Chapter 2
Ecosystem Engineers: Beaver Ponds

Abstract The beaver population of the Kabetogama Peninsula is very dense in comparison to other areas of North America. Both biotic (forage availability) and abiotic (topography, geology, hydrology) factors contribute to this dense population. Historical (1927–2003) and contemporary aerial photos were used to map beaver ponds, beaver meadows, and other features altered by beaver dam construction. The objectives of the study were to relate the extent and type of beaver works to the beaver population present. A total of 1009 pond sites were identified within the 302 km^2 Kabetogama Peninsula where flooding by beaver dams had discernibly altered the vegetation. Cover types ranged from open water to wetland forests, depending on the depth and duration of flooding. The sites were not continuously occupied by beavers over time, but were frequently recolonized. On average, each 100 beaver colonies increased the proportion of the landscape covered by open water by 2.15%. In addition, 16 of 21 permanent lakes on the Kabetogama Peninsula had lake outlet beaver dams. Collapse of the Shoepack Lake outlet dam in 2001 released an estimated 2.16 million kL of water and drained approximately 2/3 of the lake's pre-collapse area. Beaver dams built in the first several decades of peninsula recolonization (1940–1948) created the largest ponds with the greatest potential for expansion, implying that beavers are able to optimize dam location.

2.1 Kabetogama Peninsula: A Beaver Paradise

As of 2006, the 302 km^2 Kabetogama Peninsula supported 226 active beaver colonies, and beavers had built more than a thousand dams there over time. Such density of beaver colonies is among the highest in the published literature (Table 2.1). Studies reporting higher values encompass much smaller areas or focus sampling within stream corridors, ignoring mountains or other landscape features that are unlikely to support beavers. Clearly, the Kabetogama Peninsula and surrounding area provide ideal beaver habitat.

C.A. Johnston, *Beavers: Boreal Ecosystem Engineers*,
DOI 10.1007/978-3-319-61533-2_2

Table 2.1 Beaver colony densities reported in published literature, expressed per unit area and per length of survey route

Beaver density, colonies/km^2	Location	Source
0.014	Yellowstone N.P.	Smith and Tyers (2008)
0.15–0.32	Maine	McCall et al. (1996)
0.38	Northwest Territories	Aleksiuk (1970)
0.39–0.77	Central Ontario	Voigt et al. (1976)
0.46–0.62	Newfoundland	Bergerud and Miller (1977)
3.27	Illinois	Bloomquist and Nielsen (2010)
0.33–1.38	Kabetogama Peninsula	Johnston and Windels (2015a)
Beaver density, colonies/km		
0.48	Alaska	Boyce (1981)
0.52	New York State	Müller-Schwarze (2011)
0.08–1.4	Kansas	Robel and Fox (1993)
0.25–1.69	South Dakota	Dieter (1992)
0.7–4.0	California	Busher (1987)
0.15–1.91	Tierra del Fuego	Skewes et al. (2006)
1.1–1.2	Oregon	Leidholtbruner et al. (1992)
0.01–1.36	Quebec	Jarema et al. (2009)
2.59	British Columbia	Slough and Sadleir (1977)
0.83–2.23	Kabetogama Peninsula	Broschart et al. (1989)

2.1.1 Why Do Beavers Build Dams?

Beavers are semi-aquatic mammals that are uniquely adapted to living in and around water bodies. Adult beavers are nearly invincible to natural predators within the safety of their ponds, but are susceptible to predation on land by wolves and black bears (Jenkins and Busher 1979; Smith et al. 1994). Ponds provide beavers with safe access to riparian forests, allowing beavers to browse in the upland yet retreat quickly to the safety of the water when predators approach (Johnston and Naiman 1987).

Dam-building behavior by beavers is stimulated by the sound of running water. This auditory stimulus was first reported after laboratory observations of *Castor canadensis* (Hartman and Rice 1963). Wilsson later conducted experiments using captive beavers and speakers playing recordings of flowing water; the beavers consistently built dams at the speaker locations (Wilsson 1971). Even young beavers who hadn't previously built dams were stimulated by these auditory cues. The influence of sound on beaver behavior may explain how beavers are able to optimize dam location and why they rebuild dams at previous sites.

2.1.2 What Makes the Kabetogama Peninsula Such a Suitable Landscape for Beaver Ponds?

Beaver ponds require three ingredients: beavers, water, and land suitable for flooding. The Kabetogama Peninsula contains many beavers, but several landscape characteristics also promote the creation and sustainability of their ponds.

2.1.2.1 It Is Completely Surrounded by Water

Migrating beavers use the large lakes that surround the Kabetogama Peninsula as aquatic highways to access its perimeter (Smith and Peterson 1988). These three lakes, Rainy, Kabetogama, and Namakan, are not only large, but they also have convoluted shorelines (Fig. 1.2). Rainy Lake is particularly large, and its many bays extend far into Canada. The cumulative shoreline of these three lakes is more than 4000 km long (Table 2.2), providing ample access to migrating beavers.

At its western end, the Kabetogama Peninsula is separated from the mainland by a stream that drains from Kabetogama Lake (normal pool elevation = 341 m) into Rainy Lake (normal pool elevation = 338 m). The “Gold Portage” along this stream bypasses its rapids (Fig. 2.1). A dam at Kettle Falls on the eastern end of the Kabetogama Peninsula separates Namakan Lake from Rainy Lake (Fig. 1.2).

2.1.2.2 It Has Complex Topography

Tilted and eroded bedrock layers of the Kabetogama Peninsula create a complex land surface with many valleys that accumulate water. The elevation transect of the west-to-east drainage divide that bisects the Kabetogama Peninsula illustrates the peninsula’s complex topography (Fig. 2.1). Even though no streams cross this drainage divide, its topography is convoluted. The highest elevations, 418–419 m, occur at three separate locations along the catchment divide: Loiten Lake peak, Cruiser Lake peak, and Brown Lake peak. The fourth highest elevation, “Shoepack lookout” (410 m), was the site of a fire lookout tower until 1999 (Anonymous 2004).

Table 2.2 Area and shoreline perimeter of the three large lakes surrounding the Kabetogama Peninsula

	Area (km^2)	Perimeter (km)
Kabetogama	90	288
Namakan	98	443
Rainy	855	3300

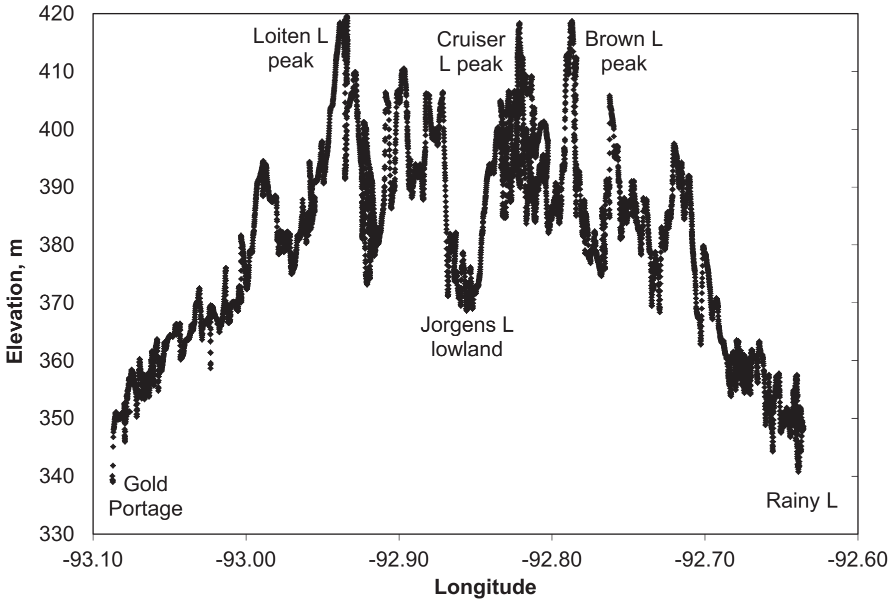

Fig. 2.1 Elevation transect of the watershed divide separating waters draining north into Rainy Lake from those draining south into Kabetogama/Namakan Lakes. I generated this by extracting the divide from the U.S. Watershed Boundary Dataset and intersecting it with one-meter digital elevation data

2.1.2.3 Its Waters Flow in Many Directions

Precipitation falling onto the Kabetogama Peninsula flows northward into Rainy Lake or southward into Kabetogama and Namakan Lakes via numerous catchments that subdivide the two halves of the peninsula (Fig. 2.2). The largest of these (28.1 km^2) drains Little Shoepack and Shoepack Lakes (catchment #8, Fig. 2.2). The longest tributary in this catchment originates in a beaver pond at 383.7 m, dropping 47 m in elevation as it flows down the 13.2 km stream path to its outlet on Rainy Lake. Only the final 0.2 km segment of the stream path is free-flowing: the upper stream flows through contiguous beaver ponds, beaver meadows, and Shoepack Lake before reaching its outlet.

The Cranberry Creek catchment (catchment #3, Fig. 2.2) is the second largest catchment on the Kabetogama Peninsula (27.4 km^2). Its waters drain northwest through Loiten, Quill, War Club, and Locator Lakes along a geologic fault line, emptying into Cranberry Bay and thence to Rainy Lake. Although beavers occupy all four of these lakes (Johnston and Windels 2015a), most of the beaver dams in the catchment are located downstream of the lakes on Cranberry Creek and its tributaries.

Three other named creeks flow off the peninsula into Kabetogama Peninsula: Deer Creek, Clyde Creek, and Sucker Creek (catchments 22–24, Fig. 2.2). As with the Shoepack Lake catchment, they are almost completely impounded by contiguous

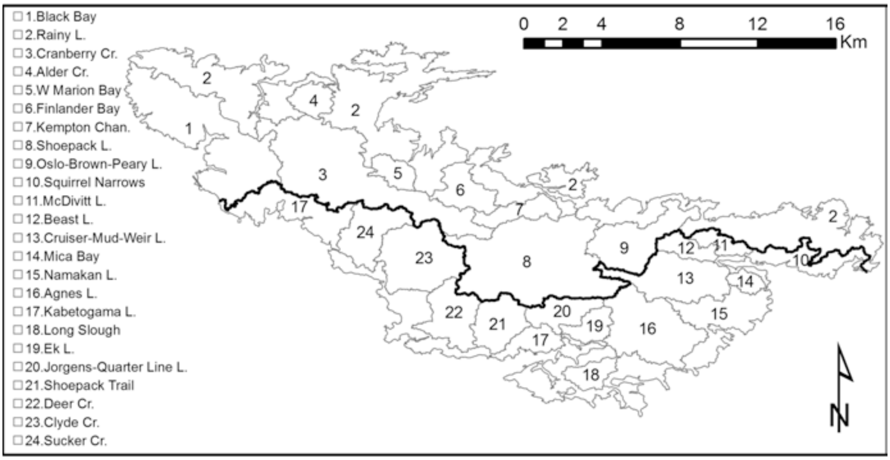

Fig. 2.2 Major catchments of the Kabetogama Peninsula, based on government databases and my unpublished map of beaver pond catchments. *Bold black line* is the watershed divide separating the Rainy Lake and Kabetogama/Namakan Lakes drainage basins that I used to prepare Fig. 2.1

beaver ponds and beaver meadows (Fig. 1.6). Other catchments of the Kabetogama Peninsula are drained by unnamed streams; I have informally named them based on their internal lakes, outlet bays, or other features (Fig. 2.2).

