NOMENCLATURE

COMMON NAMES: Beaver, North American beaver, Canadian beaver, American beaver, el Castor

Scientific Name: Castor canadensis


Castor canadensis (hereafter beaver) is endemic to North America and is one of two extant species in the genus Castor. Castor fiber (hereafter Eurasian beaver) is endemic to Europe and Asia, although its current range is severely reduced relative to its historical range. The general physical appearance of the two species is similar, but their karyotypes and several cranial and behavioral patterns are distinct (Lavrov and Orlov 1973). Multilocus allozyme electrophoresis can distinguish Castor canadensis from C. fiber using tissue or blood samples from either live or dead animals, which makes the technique useful as a management tool for restoration of C. fiber in Europe (Sieber et al. 1999).

C. c. acadicus, C. c. canadensis, C. c. carolinensis, and C. c. missouriensis are the most widespread subspecies of beaver in North America (Hall 1981), however, reintroductions following extirpation have substantially altered pristine geographic variation among subspecies. The gene pools of some subspecies have been altered through introductions and subsequent mixing with other subspecies. Some subspecies may have disappeared entirely. Because subspecies are difficult to determine even with an animal in hand, subsequent discussions will be limited to species.

Fossil remains of a giant beaver, genus Castoroides, and a number of closely related prehistoric mammals also have been found in North America (Cahn 1932). The family Castoridae dates to the Oligocene and was highly diversified in the Tertiary period in North America (Kowalski 1976). The genus Castor dates to the Pleistocene (Garrison 1967) or late Tertiary (M. Schlosser 1902).

DISTRIBUTION

Historical Range. Seton (1929) estimated the beaver population at 60–400 million before European settlement of North America. Beaver occurred throughout the subarctic of mainland Canada below the northern tundra and the mouth of the Mackenzie River in the Northwest Territories (Novakowski 1965). They were widespread in Alaska, except along the Arctic Slope from Point Hope east to the Canadian border (Hakala 1952). Within the contiguous United States, they occupied suitable wetland and riparian habitat from coast to coast, even in the arid southwest. They were generally absent from the Florida peninsula and parts of southern California and southern Nevada. Although their original range in Mexico is difficult to determine, they were present in the Colorado River and Rio Grande River (Leopold 1959) as well as some coastal streams along the Gulf of Mexico.

Despite their legendary abundance, most beaver populations were decimated by fur trappers during the 1700s and 1800s, primarily to support the European fashion for felt hats (Bryce 1904). Large trading companies, such as the Hudson Bay Company, employed Europeans and Native Americans who supplied furs without regard for method or season of take. Because trappers continually moved to new territory, they likely were unaware of their cumulative effects on entire populations. In addition, intense harvest likely caused the local destruction of population structures, contributing to regional declines (Ingle-Sidorowicz 1982). Beaver populations in the eastern United States were largely extirpated by fur trappers before 1900. Growing public concern over declines in beaver and other wildlife populations eventually led to regulations that controlled harvest through seasons and methods of take, mitigating a continent-wide recovery of beaver populations. To supplement natural recovery, during the mid-1900s beavers were reintroduced and successfully reintroduced into much of their former range, a remarkable achievement of early wildlife managers. Although the area of pristine beaver habitat has been much reduced by human land-use practices, beaver have proved to be highly adaptable and occupy a variety of human-made habitats. In addition, beaver have been intentionally or accidentally introduced into areas outside their original range. Thus, the present range of beaver is a result of natural recovery and reintroduction to their original range, introduction and expansion into areas beyond their original range, the limits of native habitat as modified by human land uses, and adaptability to new human-made habitats such as urban areas, croplands, and areas with exotic vegetation.

Present Range. Beaver populations were estimated at 6–12 million by Naiman et al. (1988). Beaver now occupy much of their former range in North America, although habitat loss and other causes have severely restricted populations in many areas (Fig. 15-1) (Hall 1981; Larson and Gunson 1983). For example, since 1834, about 195,000–260,000 km² of wetlands has been converted to agricultural or other use in the United States, much of which was likely beaver habitat (Naiman et al. 1988). Nonetheless, beaver are remarkably adaptable. They can marginally exist above timberline in mountainous areas; however, beaver have been unable to colonize Alaskan or Canadian arctic tundra, perhaps because tundra vegetation lacks essential woody plants for winter food and lodge construction or because thick ice limits surface access in winter. Although suitable beaver habitat in Canada has been reduced since pre-European settlement, fur harvest records indicate that beaver populations have fully recovered in many areas, perhaps a result of a return to earlier successional stages of forest cover (Ingle-Sidorowicz 1982). In the United States, beaver populations have continued to increase since major reintroductions ended in the 1950s. Populations in southeastern states have grown large enough to become a major nuisance to the timber industry and others (Larson and Gunson 1983). In the Far West, they have been reestablished in the Santa Ana and Colorado River systems of southern California. In Mexico, beaver may still subsist in some northern areas of Nuevo Leon and Chihuahua (Leopold 1959), although populations there likely are marginal (Landin 1980).

Beaver

Castor canadensis

Bruce W. Baker

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DESCRIPTION

Beaver are the largest rodents in North America. Most adults weigh 16–31.8 kg and attain a total length of up to 120 cm. They have heavily muscled bodies supported by large bones. Forelegs are shorter than hind legs, which results in greater height at the hips than at the shoulders. Viewed dorsally, beaver are short and thick, broadest just anterior to the hips, and taper gradually toward the nose; a short, thick neck appears almost continuous with the shoulders and head. Their most characteristic feature is a dorsally flattened, paddle-like tail, the unfurred portion of which in most adults varies from 230 to 323 mm long and from 110 to 180 mm wide (Davis 1940). The distal three fourths of the tail is covered with black, leathery, uncornified scales (Kowalski 1976). The ears are rounded, short (30 mm), fleshy, and placed high on the rear of the head. The small eyes also are located high on the head, about midway between the nose and the base of the skull. Both these adaptations enable beaver to swim with minimum exposure above the water surface.

Pelt coloration is variable within and among populations, with reddish, chestnut, nearly black, and yellowish-brown specimens possible in the same watershed. Fur of the flanks, abdomen and cheeks is usually shorter and lighter than back fur. Guard hairs are about 10 times the diameter of the hairs constituting the underfur, giving the pelt a coarse appearance. Guard hairs attain their greatest length (50 mm) and density along the back. Underfur is longest on the back (25 mm) and has wavy individual hairs, which give the pelt a downy softness. It may be dark gray to chestnut in color on the back and, like the guard hair, becomes lighter in color on the sides and ventral areas. Unlike the case in many furbearers, coloration of individual guard hairs is usually consistent throughout their length.

Two inside (medial) toes of each hind foot have movable, split nails, which beaver use as combs to groom their fur (Wilson 1973). Beaver have cloacal nostrils, valvular eyes, nictitating eye membranes, and lips that close behind large incisors, adaptations important to their semiaquatic existence. During periods of active lactation and when parturition is near, fetal corpora lutea are discernible on the chest of the adult female. During pregnancy, beaver have a subplacenta located between the placenta and uterine tissues. Although its morphology has been well described, its function is unknown (Fischer 1985). The reproductive organs of both sexes are internal and lie anterior to a common anal cloaca containing the castor and anal glands (Svendsen 1978). A notable characteristic of beaver is the strong aroma from the paired castor glands. Contents of the castor glands (castoreum) and anal gland secretion may be deposited during scent marking. Castoreum has been used as a base aroma in perfume and in making trapper’s lures.

Beaver skeletons are massive when compared to those of other mammals of similar length. The skull and mandible are thick and heavy, providing a strong foundation for large incisors (Fig. 15.2). A less rugged skull would be unable to withstand the physical stress and strain of jaw muscle contractions of sufficient strength to cut hardwoods such as oak (Quercus spp.) and maple (Acer spp.). The braincase is narrow and there is a small infraorbital canal. A prominent rostrum is anterior to the massive zygomatic arch. Adult skulls are very large (120–148 mm condylobasal length), which minimizes the possibility of confusing them with other North American rodents. Juvenile skulls are smaller and may be similar in size to those of adult nutria (Myocastor coypus), porcupine (Erethizon dorsatum), or mountain beaver (Aplodontia rufa); however, differences other than size are apparent on close examination. As in other semiaquatic mammals, the acetabulum is shifted dorsally (Kowalski 1976). The male beaver has a baculum that generally enlarges with age (Frye 1949) and can be palpated as an aid in determining the sex of live beavers and unskinned carcasses (Denney 1952). Osteological changes during growth and development of beaver were described by Robertson and Shadle (1954). The dental formula is 1/1, C 0/0, P 1/1, M 3/3. Incisors grow continuously and the chiseled edge is sharpened by grinding theppers against the lowers (Wilson 1971). The hard emarbled front surface of incisors serves as the cutting edge to fell trees and peel bark. Cheek teeth are hypodont and grow only through the deposition of cementum at the root base. Deciduous premolars are replaced at about 11 months of age by permanent premolars. Specializations such as large size, type and location of ears, eyes, and nose; size and function of front and hind legs; and a large, flattened tail appear to have individually and collectively enhanced the adaptability and survival of beaver in wetland environments.
Growth. Size of the adult beaver depends on latitude, climate, quality of available food, and extent of exploitation. In Alabama, a sample of 1450 beaver from an unexploited population showed mean body weight stabilized at 4 or 5 years of age and then diminished slightly after 9 years of age. Average weight of all specimens was 18.6 kg; maximum was 19.3 kg (review by Hill 1982). The relatively moderate climate of the midcontinent region may produce the largest beaver, where maximum weight can reach nearly 40 kg.

Growth of adults (body weight and tail size) occurs only in summer; however, kits (juveniles) continue to grow throughout their first winter (Novakowski 1965; Smith and Jenkins 1997). For northern beaver, winter ice formation on ponds and streams restricts or eliminates access to surface food, and adults and yearlings lose weight as fat stores are depleted. In southern beaver, adults and yearlings also lose weight in winter, even though their habitat typically remains ice free. Failure to maintain fat reserves during winter for beaver living in ice-free regions is likely not due to lack of adequate energy from available food, as it may be in the northern range, but instead may be associated with seasonal changes in physiology. Reduced food consumption, as described for captive beaver of a northern population, may also occur in southern beaver with the onset of warming trends in February and March, as beaver are frequently observed sunning themselves on lodges during clear sunny days of late winter, and early spring (review by Hill 1982).

In northern populations, Smith and Jenkins (1997) found that winter loss of body weight and tail size can vary among colonies by severity of winter, and sex and age composition of the colony. Beaver lost more body weight and tail size when winters were longer. Adults and yearlings that overwintered with young in the colony lost more weight than those without young. This supports Novakowski’s (1965) conclusion that older members of the colony eat less stored food when young are present, and rely instead on other adaptations to survive the winter.

