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# LONG-TERM POPULATION DYNAMICS OF THE NORTH AMERICAN BEAVER, *CASTOR CANADENSIS*, ON QUABBIN RESERVATION, MASSACHUSETTS, AND SAGEHEN CREEK, CALIFORNIA

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## ABSTRACT

Long-term research and monitoring activities on the Quabbin Reservation in west-central Massachusetts have provided an opportunity to follow changes in numbers and dynamics of a local unexploited beaver, *Castor canadensis,* population over a 45-year period. Beavers returned to the area in the early 1950s, following an absence of more than 200 years. Since then interpretation of aerial photographs, anecdotal reports from early researchers and watershed managers, and starting in 1968, complete annual censuses of all active beaver sites on the 5,018 ha Prescott Peninsula, have identified distinct periods of population change. The first 15 years were characterized by relatively slow growth. This period was followed by another 15 years of very rapid growth of the population. By the early 1980's growth had slowed, and the population experienced a period of rapid decline finally stabilizing at a level approximately 23% of its peak. Various changes in productivity, colony composition, dispersal and interactions with other wildlife species were associated with these periods of population change. The changes observed in the Quabbin Reservation beaver population are comparable to changes in an unexploited beaver population in California. Research on the California beaver population has documented similar periods of rapid growth and subsequent decline.

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# 1. INTRODUCTION

The North American beaver, Castor canadensis, was effectively extirpated from most regions of the United States due to intense hunting and trapping pressure by the mid to late 1800s (Jenkins and Busher, 1979; Larson and Gunson, 1983). During the 1900s management programs designed to protect beavers from trapping, coupled with a decline in the market for fur allowed beavers to re-colonize many parts of their former range. Active reintroduction programs were also instituted in many regions. Larson and Gunson (1983), in a summary of the 1981 status of beavers in North America, list 13 of 50 states as having current populations due to introductions, while 36 of 50 states have current populations that grew from remnant populations. One state, New York, is listed as an unknown status. Schulte and Müller-Schwarze (this volume) summarize the growth of beaver populations in the United States and Canada from 1600 to the present. Using data published by Naiman, Melillo, and Hobbie (1986) the beaver population is estimated to be between 6 and 12 million at the present time. The increase in regional beaver populations, particularly in states with high human densities, has in turn led to an increase in the number of beaver nuisance reports. This is true in all the New England states. With a decline in trapping intensity, and low to non-existent predation pressure, many beaver populations in the United States are increasing in a virtually unexploited condition. It is critical to observe and analyze the demographic trends in these populations if biologically sound and effective management plans are to be developed. Conservation biologists in Europe and the United States, can also use this population information to predict the long-term impact of beaver introductions in areas currently without any beavers, or with small populations.

Population data have historically come from regions where beavers were subjected to trapping and hunting pressure. However, in most parts of the United States, there is at present much less trapping and hunting pressure than existed in the past. This allows many beaver populations to exist under relatively natural (not human influenced) conditions. However, few long-term studies of unexploited populations in the United States have been conducted. Long-term (10 or more years) studies have been conducted in Ohio (Svendsen, 1980, 1989), New York (Müller-Schwarze and Schulte, this volume), California (Busher, 1975, 1980, 1987; Hall, 1960; Taylor, 1970), Massachusetts (Bollinger, 1980; Brooks, 1977; Fleming, 1977; Hodgdon, 1978; Howard, 1982; Lancia, 1979; Lyons, 1979a) and Minnesota (Smith and Peterson, 1988). All of these studies have, to some extent, employed livetrapping, marking and observation of animals in open systems. There was also little if any predation pressure on most of these populations, although there were predators (wolves) in the Minnesota study area. That population is also subjected to water fluctuations caused by human activity. Another long-term study is on Isle Royale National Park, Michigan (Shelton, 1966; Shelton and Peterson, 1983). Isle Royale is an isolated island with a healthy predator (wolf) population and can functionally be considered an exploited system.

This paper documents the population dynamics and demographic changes in an unexploited beaver population in western Massachusetts over a 45 year period. We also compare this population to an unexploited population in California over a similar period.