2.1.2.4 It Has Impervious Bedrock

Voyageurs National Park is at the southern end of the Laurentian Shield, a large area of some of the oldest Precambrian rocks in North America that form the ancient core of the continent (Fig. 2.3). The igneous and metamorphic bedrock consists of granite, biotite schist, and migmatite (interlayered granite and biotite schist) (Hemstad et al. 2002). This bedrock is not water-bearing except where faulted (Kanivetsky 1979), and forms an impervious base layer that keeps wetlands and water bodies perched on the bedrock surface.

2.1.2.5 It Has Impervious Soils

The Kabetogama Peninsula was submerged under the waters of early Glacial Lake Agassiz about 11,000 years before present (Teller 1985). Lake Agassiz formed during retreat of the last continental glacier, when meltwater backed up because the north-flowing rivers that drained into Hudson Bay were blocked by ice. Clayey glaciolacustrine sediments accumulated in low-lying areas of the Kabetogama Peninsula, especially on its western end (Fig. 2.4). These fine-textured soils transmit water very slowly.

Fig. 2.3 (**a**) Granite exposed by fresh rock cut along road to Ash River Visitor Center. (**b**) The root wad of a mature tree blown over in a windstorm illustrates shallow upland soils over bedrock

2.1.2.6 There Is Abundant Woody Browse

Beavers do not hibernate, instead relying on a submerged pile of twigs and branches ("cache") that they access underwater during the long winter. Quaking aspen (*Populus tremuloides*) is greatly preferred as a source of this woody browse (Slough and Sadleir 1977; Allen 1983), and Quaking Aspen-Paper Birch Forest is the most abundant forest type in Voyageurs National Park (Faber-Langendoen et al. 2007b).

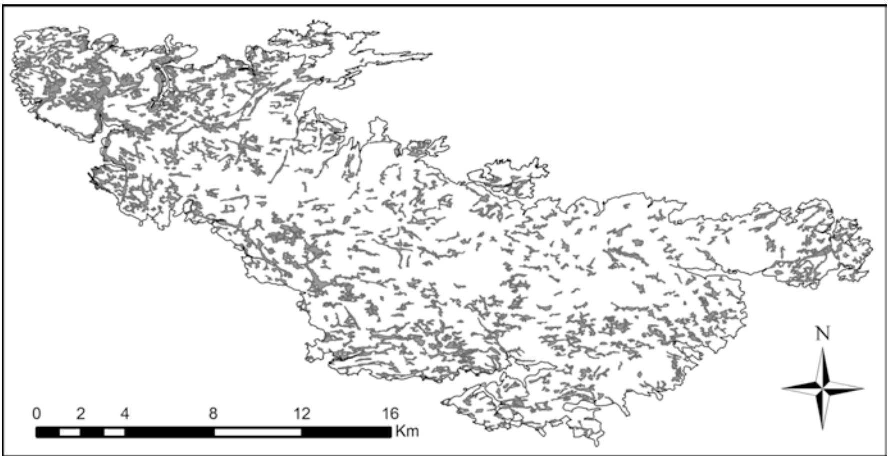

Fig. 2.4 Soils of the Kabetogama Peninsula mapped as having glaciolacustrine parent materials, derived from Soil Survey Geographic Database (SSURGO) for Voyageurs National Park

Other forest alliances at Voyageurs National Park that contain *P. tremuloides* are Spruce Fir-Aspen Forest, White Pine-Red Pine-Quaking Aspen-Paper Birch Forest, and Jack Pine-Aspen Forest.

2.2 Beaver Dam Characteristics

2.2.1 Dam Construction Materials

Beaver dams are typically constructed of mud-reinforced sticks, but dams constructed entirely of rocks and even cornstalks have been reported (Rue 2002; Jung and Staniforth 2010). In his classic book about the American beaver, Lewis H. Morgan described construction of a stick-dam, consisting of "…interlaced stick and pole work upon the lower face, with an embankment of earth intermixed with the same materials on the upper, or water face of the dam" (Morgan 1868). Morgan also described a solid-bank dam type, in which "the large amount of earth and mud, used to strengthen the work, buries and conceals the greater part of the brush and poles used to bind the embankment together."

Tree saplings and branches are a primary construction material used in beaver dams of the Kabetogama Peninsula. Branches are laid across the downstream face of the dam, parallel to the water flow (Fig. 2.5, left photo). Beavers also mound mud and grasses to make beaver dams, particularly in the early stages of construction (Fig. 2.5, right photo). In central Ontario, Doucet and colleagues (Doucet et al. 1994) reported that beavers preferentially used coniferous species and speckled alder in dam construction, reserving trembling aspen and other deciduous species

Fig. 2.5 Examples of beaver dam construction materials. *Left*: Abandoned wood and mud dam in the Kabetogama Lake drainage basin. *Right*: Dam constructed of mud and grass at a pond in the Clyde Creek drainage basin (catchment #23, Fig. 2.2)

for their food caches. I observed no such species differentiation on the Kabetogama Peninsula, but aspen branches were usually debarked prior to their use in dams; aspen bark is an important beaver foodstuff.

2.2.2 Beaver Dams on Streams

The iconic beaver dam blocks a stream, causing the flowing waters to slow and spread out, thereby creating a pond out of an area that was previously terrestrial (Fig. 2.6). Trees that are flooded die because their roots are deprived of oxygen, and trees around the pond may be cut by beavers for food or construction materials, further opening up the canopy. Stream-blocking beaver dams are the most common type on the Kabetogama Peninsula.

Solitary beaver ponds are uncommon on the Kabetogama Peninsula, however. Beaver ponds typically fill entire drainageways, so that the wetland vegetation at the upper end of one beaver pond abuts the next upstream dam. In the oblique aerial

Fig. 2.6 Pond creation by stream damming

Fig. 2.7 The longest beaver dam on the Kabetogama Peninsula, 309 m (catchment #16, Fig. 2.2)

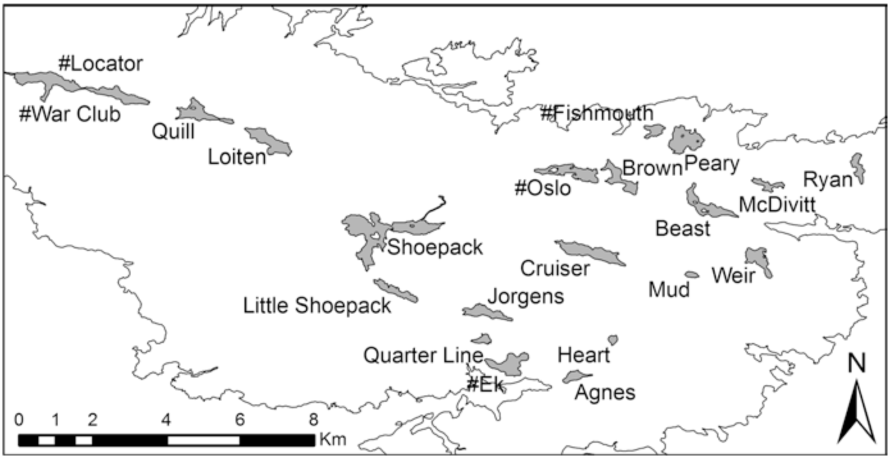

Fig. 2.8 Permanent lakes of the Kabetogama Peninsula. All lakes except those preceded by # have beaver dams at their outlets

view shown in Fig. 2.7, three beaver dams within a 0.5 km stretch of stream, each one meter higher than the next, create a massive pond/wetland complex (catchment #16, Fig. 2.2).

2.2.3 Lake Outlet Beaver Dams

Outlet beaver dams are a common feature of boreal lakes (Morgan 1868; Bertolo et al. 2008). Approximately half of 1085 "drainage lakes" sampled in the Adirondack Mountains of New York had beaver dams at their outlets (Kretser et al. 1989). In southern Finland, lake outlets were dammed more frequently than streams (Vehkaoja et al. 2015). Despite these geographically widespread examples, the prevalence and ecological influence of lake-outlet beaver dams is relatively unknown.

Of the 21 named permanent lakes and ponds on the Kabetogama Peninsula, 16 have beaver dams at their outlets (Fig. 2.8). In many cases, the purpose of such dams is not evident, because the dam building does little more than raise the lake level. For example, the beaver dam at the outlet of Ryan Lake has hardly affected its size and shape because of that lake's steep side slopes. However, beaver dams at the outlets of lakes with adjacent wetlands can flood extensive shoreline areas, greatly increasing lake area or the accessibility of upland food resources.

A downstream beaver dam raised the water level of Mud Lake, lifting the floating peat mat along its northern shore and creating a water moat that separated the peat mat from the upland (Fig. 2.9). This moat allowed beavers to swim directly to the upland and access trees for forage, rather than crossing through the dense ericaceous shrubs of the peat mat. The water level was so high that a chunk of peat mat broke

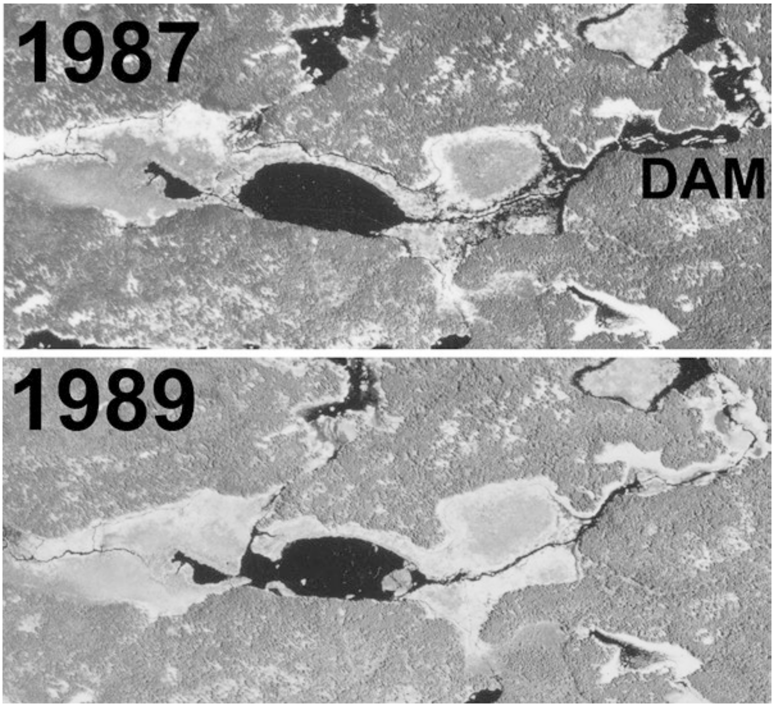

Fig. 2.9 High water levels caused by a downstream beaver dam in 1987 (*top photo*), caused a peat mat to break off and float to the opposite side of Mud Lake (*bottom photo*), changing its shoreline configuration as of 1989

off and floated to the opposite end of the lake, where it became grounded when water levels receded, thereby changing Mud Lake's shoreline configuration.

