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Beaver Recolonization in South-central Maine

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BEAVER RECOLONIZATION IN SOUTH-CENTRAL MAINE

by

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of the Requirements for the Degree of

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Following a long absence due to over-trapping, beaver (*Castor canadensis*) recolonized most of their continental range during the middle of the 20th century. The spread of beaver across the landscape was revealed by the emergence of beaver-created wetlands, or flowages. Based on the appearance of flowages on aerial photographs from 1939, 1957, 1974, and 1991, I documented the return of beaver to a 105 km^2 watershed in south-central Maine. I sought to determine if certain wetland characteristics—area, perimeter to dam length (p/d) ratio, and watershed size—influenced the order in which sites were occupied by beaver. Also, to gauge the effect of beaver on the landscape, I measured the total area of flowages and the distance from each wetland to the nearest neighboring wetland at each time period. I also observed vegetational changes that occurred in flowages after they were inhabited by beaver.

Seventy-seven flowages were created between 1939 and 1991, which caused the median distance between wetlands to decrease 68%. The area, p/d ratio, and watershed size of new colony sites decreased each time period. By 1991, 1.5% of the study area (160 ha) was affected by flooding by beaver. The vegetation of flowages underwent a general transformation from trees to herbs.

ACKNOWLEDGMENTS

I am most thankful for the guidance of my three committee members: Dr. Ray B. Owen, Jr. provided an opportunity for me to study my favorite subject, beaver-created wetlands, and infused my work with his own zest for the topic; Dr. Kate Beard was supportive, generous with her time, and occasionally extricated me from hopeless "GIS" entanglements; Dr. Malcolm L. Hunter, Jr. contributed thoughtful counsel, careful editing, and enthusiasm for "the most remarkable mammal next to humans."

I am also grateful to several other individuals for their assistance with my research. Dr. William A. Mackaness acted as a general computer consultant. Jeff DeRuyscher and Chuck Kitchens helped with digitizing. Stu Gardner joined me several nights—once in blizzard conditions—attempting to collect locations with a GPS. Fellow beaver researchers, Tom Hodgman and Tom McCall, shared ideas and information. The noontime basketball players, led by power forwards Bert Frost and Dr. Fred Servello, provided a healthy diversion. Thanks, too, to three organizations: the Department of Surveying Engineering, the Department of Wildlife Ecology, and the Hirundo Wildlife Trust.

Many, many other friends and relatives (so many I'm copping-out on a list) encouraged me during this project. My deepest gratitude to you all.

Lastly, and most importantly, I thank my wife, Elise. Her hard-work, steadfastness, and moral support (all while producing a beautiful girl named Emma) made this endeavor possible.

I dedicate this thesis to my late, beloved parents, Midge and Larry Lisle. Their love and support, and the "love of nature" they helped instill in me, made it possible.

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PROLOGUE: HISTORY OF BEAVER IN MAINE

Fossil evidence suggests that beaver (*Castor canadensis*) were widespread and abundant in North America throughout the Pleistocene epoch (2,000,000–10,000 years before present [B.P.]) (Kurten and Anderson 1980). Beaver also have been common during much of the modern, or Holocene, epoch. For example, archeological inventories of ancient cultural sites in central Maine (7500–3600 years B.P.) revealed that beaver remains were more prevalent than those of any other species (Spiess 1992). However, the European discovery and exploration of America, which began in earnest in the 16th century, precipitated the decline of many species, including beaver (Seton 1928).

Beaver were abundant prior to European contact despite coexistence with several top-level predators: mountain lions (*Felis concolor*), wolves (*Canis lupus*), and American Indians. Perhaps, the success of beaver during that time can be partly credited to Native American philosophies that encouraged conservation (Martin 1978). Nevertheless, if mores existed that helped to preserve species, they dissipated when Indians became partners in the Fur Trade.

The first European explorers showed little interest in beaver, preferring instead to fill their holds with codfish (Dickinson 1987). However, when felt hats became fashionable in Europe during the 1580s, beaver supplanted fish as the most desirable commodity in America; the fine, barbed underfur provided ideal fiber for making felt (Moloney 1931). Because populations of European beaver (*Castor fiber*) were already depleted, most of the raw material for the hat industry had to come from the New World.

Consequently, North American beaver became the backbone of the Colonial economy and the mainstay of the Fur Trade for 200 years (Clayton 1967).

Maine beaver were early principals in the Fur Trade. The first of many chronicles of harvests of beaver in Maine was made by a French captain in 1583. After trading with local inhabitants along the coasts of Nova Scotia, New Brunswick, and Maine, Etienne Bellinger returned to Europe with, "bevers skynes verie faire as many as made 600 bever hattes" (Quinn 1962). In 1620, the Plymouth Colony began a fur trade with local Indians. In 1626, the Pilgrims ventured northeast to the "Kenibeck" (Kennebec) River in present-day Maine where they exchanged a boatload of corn for 700 lbs of beaver skins. Subsequently, the Pilgrims established trading, or trucking, houses on the Kennebec, St. George's, and Penobscot Rivers. In 1631, their French rivals ransacked the Penobscot site, stealing 300 lbs. of beaver skins and considerable trading supplies (Bradford 1899). Between 1631 and 1636, beaver furs that the Pilgrims managed to retain weighed more than 12,000 lbs. Maine was the greatest source of these furs (Moloney 1931).

The Pilgrims and French were not the only competitors for beaver. By 1624, at least forty English merchantmen plied the coastal waters of Maine in search of fur-trading opportunities (Moloney 1931). In 1630, two London merchants received the Muscongus patent—30 mi^2 between Muscongus Bay and the Penobscot River. Shortly thereafter, more than 1000 lbs of beaver skins were exported from this area (Bradford 1899). By 1633, independent English merchants had built trading houses at six locations in Maine: Piscataqua River (2), Saco River, Cape Elizabeth, Casco Bay, and Pemaquid Point. On one busy day, Ambrose Gibbons, the proprietor of one of the Piscataqua sites, hosted 100 Indians who were trading beaver and other furs for European goods (Moloney 1931).

The unbridled quest for beaver continued through the 17th and 18th centuries. The effect on beaver populations, and the people who depended on them, was devastating. In 1763, following the French and Indian War, Maine Indians protested that, "English hunters kill all the Beaver they find, which had not only impoverished many Indian families, but destroyed the breed of Beavers" (Cronon 1983). Traveling in Maine in 1808, Edward Kendall wrote that the local fur trade, "can scarcely be said to exist; the native animals, like the native inhabitants, are destroyed" (Norton 1930).