Thermoregulation. Northern populations of beaver in winter must contend with the thermoregulatory cost of foraging under the ice in near-freezing water and must subsist primarily on stored food and metabolized fat (Dyck and MacArthur 1992). Some mammals can conserve energy in winter by reducing their body temperature through seasonal hypothermia. Researchers have suspected torpor in beaver, but studies of change in body temperature in response to freezing ambient temperatures have been equivocal. Dyck and MacArthur (1992:1671) found the body temperature of free-ranging beaver averaged about 37°C throughout the year, with “no evidence of shallow torpor in either kits or adults.” In contrast, D. W. Smith et al. (1991) found the mean daily body temperature of adult beaver declined by 1°C from fall to winter, but remained constant for kits. Body temperature can also vary by daily activity level. Before freeze-up, body temperature is higher during daylight hours, when beaver spend more time in the lodge, and lower at night, when they are away from the lodge (Dyck and MacArthur 1992). Thus, thermoregulation likely contributes to overwinter survival in beaver in combination with several other adaptations described in this chapter, including warmer winter fur, increased body fat, a stored food cache, a warmer microclimate in the lodge, huddling together in the lodge, and reduced activity in winter (D. W. Smith et al. 1991).

Digestion. Beaver are hind-gut fermenters. Digestion is enhanced by a prominent and unusual cardia-gastric gland on the lesser curvature of the stomach (Vispo and Hume 1995), a glandular digestive area (Kowalski 1976), and a large trilobed cecum containing commensal microbiota. Beaver consume a high percentage of cellulose, but maximize the nutritional value of woody plants by eating only the bark. They can digest about 32% of available cellulose by microbial action in the cecum, which is similar to the case in some other mammals (review by Hill 1982, Buech 1984). Beaver have a relatively long small intestine, 70% longer than in the porcupine, which suggests a high absorptive capacity (Vispo and Hume 1995). Consumption of soft green excrement directly from the cloaca (coprophagy) occurs diurnally in the beaver (observed as early as 10 days of age; Buech 1984) as well as in the Eurasian beaver (Wilsson 1971), lagomorphs, and other rodents. Feces are reingested and chewed by the beaver and pass quickly through the digestive system (Bier 1984). In contrast, lagomorphs reingest and swallow mucous-covered entire pellets.

Circulation. Beaver heart weights average 0.40% of body weight, which is consistent with heart ratios for other terrestrial mammals, but...
relatively small compared to fully aquatic mammals (Bisaillon 1982). The cardiac blood vessels are not specialized, but are typically mam­
alian and resemble those of both terrestrial and aquatic mammals (Bisaillon 1981). Beavers have no unused skin area for heat storage; capacities for certain changes in blood parameters, heart rhythm, and circulation en­
able them to make dives lasting up to 15 min without asphyxiation (review by Hil1 1982). Aleksus (1970:145) noted that “minute blood vessels permeate the entire tail, and a countercurrent heat exchange sys­
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REPRODUCTION AND DEVELOPMENT

Sexual Maturity. Beaver reach sexual maturity (defined as age at breeding that results in the first litter) at 1.5–3 years of age, although puberty may be reached several months before first breeding. Most studies have found at least some beaver had reached sexual maturity as yearlings (1.5–2.0 years old), although regional variation is evident (Gunson 1970) estimated that two thirds to three fourths of 2-year­
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Breeding. Beaver are monogamous, described by Svendsen (1989:339) as “characterized by a single adult pair and young forming a family, a relatively long pair-bond where desertion of a mate is rare, and turnover of mates usually occurs after the death of one of the pair.” Beaver typically breed in winter and give birth in late spring, producing only 1 litter/year. The potential breeding season is very long, with conception reported between November and March and parturition between February and November (review by Wigley et al. 1983). Latitude and climate can affect the breeding season, and parturition between February and November (review by Hill 1982). Aleksus (1970:145) noted that “minute blood vessels permeate the entire tail, and a countercurrent heat exchange sys­
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tem is present at the base.” This specialized circulatory feature helps con­tinue heat energy in extremely cold water and radiate heat during hot weather.
Development of Young. Growth curves of the fetuses were developed by Woodward (1977) for a 100-day gestation period. Curves may be useful for estimating peak periods of conception and parturition through extrapolation (Hodgdon and Hunt 1953).

Beaver kits are born precocial and fully furred, and weigh about 0.5 kg (review by Hill 1982). Lancia and Hodgdon (1983) studied the ontogeny of behavior in captive kits and found they were able to swim at 4 days and could dive and stay submerged at 2 months of age. Bipedal walking was noted at 1 month of age, and carrying construction materials while walking on the hind legs occurred at 90 days of age. Suckling peaked at 25 ml of milk/day at 1 month and decreased until weaned at 45–50 days. Zwarowski et al. (1974) noted that the anterior nipples produced 50–75% less milk than the posterior nipples. Kits can take some solid food at 1–4 weeks of age and switch to mostly solid food by 1 month. However, they may suckle for up to 3 months even though they obtain little milk, perhaps to maintain the mother-infant bond. The fur of kits is not water repellent at birth, but after 3–4 weeks of age they begin to spread anal gland secretions on their fur, which creates water repellency by 5–8 weeks. Captive kits began to dive underwater in response to alarm at 8–10 days of age and initiated tail slapping in response to alarm at 3–4 weeks of age (Lancia and Hodgdon 1983). Rudimentary scent marking began at 13–14 days of age. Thus, very young kits express some adult behaviors, but require a long period in the family to develop their complex construction ability and other skills required for independent life.

BEHAVIOR

Social Organization. Individual beaver spend most of their lives in small, closed, extended-family units traditionally called colonies. Although the term “colony” is commonly used for beaver, its use has been questioned (Hodgdon and Lancia 1983) because a colony more often describes a spatially associated collection of individual families rather than a single family unit. For example, a family of prairie dogs (Cynomys spp.) living in the same burrow system is called a cotérie and a group of families is called a colony. However, to maintain consistency with previous beaver literature, we use colony to represent an extended beaver family. Thus, a beaver colony typically contains the adult pair, young of the current year, or kits (<12 months old), and young of the previous year, or yearlings (12–24 months old). Sometimes older young may remain with the colony as subadults (>24 months old) before they disperse, especially if the available habitat is near carrying capacity (Busher 1987). A small percentage of colonies may contain more than one adult male or female (Busher 1983). Established colonies inhabit discrete and defended territories. Dispersing beaver of both sexes, also called floaters, remain transient until they settle with an unpaired beaver or they build dams or lodges, which may help attract a mate. Compared to many other mammals, especially other rodents, beaver populations are characterized by relatively low natality, low mortality of young, prolonged behavioral development, high parental care, and adult longevity (Hodgdon and Lancia 1983). Social interactions involving close contact are fairly infrequent outside the lodge, perhaps an adaptation to minimize predation risk on land. The most common interaction among individual beaver concerns food items and usually involves kits begging for food from older siblings or adults (Busher 1983). Adults discourage yearlings from begging by snapping their head toward the yearling. Grooming fur to maintain water repellency is a common activity inside the lodge. Beaver groom themselves wherever they can reach, but rely on other family members to groom their back fur (Paternaude and Bovet 1984). This social grooming appears to be primarily to maintain a layer of air in the fur, as does self-grooming, rather than to maintain social bonds or as an appeasement gesture (Brady and Svendsen 1981). Aggressive interactions are rare among family members, with most aggression directed as threats that do not result in fights. Studies of dominance hierarchy systems in beaver have been equivocal. Hodgdon and Larson (1973) described dominance hierarchy as age class (older dominant over younger) and sexual (adult females dominant over adult males). Busher (1983), however, found only age-class hierarchy, and Brady and Svendsen (1981) found no clear patterns in any groups.

Vocalizations and Tail Slapping. Although seven vocal sounds have been described for beaver, most investigators recognize only three that are used outside the lodge: a whine, a hiss, and a growl (Muller-Schwarze and Lancia 1983). The whine is the most frequent vocalization and can be repeated in rapid succession. Beaver of all ages whistle, but kits account for two thirds of events, either when food is at risk of being taken away or when begging for food. Food begging by kits is usually effective, which provides kits with food without the risk of obtaining it from land (Brady and Svendsen 1981; Hodgdon and Lancia 1983). Vocalizations are also used to initiate grooming and play. Although beaver are typically docile with humans, they sometimes become aggressive, a behavior sometimes preceded by a hiss or a growl. Probably the most familiar sound produced by beaver is the tail slap. The sound is made when a beaver forcefully strikes the water with its heavy paddle-like tail, a behavior that may precede diving underwater when alarmed (tail-slap dive). Tail slapping may function to (1) issue a warning signal to family members, which typically respond by moving to deep water or to the lodge especially kits, (2) drive away potential predators; and (3) elicit a response from the source of disturbance (Brady and Svendsen 1981; Hodgdon and Lancia 1983). Tail slapping is used by all ages and both sexes, but studies of variation in frequency of use by sex and age have been equivocal. Hodgdon (1978) found older beaver slapped more often than younger ones, females were more easily provoked than males, and males slapped more times per event than females. Sudden alarm often elicits immediate tail slapping. However, if beaver are unsure, they often move to deep water and orient toward the disturbance with their nose in the air, a behavior that often precedes tail slapping. Smell, sound, sight, and movement are all important stimuli for tail slapping. Smell, sound, or movement of an individual beaver to tail slapping also varies by age. Tail slapping by adults elicits the most response from all age classes, but adult beaver are the most responsive to tail slapping of other beavers. Kits are least likely to respond to tail slapping, and response and yearlings are intermediate (Hodgdon and Lancia 1983).

Scent Marking. Scent marking is a highly developed communication method in beaver. Castor glands produce castoreum, a strong-smelling, urine-based brown paste containing phenolic, neutral, basic, and acidic compounds. Anal glands (also called oil glands) produce anal gland secretions consisting of waxy esters and fatty acids. Castoreum is likely derived from diet and thus subject to seasonal variation in odor; however, anal gland secretions are unique chemical identifiers of individual beaver (Sun and Muller-Schwarze 1998). Beaver use castoreum and anal gland scents as scent marks, which they actively deposit on piles of mud and debris called scent mounds. Beaver deposit castoreum by rubbing it on scent mounds during and after construction; it is not clear how and when anal gland secretion is applied (Svendsen 1980a). Most scent mounds are constructed by adult males, who gather material in their forepaws and carry it to scent mounds in a bipedal fashion. Large numbers of scent mounds (>100) can be constructed within a territory, and they are usually placed on or near lodges, dams, and trails <1 m from water. Beaver of all ages place scent on mounds, but the frequency of marking increases with age. Males of all ages place the most scent marks (Hodgdon and Lancia 1983). In colder climates, construction and marking of scent mounds peaks soon after ice melts in the spring as beaver recover their full territory and reapply scent that faded during the winter. In warmer, ice-free regions, scent marking can occur all year, but still may be more intense during the spring dispersal period. Scent marking has been observed in December and January in Alabama, where mounds can reach 35.5 cm in height. The primary function of scent marking appears to be territorial. Scent marks may define the location and limits of the territory by creating a scent fence (Muller-Schwarze and Heckman 1980), which minimizes aggressive encounters with neighbors and discourages colonization by dispersing beaver. Beaver can distinguish the scent of castoreum fluid among family members, neighbors, and nonneighbors (beaver
When beaver venture above the ice, ambient air temperatures below 2°C (Schulze 1998). Use of foreign castor scent (as in trapping) may elicit investigation, intense scent marking, or destruction of the foreign scent as well as hissing and tail slapping behavior. In Ohio, an adult female built over 70 mounds in 1 week, likely in response to the presence of castor bait applied by trappers (Brady and Svendsen 1981). In New York, beaver obliterated foreign scent by pawing the mud, overmarking foreign scent, and transferring the mud to their own scent mounds (Muller-Schwarze et al. 1983). In addition, a territorial function for scent mounds may be expressed as a change in the motivational state of beaver. Svendsen (1980a) suggested that scent may increase the confidence of resident beaver, which smell their own scent, and decrease the confidence of nonresident dispersing beaver, thus increasing the likelihood nonresidents will flee a territory "defended" by scent mounds. Experimental field studies support a territorial function for scent marking, as Schulze (1998) found that beaver could distinguish among the scents of adjacent neighbors, far neighbors, and family members. Beaver spent more time investigating and overmarking scent from unrelated beaver than from family members. The ability of beaver to recognize relatives from nonrelatives via anal gland secretions (but not castoreum) may help prevent inbreeding as related individuals meet each other following dispersal outside their home territory (Sun and Muller-Schwarze 1997). Experimental comparisons of compounds in anal gland secretions have not yet clearly identified underlying mechanisms, but have shown that perhaps as few as two or three compounds may be important in communicating family membership (Sun and Muller-Schwarze 1998). In addition, scent marking may help orient beaver within their territory at night, although this has not been experimentally demonstrated.