An outlet beaver dam has profoundly affected Shoepack Lake, a lake that is surrounded by extensive wetlands that flood when its outlet dam is raised. A map generated using a 1×1-m digital elevation model derived from LiDAR data (Minnesota Department of Natural Resources 2015) shows areas with an elevation of 363.89 m (lake level as of the DEM acquisition date in Spring 2011) to 366.89 m, the area that would be flooded by a 3-m dam (Fig. 2.10). The flooding depicted from these elevation data matches the limits of flooding visible on a 1992 aerial photograph and altered vegetation that persisted in 2003 after the dam breach (Fig. 2.11). Based on this evidence, I calculated that the outlet beaver dam approximately tripled the area flooded, from 126 ha to 366 ha.

Nick Frohnauer was studying the muskellunge fishery of Shoepack Lake in 2001, and described its outlet dam as having a 2.16-m head above a bedrock sill; this sill limited how low the lake could drain (Frohnauer et al. 2007). The dam burst during his study due to a 12.5-cm rain event on July 23, 2001, "engendering the loss of roughly 2.16×10^6 kL of water." The cycle of dam construction and collapse had probably happened before, because Frohnauer noted remnant beaver dams near the

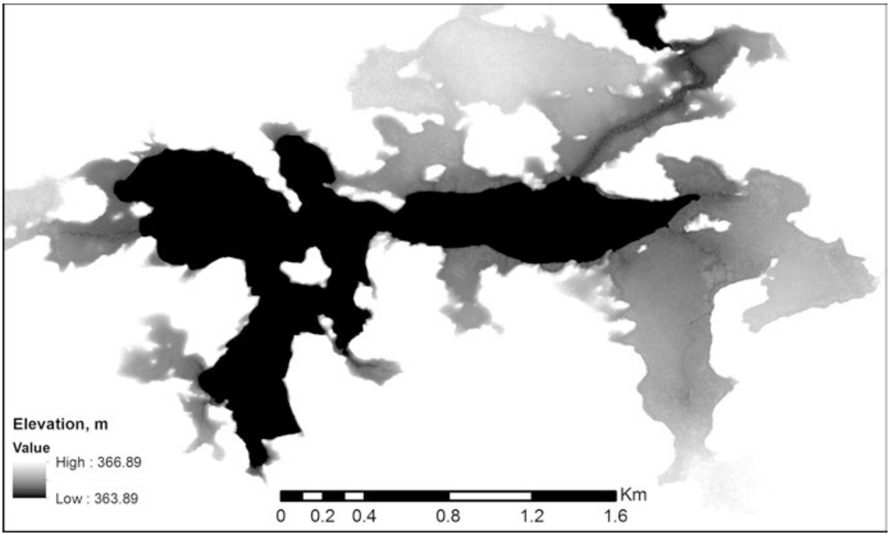

Fig. 2.10 Areas flooded by Shoepack Lake outlet beaver dam, generated from a 1-m digital elevation model, showing areas with an elevation of 363.89 m (lake level as of the DEM acquisition date in Spring 2011) to 367 m

outlet. The location of the Shoepack Lake outlet beaver dam has been very stable over time: a dam was present there as of the earliest aerial photo date in 1927. This location represents a key topographic breakpoint at a narrows along the outlet stream at which a short dam can back up a substantial amount of water.

In a landscape with developed human infrastructure, such a dam collapse could have catastrophic downstream results (Butler 1989). The Shoepack Lake dam collapse did appear to break a few downstream beaver dams, but a major dam that was 3.8 km downstream remained intact, presumably because of the many intervening beaver meadows that reduced the kinetic energy of the flood wave.

2.2.4 Beaver Dams in Peatlands

When beavers impound wetlands where vegetation is adapted to water level fluctuations or is capable of floating up and down with changes in the water level, vegetation alteration may be minimal (Johnston and Naiman 1987). Extensive peatlands (i.e., wetlands with organic soil) to the north and east of Shoepack Lake became wetter as a result of the outlet beaver dam, but retained their vegetation and were not converted to open water (1992 photo, Fig. 2.11). The vegetation in these areas consists of "Leatherleaf-Sweet Gale Shore Fen" and bog shrub species that form floating mats that lift with rising water levels (Faber-Langendoen et al. 2007a). Although the wetter conditions may alter the vegetation of floating mats (Reddoch and Reddoch 2005), these peatlands remain quite resilient to the disturbance caused by

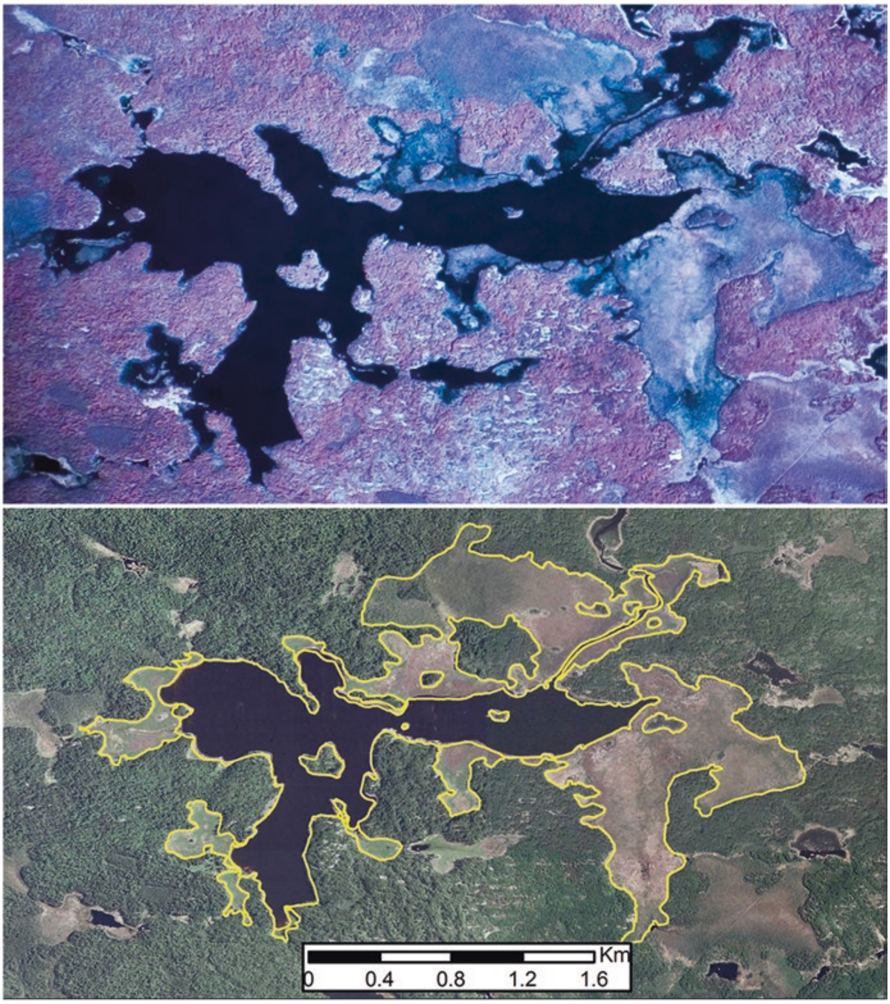

Fig. 2.11 The 2001 collapse of an outlet beaver dam reduced the impounded area of Shoepack Lake and adjacent wetlands from 366 ha in 1992 (*top*) to only 126 ha in 2003 (*bottom*). The *yellow outline* is the maximum extent of flooding

flooding. Experimental flooding of a treed bog complex in northeastern Ontario showed that shallow flooding of bog vegetation led to quick re-establishment of open bog vegetation in the floating peat mats, such that there was little loss of total biomass (Asada et al. 2005).

Beaver dams also impound wetlands that are not associated with lakes. Between 1940 and 1988, beaver dams on the Kabetogama Peninsula flooded 2183 ha of pre-existing wetlands as opposed to only 1504 ha of uplands (Johnston 1994). One-third of the wetlands flooded were converted into ponds, whereas two-thirds of the impounded wetlands were merely made wetter. Beaver dams at peatland outlets

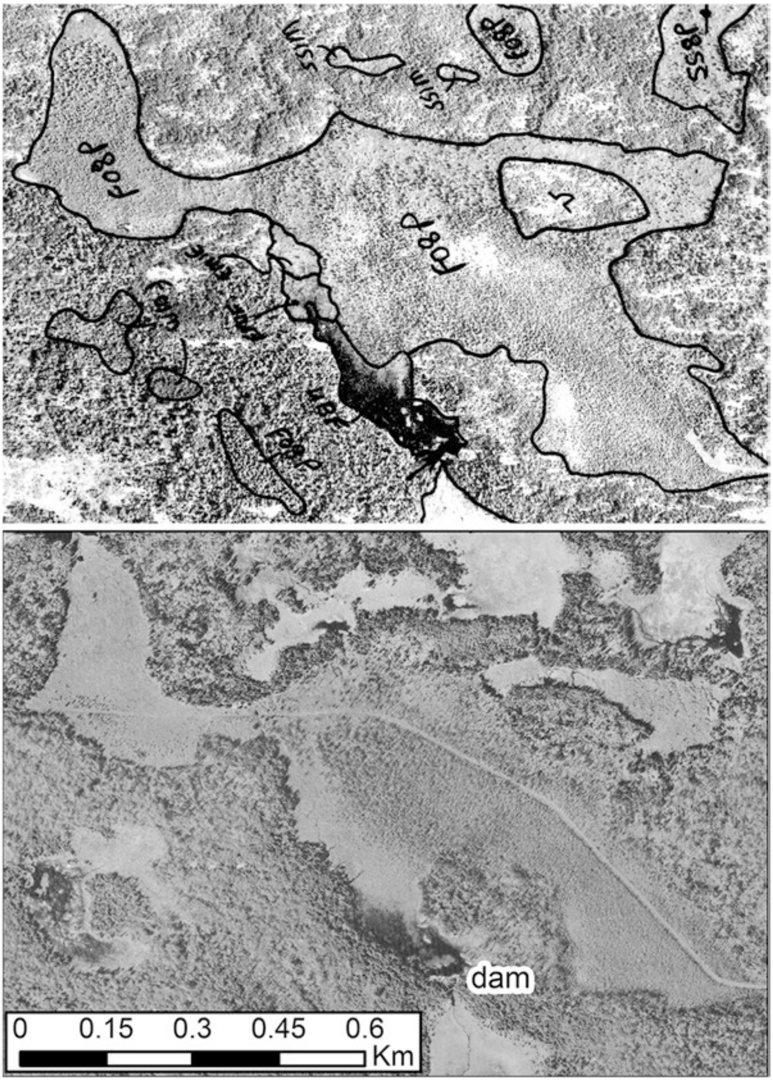

Fig. 2.12 *Top*: A beaver dam (marked by *arrow*) and pond (*dark area* labeled UBF) flood the edge of a black spruce peatland (labeled FO8P) on this 1940 aerial photo. *Bottom*: This 2008 aerial photo shows little change in the beaver dam and pond area over the 68 intervening years, although a winter logging road now traverses the peatland

push water back into the peatland, causing localized vegetation alteration and sometimes tree death, but the boundaries of beaver flooding impact are difficult to delineate because the changes are gradual (Fig. 2.12).