Shortly thereafter, beaver received a fortuitous, whim-of-fashion reprieve. In the 1830s, wool, silk, and other materials began to be used for hat-making, providing an alternative to beaver fiber. Simultaneously, raccoon (*Procyon lotor*) overtook beaver as the dominant fur in the American trade. Later in the century, fur seal (*Callorhinus ursinus*) surpassed both species in popularity (Clayton 1967). Nevertheless, a gradual diminution of beaver populations continued into the 20th century.

By the turn of the century, Maine beaver were eliminated in all but a few remote, northern towns. In response, the state legislature banned all trapping of beaver indefinitely in 1899. However, lack of legal enforcement allowed a black market trade to continue until the late 1920s when the newly-improved State Warden Service became an effective deterrent. Concurrently, federal agents, working under the auspices of the Lacey Act, which prohibits interstate shipment of illegally acquired wildlife, fined 30 Maine residents $7500 for unsanctioned fur-trading (Hodgdon and Hunt 1966).

Following 300 years of control by market forces, beaver populations again were protected by cultural constraints . As a result, beaver began a full-scale recovery in Maine. Game warden reports from the 1930s reveal a dramatic southwards expansion by the remnant population in the north.

Beaver continued to expand their range during the 1940s and 1950s, becoming reestablished in most Maine towns by 1960 (Hodgdon and Hunt 1966). In 1955, regulated trapping was reopened statewide for the first time in 56 years (Boettger 1968).

Today, evidence of beaver activity can be found almost everywhere in Maine. Perhaps, populations again are approaching levels last seen 400 years ago when commerce between Europe and America began.

INTRODUCTION

Beaver and humans are the only mammals that profoundly reshape ecosystems to form their own unique habitats. In northeastern North America, beaver add thousands of small wetlands to a panorama largely consisting of forests, glacial lakes, and assorted human enterprises. Beaver-created wetlands, or flowages, moderately increase landscape heterogeneity, which tends to increase biodiversity (Forman and Godron 1986). Also, the value of wetlands to scores of life forms suggests that beaver are an important keystone species (Bradley 1994; Hunter, in press).

The elimination of beaver during the Fur Trade allowed dams to decay, which permitted forest to intrude upon drained, herbaceous flowages. As beaver returned, reflooding their former haunts and killing trees, openings again appeared in the forested matrix. Because the spread of beaver in Maine coincided with the advent of aerial photography, the pattern of landscape colonization (based on the appearance of new flowages) was recorded periodically on aerial photographs (Lillesand and Kiefer 1987; Johnston and Naiman 1990).

In my study area, a photographic record exists for 1939, 1957, 1974, and 1991, a period during which beaver arrived (between 1939 and 1957), and then occupied most available habitats. With the photographs, I examined the pattern of beaver colonization with two questions in mind: 1) What factors influenced where beaver settled? and 2) What effect did beaver have on the landscape? I hypothesized that three wetland characteristics—area, perimeter to dam length (p/d) ratio, and watershed area—affected the location of colony sites and the order in which they were occupied. I used the p/d ratio as an index to the energy-efficiency of sites, high numbers representing short dams (less work) and long perimeters (greater potential access to food sources). The watershed area was used as a rough measure of the flow rate of streams at wetland sites. These three variables were measured for colony sites newly occupied between 1939–1957, 1957–1974, and 1974–1991. Landscape-scale changes were gauged by calculating the distance from each wetland to the nearest neighboring wetland and the total area flooded by beaver in 1939, 1957, 1974, and 1991. I also observed general successional trends that occurred in flowages during the 52-year period represented by the photographic record.

STUDY AREA

The study area is a 105 km^2 watershed extending upstream from the village of Monroe in south-central Maine (69° 02' W, 44° 37' N) (Fig. 1). The "Monroe watershed" lies primarily within the towns of Jackson and Monroe and drains into the north branch of Marsh Stream, which empties into the Penobscot River estuary 12 km east of Monroe village. Most first and second order streams in the watershed flow SSE along the same axis as the glaciers that retreated 11,000 years ago (Thompson and Borns 1985). The bedrock is oriented SW-NE, roughly perpendicular to the streams (Osberg et al. 1985). Annual precipitation averages 113 cm, and the growing season is approximately 134 days (Fobes 1946). The terrain consists of gently rolling hills; there is a 308 m drop from the highest to the lowest point in the watershed, and a 168 m difference between the highest and lowest flowages.

Several species of wetland plants are common. Abundant herbaceous species include cattail (*Typha latifolia*), burreed (*Sparganium chlorocarpum*), and blue-joint grass (*Calamagrostis canadensis*). Shrubs include sweet gale (*Myrica gale*), winterberry (*Ilex verticillata*), alder (*Alnus rugosa*) and willow (*Salix* spp.), while trees include red maple (*Acer rubrum*), ash (*Fraxinus* spp.), and spruce (*Picea* spp.).

Forest, of the hardwoods; white pine (*Pinus strobus*); hemlock (*Tsuga canadensis*) transition type, covers most of the landscape (Westveld et al. 1956). In 1966, 57% (3,830 ha) of Jackson was densely forested, while selective cuts, clear cuts, and abandoned fields comprised 29% (1,918 ha) of the town (Vonk 1975). Today, as a result of these human activities, there is an abundance of early-successional tree species such as quaking aspen (*Populus tremuloides*) and birch (*Betula* spp.).