# 2. METHODS

## 2.1. Study Areas

The study was conducted on the Prescott Peninsula, Quabbin Reservation, located in west-central Massachusetts (42° 25' N, 72° 20' W) (Figure 1). The Reservation, which con-

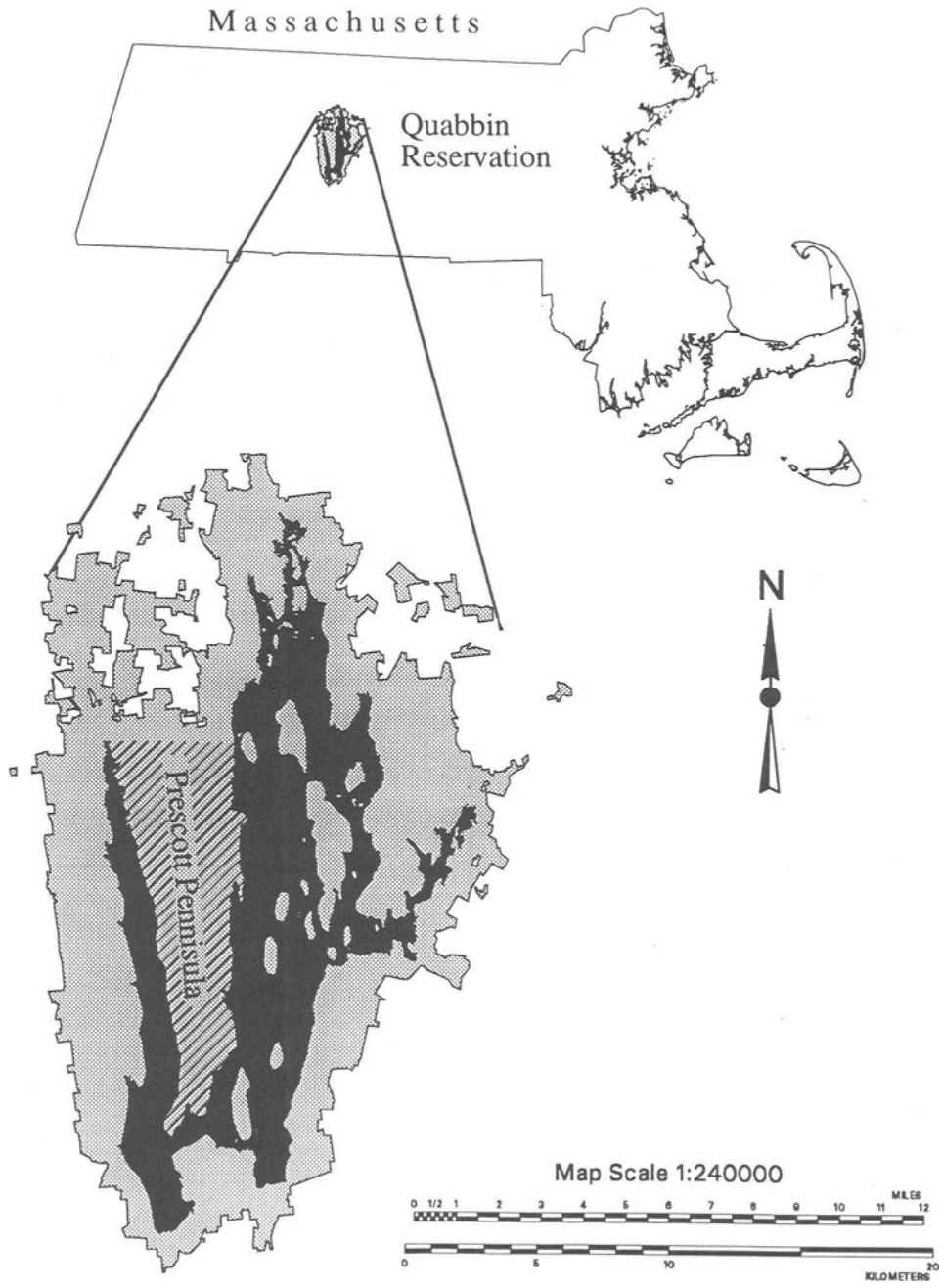


**Figure 1.** Location of Quabbin Reservation, Massachusetts. The highlighted area shows the location and relative size of the Prescott Peninsula.

tains the watershed and major reservoir for the drinking water supply for the metropolitan Boston area, was created in 1939 by damming the Swift River and Beaver Brook. The area of the reservation is 335 $km^2$ and the reservoir is 100 $km^2$. The climate consists of warm, usually moist summers and cold winters with major periods of snow. The construction of the reservoir and creation of the watershed area caused the relocation of 2500 people and the complete destruction of three towns (Hodgdon, 1978; Lyons, 1996). The reservoir was filled to maximum capacity by 1946. The Prescott Peninsula has an area of 50 $km^2$, is 16 km long and narrows from north to south (4.8 km to 0.6 km). The peninsula is heavily forested (approximately 92%) with dominant deciduous trees being red maple (*Acer rubrum*), oak (*Quercus* spp.), ash (*Fraxinus* spp.), and birch (*Betula* spp.). Eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and hemlock (*Tsuga canadensis*) are the most common conifers on the peninsula (Hodgdon, 1978).

