30-m scale. Although beaver used lakes on the outwash plain, the use of streams was greater in proportion to their availability. A relationship with decreasing closed-cottonwood-alder-wilow may indicate active lodge selection at sites with an open canopy and herbaceous vegetation. Tree canopy closure of 40-60% is positively associated with beaver activity, while tree canopy coverage outside of this range appears to be associated with less beaver activity (Allen 1983). Herbaceous vegetation is an important food component in the summer months (Jenkins 1979), and an open canopy may also allow for greater coverage of herbaceous vegetation. Although the herbaceous/graminoid vegetation type was not in the best approximating models, smaller patches and a thicker understory of this vegetation type may exist within open canopy vegetation types (Boggs 2000).

Beaver range expansion into the uplifted marsh occurred approximately 20 years after the 1964 earthquake. Surface water influence by beaver on the WCRD differed between landscape types. Contrary to prediction of a drier Copper River Delta (CRD) through pond and lake succession (Boggs 2000), ponded surface water and beaver-influence water increased over time on the uplifted marsh. On the outwash plain, surface water fluctuated over time, consistent with long term beaver occupancy patterns (Fryxell 2001).

Expansion of beavers onto the uplifted marsh was facilitated, in part, by the geomorphic setting of the uplifted marsh. The types, size, distribution, and abundance of geomorphic features of a landscape influences habitat suitability for beavers (Johnston and Naiman 1987), particularly with regards to their ability to build dams (Suzuki and McComb 1998). The size and shape of (Howard and Larson 1985; Suzuki and McComb 1998) and the amount flow (Naiman et al. 1986) in a channel influence the potential for beavers to successfully construct dams. Former tidal sloughs appear to have been favorable for dam construction. The features were also widely distributed across the uplifted marsh and provide a template for beaver colonization.

Water impoundments may also influence succession on the WCRD. Beaver influence the composition of vegetation in areas they inhabit by flooding areas (Grover and Baldassarre 1995; Wright et al. 2002), cutting woody vegetation (Barnes and Dibble 1988; Pastor and Naiman 1992) and subsequent dam loss (Wright et al. 2002). The current patterns of succession on the uplifted marsh suggest that ponds may eventually fill with sphagnum and levees will transition to a spruce-dominant vegetation type (Boggs 2000). During periods of beaver occupancy an area may be flooded by beaver impoundments. These impoundments may reduce woody vegetation (alder, cottonwood and spruce) that require aerated soils (Batzli and Dawson 1997; Boggs 2000; Mitchell and Niering 1993; Thilenius 1990). Beaver herbivory may also influence succession and woody vegetation composition through the removal of select species within woody vegetation communities (Barnes and Dibble 1988). Dam failure and subsequent water loss may also create unique vegetation communities within a landscape (Wright et al. 2002). Consequently, a pattern of occupation and abandonment may create a mosaic of vegetation types (patches) across the landscape that would not exist without the presence of beavers (Grover and Baldassarre 1995; Syphard and Garcia 2001; Wright et al. 2002).

A further understanding of beaver habitat occupancy, dispersal and patterns of use may assist in understanding this species and its interactions with the environment on the CRD. While the beaver associations with woody vegetation types and water sources is not new information, the differences in habitat selection between landscape types on the WCRD identifies distinct features within each landscape that beavers are currently exploiting. These distinct features may then be used to infer landscape-wide potential beaver habitat using remote sensing data on the WCRD.

The CRD has periodically experienced earthquakes historically. This process may occur cyclically approximately every 600 years (Reimnitz 1972), punctuated by each uplift event and followed by eventual succession, beaver colonization and subsidence. Uplift events occur in discrete windows of time often lasting just a few minutes (Reimnitz 1972). After the uplift, vegetative succession occurred relatively rapidly and is expected to continue until subsidence occurs (Boggs 2000; DeVelice et al. 2001). Beavers then exploited the vegetative succession by colonizing these new areas of hardwood trees and shrubs subsequently influencing the distribution and abundance of vegetation.

Predicted patterns of succession have not incorporated the influence of beaver on the landscape (Boggs 2000; DeVelice et al. 2001). Beaver habitat selection and subsequent influences on the landscape may assist managers in understanding of patterns of succession on the WCRD. Satellite imagery and aerial photographs may be an effective tool in determining beaver habitat associations and historic use. Managers may also consider beavers as a management tool for habitat and wetland restoration.

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