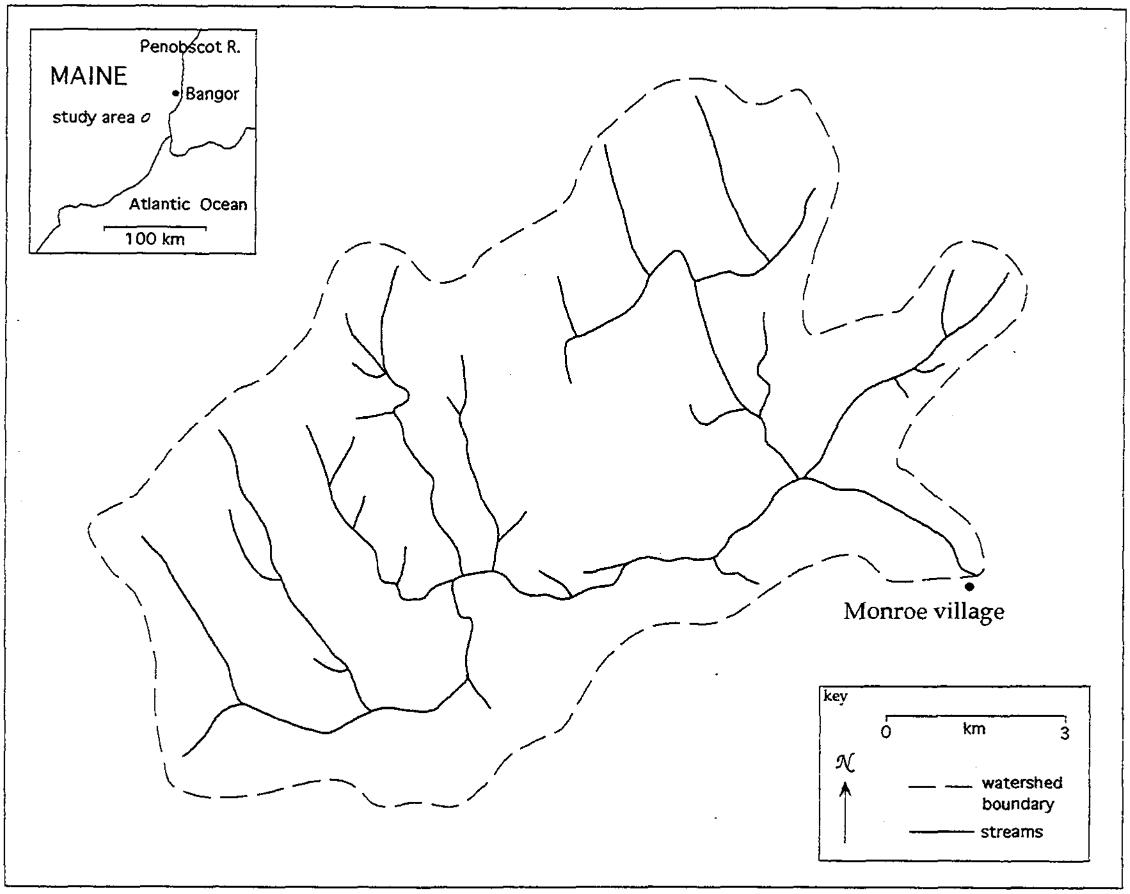

Figure 1. The Monroe watershed study area.

In 1990, the human population density in Jackson and Monroe (6/km^2) was 60% less than in 1850 when south-central Maine was a bustling agricultural area (Chace 1859; U.S. Census 1990). During the 19th century, the localized, agrarian economy supported at least ten sawmills and gristmills in the watershed (Morton 1912). The associated millponds and outlet dams (often erected at strategic sites upstream from mills to store and regulate water) may have partially mitigated the loss of beaver-created wetlands (Eves 1992).

Prior to the return of beaver, the watershed contained five large, unforested wetlands. Two of these (14 and 17 ha) are glacial kettle lakes. The other three (10, 18, and 59 ha) may have owed their openness to flooding caused by mill dams in the 19th century (Chace 1859; pers. observ.).

There were 10 beaver colonies in the study area in 1957 and 16 colonies in 1984 (Spencer 1963; Hilton 1986). Because of relatively constant, regulated trapping, the number of colonies probably was kept within this range between 1957 and 1989. Between 1989 and 1992 most of the watershed was closed to trapping (McCall 1994), which allowed colonies to increase from approximately 16 (0.15/km^2) to 30 (0.29/km^2). McCall (pers. comm.) estimated there were an average of 3.5 beaver per colony during those years.

METHODS

Use of wetland terms

I use two terms to describe wetlands inhabited by beaver. *Flowages* are wetlands that owe their structure to damming by beaver, and *colony sites* are all wetlands used by beaver (in this case, 77 flowages, two kettle lakes, and a human-made wetland). The three non-flowages were included because dams and lodges were visible on the photographs, thereby revealing the approximate arrival date of beaver. Six other non-flowages were excluded from the data on beaver use because there was no sign of beaver activity on the photographs. By contrast, the origin and approximate age of flowages was obvious because of the dramatic vegetational changes that occurred following the flooding of these previously forested basins.

To describe wetlands, I use the Cowardin et al. (1979) classification scheme. This system groups small, shallow, freshwater wetlands (<8 ha; <2 m deep [most flowages]) in the Palustrine category, which has nine classes based primarily on the type of vegetation present. Five of these classes—unconsolidated bottom (open water areas with <30% vegetative cover), emergent (herbaceous), aquatic bed (non-emergent, herbaceous), scrub/shrub, and forested (which includes dead trees)—were represented in most of the flowages in the study area. To simplify this classification, I combine the two herbaceous classes, leaving three vegetational categories, or wetland types: herbaceous, shrub/scrub (shrub), and forested. Although drowned, dead trees frequently were present in my wetlands, in no instance did I believe they dominated or controlled the ecological community, a precondition for the "forested" designation.

Despite often being conglomerations of different wetland types, flowages are distinct landscape units (Johnston and Naiman 1987). Therefore, to further simplify the description of vegetational patterns, I consider flowages singular wetlands. For example, if a flowage contained sections dominated by each of the three vegetation types, but herbaceous sections were predominant, I regarded it as an herbaceous wetland.

Data collection

Using Arc/Info software, I constructed a Geographic Information System (GIS) database containing perennial streams, flowages, and other large, unforested wetlands (living-forest wetlands were not included) present in the Monroe watershed in 1939, 1957, 1974, and 1991. Enlarged photographic prints were used to delineate wetlands (Table 1); at least four photographs were needed to capture the watershed at each time period. Flowages larger than 0.10 ha, and human-made wetlands and kettle lakes larger than 1.0 ha, were traced onto transparent acetate for digitizing. On the photographs, wetland borders usually were a distinct demarcation between basins dominated by hydrophytic shrubs and herbs, and surrounding, living forest; wetland vegetation generally appeared lighter in color and smoother in texture than upland forest. On newly-created flowages and basins otherwise full of water, the water's edge was treated as the wetland perimeter. Areas of beaver activity that did not display distinct borders (e.g. temporary "summer" dams on large streams and brand-new flowages obscured by forest) were not included. Flowages were treated as autonomous units only if separated from one another by at least 20 m of living trees or shrubs. All wetlands were field-checked to verify boundaries.