The Quabbin Reservation is managed as a watershed by the Metropolitan District Commission (MDC) an agency of the Commonwealth of Massachusetts. In addition to serving as the water supply for approximately 3 million people in eastern Massachusetts, the reservation provides forest products, recreational opportunities, wildlife observation and research, and cultural resource protection. One of the unique features of the watershed and reservoir is that human use has been strictly controlled since its inception. Until recently, there has been a complete prohibition of trapping and hunting on the reservation and, especially on the Prescott Peninsula, wildlife populations have been allowed to exist with little human interference. Beavers on the Prescott Peninsula have been, and are found on small streams, larger streams, ponds and along the shore of the reservoir.

Sagehen Creek is located on the east slope of the Sierra Nevada in Nevada county, California (Figure 2). The stream originates from natural springs at an elevation of 2400 m and flows 13.5 km to the east where it empties into Stampede reservoir at 1800 m in elevation. The Sagehen Creek basin supports a variety of habitats from moist stream-side meadows and hanging bogs to dry, rocky meadows. The meadows are interspersed with mixed coniferous forests composed of Jeffrey pine (*Pinus jeffreyi*) and lodgepole pine (*Pinus contorta*) at lower elevations and red fir (*Abies magnifica*) and western white pine (*Pinus monticola*) at the higher elevations. Savage (1973) and Trowbridge (1975) describe the vegetation in the basin. Along the stream the dominant shrubs are four willow species (*Salix* spp.) and mountain alder (*Alnus tenuifolia*). Stands of quaking aspen (*Populus tremuloides*) are also found along the stream. The climate is characterized by warm, dry summers and cool wet winters with heavy snowfall. Sagehen Creek is a relatively small stream (width ranges from 2.0 m to 10.0 m) and ponds formed by beaver activity are much smaller than those found on the Prescott Peninsula. Taylor (1970) and Busher (1975) provide detailed maps of sections of the stream. The University of California operates a field station on the stream and the rest of the land adjacent to the stream is controlled by United States Forest Service (Tahoe National Forest).

## 2.2. Census Methods

Data on the Quabbin beaver population were collected using aerial photographs and anecdotal records from game managers during the early years (1950s and 1960s), livetrapping, mark and release during the 1960s and 1970s, and autumn food cache/activity surveys from 1969 to the present. From 1969 to 1981 the autumn surveys were in conjunction with graduate research projects at the University of Massachusetts, Amherst. From 1981 to the present the surveys have been conducted through the cooperative efforts of the MDC, the United States Fish and Wildlife Service, The Massachusetts Cooperative Wildlife Re-