Scent marking by beaver may be density dependent and vary by season and location. In Maine, beaver colonies with close neighbors had more scent mounds than isolated colonies (Muller-Schwarze and Beckman 1980). In South Carolina, scent marking was positively correlated with colony density. Peak scent marking occurred in fall and winter, with very little marking activity in summer (Davis et al. 1994). Southern beaver may increase marking activity in the fall in response to increased food competition among colonies (Davis et al. 1994). Thus, scent marking in southern beaver may differ from that in northern beaver, which exhibit a peak of marking in the spring.

**Daily Activity Patterns.** Beaver are crepuscular and nocturnal. In ice-free areas, they follow a normal 24-hr period yearlong, but in northern latitudes, they do so only during spring, summer, and fall. Winter activity periods of northern beaver commonly exhibit a free-running circadian rhythm of about 26–29 hr, likely because relatively constant light conditions preclude entrainment of a photoperiod (Lancia et al 1982). To survive extreme cold in winter, beaver remain under the ice or inside a lodge, where temperatures are nearer a relatively moderate 0°C. When beaver venture above the ice, ambient air temperatures below about −10°C cause substantial energy deficits. During extreme cold, beaver may exhibit no detectable movement inside the lodge (Alekseevsk and Cowan 1969; Lancia et al. 1982), an energy-saving mechanism that may reduce caloric needs by 20% (Mckab 1963).

**Dispersal and Other Movements.** Bergerud and Miller (1977) classified the major movements of beaver as (1) movement of the entire colony between ponds within a territory; (2) short-term wandering of yearlings; (3) dispersal of beaver, usually at age 2 years, to establish new colonies; and (4) miscellaneous movement of adults, often following loss of a mate. Dispersal of 2-year-old beaver is the primary mechanism of population expansion. Dispersing individuals may return to the home colony for short periods of time, which suggests that dispersal is innate rather than learned from or encouraged by any aggressive behavior of parents (Hodgdon 1978). Dispersal of subadults often coincides with the birth of kits in the spring and/or high runoff, especially where ice is absent and temperatures in ice-free areas are less restricted, as some dispersal occurs in late February and March, and scent marking and territorial defense may occur throughout the winter. Beaver in poor-quality habitat, or where trapping or other control measures have reduced populations below carrying capacity, may disperse at a higher rate than those in good-quality saturated habitat. Thus, habitat conditions may affect the length of time beaver remain in the family unit as subadults. However, beaver also may exhibit high dispersal in fully occupied habitat, which suggests dispersal patterns are inconsistent (Gunson 1970; Van Deelen and Pletcher 1996). Stochastic models of beaver population growth have assumed density-dependent dispersal rates (Molini et al. 1980). Distance of natural dispersal varies greatly, sometimes depending on the location of suitable but unoccupied habitat. Direction of dispersal can be either upstream or downstream within a watershed, or beaver can cross watersheds by overland travel of up to several kilometers. In a study of 46 dispersing beaver in New York, 74% initiated dispersal downstream, 35% moved to neighboring colonies, and females moved farther than males (Sun et al. 2000). In that study, 14% of dispersers were 1 year old, 64% were 2 years old, and 21% were 3 years old. If the entire colony moves to a new location, then movement usually occurs before parturition, single animals usually disperse before pairs (Hodgdon 1978). Distances moved and time of movement are important considerations in formulating management strategies.

**Home Range.** Home range of a beaver depends on sex, age, social organization of the family unit, type of occupied habitat, and seasonal constraints. During the trapping season, parental care for kits in and near the lodge or den can restrict the distance that adults can forage, with females staying closer to kits than do males. As young become more independent in the fall, the home range of adults may increase, although this is not always the case. In areas where ice confines movements in winter, home range is also constrained. For example, a radio telemetry study of beaver in the taiga of southeastern Manitoba showed those in family units had smaller average summer home ranges (8 ha) than those in nonfamily units (18 ha) and that home ranges were larger in summer and fall than in winter (Wheatley 1997a, 1997b).

Habitat features, especially shoreline configuration, strongly affect home range shape and size. Home ranges tend to follow the irregular shoreline patterns of lakes, ponds, rivers, and streams. Small ponds may contain only a single family unit with a relatively circular home range, but in lakes, streams, and rivers, the home ranges of beaver are typically larger and more linear (Novak 1987; Wheatley 1997c). However, these habitat-related patterns may break down when beaver are not living in a sedentary family unit or during seasonal movements (Wheatley 1997c). In addition, intraspecific competition, or territoriality, is an important mechanism, which helps to regulate population density. Boyce (1981a) suggested that territoriality likely was responsible for a minimum intercolony distance of 1 km. Beyond that distance, availability of suitable sites for foraging, dams, and lodges more strongly influenced the distribution of colonies.

**Population Density.** Beaver population density varies spatially and temporally. Because the home ranges of adjacent beaver families are usually separated by unoccupied habitat, density estimates typically include some unoccupied habitat. Factors that cause a decrease in the density of beaver populations include human exploitation (trapping), water quality, habitat suitability, area available for new colonization, length of habitation time relative to available resources, epizootic diseases, local predation events, and territoriality. There is a wide range in the density of beaver colonies, from near zero to at least 4.6/km² (reviews by Hill 1982; Novak 1987). Observers in different regions have attempted to estimate the maximum density or saturation point in local populations. Saturation has been reported to vary from 0.4 colony/km of stream in northern Alberta to 1.2 colonies/km of stream in New York and Utah (reviews by Hill 1982; Novak 1987). In the headwaters of four Alabama watersheds, saturation approached 1.9 colonies/km of stream (Hill 1976).

Trapping can suppress beaver populations below habitat-based carrying capacity and is an important consideration in understanding population dynamics. Trapping often removes a larger percentage of adult beaver than it does other age classes; thus, it can increase adult
mortality and affect both the density and age structure of populations. Intense trapping over many years can entirely decimate populations, as it did during European settlement of North America. In previously unexploited populations, trapping can cause rapid population reductions. In a Wisconsin study, where trapping was resumed after 19 years of protection, beaver populations were reduced by 21% in the first year and 53% in the second year (Zeckmeister and Payne 1998). Trapping can also alter the age structure of populations as removal of adults from established territories frees suitable habitat, allowing beaver to disperse earlier from their natal colony and increasing their survival (Boyce 1981b). Comparing harvested and unharvested beaver populations in New York, Muller-Schwarz and Schulte (1999) found that in unharvested populations, beaver colonized steeper stream gradients, young remained longer in the natal colony, preferred forage species were depleted and less preferred species were used more often, and beaver foraged further from their pond, lodge, or den.

Density of beaver populations that occupy particular sites may also vary as a function of the length of time sites have been occupied. For example, beaver located on the Prescott Peninsula in Massachusetts following an absence of more than 200 years, the population showed slow growth the first 15 years, then 15 years of very rapid growth, and then a rapid decline in numbers until it stabilized at 23% of its peak. POPulations in Sagehen Creek, California, also followed a pattern characterized first by slow growth, then rapid growth, then rapid decline to a level of relative stability (Buscher and Lyons 1999). Observers monitoring short-term trends in beaver populations should consider these and other intrinsic population regulation mechanisms (such as territoriality) as factors that might explain population change. These intrinsic factors can be important confounding variables when attempting to interpret population trends.

Structure is added by anchoring leafy branches, peeled branches, or other material to the substrate (stream bottom, stream banks, large rocks, or coarse, woody debris). Branches in the bulk of the dam may be anchored and intertwined perpendicular or parallel to the flow of water; however, material on the downstream side is usually placed with the cut end pushed into the stream bottom or bank and the branched end pointing upstream to support and stabilize the dam.

Bear use woody vegetation (bark may be peeled and eaten before placement in dams) and many other materials in dams. Dams can include conifers, sagebrush (Artemisia tridentata), tamarisk (Tamarix pentandra), aquatic plants, corn cobs, corn stalks, plastic, metal, or other debris. Interestingly, when preferred foods are limited and less-preferred foods are more abundant, beaver will select stems that are less palatable for dams and save the more palatable stems for food, especially for use in their winter food cache (Barnes and Mallik 1996; B. W. Baker, unpublished data). For example, Barnes and Mallik (1996) found that beaver preferred stems that were 1.5–3.5 cm in diameter and grew close to shore for dam-building material (mostly alder, Alnus spp.). They searched for and selected larger stems (>4.5 cm) that were further from the shore as food items. Thus, beaver increased risk of predation to obtain food but not dam-building material. Barnes and Mallik (1996) speculated that smaller stems were also better for construction of dams, as they might be easier to work with and provide a tighter seal against leaks. However, conventional wisdom suggests that larger material might make stronger dams in regions that experience high spring flows, although this hypothesis has not been tested experimentally. When woody material is in place, beaver seal the upstream side of the dam with mud and herbaceous vegetation (grass, leaves). They typically use mud from the stream bottom immediately upstream of the dam, making this area of the pond the deepest. If the pond overflowed the channel as it develops behind the dam, then beaver will often extend the dam laterally by building shallow wings. Canals built to extend the dam are built in succession, with water from each pond backed up to the base of the upstream dam, creating a stair-step pattern of dams and ponds, which flattens the slope of the drainage.