Table 1. Characteristics of aerial photographs used to record wetland information in the Monroe watershed.

year	scale	film type	source
1939	1:4,877	black and white	U.S. Soil Conserv. Service
1957	1:10,600	black and white	Sewall Co. Old Town, ME
1974	1:9,907	black and white	Sewall Co. Old Town, ME
1991	1:10,140	color infrared	U.S. Geological Survey

At least four road intersections on each photograph were used as registration points, or tics, to provide placement, orientation, and scale to the digitized wetlands. Universal Transverse Mercator (UTM) coordinates at the road intersections were determined using U.S. Geological Survey (USGS), 7.5-minute, 1:24,000-scale, topographical maps. The wetlands delineated from the individual photographs were joined to form a single map, or GIS coverage, of the watershed in each of the four photographic years (photo-years). Each wetland was assigned four attributes: name, number, origin (human, beaver, or kettle), and date when first seen on the photographs (see Appendix). The numbering system begins at the western edge of the watershed and progresses east, moving down each of seven main tributaries. Origin was credited to the animal or geological event deemed most responsible for the physical structure of the wetland. Some wetlands were influenced by two, or all three, factors.

The boundaries of most flowages present during more than one photo-year appeared to be relatively static. However, minor border incongruities were revealed on GIS overlays of the various coverages. I assumed most of these discrepancies were attributable to two factors other than actual boundary movements. First, technological advances in photography and differing flight altitudes gave each set of photographs unique distortion qualities; secondly, discrepancies inevitably occurred when delineating the same wetland more than once, and with two different tools (a felt-tipped pen and a digitizing cursor). Therefore, to eliminate these distortions, I used a copy of the 1991 coverage to fashion maps of the other years. A 1974 coverage was composed by deleting flowages created after that date from the 1991 map. A similar process was performed for the 1957 and 1939 coverages. The borders of the few (usually large) wetlands that did display conspicuous inter-photo-year growth (no wetlands decreased in size between 1939 and 1991) were adjusted accordingly after overlaying the final coverages on the originals, which were used as guides.

The area, perimeter length, and nearest-neighbor distances of wetlands were calculated with the GIS. Centroids, which Arc/Info assigns automatically to polygons (wetlands), were used to measure inter-wetland distances. Dams were measured directly from the photographs by dividing photographic distance by photo-scale (representative fraction). Where more than one dam occurred in a flowage, which was often the case, lengths were totaled. To double-check accuracy, approximately 10% of the dams also were measured in the field. The watersheds of wetlands were drawn from the contour lines of 7.5-minute topographical maps and measured using a Tamya Technics planimeter.

Streams were digitized from four, 7.5-minute, topographical maps. UTM coordinates at each corner of the maps were used as registration points. The four sections were joined to form a single coverage. The stream order of each stream segment was determined using the Strahler method (1957). With this method, the confluence of two first order streams creates a second order stream; the confluence of two second order streams produces a third order stream, and so on. Only perennial streams large enough to sustain flowages were included (flowages need a certain minimum influx of water to compensate for loss to evapotranspiration and porous dams). The stream and wetland coverages were merged. Again, minor incongruities existed between the two coverages because they were gathered from different data sources. Therefore, where necessary, streams were adjusted to connect accurately to wetland inlets and outlets.

RESULTS

Physical characteristics and location of colony sites

Beaver first arrived in the Monroe watershed between 1939 and 1957. In subsequent years, they occupied two kettle lakes and one human-made wetland (all by 1957), and created many flowages: 7 by 1957; 32 by 1974 (+357%); and 77 by 1991 (+141%).

The mean size of new colony sites decreased with time: 1939–1957 (10.9 ha); 1957–1974 (1.3 ha); and 1974–1991 (1.2 ha) (Fig. 2). Of the 10 wetlands occupied by 1957, five were greater than 10 ha. Furthermore, three of the four remaining wetlands were within 200 m of one of the larger wetlands. By 1991, flowages occurred in a broad range of sizes. The second and third largest wetlands in the study area—24.4 and 20 ha—were created by beaver. However, most flowages (72; 93.5%) were less than four ha in size.

The mean p/d ratio of new colony sites also decreased with time: 1939–1957 (117:1); 1957–1974 (26:1); and 1974–1991 (18:1) (Fig. 3). Many of the earliest flowages were located where small, bedrock ridges (~2 m high) created natural dams. To be complete, the ridges needed damming only where years of stream flow had caused short breeches (3–4 m) in the granite. The two flowages with the highest p/d ratios (227:1 and 323:1) were of this nature. Conversely, many latter flowages, unaided by natural barriers, had relatively long beaver dams, which resulted in small p/d ratios. Interestingly, the qualities associated with narrow, bedrock outlets had previously attracted human dam builders; mill dams and outlet dams once stood at several of the locations later (and probably formerly) dammed by beaver.

Most sites occupied by beaver were on small streams (Table 2; Fig. 4). Although the watersheds of all flowages created by 1991 ranged in size from 8

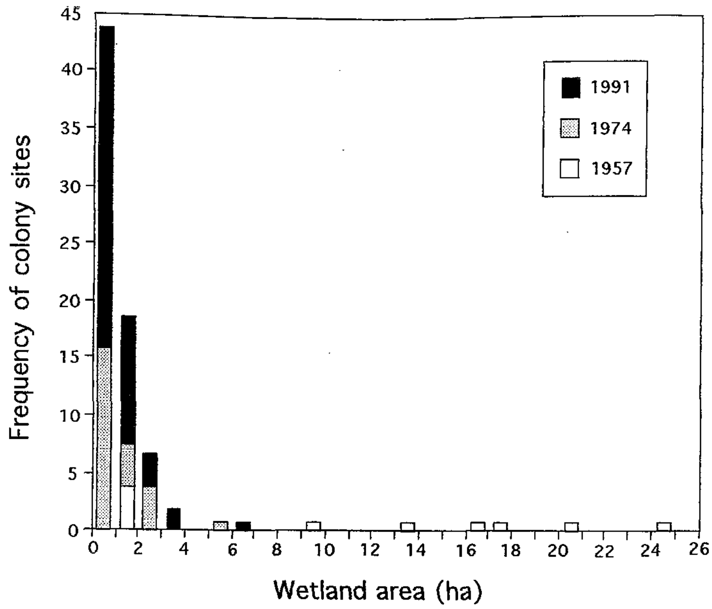

Figure 2. Distribution of colony sites in the Monroe watershed by size and date of origin (1991 for sites occupied between 1974 and 1991, 1974 for sites occupied between 1957 and 1974, and 1957 for sites occupied between 1939 and 1957).