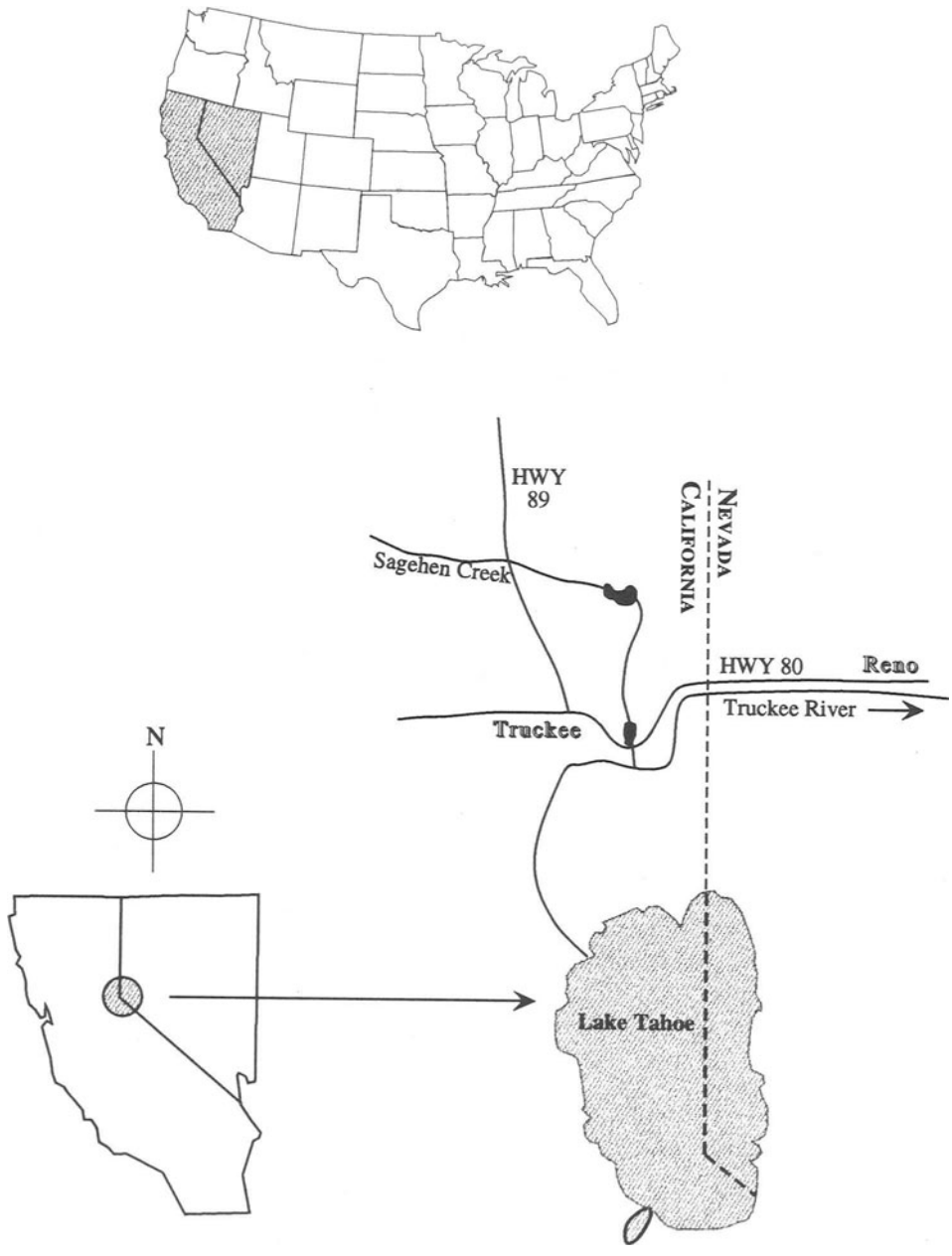


**Figure 2.** Geographic location of the Sagehen Creek Study area. The location is illustrated by showing its placement in the United States (top map), its placement in the California/Nevada region (map on left), and in a site specific map. In the site specific map Sagehen Creek is shown flowing into a connected reservoir system which is connected to the Truckee River.

search Unit, and the University of Massachusetts, Amherst. The surveys which are conducted in late November or early December each year, consist of having observers walk predetermined routes along streams, ponds, and through other potential beaver habitat on the Prescott Peninsula. A separate boat survey is used to locate active beaver sites along the reservation shoreline. Active beaver sites are identified by the presence of a food cache (usually located near a lodge), recent tree and shrub cutting, and evidence of lodge and dam maintenance (fresh mud and/or freshly cut branches). Observers record the size and composition of the cache and record any beaver sightings. Universal Topographic Map (UTM) coordinates are recorded for each active site.

The Sagehen Creek population has been censused by livetrapping, mark and release methods, coupled with intense observation of the colonies primarily during the summer and autumn. Data reported in this paper end in 1991 although anecdotal information from summer surveys the past few years is also available. Busher (1975, 1980, 1987), Busher, Warner, and Jenkins (1983), and Taylor (1970) provide more detailed information on the actual livetrapping technique.

## 2.3. Initial History of the Two Populations

Shaw (1948) reported that by the early 1900s beavers were returning to Massachusetts after being extirpated 200 years earlier. Beavers were first observed on the Prescott Peninsula in 1952 (Hodgdon, 1978) a few years after the reservoir had been filled. This paper presents the reconstruction of the Quabbin beaver population on the Prescott Peninsula from that time to the present (1997).

The Sagehen Creek population was started by the introduction of four adults (two pairs) by the California Department of Fish and Game in 1945 (Hensley, 1946). The population was initially studied by Joseph Hall (1952–1955). He was followed by Richard Gard (1954–1957), David Taylor (1958–1970), and Peter Busher (1973 -1980). Ellen Woodard studied the population from 1984–1991.