Large peatlands can also act as barriers to beaver activity because their surface waters are not channelized, making them less conducive to dam construction. A 363 ha area west of Shoepack Lake contains only a single beaver dam because of the large peatlands present.

2.2.5 *Beaver Dam Persistence*

In contrast with beaver dams in the western U.S. that are frequently washed out by high water levels or channel migration, the beaver dams of the Kabetogama Peninsula are quite persistent; the same locations are used over and over again. In some cases, many generations of beaver colonies maintain the dam over time. For example, a persistent beaver dam occurs south of Oslo Lake in catchment #9 (Fig. 2.2). A smaller beaver dam existed at this spot in 1927 and 1940, and the present dam has held water continuously since 1949 (Fig. 2.13). Aerial censusing of beaver lodges in 1984, 2000, and 2006 showed this site to have an active beaver colony in all 3 years.

Some abandoned beaver dams continue to hold water despite lack of beaver maintenance, as long as the dam is not breached. Over the period of aerial photo record used to study the Kabetogama beaver ponds, the only beaver dams that have completely washed out without a trace are along the downstream reaches of Cranberry Creek (catchment #3, Fig. 2.2). Some beaver dams disappear from view because they are overtopped by water from a taller dam downstream. River otters (*Lontra canadensis*) dig passages through beaver dams for under-ice access between adjacent water bodies, but normally this doesn't drain the entire pond (Reid et al. 1988).

I analyzed the historical beaver dam map that was prepared by Lewis H. Morgan in 1868 (Morgan 1868) to address the question, "Can the artifacts of beaver engineering be detected after a century or more?" I compared Morgan's map with contemporary digital imagery for the Ishpeming, Michigan region (Johnston 2015). Of the 64 beaver dam and pond sites mapped in the 1860s, 72% were still discernible in 2014. Land use changes that altered the terrain (mining, residential development) or stream paths (channelization) were the main sources of beaver pond loss. This remarkable consistency of beaver pond placement over the last 150 years is evidence of the beaver's resilience.

The persistence of beaver presence over geologic time has been demonstrated by relict beaver dams found buried in peat or sediment deposits, indicating a legacy of beaver activity. Sites described occur in Finland (Aalto et al. 1989), southeastern New England (Kaye 1962), western U.S. mountains (James and Lanman 2012; Persico and Meyer 2009), the Canadian Yukon (Lewkowicz and Coultish 2004), and a former bog buried under urban debris in Columbus, Ohio (Garrison 1967).

2.2.6 *Large Beaver Dams*

Lewis Morgan was particularly impressed with the length of a 79-m beaver dam in northern Michigan (Morgan 1868), which still exists today (Johnston 2015). However, Morgan's dam is only one-tenth the size of the world's longest beaver dam, 850 m, which was found in 2007 using DigitalGlobe satellite imagery for Northern Alberta, Canada (Thie 2016). That beaver dam backs up surface water in a large alluvial fan wetland, which lacks a discernable inlet or outlet stream.

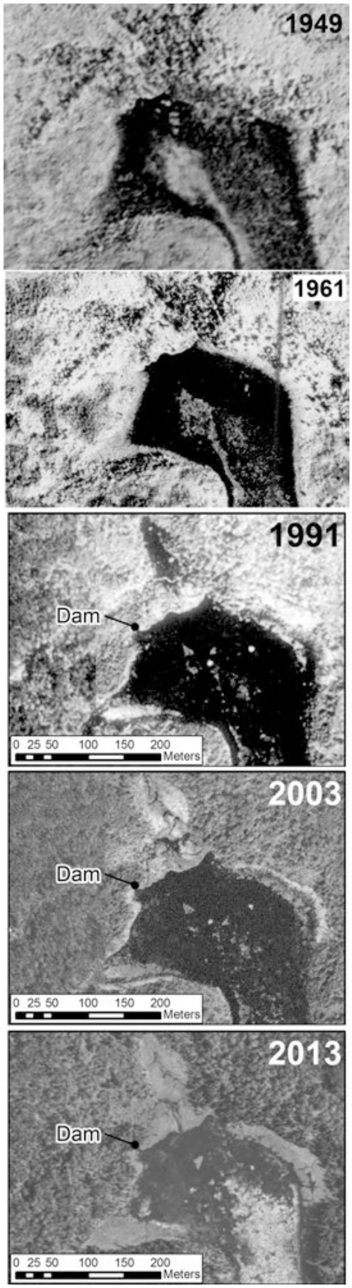

Fig. 2.13 Persistent beaver dam and pond near Oslo Lake, 1949–2013

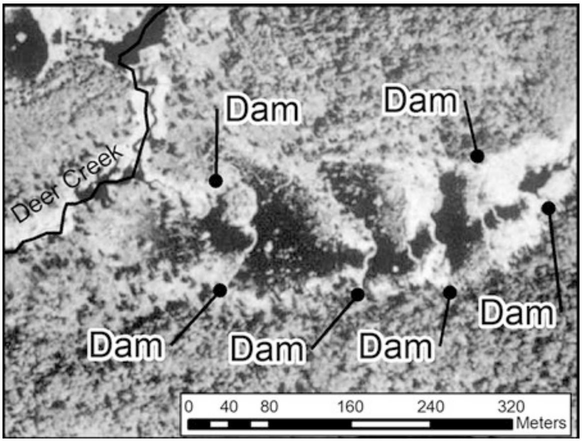

Fig. 2.14 Multiple beaver dams spanning a 140-m wide lowland near Deer Creek, 1992 (catchment #22, Fig. 2.2)

The longest beaver dam on the Kabetogama Peninsula measured 309 m (Fig. 2.7), and was located at the confluence of two tributaries in catchment #16 (Fig. 2.2). Aerial photos showed that the dam was breached sometime between 1997 and 2003, and had not been repaired as of 2015.

The tallest beaver dam I have personally observed, estimated to be 4.5 m tall, was in the Adirondack Mountains of New York. A 2.16 m beaver dam was documented on the Kabetogama Peninsula (Frohnauer et al. 2007), and the tallest dam mentioned by Morgan's 1868 beaver treatise was 3.7 m (Morgan 1868).

2.2.7 Unusual Beaver Dams

In contrast to the Shoepack Lake outlet dam, the location of some beaver dams seems illogical given the effort required to construct them versus the habitat gains achieved. An unusual series of beaver dams was observed on a minor tributary of Deer Creek (Fig. 2.14). They are very close together: there are six primary dams and two minor dams within a 350 length of stream. The dams span a 140-m wide valley, and the longest is about 160 m. The dams were initiated in 1961 and were full of water in 1991, but had drained and reverted to wet meadow by 2013.

I have observed several Kabetogama beaver ponds with multiple outlets on drainage divides, an arrangement which seems to defy the laws of hydrology (Johnston 2000). This phenomenon can be clearly seen in Fig. 2.15, where dams occur at the opposite ends of an impounded black ash swamp in level terrain that drains to Black Bay (catchment #1, Fig. 2.2). This pond receives water from an upslope wetland ("inlet"), but is not on a mapped stream. Such ponds are usually shallow and in suboptimal locations: this pond was initiated in 1987, and was abandoned after 2008.

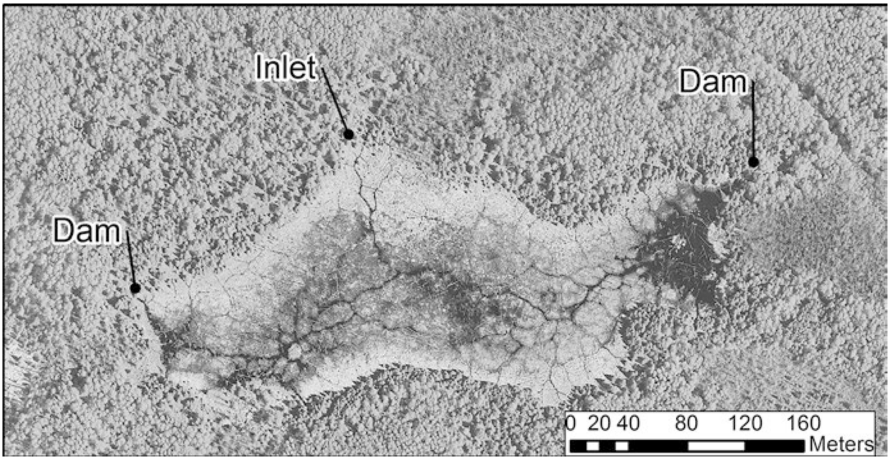

Fig. 2.15 Beaver pond with outlet dams on opposite ends. This dam occurs in very level terrain that drains to Black Bay (catchment #1, Fig. 2.2). Fallen dead tree boles appear throughout, but are easiest to see in the water ponded at the eastern end. Aerial photo taken in 2009

Fig. 2.16 Section of the Agnes Lake trail that was flooded by a beaver dam

Beaver flooding of roads and other infrastructure can be a problem in developed areas (Boyles and Savitzky 2008; Jensen et al. 2001; Johnston 2012). Although there is little built infrastructure on the Kabetogama Peninsula, beaver flooding has impacted trails (Fig. 2.16). When beaver pond expansion started to flood the access road to the

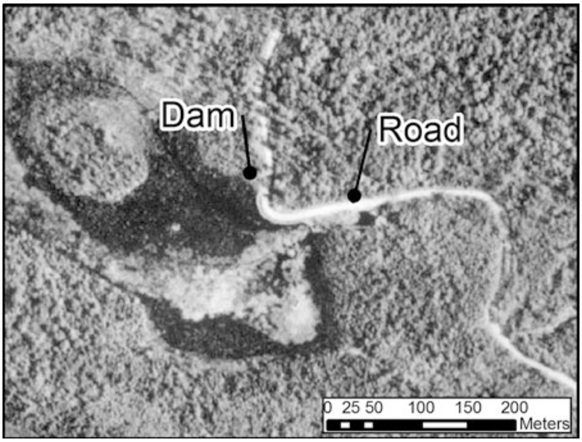

Fig. 2.17 Curved beaver dam constructed by beavers between sandbags placed along the old Ash River Visitor Center access road, 1992

Ash River Visitor Center on the mainland, resourceful park staff used beaver psychology to trick the beavers into constructing a remedy to the problem. They placed piles of sandbags at regular intervals along the side of the road, and the beavers built a dam between them, using the sandbag piles as anchors. The result was a dam that curved along the side of the road (Fig. 2.17). The water level in the pond was at eye level to drivers passing the dam! When the access road was relocated in the 1990s, the road was wisely moved to higher ground, but the curved dam still remains.