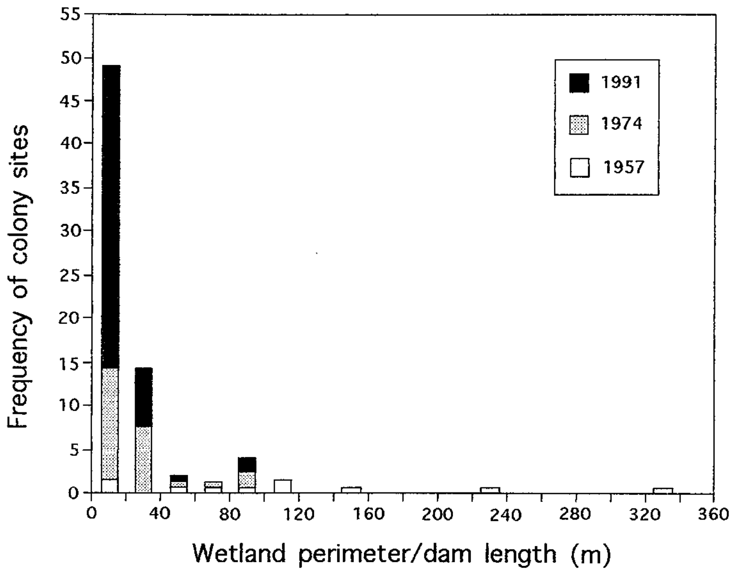

Figure 3. Distribution of colony sites in the Monroe watershed by perimeter to dam length ratio and date of origin (1991 for sites occupied between 1974 and 1991, 1974 for sites occupied between 1957 and 1974, and 1957 for sites occupied between 1939 and 1957.

Table 2. The expected vs. actual distribution of flowages in the Monroe watershed based on the total length of each stream order.

stream order	length (m)	percent of all streams	expected no. of flowages	actual no. of flowages
1	32,975	42	32	60
2	25,695	32	25	16
3	16,223	21	16	1
4	4,018	5	4	0
total	78,911	100	77	77

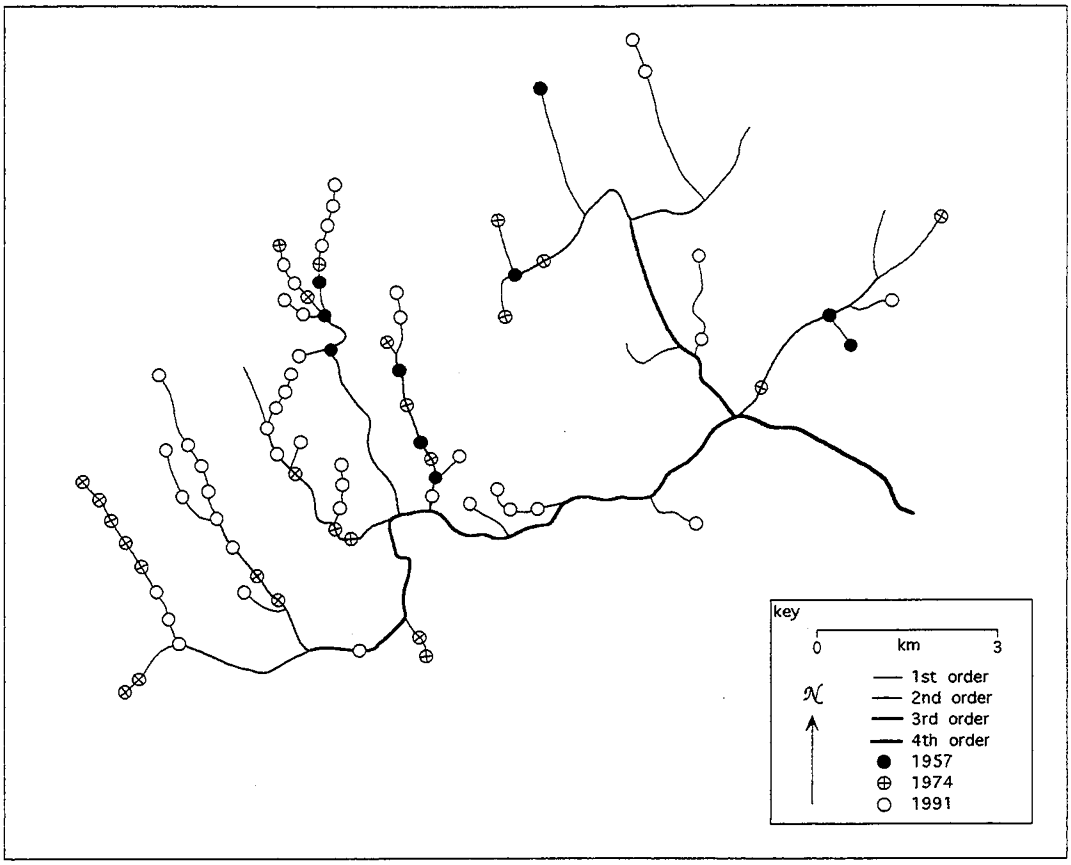

Figure 4. The location, stream order, and date of origin of colony sites in the Monroe watershed (1991 for sites occupied between 1974 and 1991, 1974 for sites occupied between 1957 and 1974, and 1957 for sites occupied between 1939 and 1957).

to 1,833 ha, 48 (62.5%) were less than 200 ha. Stream sections with watersheds larger than 1,833 ha were used sparingly. Above Monroe village, no permanent flowages were established along 19 km of third and fourth order streams; three dams were constructed along this section during the summers of 1991–93, but they were destroyed the following winters by ice flows and high water (therefore, distinct borders, typical of flowages, did not develop). The mean watershed size of new colony sites also decreased with time: 1939–1957 (345 ha); 1957–1974 (305 ha); and 1974–1991 (167 ha) (Fig. 5).