Both populations have received extensive attention from researchers examining various aspects of the populations. The Quabbin population was initially studied in the mid 1960s by Stanton (1965) and Keiper (1966) who investigated waterfowl use and macroscopic bottom fauna associated with beaver areas respectively. Hodgdon (1971, 1978) provided an extensive analysis of the population dynamics and Lancia (1979) examined the activity period of beavers using radio telemetry. Later, Brooks (1977) and Fleming (1977) tested the effects of sterilization on family structure (Brooks, Fleming, and Kennelly, 1980). This work was followed up by Bollinger (1980) and Lyons (1979a, 1979b). Olsen (1980) and Howard (1982) also contributed by examining beaver physiological condition and habitat suitability respectively. Busher (1991, 1996) investigated the selection and use of woody species during the autumn food caching period and Busher and Lyons (1988) conducted the last extensive livetrapping, mark and release effort on the Prescott Peninsula.

On Sagehen Creek, Joseph Hall investigated the use of aspen and willow by beavers (Hall, 1956, 1960). Richard Gard studied the impact of beaver activity on the aquatic macrofauna (Gard, 1958, 1961), and David Taylor conducted a long-term analysis of population and habitat changes (Taylor, 1970). In the early 1970s, Peter Busher constructed the first radio transmitters used on beavers in the United States and examined beaver movements and activities (Busher 1975). Busher followed this study by examining the population dynamics and behavior of beavers on Sagehen Creek (Busher, 1980, 1987; Busher and Jenkins, 1985; Busher, *et al.*, 1983). From 1984 to 1991 Ellen Woodard examined the behavior, activity patterns and foraging behavior of the Sagehen Creek population (Woodard, 1994).

# 3. RESULTS

## 3.1. Prescott Peninsula Population

The Prescott Peninsula population history (Figure 3) is typified by five phases. The initial phase (1952–1968) was a time of very slow population growth. During this time period the number of colonies increased from 2 to 16, which is a change of 0.82 colonies per year.

A second phase was observed beginning in 1968 (when extensive annual ground surveys began) and continued through 1975. During this time period the number of colonies increased from 16 to 46, which is an average change of 4.29 colonies per year. An increase in the number of shore colonies contributed to this rapid increase phase (Table 1).

The third phase in the population occurred between 1975 and 1983, which was a time of fluctuating population levels at a high density. Overall, the population declined by 4% (46 to 44 colonies) during this period, although year-to-year fluctuations were as high as 20%. During the second and third phases (1969–1983) there was rapid colonization of new sites on both the peninsula and the shore, and by 1983 many marginal sites were occupied.

A fourth phase occurred between 1983 and 1988 when the number of colonies declined from 44 to 12. This is a mean annual decline of 6.4 colonies. The decline during this period was precipitated by a reduction in the number of shore colonies from 13 in 1983 to one in 1985, 1986 and 1987. By 1988 no shore colonies were present.

The period from 1988 to the most recent survey in 1996 represents the fifth phase in the population. During this time the number of colonies has ranged from a low of 10 to a high of 15. The average change (a decrease) is 0.125 colonies per year during this period of relative stability at low population levels.