The sound of running water is the primary cue for beaver to maintain and sometimes initiate dams (e.g., a noisy road culvert). Although beaver typically work on dams individually, sudden or loud sounds of running water may elicit cooperative behavior, especially to repair a dam in the dam (Aeschbacher and Pillen 1983). Beaver of all ages inspect and repair dams, but adults perform most of the work. The literature is inconsistent about the relative efforts of males and females (Hodgdon 1978; Buscher 1983). Beaver may initiate and maintain dams at any ice-free time of year; however, in many areas there is a peak of activity in the fall before freeze-up and again in the spring after high flows have subsided. The size and number of dams in a colony and the surface area and volume of water in ponds vary greatly depending on duration of occupancy, topography, substrate, flow levels, available vegetation, and other factors. As water spreads from primary dams within main channels, beaver often build small dams on the surface of the floodplain to further spread and direct water. Thus, individual dams and ponds can be very large or very small, with area inundated generally increasing through the first few years of beaver occupancy. Beavers often dig canals to facilitate movement of food and building material within and among their ponds or increase water depth for ice-free access to a lodge or food cache. The longer that beaver occupy a site, the more likely it is that beaver will build or extend canals and build new foraging areas. Canals built within the pond may not be visible unless the pond is drained, but canals built in the floodplain may become obvious features of the landscape. Some canals may contain burrows with an underwater entrance to provide a refuge from predators.

Beaver also create surface trails or "slides" as they transport woody material from their foraging area back to ponds and canals. These trails make it easier for beaver to drag material across the ground, permitting them to move material across greater distances. This is especially obvious in steep terrain, where gravity aids movement of material and can increase the effective foraging distance by several hundred meters. Lodges and Bank Dens. Beaver construct bank dens and lodges, which are used for protection from predators and weather. Bank dens are often dug under a large tree or shrub on the stream bank to provide support for the roof of the den. They have a nest area above the water level, an underwater entrance, and small holes in the surface soil to permit air exchange. Where beaver live exclusively in rivers or deep lakes, bank dens are typically the only housing structures that are built. Even where beaver eventually build dams and lodges, they often live in a bank den until more permanent structures are completed. The only place that bank burrows are completely absent is where the substrate prohibits their construction, such as areas with very rocky soils or permafrost. In many areas, lodges and bank dens are used.

Lodges can be built in ponds or shallow lakes, where they are surrounded by water, or they can be built on the shore, often as an upward extension of a bank den. In this case, in which they often are called a bank lodge, beaver add sticks on top of the bank den and cut a hole to create a nest chamber. This process can be extended over several years if dam height and water level increase. Construction of a lodge in open water is similar, with sticks piled high enough to enable beaver to cut a nest chamber above the water surface. Mud is added to the surface of the lodge to provide a weather seal, but a portion of the top remains unsealed to allow air exchange. Beaver may have multiple active and inactive lodges within their territory. In addition to mud and freshly cut branches or dead sticks, beaver lodges may include some rocks or other
material, although not as much as in dams. The presence of fresh mud or green branches on lodges is often used as an indicator of an active colony. As with dams, lodge construction is often most active in the fall immediately before freeze-up. In ice-free regions, construction of dams and lodges occurs all year, but is less active in the summer.

Food Caches. In regions where ponds or streams freeze during the winter, beaver build food caches, which they access from their lodge by swimming under the ice. The use of food caches is uncommon or absent where beaver inhabit ice-free regions. Beaver typically build a cache by first floating cut branches in a deep part of the pond and then adding new material under this raft. The branches eventually become water-logged and sink to the bottom, holding the cache in place. The upper layer of the cache, called a cap or raft, becomes frozen in ice and unavailable to beaver. Interestingly, beaver often use inedible or less-preferred species for the cap and place more-preferred food items deep enough in the cache to remain ice free and accessible throughout the winter (Slough 1978; B. W. Baker, unpublished data). Differential use of woody plants in food caches and dams can also occur. For example, beaver in Ontario preferentially used conifers and alder in dams and aspen (Populus tremuloides) and maple in food caches (Doucet et al. 1994a). Quality of food items in caches is especially important in colder climates, where gestation, parturition, and feeding of newborn young occur under the ice. Construction of a winter food cache usually occurs in late fall and is often initiated by the first hard frost. Beaver may build multiple food caches in a single colony and often do not consume the entire cache during the winter. In the spring, barked stems from the cache may be used to maintain the dam. During ice-free months, beaver sometimes forage by cutting stems on land and returning to a favored location at the edge of a pond to consume them in safety, leaving a pile of peeled stems suggestive of a winter food cache.

ECOLOGY

Diet. Beaver are choosy generalist herbivores, consuming a diet of herbaceous and woody plants, which varies considerably by region and season. The number of plant species in the diet is highest in the southern part of the range and decreases toward the northern and alpine limits of the range (Novak 1987). Herbaceous plants make up much of the diet when they are available and succulent (actively growing). In the central and southern United States, beaver eat a variety of aquatic and riparian forbs and grasses as well as cultivated row crops and grains. Roberts and Arner (1984) found that beaver in Mississippi depended on the bark of woody plants in late fall and winter, but abruptly shifted their diet to herbaceous species after spring greenup in March. Using stomach analysis, they identified 16 genera of herbaceous plants, 15 species of trees and shrubs, and four woody vines in the yearlong diet. Woody material constituted 53% of the annual diet (86% in winter, 16% in summer); grasses occurred in 25% of stomach samples, including some collected in midwinter. In an Ohio study, herbaceous plants accounted for 90% of the feeding time during summer and 40–50% during spring and fall (Svendsen 1980b). In the Mackenzie Delta, Northwest Territories, leaves and the growing tips of willow (Salix spp.) were the main foods in July and August. Bark of willow (76%), poplar (Populus balsamifera) (14%), and alder (A. crispa) (10%) made up the diet the rest of the year (Aleksiuk 1970b). The protein-calorie ratio was 40 mg cal/kg in summer and 8 mg cal/kg for the rest of the year, indicating that beaver in northern areas shift their diet to high-protein willow leaves whenever they are available. In northern latitudes, water lily (Nymphaea, Nuphar) is often the most important food species. Where aspen or poplar is available, it is usually more preferred than willow (Novak 1981). Cafeteria-style feeding experiments in Ontario showed the following preferences (in descending order): aspen, white water lily (Nymphaea odorata), raspberry (Rubus idaeus), speckled alder (A. rugosa), and red maple (A. rubrum). Similar experiments in Nevada showed that beaver preferred aspen and avoided Jeffery pine (P. jeffreyi) (Basey 1999).

Selection of forage items by beaver may be related to a variety of physical and chemical factors. Evidence suggests that beaver may select aspen resprouts based on their age-related growth form (Basey et al. 1988, 1990). Aspen reproduces asexually by resprouting within a clone. Aspen clones that have been repeatedly cut by beaver produce juvenile-form root sprouts (large leaves with an absence of lateral branching), which are avoided by beaver when compared to available adult-form root sprouts (small leaves with lateral branching). Although juvenile-form root sprouts have more protein and likely provide better nutrition, they contain secondary metabolites that apparently cause avoidance by beaver. The importance of secondary metabolites to selection was further demonstrated in experiments where leaf extracts from different deciduous and coniferous species were painted on aspen leaves and then presented to beaver. Selection favored aspen leaves painted with extracts from deciduous species more so than those painted with extracts from coniferous species (Basey 1999).

Retention time of forage passed through the digestive tract varies with diet composition (likely due to lignin and fiber content) and may also influence food selection by beaver. Experiments have shown that beaver retention time is correlated, species with a shorter retention time, such as aspen, are more preferred than those with a longer retention time. Beaver “select a diet that maximizes long-term energy intake, subject to digestive limitations” (Doucet and Fryxell 1993:201). Thus, retention time may influence intake rates and energy gained from different forage species, indicating it may be an important factor in food selection by beaver (Fryxell et al. 1994).

Physical features of the food item may also influence selection. In an experimental study of foraging behavior, Doucet et al. (1994b) found plants, as well as acorns when available (Grinnell et al. 1937; Novak 1987). There is wide regional variation in the number and composition of woody plant species used. As few as 3 species may be used by colonies in the northern range (Aleksiuk 1970b), but in the southern range, 22 species were reported in Louisiana and 38 species in South Carolina (review by Hill 1982). In a review of regional food habits, Novak (1987) suggested that local populations of beaver in southern areas included more woody plant species in their diets than did northern populations, but at regional scales the number of woody species used was similar. Beaver also may repeatedly gnaw the bark of pine trees to obtain sap (Svendsen 1980b) or sweet gum (Liquidambar styraciflua) trees to obtain storax, an aromatic balsam, which they lick from the injured site. In many areas, especially in their northern and western range, any substantial use of conifer is considered unusual and a sign that more-preferred species are lacking (Novak 1987). Dietary use of conifer also may be seasonal, as beaver in Massachusetts selected against pine during the fall, but not during the rest of the year (Jenkins 1979).

Food Preference. Preference for a particular food item indicates “it constitutes a significantly larger fraction of the diet than an unbiased sample of items of the various food types available” (Jenkins 1981:560). Thus, some foods may constitute a large percentage of the diet, but may not be preferred over less available, but more favored species.

Willow is the most available and the most used woody riparian species in much of the beaver’s range. In many areas of the far north, Rocky Mountains, and intermountain west, beaver may depend entirely on willow to supply winter forage and building material (Aleksiuk 1970b). Where aspen or poplar is available, it is usually more preferred than willow (Novak 1981). Cafeteria-style feeding experiments in Ontario showed the following preferences (in descending order): aspen, white water lily (Nymphaea odorata), raspberry (Rubus idaeus), speckled alder (A. rugosa), and red maple (A. rubrum). Similar experiments in Nevada showed that beaver preferred aspen and avoided Jeffery pine (P. jeffreyi) (Basey 1999).
that beaver could only distinguish differences in canopy biomass on a very coarse scale, which suggests they selected stems using diameter as an index of biomass. Beaver also select foods by taste, sometimes biting off small samples of bark before cutting down an entire tree. In feeding experiments, beaver avoided aspen that had been painted with an extract of red maple (Muller-Schwarz et al. 1994). In areas with a variety of trees available for food, red maple may be the only tree left standing at the edge of an older beaver pond. Odor may also affect selection. In a similar experiment using extracts of predator feces painted on aspen logs, there was a strong preference against the odors of coyote, lynx, and river otter. Thus, predator odors may be a useful management tool for preventing beaver damage (Engelhart and Muller-Schwarz 1995).

Central-Place Foraging. Beaver typically cut woody vegetation from terrestrial locations for food or construction material and bring it back to a central place, such as a pond, cache, aquatic feeding station, lodge, burrow, or dam. Because this behavior creates exposure to predation and has high energetic costs, beaver have been used to test general predictions of central-place foraging theory. These predictions suggest that beaver should modify their behavior to concentrate foraging near the central place and should increase their selectivity for size and species away from the central place (Fryxell 1992). Most studies have confirmed these general predictions, but exceptions to these patterns occur. For example, studies confirmed that beaver typically cut increasingly smaller stems (less provisioning time) further from the central place, as predicted by optimal foraging models (Jenkins 1980; Belovsky 1984; Fryxell and Doucet 1990). In contrast, where relatively small (1.5–30 mm) stems are the only woody plants available, beaver may select larger stems even when located further from the central place (McGinley and Whitman 1985). Selection for larger stems is particularly evident where beaver occupy shrub habitats, such as those containing only smaller species of willow and alder. In some cases, repeated cutting by beaver can cause trees to develop and maintain a shrubby growth form (e.g., Fremont cottonwood, Populus fremontii; McGinley and Whitman 1985). For example, in small diameter. Estimates have been derived for aspen (Aldous 1938; Dyck and MacArthur 1993) to 2.0 kg/day (review by Stegeman 1954). In a study of the energy content and digestibility of cached woody biomass, Dyck and MacArthur (1993) concluded that the total winter energy requirements could not be met from the submerged food cache in their study colony. Supporting research has shown that when food is limited, beaver may metabolize body tissue during winter.