Landscape changes

The return of beaver to the Monroe watershed led to a general transformation of wetlands from a forested to a herbaceous state. The 77 sites that eventually became flowages were forested in 1939. By 1991, most trees had drowned, and the vegetation in the flowages was predominantly herbaceous with a lesser component of shrubs and trees (McCall 1994; pers. observ.) The total area that beaver affected in this manner was 77.4 ha by 1957, 107.7 ha by 1974 (+39%), and 160 ha by 1991 (+48.6%). The final figure is 1.5% of the study area. The three wetlands that beaver occupied, but did not create, experienced no dramatic vegetation changes. The relatively stable kettle lakes appeared to have larger shrub components (e.g. *Myrica gale*) before, and after, the arrival of beaver than did most flowages.

The addition of flowages to the landscape decreased inter-wetland distances. The median distance between wetlands and their nearest neighbors declined 68% between 1939 and 1991: 1939 (997 m), 1957 (384.5 m), 1974 (423 m), and 1991 (322.5 m) (Fig. 6).

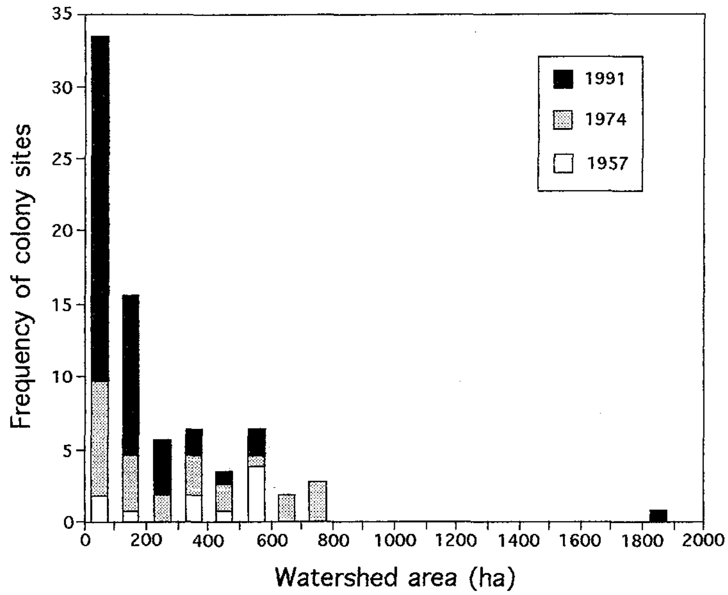

Figure 5. Distribution of colony sites in the Monroe watershed by (sub-) watershed size and date of origin (1991 for sites occupied between 1974 and 1991, 1974 for sites occupied between 1957 and 1974, and 1957 for sites occupied between 1939 and 1957).

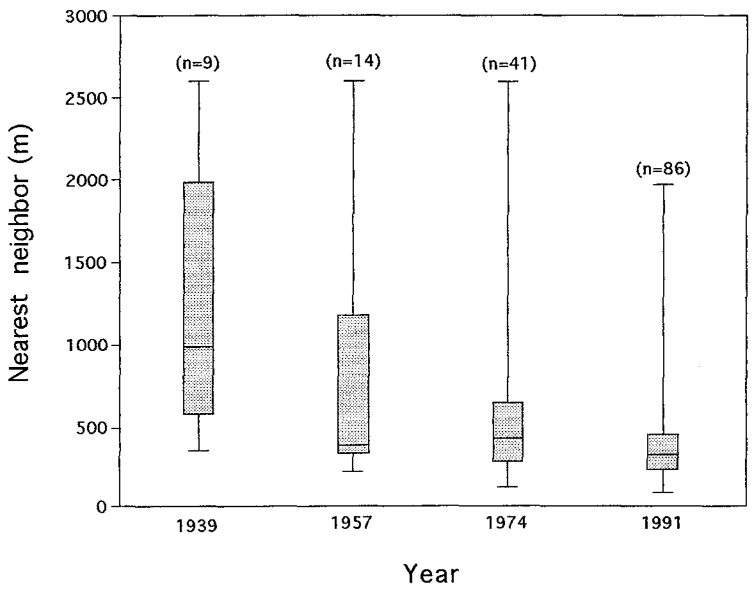

Figure 6. Nearest neighbor distances of all wetlands in the Monroe watershed during each photographic year. Lines within boxes are medians, ends of boxes are quartiles, and vertical lines show the range of values.

DISCUSSION

Assumptions

My conclusions regarding the pattern of beaver colonization are based on three assumptions. 1) Initially, lack of food did not restrict beaver from any wetlands or stream sections. Extensive logging and abandonment of agricultural fields throughout the last 100 years encouraged widespread growth of early-successional hardwoods, a primary food of beaver. Also, beaver had not been present to deplete food stores for a long period of time. 2) Population pressures did not, at any time, force beaver to use marginal habitat. Populations were held in check by regulated trapping from soon after beaver arrived until 1989. 3) Beaver moved into, and within, the study area along the stream system, and not overland. Although beaver do occasionally move overland between watersheds, waterways are their primary dispersal paths.

Habitat selection

When beaver first returned to the Monroe watershed, they settled in, or near, relatively large wetlands (Fig. 2)—a pattern also witnessed in Minnesota (Naiman et al. 1988). Large wetlands may have been selected because they provided more food and security than smaller wetlands. Aquatic plants and early-successional hardwoods, especially aspen, are preferred foods of beaver (Northcott 1971; Jenkins and Busher 1979). If the density of these plants was relatively constant among the wetlands of the Monroe watershed, then large wetlands, with greater surface areas and longer perimeters, provided more of both food types. A possible manifestation of this relationship was observed by McCall (pers. comm.); although beaver normally cache hardwoods underwater to eat in winter, in large wetlands they sometimes over-wintered without caches. This behavior may have been an indication of ample reserves of herbaceous food available under the ice.

Security from predators also may be enhanced in large, food-rich wetlands. Plentiful food sources would eliminate or postpone two activities that increase vulnerability: foraging far from the safety of water, and searching for new habitat. Also, beaver activity in large wetlands is likely to be less concentrated, and therefore less predictable to predators, than in small wetlands. Large wetlands that contain "permanent" water bodies, such as kettle lakes, offer an additional advantage. In these wetlands, dams may be unnecessary or inexpensive to maintain, and, unlike in flowages, dam failure does not eliminate protective reservoirs.