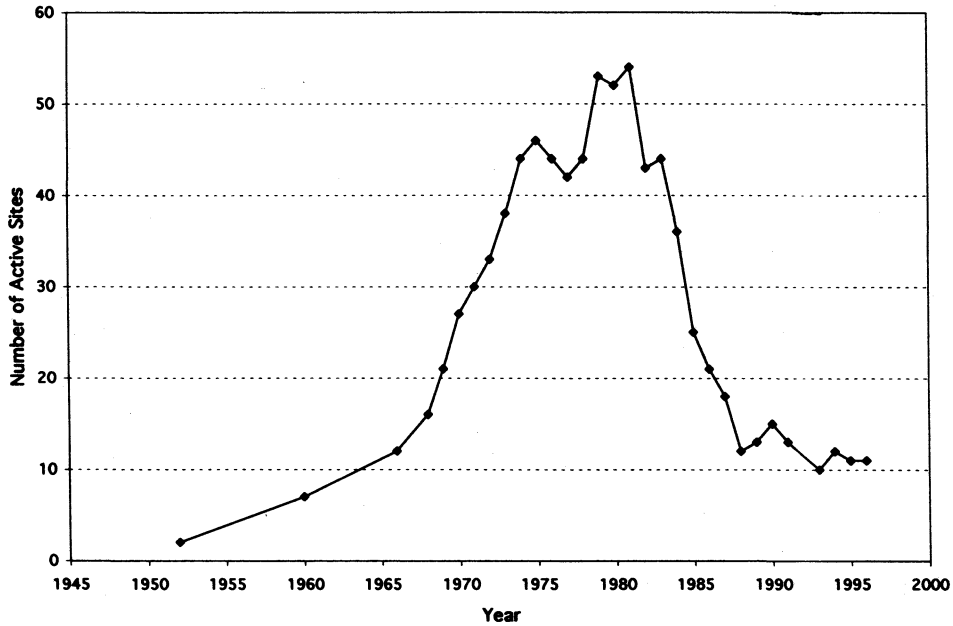


**Figure 3.** Results of beaver population surveys on Prescott Peninsula, Quabbin Reservation, Massachusetts, 1952–1996.

**Table 1.** Number of active beaver colonies on Prescott Peninsula, Quabbin Reservation, Massachusetts, 1952–1996

| | Number of active sites | | |
|---|---|---|---|
| Year | Interior | Shore | Total |
| 1952 | 2 | 0 | 2 |
| 1960 | 7 | 0 | 7 |
| 1966 | 12 | 0 | 12 |
| 1968 | 16 | 0 | 16 |
| 1969 | 18 | 3 | 21 |
| 1970 | 21 | 6 | 27 |
| 1971 | 24 | 6 | 30 |
| 1972 | 22 | 11 | 33 |
| 1973 | 23 | 15 | 38 |
| 1974 | 26 | 18 | 44 |
| 1975 | — | — | 46 |
| 1976 | 30 | 14 | 44 |
| 1977 | 28 | 14 | 42 |
| 1978 | 30 | 14 | 44 |
| 1979 | 36 | 17 | 53 |
| 1980 | 35 | 17 | 52 |
| 1981 | 39 | 15 | 54 |
| 1982 | 29 | 14 | 43 |
| 1983 | 31 | 13 | 44 |
| 1984 | 24 | 12 | 36 |
| 1985 | 24 | 1 | 25 |
| 1986 | 20 | 1 | 21 |
| 1987 | 17 | 1 | 18 |
| 1988 | 12 | 0 | 12 |
| 1989 | 13 | 0 | 13 |
| 1990 | 13 | 2 | 15 |
| 1991 | 11 | 2 | 13 |
| 1993 | 7 | 3 | 10 |
| 1994 | 9 | 3 | 12 |
| 1995 | 11 | 0 | 11 |
| 1996 | 10 | 1 | 11 |

The age-class composition of the population (Table 2) is drawn from data presented by Hodgdon (1978) and from Busher and Lyons (1988). In 1969 at the beginning of the increase phase there were 35.6% adults, 5.8% 2-year-olds, 25% yearlings, and 33.7% kits. By 1974 when the population was approaching the first peak Hodgdon (1978) reported a total population size of 257 animals. The composition in 1974 was 37.4% adults, 3.5% 2-year-olds, 28.8% yearlings, and 30.4% kits. The total number of animals, and the age composition changed dramatically by 1988. Busher and Lyons (1988) reported only 40 animals in the population and an age-class composition with 47.5% adults, 20% 2-year-olds, 17.5% yearlings, and 15% kits. This year (1988) represents the end of the decline phase and the beginning of the stabilization phase at low population levels.

## 3.2. Sagehen Creek Population

Sagehen Creek includes a much smaller area than the Prescott Peninsula and supported a smaller number of beavers and colonies. For Sagehen Creek the number of bea-

**Table 2.** Age-class composition on the Prescott Peninsula, Massachusetts, during selected years

| Year | Adult | 2-year-old | Yearling | Kit | Total number |
|---|---|---|---|---|---|
| 1969 | 35.6 | 5.8 | 25 | 33.7 | 104 |
| 1974 | 37.4 | 3.5 | 28.8 | 30.4 | 257 |
| 1988 | 47.5 | 20 | 17.5 | 15 | 40 |

In 1969 the population was at the beginning of the increase phase, in 1974 the population was at the end of the increase phase and entering the high density phase, and in 1988 the population was entering the low density phase.

vers (not the number of colonies) is represented (Figure 4). Additionally, the stream is bisected by California State Highway 89, and the section west of the highway has been studied most intensively and only data from this section are presented here. The Sagehen Creek population, much like the Prescott Peninsula population, had an initial phase of slow growth, a second phase of more rapid increase, followed by a third phase of relative stability at high numbers, and a fourth phase of sharp decline. The decline was followed by only a few years of relative stability at low numbers. The Sagehen Creek population, unlike the Prescott Peninsula population, had a fifth phase characterized by rapid population growth. This phase was in turn followed by a second decline phase (1979–1991).