Habitat Requirements. The ability of beaver to alter existing habitat conditions to meet their needs has allowed populations to inhabit a variety of natural and human-made habitats in North America. They have successfully colonized tundra and taiga in the far North, bottomland hardwood forests and marshes in the deep South, riparian areas in both cold and hot deserts, and elevations that vary from sea level to about 3400 m (reviews by Hill 1982; Nowak 1987). Although beaver can occupy a wide variety of habitats, some generalizations are evident. A comprehensive evaluation of beaver habitat requirements in the Rocky Mountains showed they generally preferred wide valleys with a low (<6%) stream gradient, which offered relatively more food and reduced risk of severe floods (Retzer et al. 1956). Beaver typically inhabit streams with at least intermittent flow and lakes or ponds with standing water, but they can also inhabit bogs that lack open water. In Minnesota, they occur in sedge-moss and other bogs, where they can enlarge natural moats to create ponds of standing water and build floating lodges able to adjust to fluctuating water levels, and thus maintain protection from predators (Rebertus 1986).

Early studies of beaver formed the foundation for later mathematical models, which quantitated habitat requirements and created a framework for making and testing predictions. Slough and Sadler (1977) sampled colony density and associated habitat conditions at 136 lakes and 45 stream sites in Ontario and used regression analysis to develop a land classification system for beaver. Howard and Larson (1985) used principal component analysis of habitat variables to predict beaver colony density in Massachusetts. Percentage hardwood vegetation, watershed size, stream width, and stream gradient were important predictors in their classification system. Allen (1983) used existing literature and expert opinion to develop a general habitat suitability index (HSI) model for beaver, which used nine variables to rate habitat quality on a scale of 0.0–1.0. These variables included measures of canopy cover, height, stem diameter, species of trees and shrubs, stream gradient, water level fluctuation, and shoreline development (ratio of length and area). The HSI model assumed a minimum habitat area of 0.8 km² of stream or 1.3 km² of lake or marsh as a prerequisite of suitable beaver habitat. This model has been widely used by environmental planners to quantify potential impacts from development projects and mitigate habitat loss.
Other researchers have developed alternative habitat models and modified existing models for different habitats and regions. For example, researchers in prairie regions found beaver selected riparian lodge-site locations in areas that had thick, concealing vegetation cover (which was often left uncut) and steep shoreline banks (Dieter and McCave 1989). In the Truckee River basin of California, physical features of the stream, such as a lower gradient and a greater depth and width, were more important than vegetation in describing the location of lodge sites selected by beaver (Beier and Barrett 1987). In contrast, Barnes and Mallik (1997) found that concentration of woody plants 1.5–4.4 cm in diameter and size of the stream and its upstream watershed area were important predictors of dam-site location in northern Ontario. In Oregon streams, McComb et al. (1990) found that beaver selected dam sites where the substrate was less rocky, the water was shallower, the channel had a lower gradient, and woody vegetation (e.g., Aldus) had a greater canopy cover. They concluded that Allen's (1983) HSI model was useful in predicting habitat quality for beaver at their sites, but required some site-specific modifications.

In contrast, others have found that Allen's HSI model was a poor predictor of beaver habitat quality in their region. For example, a Kansas study suggested that water quality, river substrate type, and adjacent agricultural land-use practices are important predictors of riparian habitat quality for beaver in the central United States (Rebel et al. 1993). In an Oregon study, many potential beaver sites were highly rated by the HSI model even though they were unoccupied by beaver at the time of study, which suggested poor model performance to the investigators (Suzuki and McComb 1998). However, low density or absence of beaver in apparently suitable habitat is not unusual and may be caused by many non-habitat-based factors, such as trapping, disease, territory, or simply the inherent variation of natural systems. At occupied sites, cutting of preferred species by beaver may alter the density and species composition of vegetation, and thus affect how the habitat might be rated by habitat models (Suzuki and McComb 1998).

MORTALITY

Predation. Predation by the timber wolf (Canis lupus) can be an important limiting factor of beaver populations where they occur together. Wolves prey on beaver during the ice-free period, when nearly half their diet may consist of beaver (Potvin et al. 1992). In Algonquin Park, Ontario, as white-tailed deer (Odocoileus virginianus) populations declined over a 9-year period, beaver gradually became the most important prey item: 35% of wolf scats had beaver remains (Voigt et al. 1976). In an experimental study in Quebec, density of beaver colonies increased 324% following the removal of wolves (Suzuki and McComb 1998). Habitat conditions that force beaver to forage farther from water may influence predation rates by wolves. On Isle Royale, beaver foraged farther (>100 m) from ponds when wolf populations were low and closer (<35 m) to ponds when wolf populations were high (D. W. Smith, unpublished data). Thus, the impact of wolf predation on beaver populations can be locally significant, but varies greatly depending on wolf density, alternative prey availability, and other factors.

Coyotes (Canis latrans) and mountain lions (Puma concolor) also prey on beaver, as do some other mammalian predators of generally minor importance, such as bears (Ursus spp.), wolves (Canis spp.), river otters (Lontra canadensis), lynx (Lynx canadensis), bobcat (Lynx rufus), and mink (Mustela vison) (review by Hill 1982). However, unusual circumstances can alter typical predation patterns. Black bear (U. americanus) predation strongly suppressed beaver populations on an island in Lake Superior (Smith et al. 1994). In this case, bears colonized one of two similar islands in the 1970s that beaver had colonized in the late 1940s or early 1950s. As the bear population grew, they focused their predation on beaver, the only source of meat on the island, digging into 18 of 26 beaver lodges and causing surviving beaver to concentrate foraging on trees <30 m from water.

Disease. Water-borne tularemia is a zoonotic disease caused by the bacterium Francisella tularensis biowar palaearticus (type B), which commonly occurs in semiaquatic mammals such as beaver and muskrat (Ondatra zibethicus) and occasionally becomes epizootic. Type B tularemia is not fatal to humans and is responsible for only 5–10% of human tularemia infections in North America. Type A tularemia is responsible for the remaining human infections. It can be fatal to humans and has a terrestrial cycle in rabbits (Sylvilagus spp.) and ticks (Morrer 1992). Tularemia infections in beaver are typically subclinical without noticeable effects on the individual or the population, but they can be fatal to beaver and cause mass mortality from local or regional epidemics. Tularemia in beaver sometimes can be traced to infections in terrestrial rodents that deposit urine or feces in water, or die in water, which then harbors F. tularensis bacteria. For example, an outbreak of tularemia in Montana during 1939–1940 caused widespread mortality of beaver (several hundred carcasses were found) and coincident infection and mortality of meadow voles (Microtus pennsylvanicus) that inhabited the grassy streambanks (Jellison et al. 1942). Interestingly, rabies has been documented in beaver, but little is known about its pathogenesis or epizootiology (J. Rupprecht, 47th Wildlife Disease Association Conference, oral commun., 1998).

Other Mortality. Starvation can be an important cause of mortality, especially at northern latitudes, when beaver are unable to construct a food cache large enough to sustain them through the winter (Kendrick 1970; Bergerud and Miller 1977). Sudden snowmelt in midwinter or violent spring breakups can raise water levels in streams and may destroy lodges and occupants or drown large numbers of beaver under the ice (Hakala 1952).

BEAVER AS A KEYSTONE SPECIES AND AN ECOSYSTEM ENGINEER

A keystone species is one that greatly influences the species composition and physical appearance of ecosystems (Paine 1969) and whose effects on ecosystem structure and function are both large and noticeable over a relatively large area as well as being persistent over time (Habitat Index System — HSI). An ecosystem engineer is a species that directly or indirectly controls resource availability by causing “physical state changes in biotic or abiotic materials” (Jones et al. 1997:1946). The beaver is a definitive example of both a keystone species and an ecosystem engineer.

The dam-building, canal-building, and foraging activities of beaver have profound effects on ecosystem structure and function. Beaver dams slow current velocity, increase deposition and retention of sediment and organic matter in the pond, reduce turbidity downstream of the dam, increase the area of soil–water interface, elevate the water table, change the stream gradient, alter stream discharge rate by retaining precipitation runoff during high flows and slowly releasing it during low flows, alter stream gradients by creating a step-like profile, and increase resistance to disturbance (reviews by Naiman et al. 1988; Gurnell 1998). Canals dug by beaver spread impounded water across a larger surface area, and thus magnify the effects of single dams. The foraging activity of beaver alters the species composition, density, growth form, and distribution of woody vegetation. These effects on vegetation and the physical characteristics of streams strongly alter the composition of the animal community. Because research did not begin until after beaver populations recovered following near extinction by presettlement trapping and extensive habitat loss, researchers have observed a human-impacted and likely conservative picture of how beaver have altered ecosystem structure and function (Naiman et al. 1988).

Effects of Beaver on Geological Processes. In 1938, researchers evaluating the formation of broad, flat alluvial valleys in the Catskill region of New York discovered that geological processes alone could not explain observed sediment deposition rates (Ruedenham and Schoonmaker 1938). They suggested that during the 25,000 years since the last glaciation, layer on layer of sediment-filled beaver ponds caused extensive and extensive habitat loss, researchers have observed a human-impacted and likely conservative picture of how beaver have altered ecosystem structure and function (Naiman et al. 1988).
plain horizontal from bank to bank” (Ruedenmann and Schoonmaker 1938:525). Unfortunately, the theory of beaver-assisted alluvial valley formation remains largely unproven by rigorous research across varied landscapes. One exception is a study in Glacier National Park, Montana, where comparisons of sediment depth and pond age confirmed that beaver ponds gradually accumulated sediment as they aged (Meseen, seventh edit. 1999). This, in turn, meant that beaver ponds will eventually fill with sediment and become beaver meadows. This process of accelerated meadow development by beaver dams is likely more important in meandering, low-gradient, valley-bottom streams, where conditions favor stable dams that spread sediment-laden water over a large surface area, rather than in steep, V-shaped, high-energy streams, where beaver dams tend to fail at a greater rate.

Beaver dams also affect erosional processes within stream channels, typically increasing channel aggradation. As sediments fed water enters a beaver pond, it slows in velocity and drops sediment, increasing aggradation. However, water downstream of dams can be underloaded with sediment and increase erosional forces as the stream regains lost sediment (Metcenmeier and Butler 1999). This can lead to a localized increase in bank sloughing below beaver dams in areas with erosive soils. In most cases, the net effect of beaver dams is to decrease channel and streambank erosion and increase channel aggradation (Parker et al. 1985). Catastrophic beaver dam failures are rare events, but can occur following unusually large rainfalls or high spring runoff. In 1994, a beaver dam in central Alberta failed and released 7500 m³ of water, causing a flood wave that was 3.5 times the maximum recorded discharge for the stream (Hillman 1998). In this case, the flood wave was largely attenuated by downstream wetlands, including several beaver ponds.