Many of the first sites settled by beaver also had high p/d ratios (Fig. 3). This pattern, too, is reflective of the early use of large, long-perimeter wetlands. However, it also suggests beaver select wetland basins with narrow outlets. Unlike most animals, stream-dwelling beaver need to devote a portion of their energy budget to creating and maintaining their own habitats. Short dams require less work than long dams, and, for the same amount of energy, can be built higher, which increases wetland area. Consequently, beaver returning to the Monroe watershed were quick to exploit landscape features, such as bedrock ridges, that minimized the length of dams, and hence the cost of habitat maintenance.

Regardless of their size or structure, all flowages were established on small streams (Fig. 5). Apparently, large streams were avoided because of their potential for destroying dams during periods of high run-off. The reservoirs that dams create are critical for escape cover, conveyance, storage of food caches, foraging, and predator barriers at lodge entranceways. Therefore, the loss of a dam, especially in winter, is a serious threat to survival. Also, the burden of habitat maintenance is reduced if dams are able to retain their structural integrity through the year.

The size of the watersheds of new colony sites decreased with time. However, this does not necessarily indicate a general upstream movement by beaver. Although some streams were colonized in a stair-step fashion, many latter flowages were located low in the watershed on small tributaries of the main stem (Fig. 4). If the beaver that settled these sites originated within the watershed, then dispersal occurred in both an upstream and a downstream direction.

Landscape changes and ecological effects

The long-term absence of beaver altered vegetational succession in wetlands. Flowages usually occur in low-gradient basins along streams (Retzer et al. 1956; Hill 1990). In the undulating terrain associated with the Appalachian mountain chain, sites of this nature are relatively fixed in number between glaciation events. Therefore, most basins used today probably were occupied prior to the Fur Trade. By causing flooding, beaver likely maintained these areas as open, herbaceous wetlands. However, when beaver disappeared, dams eroded, soils dried, and woody plants colonized the forest openings. In 1939, sites destined to become flowages were vegetated largely by trees and tall shrubs (probably *Alnus*). Subsequent flooding by beaver changed these areas back to primarily herbaceous wetlands.

Field checks revealed that beaver had occupied most wetland basins in the Monroe watershed by 1991. Consequently, the total area altered by beaver has probably plateaued at about 160 ha (1.5% of the study area). By comparison, 13% of a 250 km^2 area in Minnesota was affected by beaver

(Johnston and Naiman 1990). There, maximum topographic relief was 80 m versus 308 m in the Monroe watershed. This difference suggests that relief plays an important role in determining the effect of beaver on the landscape.

The resurgence of beaver in this century implies that millions of wetland hectares were added to North America. However, the moist, streamside basins where most flowages occur usually are classified as wetlands regardless of beaver activity (Wilde et al. 1950: Cowardin et al. 1979; USFWS 1991). Therefore, most beaver-*created* wetlands actually are habitats that beaver have *altered* from one wetland class to another (e.g. forested to herbaceous).

Although the return of beaver may not have increased the total area of wetlands, it probably did increase wetland productivity. Generally, water level changes contribute to the productivity of wetlands more than any other factor; fluctuations allow oxidation of anaerobic soils, which accelerates organic decomposition, resulting in the release of limiting nutrients such as nitrogen and phosphorus (Mitsch and Gosselink 1986; Weller 1987). The behavior of beaver, and the dynamics of their populations, guarantees that dams are continually built, repaired, abandoned, and rebuilt, thus ensuring oscillating water levels. Furthermore, because most flowages have small watersheds, they also are likely to experience fluctuations caused by climatic factors; draw-downs can occur during summer when water loss exceeds water gain, resulting in an oxidized perimeter band, and subsequent enrichment.

The addition of 77 flowages to the Monroe watershed increased the proximity of wetlands to one another, a condition that appears to benefit many species. For example, to satisfy foraging requirements, black ducks (*Anas rubripes*) often include several wetlands within their home ranges (Ringleman et al. 1982). Consequently, when the density of wetlands increases, the need for energy-costly flight decreases. This may improve reproductive performance because increased flying negatively alters the energy budget of ducks producing eggs (Wooley and Owen 1978; Owen and Reinecke 1979). Also, an increase in the number of habitat patches within a given area disperses waterfowl, which reduces intraspecific competition and predation (McCall 1994).

In Iowa, the number of marsh bird species decreased as wetlands became more isolated (Brown and Dinsmore 1986). The same effect was observed in Maine where isolated wetlands received less use by 15 species of water birds than did wetlands that occurred close together (Gibbs et al. 1991). Gibbs (1993) concluded that an increase in inter-wetland distances in south-central Maine, caused by the elimination of wetlands less than 10 acres (4 ha), would heighten the risk of extinction for small birds and mammals, and turtles. It seems probable that the return of beaver, and hence flowages, had the opposite effect while also increasing the abundance of many species.

Of course, the decrease in inter-wetland distances, like the increase in the number and total area of flowages, represents the return of the landscape to a more normal condition. Prior to the arrival of Europeans, beaver flowages probably were an integral part of the North American landscape. However, centuries of unregulated trapping depleted stream systems of beaver, and beaver-created wetlands. In this century, beaver have, to the benefit of many species, reestablished their unique wetlands in the landscape mosaic.

MANAGEMENT IMPLICATIONS

Today, beaver are a controversial species that can have well-known, adverse effects on human property. However, our perception of beaver should be formed in an historical light. For hundreds of years there were very few beaver-related "problems" because beaver were eliminated by the avarice of the Fur Trade. In the absence of beaver, vegetational succession also was altered, allowing forests to colonize wetlands (much of the timber we now lose to beaver had a chance to grow where it did only because of our past excesses). But the removal of beaver from the ecosystem was an unnatural, and ecologically unhealthy, situation.

If one accepts the premise that "natural" ecosystems are better than ones greatly disturbed by humans, then the return of beaver is a positive event. Many species, including humans, derive extensive benefits from beaver-created wetlands. The challenge to managers is to make people aware of this fact, while also minimizing human-beaver conflicts.

Problems associated with beaver (e.g. clogged culverts) are often blamed on "over-population." However, in the Monroe watershed the majority of flowages created between 1939 and 1991 were located away from roads and houses; only two of 77, both inactive during the study, were located beside roads. Also, only a fraction of flowage sites were occupied by beaver at any one time. Therefore, habitats removed from roads and houses were, in a physical sense, always available.