The initial period of slow growth was between 1948–1956. Beavers colonized the eastern sections of the stream first, but by the late 1940s and early 1950s were also using areas west of the highway. The population increased from an estimate of two animals in 1948 to 10 in 1956. The average increase was 1.0 beavers per year during this period.

During the second phase, from 1956 to 1959, there was a sharp increase from 10 animals to approximately 20 animals for an average annual increase of 3.3 animals. The

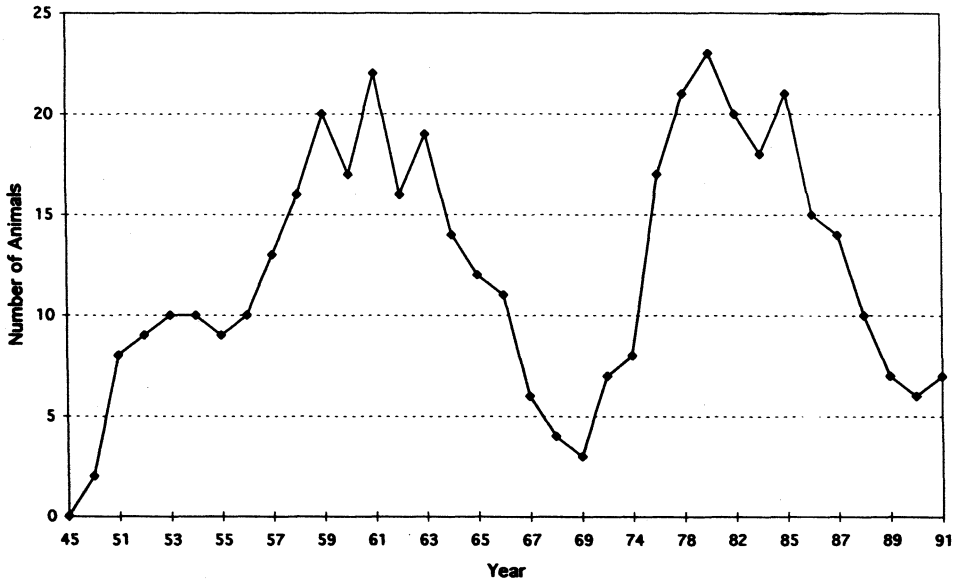


**Figure 4.** Results of the beaver surveys on the western section of Sagehen Creek, California, 1945–1991.

beavers colonized the upper sections of the stream during this time and the family groups became well established.

The period 1959–1963 (phase three) represented 5 years of relative stability in number of animals (ranging from 18–22). Twenty animals were present in 1959 and 20 were present in 1963. Taylor (1970) reports four well established family groups on this section of stream during this period.

The fourth phase (1963–1969) was characterized by a sharp decline in the number of beavers. Taylor (1970), reported that by 1969 there was only one active colony on this section of stream and it was composed of only one pair of adults. There was an average decrease in the number of beavers during this period of 3.0 animals per year.

During the fifth phase (1969–1979) the number of beavers increased from 2 to 23, which is an average increase of 2.1 beavers per year (Busher, 1987). The number of colonies ranged between two and four during this phase. In 1982 R. N. Brown conducted an unpublished, one summer study and reported a small decline in number to 20 beavers. This was the beginning of a second decline phase.

Ellen Woodard studied the population from 1984 to 1991, and documented the decrease in number of beavers during these years. Woodard reported that the population declined from 18 animals in 1984 to 7 animals in 1991. The beaver numbers were affected by two drought years, and animals moved from the western section of the stream to the eastern section at that time (Woodard, 1994; and pers. comm.).

## 4. DISCUSSION

The Prescott Peninsula and Sagehen Creek beaver populations show a similar pattern of growth, stabilization and decline. The populations are different in that the Prescott beavers have stabilized at a low density while the Sagehen beavers increased a second time and then declined again. While the dynamics of the two populations are similar, the areas are quite different in geographic location, size, vegetation, topography, elevation, and stream characteristics. The Prescott Peninsula has a number of large persistent ponds fed by small streams, while Sagehen Creek is one small stream (average width is approximately 5 m). From both management and conservation biology points of view the growth, peak and subsequent decline of both populations provide insight into beaver population dynamics in unexploited populations.