2.3 Beaver Pond Characteristics

2.3.1 Beaver Impoundments, Pond Sites, and Clusters

Most of the analyses that follow are based on data extracted from maps that my colleagues and I prepared for the Kabetogama Peninsula by examining aerial photos from multiple years (Table 2.3).

We delineated areas in which elevated water levels from beaver dams had flooded, killed, or otherwise altered the vegetation present, and classified them according to National Wetlands Inventory conventions (Cowardin et al. 1979). These patches were delineated manually or electronically on aerial photo prints or digital images, and digitized using an ArcMap Geographic Information System (GIS) (Johnston and Naiman 1990b). We called the final product "beaver impoundment" maps, because they show more than just ponds. There were 3521 individual polygons on the 2005 beaver impoundment map, the most recent one prepared. GIS shapefile versions of these impoundment maps (1940–2005) can be viewed online and downloaded (Johnston and Windels 2015b).

Table 2.3 Aerial imagery used to generate beaver impoundment maps

Flown	Scale	Type	Commissioning agency
May 1927	1:9082	BW film	Department of the Interior, Canada
Jul 1940	1:20,000	BW film	U.S. Agric. Stabilization and Conservation Service
Sep 1948, Aug 1949	1:15,840	BWIR film	St. Louis County, Minnesota
Aug 1961	1:15,840	BWIR film	St. Louis County, Minnesota
Jun 1972	1:15,840	BWIR film	Voyageurs National Park
Jul 1981	1:24,000	Color film	U.S. Forest Service
May 1986	1:24,000	CIR film	Natural Resources Research Institute
May 1987	1:24,000	CIR film	Natural Resources Research Institute
May 1988	1:24,000	CIR film	Natural Resources Research Institute
May 1989	1:24,000	CIR film	Natural Resources Research Institute
May 1990	1:24,000	CIR film	Natural Resources Research Institute
Sep 1997	1:15,840	CIR film	Minnesota Department of Natural Resources
May 2003	1 m pixels	Color digital	National Agricultural Imagery Program
Sep, Oct 2005	1:15,840	CIR film	Minnesota Department of Natural Resources

BW black and white panchromatic, *BWIR* black and white infrared, *CIR* color infrared

The beaver impoundment maps did not distinguish individual dams; they delineated polygons of contiguous vegetation of the same class. To identify the complex of vegetation and open water associated with an individual dam, we created digital maps of the local catchments draining to each beaver dam and intersected the beaver impoundment maps with them to generate a "pond site" map. Pond sites are bounded at the downstream end by the beaver dam that caused the ponding, and at the upstream end by unimpounded vegetation or the next upstream beaver dam. Pond sites usually contain a complex of water and wetland vegetation, and may or may not contain an active beaver colony in any single year.

As of 1997, there were 1009 pond sites on the Kabetogama Peninsula. The average area per pond site was 3.6 ha, and the maximum pond site area was 39.3 ha. A frequency distribution by pond site area showed the smallest sizes to be most abundant, with only 42 pond sites having areas of 12 ha or greater (Fig. 2.18).

Contiguous beaver-altered areas were merged into a single "cluster" by dissolving the internal GIS boundaries separating adjacent impoundment polygons. Each cluster usually contained more than one pond site. In 1940, there were 71 pond sites but only 47 clusters, a ratio of 1.5 pond sites/cluster (Fig. 2.19a). By 1986, the 835 pond sites were contained in only 346 clusters, a ratio of 2.4 pond sites/cluster. The number of clusters grew at a slower rate than the number of pond sites because beavers were attaching new pond sites onto existing clusters in addition to creating new clusters. Although pond site density increased by an order of magnitude between 1940 and 1986, from 0.3 pond sites/km^2 to 3.0 pond sites/km^2, cluster density peninsula-wide remained at about 1.1 clusters/km^2 after 1961. Cluster density actually declined after 1972 in one region that was densely populated by beavers (Fig. 2.19b). This decrease, within a 382 ha area that encompassed catchments 21–24 (Fig. 2.2),

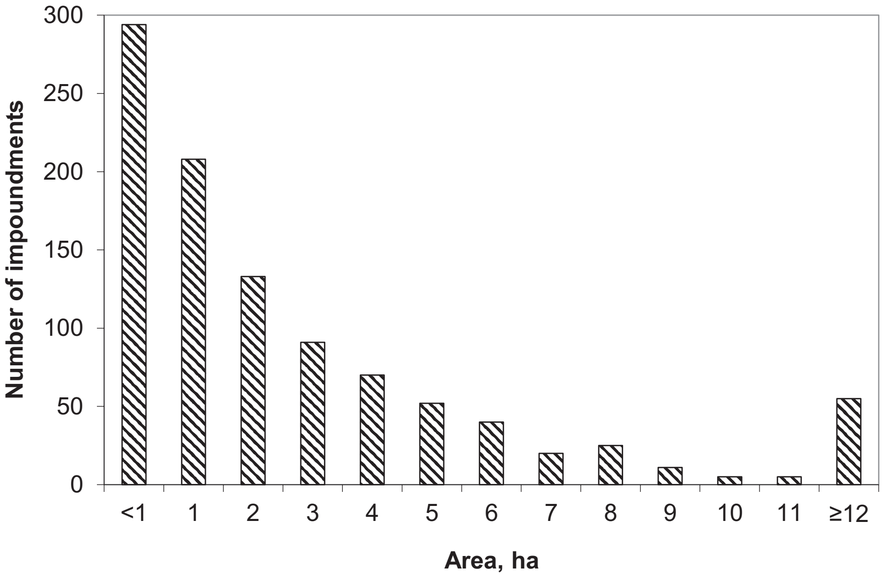

Fig. 2.18 Size frequency distribution, area per pond site as of 1997

occurred because beavers were building ponds that were connecting the clusters together, filling entire valleys with beaver impoundments. These beaver impoundment corridors are favored as travel routes by gray wolves (see Chap. 10).

2.3.2 Influence of Geomorphology on Pond Shape and Boundaries

Land suitable for flooding, one of the three ingredients required for beaver ponds, affects the size and shape of beaver ponds. The Shoepack Lake outlet dam was only about 50 m long, yet it altered water levels 4.4 km upstream due to the large size of Shoepack Lake and its surrounding wetlands (Figs. 2.10 and 2.11). In contrast, the Deer Creek tributary dams were as much as three times longer than the Shoepack Lake outlet dam, but raised water levels only 50–110 m upslope (Fig. 2.14). Stream channel geomorphology has been used to model the capacity of riverscapes to support beaver dams (Macfarlane et al. 2017; Jakes et al. 2007).

I examined the influence of geomorphology on beaver pond configuration, contrasting the shape and boundaries of ponds created by flooding uplands versus those created by flooding wetlands (Johnston and Naiman 1987). Streams flowing through uplands tend to have V-shaped valleys, so beaver ponds created by flooding uplands have steeply sloping bottoms and straight, abrupt side boundaries (Fig. 2.20). In contrast, the flat topography of beaver-flooded wetlands allows a low beaver dam to impound a relatively large area with shallow

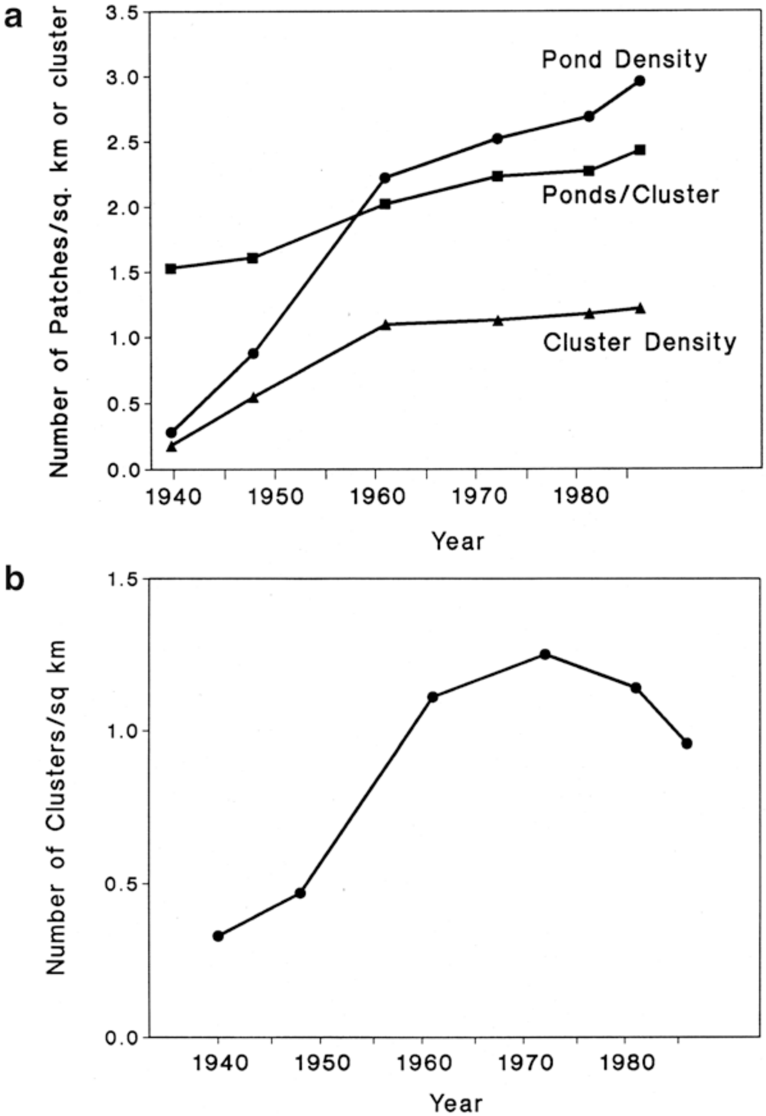

Fig. 2.19 (**a**) Density of pond sites and pond site clusters per unit land area (number of patches/km^2) and average number of pond sites per cluster within the Kabetogama Peninsula, 1940–1986. (**b**) Density of clusters (number of patches/km^2) in a 382 region that was densely populated by beavers, 1940–1986