Beaver ponds may also act as a filter to decrease nonpoint-source water pollution. In a study of Currant Creek, Wyoming, a highly erosive second-order stream, concentrations of suspended solids, total phosphorus, and nitrogen were lower in beaver ponds (Curtis et al. 1998). Beaver ponds also influence water quality by affecting the number and composition of bacteria in the stream. In Wyoming, one species of bacteria apparently increased and others decreased as water flowed through beaver ponds; however, results were confounded by the effects of different livestock grazing systems (Skinner et al. 1984).

Effects of Beaver on Coastal Processes. In addition to geological effects, beaver alter the landscape by creating layers of spatially distinct volumetric units, or patch bodies, which include the bedrock, the water-saturated anerobic soil under the pond, the moist aerobic soil at the water’s edge, the pond, the zone concentrated to the pond or central place, and the overlying atmosphere (Johnston and Naiman 1987). These patch bodies create a shifting mosaic of conditions in the landscape, which varies spatially and temporally as beaver populations colonize new territory or abandon old sites (Naiman et al. 1988). The inherent habitat matrix strongly influences how these patch bodies affect ecosystem processes. Effects are greatest where contrast is greatest. Beaver that create dams in existing wetlands have less effect than those in well-drained forests. In a study that compared stream riffle sites upstream and downstream of beaver ponds, sites immediately below dams had lower invertebrate richness and diversity, but higher total invertebrate abundance, than riffle sites in the spring and summer, but were similar in the fall (McDowell and Naiman 1986). The number of species in ponds was similar to that in the natural stream channel, but resembled that in slow-water habitats of larger order streams, indicating that invertebrates in the beaver ponds may not be unique in the watershed (Naiman et al. 1988). In a study that compared stream riffle sites above and below beaver dams in the Adirondack Mountains, sites immediately below dams had lower invertebrate richness and diversity, but higher total invertebrate abundance, predator, and collector-gatherer densities (M. E. Smith et al. 1991).

Beaver may also affect the invertebrate community by changing the structure and chemistry of plant hosts. In a study of leaf beetles (Chrysomela conflua) and their cottonwood (P. fremontii × P. angustifolia) hosts, beetles were attracted to beaver-cut cottonwood regrowth even though it contained twice the level of defensive chemicals (to protect the plant from herbivory) as normal juvenile regrowth (Martinsen et al. 1998). In this case, beetles may have sequestered these chemicals for their own defense against mammalian predators. Beetles also may have obtained a nutritional benefit from beaver-cut regrowth because it contained more total nitrogen than non-grazed growth. Thus, beetles grew faster and were heavier at maturity.

Beaver impoundments also may affect local mosquito populations, but not necessarily as conventional wisdom might suggest. At a New York site, observers noted marked reductions in mosquito populations after beaver impounded an area of poorly drained forest (Butts 1992). Before impoundment, the area supported large larval populations of the Aedes mosquito, which is unable to breed in the permanent water developed by beaver.

Beaver activity strongly alters the biogeochemical characteristics of watersheds through the accumulation, availability (standing stocks), and translocation of nutrients and ions (Naiman et al. 1994). In a comparison of stream riffle areas to beaver ponds, Naiman et al. (1988) showed riffles had only 48% of the carbon inputs, 5% of the carbon standing stock, and 6% of the carbon outputs as did beaver ponds. In addition, the turnover time of carbon in beaver ponds averaged 161 years, much slower than the 24 years found in riffles. Beaver ponds affect the amount and distribution of nitrogen in the system, as ponds create anoxic conditions, slow flows, and increase oxygen demand by draining organic matter. In Quebec, a beaver-modified section of stream “accumulated 10 times more nitrogen than before alteration” (Naiman and Melillo 1984:150). Anoxic conditions caused by water-saturated soils in beaver ponds fundamentally alter biogeochemical pathways (Naiman et al. 1994). When beaver create ponds in forested uplands, most upland vegetation dies from inundation and woody material cut by beaver is moved to the stream for dams and lodges. The organic horizons of pond sediments accumulate chemical elements from formerly upland plants that become available for vegetation growth when the ponds fill with sediments or dams fail and abandoned sites become beaver meadows. Even small dams can accumulate a tremendous amount of sediment. For example, dams containing 4–18 m³ of wood retained 2000–6500 m³ of pond sediment in a boreal forest system in Quebec (Naiman et al. 1986). In a long-term Minnesota study, beaver activities increased the standing stock of chemical elements in the organic horizon of ponds by 20–295% (Naiman et al. 1994). Transport of water through beaver ponds can also neutralize acids, increase pH, and increase dissolved oxygen concentrations in acidic stream systems (M. E. Smith, et al. 1991). Thus, the activities of beaver can strongly modify the biogeochemical characteristics of stream systems and fundamentally influence forest ecosystem dynamics at landscape scales.

Effects of Beaver on Invertebrates. Beaver ponds affect the species composition and abundance of stream invertebrates as the community responds to increased sediment deposition and still water behind dams. Invertebrate taxa that prefer running water are replaced by pond taxa. Community function is changed as collectors and predators increase in importance and shredders and scrapers decrease in importance (McDowell and Naiman 1986, Naiman et al. 1988). In Quebec, density and biomass of invertebrates in pond sites were two to five times greater than in riffle sites in the spring and summer, but were similar in the fall (McDowell and Naiman 1986). The number of species in ponds was similar to that in the natural stream channel, but resembled that in slow-water habitats of larger order streams, indicating that invertebrates in the beaver ponds may not be unique in the watershed (Naiman et al. 1988). In a study that compared stream riffle sites above and below beaver dams in the Adirondack Mountains, sites immediately below dams had lower invertebrate richness and diversity, but higher total invertebrate abundance, predator, and collector-gatherer densities (M. E. Smith et al. 1991).

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Effects of Beaver on Fish. Dams, ponds, canals, and foraging of beaver may alter the density, distribution, species composition, and population characteristics of fish populations. Trout habitat in streams is usually improved by beaver where low flows or cold water temperatures limit trout distribution or production. However, trout may be harmed if water is warmed beyond their tolerance. Beaver benefit trout by creating deep pools, which resist rises in water temperature during the hot summer months. Trout forage more easily in deep pools, which prevents formation of anchor ice and maintain cooler temperatures in summer. Beaver provide additional benefits by increasing the size of the wetland area, improving physical cover, and increasing the invertebrate forage base because of changes in the substrate and higher water temperatures in ponds (reviews by Hill 1982; Olson and Hubert 1994). In Wisconsin, standing stock (kg/ha) and density of brook trout (Salvelinus fontinalis) in beaver ponds were correlated with surface area, mean water depth, water volume, discharge into pond, elevation, and a morphoedaphic index (Winkle et al. 1990). However, where trout populations are limited by high water temperature in the eastern United States, beaver ponds may increase temperatures beyond tolerable limits, and beaver dams are often removed to improve trout habitat. However, a study of the thermal effects of beaver dams in Wisconsin found no consistent relationship between size or number of beaver ponds and degree of downstream warming (McRae and Edwards 1994). They found that large ponds may act as thermal buffers, which dampen daily fluctuations in water temperature and only slightly raise downstream temperatures. Thus, large-scale beaver dam removal in headwater streams may have net negative consequences on trout populations as their positive effects on invertebrates and ecosystem processes are lost.

Beaver dams may be detrimental to populations of trout and salmon if they restrict or prevent fish passage. However, some studies have shown that trout can pass over beaver dams during high water and may pass through newly constructed dams at any season (review by Olson and Hubert 1994). In the Pacific Northwest, many beaver dams are partially washed out each year by winter high water. However, dams can still benefit fish that use the remaining ends for cover, thus providing value as coarse, woody debris. During summer low flows in this area, beaver dams improved rearing habitat for coho salmon (Oncorhynchus kisutch), as beaver ponds were larger and contained more coarse and higher flows than pools without beaver (Leidholt-Bruner et al. 1992). Beaver activities can have profound effects on fish community structure. In an experimental study of a headwater stream in northern Minnesota, beaver ponds appeared to act as reproductive “sources” populations for fish, which dispersed to adjacent streams, which functioned as reproductive “sinks” in the landscape. Thus, the boundary influences of beaver ponds were “critical in controlling fish dispersal between ponds and streams and the subsequent abundance and composition of fish in lotic ecosystems” (I. J. Schlosser 1995:908). The age and size of beaver ponds also affect stream dynamics. In Georgia, fish species richness per pond increased until ponds were 9–17 years old and then decreased as ponds aged in headwater streams, but showed little change relative to pond age in downstream sections (Snedgrass and Meffe 1998). In larger ponds, fish species shifted from lotic to lentic species, and larger predators replaced small-bodied minnows in older ponds. The size of beaver ponds is also important. As expected from general species–area relationships, fish species richness increases with size of pond, but very small beaver ponds can have higher than expected richness compared to ponds of a similar size not impounded by beaver (Keast and Fox 1990). Thus, beaver have a strong effect on fish species richness, but the effect is dependent on the size and age of beaver ponds and how ponds are distributed within the landscape.

Effects of Beaver on Vegetation. Beaver affect vegetation by building dams and removing woody plants as food and building material. Beaver dams raise the water table by creating a pond area that may be inundated by several meters of water and an umbrella-shaped zone of influence that radiates out from the pond, creating a new water table gradient controlled by soil texture and other factors. The soil behind dams can act like a sponge, retaining water during wetter months and slowly releasing it during drier months. In areas of low or irregular precipitation, beaver dams may convert streams from intermittent flow to perennial flow. Changes in the amount, timing, or duration of available water can create a competitive advantage for many species of riparian–wetland plants, thus increasing their survival and dominance in the landscape. For example, in some western shrub–steppe ecosystems, beaver may help control invasive tamarisk by creating a competitive advantage for willow as dams alter hydrologic ratios, maximizing plant production in incised stream channels (B. W. Baker, pers. obs.). Higher water tables caused by beaver ponds generally kill upland vegetation and promote establishment and growth of wetland vegetation.

Beaver can improve conditions for seedling establishment of willow, cottonwood, and other riparian species. Sediment deposited behind beaver dams creates an ideal moist soil substrate, which can become exposed as water levels in the pond decrease due to a dam washout or other cause. Beaver cuttings may be an important mechanism of plant establishment for some woody species such as willow (Cottrell 1995). Stems that are cut by beaver but not eaten can become imbedded in dams, lodges, or moist soil in or near ponds and sprout adventitious roots and new stem growth. Because a high percentage of stem segments is not consumed by beaver, they may substantially contribute to plant establishment, although the relative importance of this method is not well understood at the community level.

Cutting by beaver can stimulate vigorous resprouting, which may increase biomass production in many woody riparian species. Plants can sprout new shoots by activating dormant meristems located below the cut on the same stem or on ground plant tissue, or from previously developed root suckers. In a study of red willow (S. lasiandra) in Oregon, trees that had a higher percentage of stems cut by beaver responded by producing a higher percentage of regrowth than noncut stems (see above; Olson and Hubert 1994). Where stem cutting is concentrated in late fall to build dams or prepare a food cache, plants are dormant when cut and respond with new shoots in the next spring in an attempt to recover former root-shoot ratios, maximizing plant production and minimizing plant damage. Cutting by beaver can also stimulate plants to initiate growth earlier in the spring, further increasing stem production (Kindschy 1989). However, biomass of new shoots can be decreased if regrowth is browsed by native ungulates or livestock.