The Prescott Peninsula population initially exhibits the classic sigmoid growth pattern that is often associated with populations colonizing new habitat (Caughley, 1977, Elton, 1958). The rapid decline between 1984 and 1988 indicates that beavers had colonized all available habitats including many marginal areas. Hall (1960) suggested that beavers will utilize a food resource in an area then move to another area leaving the first site vacant for a number of years. This behavior of habitat rotation allows food resources to rebound after beaver occupation. On the Prescott Peninsula many marginal areas were occupied by the early 1980s. For beavers living in these marginal areas, once the food resources were depleted and they were forced to move, there were few if any high quality unoccupied sites available on the peninsula. Thus, beavers were forced to leave the peninsula or perish. The drastic decline in the number of shore colonies from 1988 to the present suggests that shore sites are not optimal for beaver occupation. The shore sites are subject to water fluctuations during drought years when the reservoir is not full. However, the reservoir has not been at low levels every year since 1988.

Further evidence that the Prescott Peninsula is at carrying capacity for beavers is the change in the age-class composition that occurred between the time of peak population

size (early 1970s) and 1988 (the last trap, mark and recapture study). In 1974 Hodgdon reported that 59.2% of the population was pre-reproductive animals (yearlings and kits) (Hodgdon, 1978). In 1988 only 32.5% of the population was pre-reproductive. In 1974, 2-year-old beavers were only 3.5% of the total population while in 1988 they were 20%. This suggests a reduction in dispersal of these young adult animals. Lack of dispersal in beavers is observed at very high population densities associated with habitat saturation (Bergerud and Miller, 1977; Novakowski, 1965; Busher, 1987; Müller-Schwarze and Schulte, this volume). However, lack of dispersal can also occur at lower densities or in areas where little or no quality habitat is available (after all the marginal sites have been used and abandoned). When Hodgdon (1978) observed a high rate of 2-year-old dispersal at high densities there were still suitable (although marginal) areas available for dispersing animals. However, once these marginal sites had been occupied and then later abandoned, they were not suitable sites able to sustain dispersing 2-year-old beavers.

A second factor that may have influenced the beaver population is the occurrence of whitetail deer, *Odocoileus virginianus*, on the peninsula. The deer population was very dense through the 1980s. Deer reduce the regeneration of trees by eating the saplings. There is evidence that deer activity on the peninsula was inhibiting forest regeneration. Thus, woody species that beaver would have used for food after they regenerated were being removed by deer. This interaction between deer, regenerating forage trees, and beaver could account for the most recent population phase (a low density, stable population). A controlled deer hunt on the peninsula was instituted in 1990 and an increase in forest regeneration is being observed. The Prescott Peninsula beaver population may show a similar rebound phase much like the Sagehen Creek population in the future.

Both study areas have been subject to beaver habitat classification studies. Howard and Larson (1985) developed a stream habitat classification system for beaver using information from the Prescott Peninsula population. They found that water reliability variables significantly affect colony site longevity, while food availability was considered less important. However, they do note that the relationship between water reliability and aquatic plant productivity is critical since beaver may use aquatic plants for food during both summer and winter.

Beier and Barrett (1987) evaluated habitat use and impact by beavers in the area around Sagehen Creek. They state that, "Stream gradient, stream depth, and stream width were clearly the most important factors related to beaver habitat use..." They continue by saying that, "Vegetation variables added little explanatory power to the functions." They considered the suitable beaver habitat in the entire Truckee River basin (including Sagehen Creek) to be saturated with beavers when the study was conducted (May–August, 1985). The second decline phase of the Sagehen Creek beaver population in the late 1980s supports this view of habitat saturation. It is possible that after two periods of high beaver numbers (early 1960s, 1970s) the vegetation in potentially marginal habitat may have been effectively depleted. Stream width is a critical variable in the Beier and Barrett study. Many sections of the western part of Sagehen Creek are 5.0 m or less in width well below the average width of 8.1 m associated with active colonies. Thus, the combination of marginal physical requirements of the stream, coupled with intensive occupation and food utilization by beavers may have led to the latest population decline. Summer and autumn surveys on Sagehen Creek are being planned for 1999 to determine the extent of re-colonization of the area.

These two unexploited populations, while geographically different, do provide a picture of what can be expected when beavers are introduced to or move into an area. Habitat classification studies such as those by Beier and Barrett (1987), Hartman (1996), Howard and Larson (1985), and Slough and Sadlier (1977), are useful in predicting areas that will

support long-term beaver occupation. However, as is evident from the Prescott Peninsula population, even marginal sites will be utilized in virgin habitat when populations are dense. These data from two unexploited populations will aid conservation biologists and wildlife managers when they develop long-term (10–50 year) beaver management plans.

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