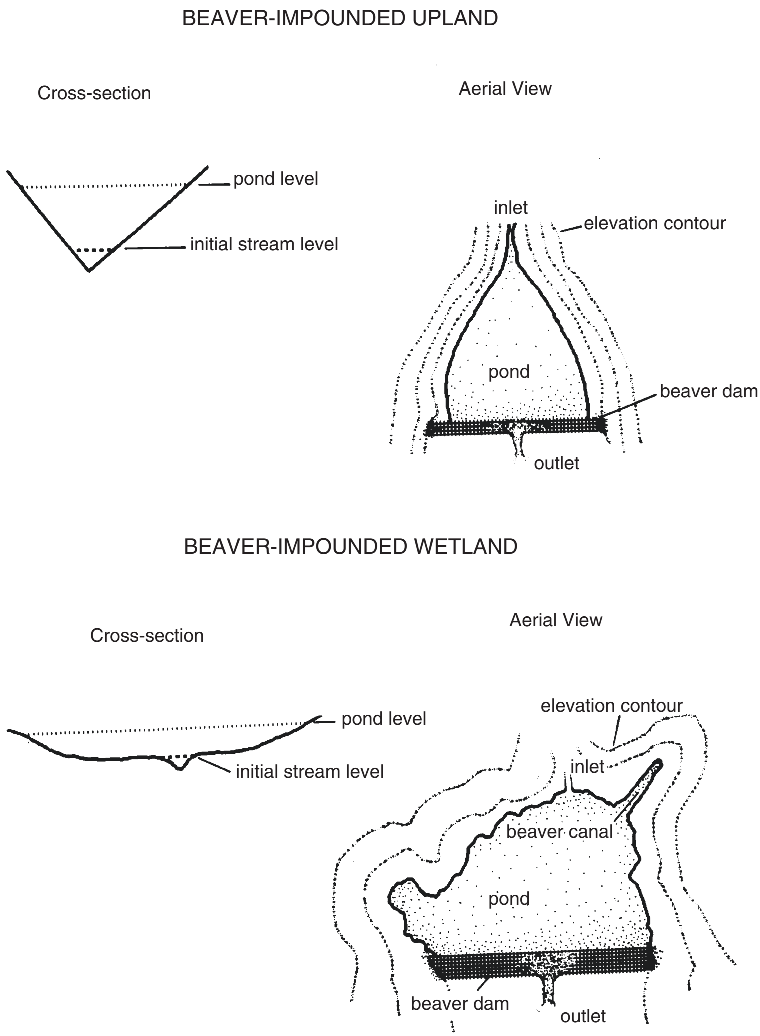

Fig. 2.20 Cross-sectional and plan views of a hypothetical beaver pond created by flooding an upland versus a wetland. From Johnston CA, Naiman RJ (1987) Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1(1):47–57, with permission of Springer

Table 2.4 Comparison of beaver foraging patterns in the riparian zones around a flooded wetland (Arnold Pond) and a flooded upland pond (Ash Pond) near Duluth, Minnesota

Characteristic	Wetland pond	Upland pond
1. Perimeter of upland riparian zone, meters	800	500
2. Mean maximum foraging radius, meters (± S.D.)	16.1 ± 10.9	25.8 ± 12.7
3. Area of riparian foraging, sq. meters (row 1 * row 2)	12,880	12,900
4. Foraging occurrence within 20 m of pond (% of plots browsed)	33%	83%

From Johnston CA, Naiman RJ (1987) Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1(1):47–57, with permission of Springer

water. Boundaries of ponds in beaver-impounded wetlands are more gradual and diffuse than ponds in beaver-impounded uplands because the land flooded has a gentle slope. This can affect the "permeability" of the pond boundary to beaver movement into the riparian zone: a beaver threatened by predators can quickly return to the deep water of an impounded upland pond, whereas the distance is longer to the safety of deep water in an impounded wetland pond. This can affect riparian foraging patterns. A comparison of woody plant foraging around a upland beaver pond versus a wetland beaver pond showed that, even though the area subject to browsing was nearly identical at the two ponds (about 12,900 m^2), riparian foraging was less evenly distributed around the flooded wetland than the flooded upland (Table 2.4).

2.3.3 Pond Site Optimization

Beaver ponds can be grouped into cohorts representing their creation sequence, such that all the beaver ponds visible on the earliest aerial photos are the first cohort, and beaver ponds added as of the next aerial photo date are the second cohort, etc. I did this with the beaver ponds created on the Kabetogama Peninsula using aerial photos taken at approximately decadal intervals from 1940 through 1986 (Johnston and Naiman 1990a).

The number of pond sites increased dramatically over the half-century period, from 71 sites in 1940 to 835 sites in 1986. The rate of new pond creation was greater in 1940–1961 (25 new sites/year) than it was in 1961–1986 (10 new sites/year). New ponds established in 1940, 1948, or 1961 were also significantly larger ($F = 8.85$, df = 5, $P = 0.0001$) than new ponds established in 1972, 1981, or 1986, so that the average area of a pond established in 1986 (1.2 ha) was only one-third the average area of a new pond in 1948 (3.9 ha). Not only were 1940-cohort ponds significantly larger to begin with, they also grew at a faster rate once established, doubling in average area

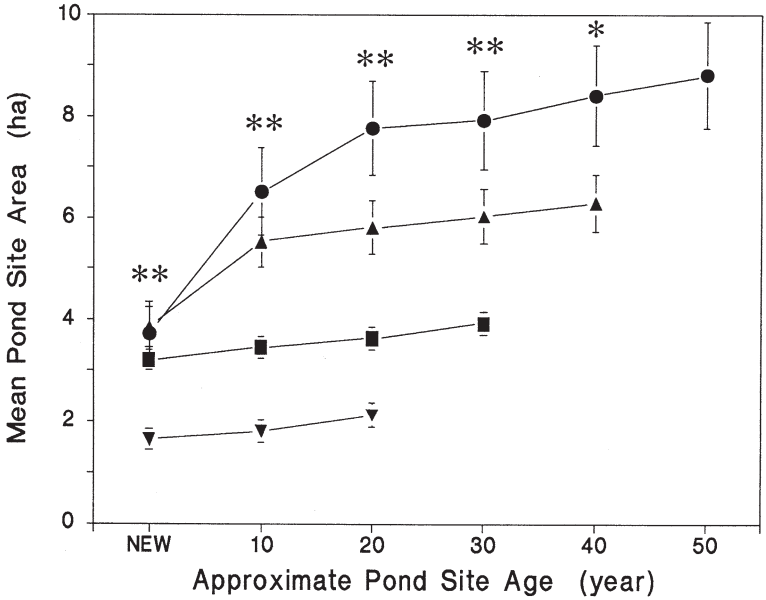

Fig. 2.21 Average pond-site area, by pond cohort. *Circle* = 1940 pond cohort ($y = 1.27 \ln(x) + 3.72$), *triangle* = 1948 pond cohort ($y = 0.63 \ln(x) + 3.85$), *square* = 1961 pond cohort ($y = 0.18 \ln(x) + 3.16$), *inverted triangle* = 1972 pond cohort ($y = 0.14 \ln(x) + 1.62$). * and ** indicate significant effects of pond-site age on average pond area (Kruskal–Wallis one-way ANOVA) at 0.05 and 0.01 significance levels. From Johnston CA, Naiman RJ (1990a) Aquatic patch creation in relation to beaver population trends. Ecology 71:1617–1621, with permission of John Wiley & Sons

after only two decades (Fig. 2.21). The 1948-cohort ponds also grew rapidly during the first decade after establishment, but the growth of the 1961 and 1972-cohort ponds was small (0.1–0.8 ha/decade) and linear over time (Johnston and Naiman 1990a).

The combination of high rates of pond creation, larger initial pond area, and rapid growth made the 1940, 1948, and 1961 pond cohorts the most spatially influential (Fig. 2.22). As of 1986, these cohorts constituted 75% of the total number of ponds and 90% of the total area impounded. The establishment of new ponds was the primary cause of increased cumulative pond area prior to 1961 (70% of the total increase), the rest being due to the enlargement of existing ponds. Therefore, ponds constructed by beaver during their first few decades of occupancy have the greatest impact on the landscape (Johnston and Naiman 1990a).

How is it possible that beavers are able to optimize their dam location so as to create the largest ponds first? It has been established that beavers build dams in response to the sound of running water (Wilsson 1971; Hartman 1975), so the stream pour points at these optimal dam sites probably convey auditory clues to beavers that prompt them to build there.

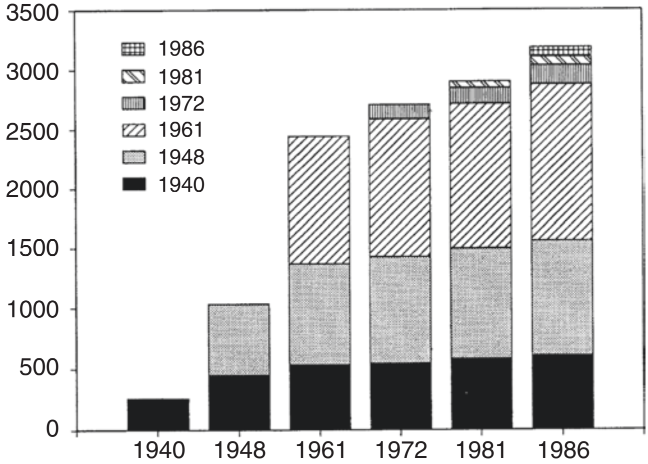

Fig. 2.22 Cumulative pond area, by age class. From Johnston CA, Naiman RJ (1990a) Aquatic patch creation in relation to beaver population trends. Ecology 71:1617–1621, with permission of John Wiley & Sons

2.4 Vegetation Alteration by Beaver Dams

2.4.1 Cover Types of Beaver Impoundments

The raised water level of beaver dams not only creates open water ponds, but also affects a variety of riparian vegetation communities. Beaver dam construction in forested regions causes a fairly predictable sequence of vegetation changes: (1) flooded forest, (2) tree death and toppling, (3) pond containing submergent, floating-leaved, and emergent wetland plants, (4) drained pond with exposed sediments, and (5) drained pond revegetated to grasses and sedges (Johnston 1994; Sturtevant 1998; Little et al. 2012). Beaver colonies move around to new locations and often reflood areas that they have previously abandoned, so that at any one time the beaver-impacted landscape is a shifting mosaic of these various vegetation stages (Naiman et al. 1988).