The interaction of stem cutting by beaver and intense browsing by livestock or native ungulates can strongly suppress regrowth and may result in declining riparian plant communities. Summer browsing by livestock (Cervus elaphus) congregate along riparian areas can be particularly detrimental to recovery of beaver-cut willow, when new green shoots become highly preferred as grasses cure and become less palatable (Kindschy 1989). Intense browsing by native herbivores can also severely suppress regrowth of beaver-cut stems. When beaver cut tall stems, regrowth occurs at or near ground level, placing the apical portions of stems within easy reach of herbivores. Browsing the tips of stems (leaders) releases apical dominance and may cause plants to develop a short stature. In an experimental study at Rocky Mountain National Park, Colorado, intense elk (Cervus elaphus) browsing of willow (S. monticola) regrowth during 3 years following simulated beaver cutting produced plants of low vigor, which were small, short, and hedged with a high percentage of dead stems (B. W. Baker, unpublished data). In contrast, regrowth of unbrowsed plants was vigorous, large, tall, highly branched, and leafy with a low percentage of dead stems. Browsed and unbrowsed plants recovered more stems per plant (about 70 after 3 years) than were present before simulated beaver cutting, but elk browsing strongly suppressed recovery of plant biomass. After 2 years of regrowth, browsed plants had recovered only 6% of their precut biomass, whereas unbrowsed plants had recovered 84%. Thus, beaver cutting and elk browsing may interact to decrease woody plant height and biomass, eventually reducing beaver habitat suitability and the positive effects of beaver on community structure and function.

Foraging by beaver can significantly alter forest composition and plant succession. Besides humans, beaver are the only species in North America that can affect overstory vegetation by felling mature trees (Johnston and Nauman 1990b). In contrast to many other herbivores, beaver foraging is restricted to a central place within riparian
300 Rodents

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riparian and aquatic vegetation and availability of standing water for larval development. These habitat changes may dramatically increase bird species richness, diversity, and abundance (Krueger 1985; Medin and Clary 1990). Active beaver sites contained 92% of 106 bird species observed in 70 New York wetlands (Grover and Baldassarre 1995). Beaver sites also were important habitat for red-winged blackbirds (Agelaius phoeniceus), Brewer’s blackbirds (Euphagus cyanocephalus), common snipe (Gallinago gallinago), and spotted sandpipers (Actitis hypoleucos) in Wyoming (Brown et al. 1996). In South Carolina, beaver ponds were an important avian habitat in all seasons, but reached maximum bird diversity in spring and summer and maximum number of individuals (all bird species combined) during fall migration (Reese and Hairs 1976). Beaver ponds are especially important in arid environments, where riparian–wetland habitat provides an oasis for birds. Any increase in area or structural complexity of riparian vegetation usually benefits the avian community.

**ECONOMIC STATUS, MANAGEMENT, AND CONSERVATION**

**Economic Value.** The ecological role of beaver discussed in the previous section has tremendous indirect economic benefit through wetland creation, water storage, improved water quality, erosion control, sediment deposition, and recreation. These indirect benefits may far outweigh the direct monetary value obtained from their fur, and may offset any direct or indirect costs due to beaver damage. However, because the monetary value of these indirect ecological benefits has not been quantified, fur trapping and damage control are typically considered of primary economic importance.

American beaver fur for food and clothing and early Europeans valued the underfur of beaver pelts for the manufacture of felt hats. In 1610, France granted Samuel de Champlain the first fur-trading monopoly in North America, initiating 200 years of intensive beaver trapping, which continued until the early 1900s, when beaver populations had been nearly extirpated and demand for felt hats had declined (reviews by Hill 1982; Hill and Novakowski 1984; Novak 1987). Since then, strict harvest regulations, reintroduction programs, and cutting and burning of climax boreal forests (setting back succession) have greatly benefited beaver populations. Annual harvests during the 1980s sometimes exceeded 1 million beaver pelts, more than recorded at any other time (Novak 1987). Although beaver trapping is still an important part of the fur industry in Canada and the United States, erratic and relatively low pel t prices have caused the economic importance of trapping beaver (numbers marketed and value of pelts) to decline relative to furbers such as red fox (Vulpes vulpes), mink, and several other species (Hill and Novakowski 1984; Novak 1987). In addition, the value of beaver pelts varies by region, with those from warmer southern climates valued lower and those of colder northern climates valued higher.

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**Harvest Regulations.** Harvest regulations for beaver have included limits on the number of beavers taken in a season, seasons closed for harvest, and burning of climax boreal forests (setting back succession) have greatly benefited beaver populations. Annual harvests during the 1980s sometimes exceeded 1 million beaver pelts, more than recorded at any other time (Novak 1987). Although beaver trapping is still an important part of the fur industry in Canada and the United States, erratic and relatively low pel t prices have caused the economic importance of trapping beaver (numbers marketed and value of pelts) to decline relative to furbers such as red fox (Vulpes vulpes), mink, and several other species (Hill and Novakowski 1984; Novak 1987). In addition, the value of beaver pelts varies by region, with those from warmer southern climates valued lower and those of colder northern climates valued higher. Pelt prices are a primary incentive for most trappers. Prices influence annual harvest levels and the ability of resource managers to use recreational trapping as a tool to reduce beaver populations or remove unwanted individuals.

**Trapping Techniques.** Trapping regulations or trapping bans can limit beaver trapping as a management tool. In recent years, recreational trapping has been the target of animal rights groups, which have successfully used the public initiative/ballot referendum process in some states (e.g., Amendment 14 in Colorado, November 1996) to eliminate or severely curtail trapping of furbers. The long-term implications of trapping bans on beaver populations in these areas remain to be determined. One possible outcome may be that in some areas where private landowners once considered beaver a valuable fur resource they may instead be viewed as a pest species, with negative consequences to populations (Hill 1982). Regulations that control or ban recreational trapping in many jurisdictions do not apply to landowners who are protecting private property.

**Beaver Damage.** Expanding populations of humans and beaver inevitably lead to property damage. From the point of view of a landowner or other person experiencing damage, the cause is “nuisance beaver”; however, from the point of view of a beaver or some concerned citizens, the cause is “nuisance people.” From either view, beaver damage can be expensive and costly.

Beaver damage varies by type, magnitude, and region. Common complaints regarding beaver damage include flooding of roads (often by plugging culverts) and pastures, eating or flooding agricultural crops (e.g., corn), damage to timber by flooding and cutting (mainly in the relatively flat Southeast), burrowing damage to dikes, ditches, and dams (mainly the arid West), cutting or flooding ornamental plants around homes or businesses, flooding habitat of rare plants or animals, damaging wild trout habitat, damaging fish ponds by plugging the overflow pipe, and potentially increasing the risk of human infection via Giardia lamblia, although some data suggest this is unlikely (Hill 1982; Woodley et al. 1985; Hammerson 1994; Olson and Hubert 1994). Annual cost of damage can be very high. In the early 1980s, annual beaver damage in the United States was estimated at $75–100 million; in the Southeast, the 40-year cumulative damage was estimated at $4 billion (review by Novak 1987).

The importance of timber damage in the southeastern states was recognized soon after beaver were reintroduced; timber damage there far exceeds all other types of complaints (review by Hill 1982). Timber damage was reported by 67% of respondents to landowner questionnaires in Alabama (Hill 1976). In South Carolina, a 1984 survey showed beaver flooded >35,000 ha of timber, often flooding trees during the entire growing season with low dams <0.5 m high (Woodward et al. 1985). If the root systems remain inundated for one to two growing seasons, many species of tree usually will die. Beaver kill timber of all size classes, with loss of larger trees causing greater financial impact on producers. Beaver frequently gnaw bark from hardwoods, which increases the risk of disease and subsequent rotting.

**Damage Control.** Killing unwanted individual beavers and controlled harvests of beaver populations are the most common, and often the most effective, methods of reducing beaver damage, even though lethal control is becoming increasingly less acceptable to the public. In Mississippi, about 20,000 beaver are harvested annually, with 80% of carcasses discarded without use of meat or fur (Schulte and Muller-Schwarze 1999). Nonetheless, annual harvest may be the most prudent approach to animal damage problems, particularly where such harvest can involve citizen participants with no resultant public expense (Hill 1974, 1976). Trapping techniques for taking beaver vary with trapper preference and climatic conditions, the greatest differences occurring between areas that have extremely thick ice and those that are ice free. Successful harvest techniques involve shooting, snaring, and trapping with either No. 3 or No. 4 leghold traps or No. 330 Conibear traps (Hill 1982, Miller and Yarrow 1994). Shooting beaver from boats or from land may or may not be an effective control method (Hill 1982; Olson and Hubert 1994) and raises significant safety concerns. Alligators (Al­ligator mississippiensis) have been evaluated as a control method in the Southeast, but are generally not effective (Hill 1982). Poison bait substances, such as stryamine alkaloid baits and compound 1080, have been evaluated as a lethal control method, but are not approved for this purpose. They also pose political and practical problems, which will likely preclude their development (Hill 1982; Hammerson 1994). Thus, if the decision is to kill problem beaver, then trapping likely remains the most effective method.

However, trapping beaver can be an ineffective control measure if landowners create a sink population by trapping beaver from their own land but fail to reach consensus for control among adjacent landowners containing a source population of beaver. Even when consensus for control is reached, migration of beaver from less-controlled sites to more-controlled sites imposes an external cost (negative diffusion externality) when landowners must incur the future cost of repeated trapping (Bhat et al. 1993). When attempting to minimize beaver damage to timber resources, the cost of trapping must be weighed against the ben efits of increased timber production. Integrating a trapping plan with a timber plan via a cost-minimizing, area-wide bioeconomic model may
help strike the optimal balance between timber damage and trapping costs and maintain a more even density and distribution of beaver in the management area (Bhat et al. 1993).

Timing of trapping is also important where inundation of timber is the primary problem. In this case, it may be most effective to eradicate problem beaver colonies by the end of May and continue to remove im­
migrating individuals until September to prevent the establishment of new colonies (reviews by Hill 1982; Hammerson 1994). In some situations, beaver may tolerate relatively high levels of beaver damage without any major effect on the forest. It is usually best to remove at least 30% of the colonies before the peak in beaver abundance (Hammerson 1994; Olson and Hubert 1994). The most widely used method to control flooding is to dynamic or other­wise remove problem beaver dams. However, this method is usually the least effective because beaver will often rebuild dams within a few days if building materials are still available. Altering habitat to make sites unsuitable to beaver may be possible in some cases, but may require habitat changes that are unacceptable to landowners.

Methods for controlling beaver or their damage often require spe­
cial training, materials, and permits. State and local regulations should be consulted before attempting to control populations or to mitigate damage, such as by installing water control structures that affect in­
stream flow.