Beaver harvest hardwoods around the perimeter of flowages, and generally leave conifers (e.g. hemlock, balsam [*Abies balsamea*] and spruce), which they seldom eat (Jenkins 1974). This behavior degrades habitat by creating riparian zones dominated by unpalatable conifers (Northcott 1971;

Bergerud and Miller 1977; Naiman et al. 1988). Following several decades of beaver presence in the Monroe watershed (and most of Maine), stocks of riparian hardwoods are reduced. As a result, use of less traditional sites (e.g. road embankments) may be increasing as beaver search for new food sources. If there is a correlation between degradation of beaver habitat and increased human-beaver conflicts, then an increase of food stocks in flowages would help solve the problem (combined with the tools presently employed: water-level-control devices and regulated trapping).

In Maine, statutes prohibit timber harvesting along streams, wetlands, and lakes, in recognition of the ecological value of these ecosystems. However, if amendments were created that allowed the cutting of conifers around flowages (assuming it was done in an environmentally-sensitive manner), early-successional hardwoods would become more common, and beaver habitat would be improved. State wildlife managers could carry this approach one step further by selecting a number of high-quality wetlands (large size, high p/d ratio, and moderate stream flow rate) to be managed specifically for aspen and other hardwoods. These strategies might decrease human-beaver conflicts by "holding" beaver in more remote locations. Also, by stimulating beaver activity, wetland productivity would increase. Increased wetland productivity would benefit many wild species, as well as trappers, hunters, and people who, in a non-consumptive manner, enjoy wildlife.

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APPENDIX. Select characteristics of wetlands in the Monroe watershed.

Wetland Name	ID #	Origin*	Year**	Area (m^2)
Great Farm	1	B	74	27,084
Stantial	2	B	74	54,776
Dollar	3	B	74	14,151
Penny	4	B	74	2,451
Nickle	5	B	74	4,980
Dime	6	B	91	5,358
Quarter	7	B	91	7,115
Norum	8	B	74	7,971
Bega	9	B	74	24,101
Hemlock	10	B	91	28,172
Common Hill	11	B	91	9,069
Long	12	B	91	68,302
Mill Pond	13	B	91	11,174
Tee	14	B	91	28,390
Bucky	15	B	91	14,867
Kate	16	B	91	9,680
Mac	17	B	91	10,879
Elbow	18	B	91	4,612
Dissected	19	B	74	13,763
Tad	20	B	91	8,073
Duck	21	B	74	23,341
Great Farm Brook	22	B	91	14,014
Mason Hill	23	B	74	1,238
Roundy	24	B	74	6,015
Hardluck	25	B	91	10,753
Upper Ludden	26	B	91	2,089
Middle Ludden	27	B	91	1,385
Ludden	28	B	91	16,379
Cryptic 1	29	B	91	13,192
Cryptic 2	30	B	91	9,338
Cryptic 3	31	H/B	74	9,966
No Trespass 1	32	B	91	6,354
No Trespass 2	33	B	91	2,610
No Trespass 3	34	B	91	1,979
No Trespass 4	35	B	74	20,419
No Trespass 5	36	B	74	12,693
Drakewood 1	37	B	91	2,536
Drakewood 2	38	B	91	32,481
Hook	39	B	91	35,325
Drake E	40	B	91	7,312
Drake BC	41	B	74	1,181
Drake Extension	42	B	57	10,355
Skip's	43	B	74	6,492

Drake H	44	B	91	1,688
Drake A1	45	B	91	7,773
Drake A	46	B	74	3,499
Drake	47	N/B/H	39	169,181
Lisle	48	B	91	14,110
Emma	49	B	91	2,684
Lower Drake	50	B/H	39	179,118
Eversong	51	B	91	6,613
Decoy Impound.	52	H	74	12,557
Midge	53	B	91	7,133
Elsie	54	B	91	7,345
Pers Bog Upper	55	B	74	9,578
Pers Bog	56	B	57	200,308
Pers Bog Flowage	57	B	74	13,369
Pers Bog Lower	58	B	57	19,583
Pers North Annex	59	B	74	9,967
Pers Annex	60	B	91	18,711
Pers	61	B	39	98,568
Pers South Annex	62	B	91	17,091
Pit Pond	63	B	91	3,779
Nason	64	B	91	4,547
Marsh Upper 2	65	B	91	6,083
Marsh Upper	66	B	91	2,491
Plummer Hill	67	B	91	5,681
Olney South	68	B	74	7,431
Olney Brook	69	B	57	244,756
Olney North	70	B	74	7,695
Olney East	71	B	74	8,574
Croxford	72	B	57	19,701
Demmon Upper	73	B	91	14,023
Demmon	74	B	91	8,749
Chase Bog	75	H/B	39	587,416
Federal	76	H	74	27,342
Snagtooth 2	77	B	91	5,867
Snagtooth 1	78	B	91	23,116
State	79	H	74	36,339
York Flowage	80	B	74	3,409
York Kettle	81	N/B	39	15,247
York Pond	82	H/B	39	14,960
Hidden	83	B	91	3,610
Glyceria	84	B	57	11,095
Northern Pond	85	N/B	39	135,683
Harmony	86	B	74	9,576

*B=beaver, H=human, and N=natural. **when first seen on photographs.

BIOGRAPHY

Laurence "Skip" Lisle, II was born in Townshend, Vermont on May 17th, 1958. He graduated from Bellows Falls (Vermont) Union High School in 1976. In 1980, he earned a B.S. Degree in Geography at Plymouth (New Hampshire) State College where he also played on the football and baseball teams. He has attended the Shelter Institute Owner/Builder School in Bath, Maine, and the Audubon Ecology Camp in Bremen, Maine.

Skip has worked as a cordwood dealer, house painter, carpenter, and biologist. His carpentry experience includes timberframing (post and beam) and colonial renovation. In 1986, he assisted a sharp-tailed grouse research project in Idaho for the Bureau of Land Management. His lifelong avocation has been to improve the habitat value of a family-owned woodlot and wetland in southern Vermont. A second avocation saw him play ten years for the Saxtons River (Vermont) Pirates semi-pro baseball team.

In 1990, Skip and his wife Elise were married. They have a daughter, Emma, who was born in June, 1992. Also in 1990, Skip entered graduate school at the University of Maine at Orono. There, he worked two summers for the Department Wildlife Ecology mapping wetlands and recording beaver activity. He received his Master of Wildlife Conservation degree in May, 1994.