The impoundment maps classified the cover types of beaver-altered ponds and wetlands (Table 2.5). Open water beaver ponds were relatively easy to detect, but the boundaries of beaver-altered wetland vegetation were more subtle. For example, the beaver dam that impounded the peatland in Fig. 2.12 not only created open water (labeled UBF), but also raised the water level sufficiently to alter the vegetation in an upslope marsh (labeled EM1F) and wet meadow (labeled EM1E). These cover types were bounded along the north and northeast by peatland that was judged to be unaffected by the raised water level, labeled FO8P. The beaver impoundment encompassed the open water pond, marsh, and wet meadow, but the FO8P peatland

Table 2.5 National Wetlands Inventory (NWI) classification codes used, and grouping into six general classes

General class	NWI class and subclass	NWI description	NWI water regime(s)
Dead woody	PSS5	Scrub/shrub dead	B, E, F
	PFO5	Forested dead	B, E, F
Pond	PAB3	Aquatic bed rooted vascular	F, H
	PUB	Unconsolidated bottom (i.e. open water)	F, H
Meadow	PEM1	Emergent persistent	A, B, E
Marsh	PEM1	Emergent persistent	F
Bog	PSS3	Scrub/shrub broad-leaved evergreen	A, B, E, F
	PSS4	Scrub/shrub needle-leaved evergreen	A, B, E, F
	PFO3	Forested broad-leaved evergreen	A, B, E, F
	PFO4	Forested needle-leaved evergreen	A, B, E, F
Deciduous swamp	PSS1	Scrub/shrub broad-leaved deciduous	A, B, E, F
	PFO1	Forested broad-leaved deciduous	A, B, E, F

The "System" for all NWI classes used was Palustrine (P). Water regimes: A—temporarily flooded, B—saturated, E—seasonally flooded-saturated, F—semi-permanently flooded, H—permanently flooded. Additional information about classes at http://www.fws.gov/wetlands/Data/Wetland-Codes.html. From Johnston CA, Windels SK (2015a) Using beaver works to estimate colony activity in boreal landscapes. Journal of Wildlife Management 79 (7):1072–1080, with permission of John Wiley & Sons

was not included in it. GIS analysis was used to quantify the cover types mapped for a 250 km^2 area of the Kabetogama Peninsula (Johnston and Naiman 1990b; Johnston and Windels 2015a, b).

The cumulative area affected by beaver dams increased rapidly from 1940 to 1961, increased at a slower pace from 1961 to 1986, and was relatively stable at about 32 km^2 (12.8% of the landscape) after 1986 (Fig. 2.23). The area of open water pond increased from only 0.12 km^2 in 1940 to 9.8 km^2 in 1990, when it constituted 30% of the landscape, but decreased to half that area in 2003 and 2005. These pond changes were associated with the increase, stabilization, and decrease in the Kabetogama beaver population (Johnston and Windels 2015a).

The Kabetogama Peninsula was mostly wooded prior to the expansion of beavers, vegetated by deciduous and coniferous upland forests, conifer bogs, and swamps (Marschner 1930). Therefore, it is surprising that only about one-third of beaver-impounded vegetation is woody (i.e., deciduous, bog, or dead woody) (Fig. 2.23). Although woody vegetation can persist in floating bog and fen mats, trees rooted in mineral soil die under prolonged flooding (Figs. 2.15 and 2.16). Therefore, beaver-impounded forests are generally short-lived, converting to open water ponds or herbaceous wetlands as the trees topple (Fig. 2.24, top photo). Impounded live deciduous trees and shrubs covered about 5 km^2 during 1961 through 1981, but the area in this cover type was lower after 1981. Impounded bog area has been small but relatively stable over time.

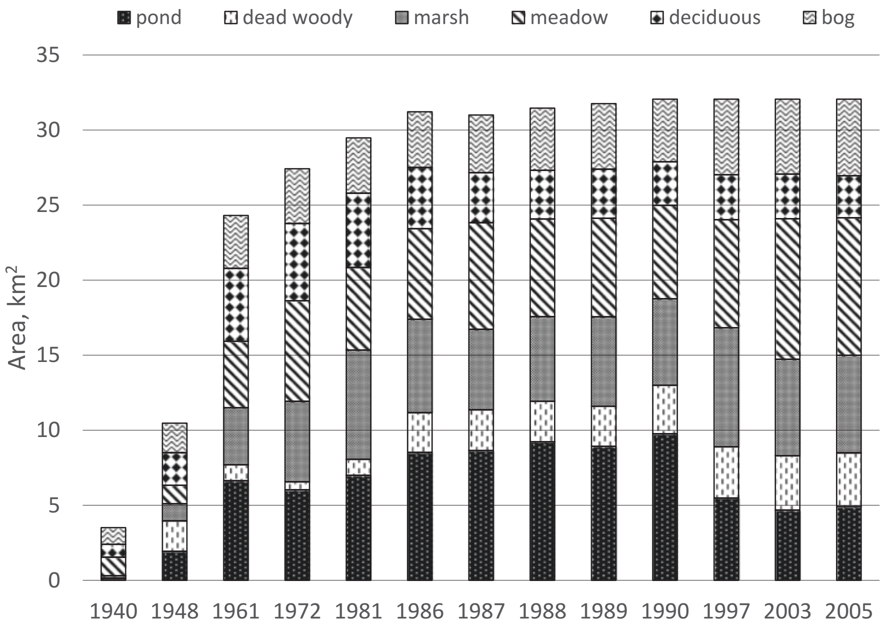

Fig. 2.23 Area of major vegetation types associated with beaver impoundments within a 250 km^2 area of the Kabetogama Peninsula, 1940–2005

2.4.2 Beaver Meadows

Beaver meadows (Fig. 2.24, bottom photo) have been described by a number of researchers around the world (Westbrook et al. 2011; Little et al. 2012; Polvi and Wohl 2012; Simonavičiūtė and Ulevičius 2007; Wright et al. 2003), and are the most abundant cover type of Kabetogama pond sites (Fig. 2.23). Beaver meadows are established when herbaceous vegetation quickly becomes rooted on the exposed bottom sediments of drained beaver ponds. Alternatively, the death of woody plants in floating peat mats can increase the dominance of sedges and other herbaceous species (Mitchell and Niering 1993; Reddoch and Reddoch 2005). The Field Guide to the Plant Community Types of Voyageurs National Park (Faber-Langendoen et al. 2007a) includes two main types of herbaceous wetland vegetation associated with beaver impoundments, Northern Sedge Wet Meadow and Canada Bluejoint Eastern Meadow. Individual plant species occurring in these herbaceous communities are further described in Chap. 6.

On the Kabetogama Peninsula, wet meadows constituted 12–29% of impoundment area between 1948 and 2005, reaching their maximum area in 2003 and 2005 as the beaver population dropped and abandoned ponds drained (Johnston and Windels 2015a). Marshes, including floating sedge mats, constituted 20–25% of

Fig. 2.24 Field photographs of beaver impoundment vegetation. *Top*: This beaver pond with standing dead trees was first created in 1992, 11 years before this photo was taken. *Bottom*: White pine (*Pinus strobus*) saplings and willow (*Salix* spp.) shrubs begin to encroach on the edges of a beaver meadow that had persisted for 30 years

impoundment area between 1972 and 2005. In the absence of renewed disturbance, beaver meadows may succeed to shrubs and trees (Remillard et al. 1987), but this process is very slow on the Kabetogama Peninsula. Woody plant succession was only beginning to occur at one of the field sites that we studied, called Found Pond, after 30 years of being a beaver meadow.

2.4.3 Vegetation of Active Versus Inactive Beaver Pond Sites

Beavers are of course a key ingredient in the creation of beaver ponds, so it makes sense that pond sites that are actively being maintained by a resident beaver colony should differ from those that have been abandoned. Comprehensive beaver colony maps had been prepared for the National Park Service using autumn aerial censuses of beaver lodges in 1984, 2000, and 2006. By pairing that information with the pond site maps, we were able to analyze the vegetation of active versus inactive beaver pond sites (Johnston and Windels 2015a).

For each of the three dates, active pond sites were larger and contained greater pond and marsh area than did inactive pond sites (t tests, $P < 0.001$; Fig. 2.25a). Sites active two or three times (i.e., active in 1984, 2000, and 2006) were significantly larger than the two other site groups, and the area per pond site of open water pond and marsh increased significantly with increasing frequency of beaver occupancy (Fig. 2.25b). The area of wet meadow vegetation was greater in twice-active than inactive pond sites, but wet meadow as a fraction of total pond site area was greatest in once-active and inactive pond sites. On average, bog vegetation constituted 12–16% of pond site area regardless of beaver activity, and the area of bog vegetation was significantly greater in thrice-active than in inactive pond sites. Dead woody vegetation was not significantly different across the three groups. These data illustrate that the same vegetation classes occur in both active and inactive pond sites, but that the area and relative proportion of open water and herbaceous vegetation classes differ across levels of beaver activity.

Classification (CART) trees were developed to estimate the activity of individual pond sites using the three lodge maps and the beaver impoundment cover type maps, with overall accuracies of 78–82% (Johnston and Windels 2015a). The CART model derived from the 2000 lodge map paired with the 2003 beaver impoundment map retained only two variables: pond area per site and pond plus marsh area per site. The first split in the tree classified as inactive those sites with very small pond areas (<0.255 ha) and the second split classified as inactive those sites with pond plus marsh areas <2.633 ha (Fig. 2.26). The remaining sites were estimated to be active. CART models developed for the other two dates also incorporated pond and pond plus marsh area, as well as the area of woody deciduous cover (Johnston and Windels 2015a).

2.4.4 Changes in Beaver Population Alter Beaver Impoundment Cover Types

Knowing that beavers alter the relative proportion of vegetation cover, my colleagues and I modeled beaver landscape alteration over a longer time period, using aerial beaver lodge counts that had been conducted for the Kabetogama Peninsula

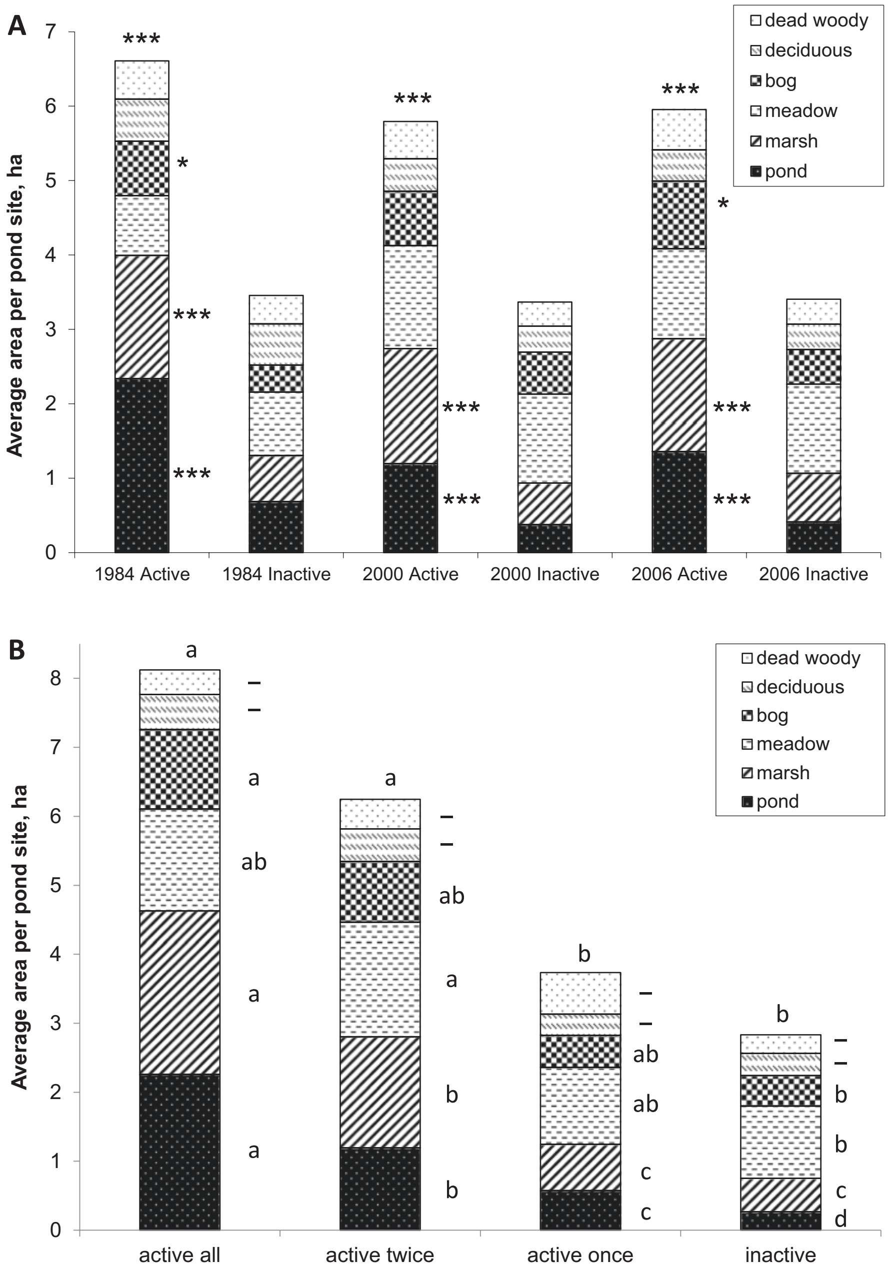

Fig. 2.25 Vegetation types associated with active versus inactive beaver pond sites. (**a**) Average area of vegetation types for active versus inactive pond sites during lodge map census years 1984, 2000, and 2006. Bars or portions of bars with * indicate significant differences (***$P < 0.001$, *$P < 0.05$). (**b**) Average area of vegetation types for beaver pond sites that had been active once, twice, thrice, or inactive according to lodge maps. Bars or portions of bars sharing the same lowercase letter are not significantly different (Tukey's multiple comparisons of means, $P < 0.05$). – = no significant difference among groups. From Johnston CA, Windels SK (2015a) Using beaver works to estimate colony activity in boreal landscapes. Journal of Wildlife Management 79 (7):1072–1080, with permission of John Wiley & Sons

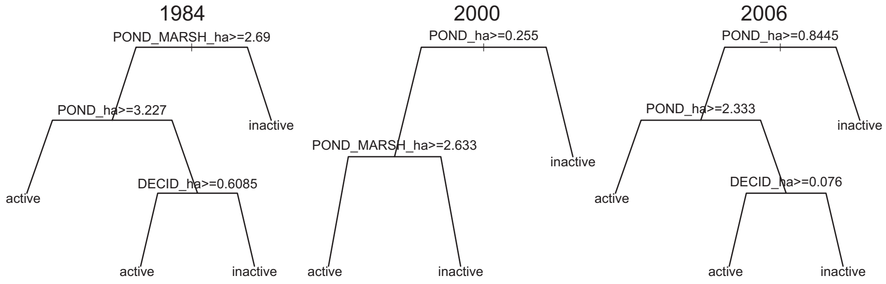

Fig. 2.26 Classification trees for distinguishing activity of beaver pond sites based on associated cover types, derived from 1984, 2000, and 2006 lodge maps and their corresponding impoundment maps. Sites meeting the decision criterion go to the left split, whereas those not meeting the criterion go to the right. DECID_ha = area of beaver-impounded deciduous woody vegetation in hectares, POND_ha = beaver pond water area in hectares, POND_MARSH_ha = area of beaver-impounded marsh and pond area in hectares. From Johnston CA, Windels SK (2015a) Using beaver works to estimate colony activity in boreal landscapes. Journal of Wildlife Management 79 (7):1072–1080, with permission of John Wiley & Sons

annually since 1958 (Berg 1987). In contrast to the three lodge maps that were used in the previous analysis, the annual lodge counts were not spatially explicit. Our initial model matched the aerial beaver colony counts with beaver impoundment maps representing approximately 10-year intervals between 1940 and 1986, a period of rapid beaver population increase. The initial regression model showed that beaver populations were best predicted by the proportion of land area in impounded shallow marsh, and were negatively related to the proportion of land area in seasonally flooded meadow (Broschart et al. 1989).

This model failed, however, when applied to more recent maps (1987–2005) because the vegetation alteration caused by the recolonization and abandonment of pond sites evolved as the beaver landscape matured and the beaver population peaked and declined (Fig. 2.27). Total active lodge density was only 0.33/km^2 during the first transect survey in 1958, increased to 1.1/km^2 during the mid-1980s, then decreased to 0.9/km^2 thereafter. The new landscape-scale regression model that we developed related the number of beaver colonies to open water pond area as a proportion of land area, estimating that each 100 additional beaver colonies would impound 2.15% of the landscape (Johnston and Windels 2015a).

2.5 Beaver Excavation

Beavers engineering includes excavation. Beavers excavate the mud behind their dams and around their lodges, applying the mud to the structures. Beavers also excavate canals so as to create deeper water access to riparian foraging areas. Beaver canals that are not obscured by overlying water or overhanging vegetation are often visible on detailed aerial imagery (Figs. 2.15 and 2.28a). Beaver canals are also detectable using vertically precise digital elevation model (DEM) data. Figure 2.28b

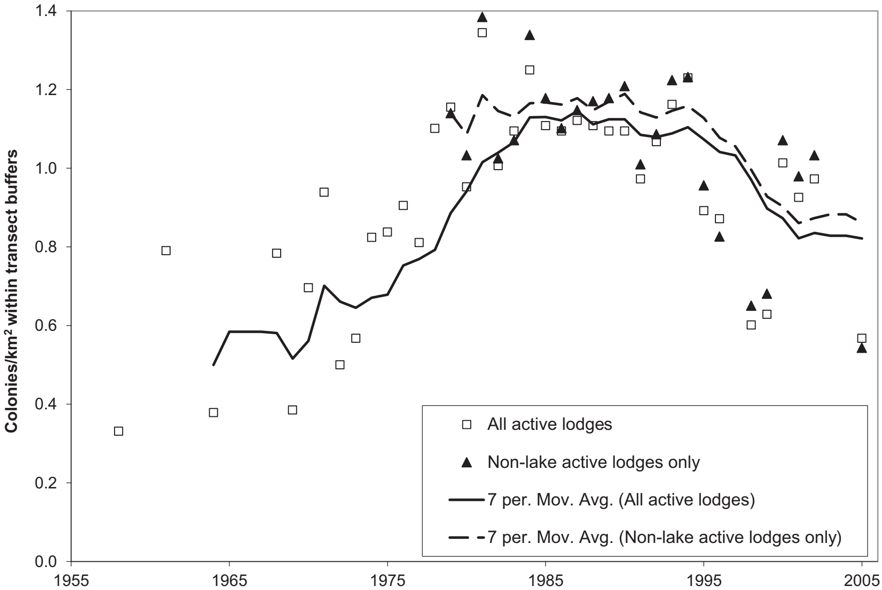

Fig. 2.27 Beaver colony density at Voyageurs National Park, Minnesota based on aerial survey transects, 1958–2005. Point symbols indicate average annual colony density per square km, including and excluding lake lodges. Linear trends are seven-period moving averages of the point data. From Johnston CA, Windels SK (2015a) Using beaver works to estimate colony activity in boreal landscapes. Journal of Wildlife Management 79 (7):1072–1080, with permission of John Wiley & Sons

is color-coded to represent elevations within a 1.1 m range, using a LIDAR-derived DEM depicting 1 cm elevation differences. The beaver canals are 20–50 cm deep (Fig. 2.28). Beaver canal excavation to access upland food reserves can increase average wetland perimeters by over 575% (Hood and Larson 2015).

2.6 Conclusions

- Beaver ponds require three ingredients: beavers, water, and land suitable for flooding.
- The Kabetogama Peninsula is an ideal area for beaver ponds because: (1) it is completely surrounded by water, (2) it has complex topography, (3) its waters flow in many directions, (4) it has impervious bedrock, (5) it has impervious soils, and (6) there is abundant woody browse.
- Beavers build dams on streams, in peatlands, and at lake outlets. When beaver dams flood peatlands, the vegetation often forms floating mats that lift with the rising water level.
- The lake outlet dam at Shoepack Lake raised water levels 4.4 km upstream and tripled the lake's surface area by flooding adjacent wetlands.

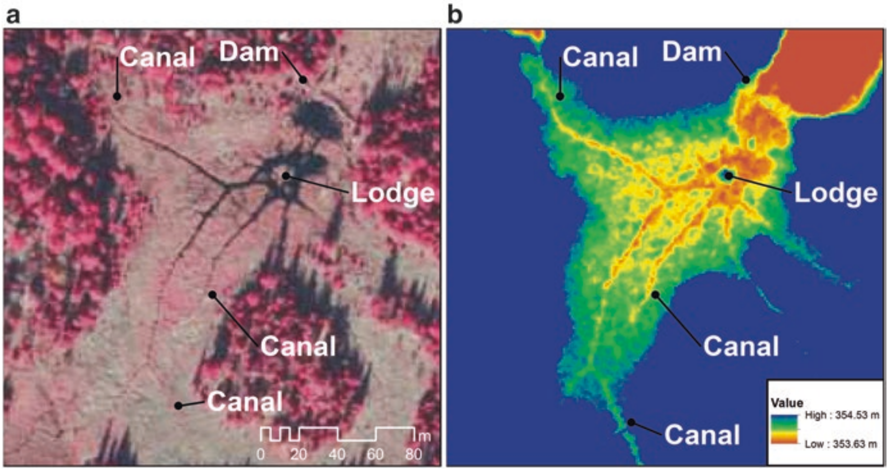

Fig. 2.28 Beaver-excavated features. (**a**) Water appears as black patches behind dam, around lodge, and in linear canals in this color infrared image. (**b**) LIDAR-derived DEM has been color-coded to show beaver-excavated canals that are 20–50 cm deep

- The longest beaver dam on the Kabetogama Peninsula is 309 m, but the longest beaver dam in the world is 850 m.
- Beaver dams on the Kabetogama Peninsula are quite persistent. Some have been continuously occupied by beaver colonies. Others go through cycles of abandonment and rebuilding. Dams may be breached by high water flows, but are usually rebuilt at the same location.
- Some beaver ponds have dams at multiple outlets draining in different directions.
- Beaver impoundments have altered 12.8% of the Kabetogama Peninsula over time.
- When colonizing a new area, beavers choose to flood first the sites that will create the largest ponds with the greatest potential for areal growth. Smaller ponds are created after the best sites are used up.

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http://www.springer.com/978-3-319-61532-5

Beavers: Boreal Ecosystem Engineers
Johnston, C.
2017, XXXIX, 272 p. 21 illus., 4 illus. in color., Hardcover
ISBN: 978-3-319-61532-5