Public Opinion. Public opinion is an important consideration when choosing methods to control beaver damage. Many people have an emotional attachment to beaver and are vehemently opposed to any control methods that may cause their pain, suffering, or death. However, attitudes toward beaver control methods vary greatly among individ­
uals, communities, regions, and types of land tenure. Rural residents, especially in agricultural areas, may have less opposition to lethal con­trol than urban residents. People who experience beaver damage may accept harsher control than those without problems. Cultural values attributed to the presence of beaver also vary by region. Beaver may be more socially and economically valued in regions of Canada and the northern United States than in the Southeast, where fur values are lower, damage to timber and development is more severe, and beaver have less historical and cultural value.

Social acceptability of beaver control depends on many factors. Residents in suburban areas of New York were willing to accept increas­ingly invasive control when they had increasingly severe concerns about problems (Loker et al. 1999). Contrary to predictions, residents were willing to use more severe control measures for nuisance and economic damage problems than for concerns about public health and safety (re­sults combined for white-tailed deer, Canada geese, and beaver). In another New York survey, nearly 50% of stakeholders took lethal ac­tions to solve beaver problems; highway superintendents were more likely than the general public to attempt to solve beaver problems and to use actions that were nonlethal but invasive (Enck et al. 1997). In Wyoming, managers of private and public lands were concerned that beaver caused problems when they blocked irrigation ditches, gridded timber, blocked culverts, and flooded pastures, roads, crops, and timber. However, 45% of private landowners with beaver on their land and all public land managers were interested in the proactive use of beaver for riparian management (McKinstry and Anderson 1999).

Population and Harvest Management. Do beaver populations “need” to be harvested so they do not “eat themselves out of house and home”? This management philosophy is pervasive in the culture of laypeople and professional wildlife managers. But is it true? Why would beaver need the help of humans to control their populations, whereas nongame mammals seem to manage just fine without it (aside from pervasive anthropogenic stressors)? How does the absence of wolves or other predators affect beaver carrying capacity? Clearly, answers to these questions are beyond the scope of this chapter, but recent evidence provides some interesting discussion points. For example, densities of beaver colonies did not differ in a comparison of unexploited, saturated populations and exploited, thinned-out populations. Beaver in the sat­
urated populations, however, colonized steeper gradients, had families with a larger percentage of 3-year-olds, depleted preferred trees and fed on less palatable species, and extended trails to more distant foraging sites (Muller-Schwarze and Schulte 1999). Because the maximum density of colonies (usually a minimum distance of about 0.9 km be­tween colonies) may be controlled by territorial behavior rather than by habitat selection, beavers in areas with smaller populations may be­come saturated or self-limiting below habitat-based carrying capacity.

Beaver typically maintain intercolony distances and body weight re­
gardless of population density. In some areas, forage near the central place may be less palatable or compete with other plants, causing colonies to periodically move to former beaver habitat that has
recovered or to new habitat. In other areas, beaver may persist indefinitely within the same stream reach. In the Rocky Mountains, beaver may temporarily abandon mixed aspen-conifer sites after removing available aspen from nearby uplands, but may indefinitely occupy riparian-willow sites, where dams create moist, bare soil and a high water table, which helps establish and perpetuate the willow community. Despite lack of any inherent control needs, beaver harvest provides valuable recreational and income opportunities for trappers and is the primary means of reducing beaver damage to timber and other resources. Thus, justification for beaver harvest should be based on the economic value of fur trapping or “managerial decisions [that] address conflicts between beaver and humans, and not necessarily any requirements of the beaver themselves” (Muller-Schwarze and Schulte 1999:176).

Beaver populations are managed by state, provincial, and territorial wildlife agencies in the United States and Canada. Agencies are responsible for setting seasons, setting bag limits or area-specific quotas, licensing trappers, stamping or tagging pelts, licensing fur dealers and auction houses, and enforcing laws and regulations (Novak 1987). Trapper education is an important part of beaver management. Trappers in the field influence the age, sex, and distribution of animals removed as they make decisions about how, when, and where to set and check traps. Harvest rates, or quotas, are based on allowable harvest to maintain sustained yield. Rates suggested by different studies have varied from 10% to 70%, depending on habitat type, elevation, and region. The most typical recommended annual harvest rate is 20–30% of the population, which is about 1.0–1.5 beaver/colony/year. Beaver are highly vulnerable to overharvest, so managers must closely monitor populations. Their slow rate of reproduction and delayed sexual maturity preclude reproduction as a means to offset intensive annual harvest.

Regional differences among habitat types and land management prescriptions warrant regional beaver management plans (Snodgrass 1997). Managing beaver by managing their food supply may be possible in some regions. For example, prescribed burning may encourage aspen production in mixed-conifer habitat, but may be of limited value where multiple forage species are available.

Using Beaver for Habitat Restoration and Improvement. The ability of beaver to store water, trap sediment, reduce channel erosion, and enhance establishment and production of riparian vegetation can be used as a proactive management tool to restore degraded riparian habitat. Beaver were abundant in forested, shrub-steppe, and some hot desert habitats in the western United States until fur trapping decimated populations. Ranchers followed trappers in settlement of the West, and immense numbers of sheep and cattle subjected newly beaver-free riparian areas to intense overgrazing. Overgrazing stripped streambanks of soil-binding vegetation, and channels responded with accelerated erosion and severe downcutting (see Elliott et al. [1999] for a discussion of possible mechanisms to explain observed channel incision). Mechanical restoration and revegetation (willow, cottonwood) of incised channels can be expensive, labor-intensive, and often
Beaver have also been useful as a timber management tool in the southeastern United States. Flooding by beaver ponds kills existing noncommercial vegetation, thus preparing sites for reforestation with commercially valuable timber. By draining ponds and removing beaver, landowners can reduce the cost of clearing land, often a major component of timber production (Houston et al. 1992).

Population Estimation. Population density of beaver is usually expressed as number of colonies or individuals in areal or linear units. Areal estimates are more appropriate where wetlands and herbaceous growth are diffuse and linear estimates are better where beaver habitat is limited to well-defined watercourses. Estimates of number of individuals are often derived from colony counts, but are not meaningful unless the mean number of beaver per colony is based on local data and not the general literature. Multiplying number of colonies by the general average of 5 or 6 beaver per colony only adds false precision to population estimates.

Estimates of mean colony size are very difficult to obtain and vary temporally and spatially, but are important in setting harvest quotas (Novak 1987). Colony size can be estimated by using night-vision scopes to count beaver as they move about their territory, driving beaver from their lodges using smoke or dogs, draining the pond and dismembering the lodge (not recommended), attempting to trap all the beaver in a colony (difficult to accomplish, thus a conservative estimate), and employing models that use age and reproductive data from populations of trapped beaver (Novak 1987) or data on the interactions among natality, mortality, and dispersal (Bishir et al. 1983).

Size of the food cache may be a useful predictor of colony size, but more research is needed to better understand relationships, as studies in different regions have been equivocal. In Montana, aerial cache surveys of prairie rivers located about 90% of caches, but colony size varied among years and areas. Thus, cache counts alone are not good predictors of population size or trend (Swenson et al. 1983). Estimates of cache size are more meaningful, thus the interactions among natality, mortality, and dispersal (Bishir et al. 1983).

Beaver restoration in western riparian areas may also help control tamarisk, an invasive woody species (Fig. 15.4). In northwestern Colorado, beaver used tamarisk, sagebrush, and greasewood (Sarcobatus vermiculatus) as building material for a series of dams, which coincided with increase in the distribution and abundance of coyote willow (S. exiguus) relative to tamarisk (B. W. Baker, unpublished data). A similar response as a restoration tool, even where willow or other suitable winter food may be lacking (Fig. 15.4). Livestock grazing must be managed before beaver reintroduction to allow development of an adequate biomass of herbaceous aquatic and riparian vegetation for summer beaver food and to permit establishment and growth of willow or other woody riparian vegetation for winter beaver food. Aspen, cottonwood, or willow can be provided at reintroduction sites, or where beaver have initiated dam building on their own, to encourage beaver to remain at the site and to provide them with stronger dam-building material, which might otherwise be lacking (Apple et al. 1985). In some cases where overwinter food is lacking, beaver may subsist on herbaceous vegetation long enough to build dams and ponds. These features may initiate a positive riparian response, which stimulates growth of willow or other suitable winter food. A winter food cache provides beaver with more permanent habitat and the ability to successfully raise young. Thus, beaver can create a positive feedback mechanism by temporarily expanding into marginal habitat (naturally or by introduction), improving conditions for the establishment and survival of woody riparian vegetation, and persisting long enough to raise young, which can disperse to new marginal habitat.

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**Figure 15.4.** A conceptual model of the use of the beaver (*Castor canadensis*) activity as a possible mechanism for riparian restoration in shrub–steppe ecosystems.
Aerial surveys have been widely used to estimate the size and distribution of beaver populations, but evaluations of their efficiency, accuracy, and precision in terms of costs and benefits suggest their value is highly variable (Novak 1987). Surveys are usually conducted in the fall after leaf drop but before freeze-up. Results depend on search methods, topography, overstory vegetation, type of aircraft, and behavior of beaver (reviews by Hill 1982, Novak 1987). For example, aerial surveys only located 41 of 146 ground-located beaver colonies in Kansas riverine habitat, where beaver lived in bank dens and did not build food caches (Robel and Fox 1993).

Various combinations of aerial photography, aerial videography, and geographic information systems (GIS) can also be used to survey beaver populations and evaluate habitat conditions. Aerial photographs can be used as a reconnaissance aid to locate beaver habitat in remote locations for later ground or aerial surveys, to map locations of dam ponds, and lodges via photointerpretation methods; to find and/or plot colony locations during ground surveys (<1:3000-scale best); and to create overlays of beaver locations and habitat features that can be digitized into a GIS (Parsons and Brown 1978; Novak 1987; Baker et al. 1992; Werth and Boyd 1997). A GIS is essential for some types of landscape-level analysis of beaver habitat and may be better than manual methods for others, depending on costs and technical requirements (Johnston and Naiman 1990c). Global positioning systems (GPS) allow users to plot exact locations of active or inactive dens and ponds, which can be integrated with GIS systems to develop highly accurate beaver habitat models or monitoring programs. Aerial videography via a helicopter-mounted video camera may be useful for locating and monitoring beaver populations, especially in underbrushy riparian systems that are difficult to observe from low-level, fixed-wing aircraft (B. W. Baker, pers. obs.). Video has the advantage of instant availability on return from the flight and can be integrated with onboard GPS systems to create georeferenced data for computer analysis; however, videography is less useful than aerial photography for creating images for use in the field.

Sex Determination. Sex of beaver carcasses can be determined by the presence of the baculum and testes in males and the uterus in females, but the lack of any obvious external sex characters makes sex determination in live animals difficult (Novak 1987). The sex of live adult beaver can be determined by probing the cloaca or palpating the abdominal region for the baculum and testes, by noting the presence of four enlarged precastoral mammae in pregnant females (after 2 months), by giving beaver the anesthetic combelen (which causes the penis to become flaccid), by detecting Barr bodies in blood smears, and by giving beaver the anesthetic combelen (which causes the penis to be bleached or dyed. Hind feet webs also can be tattooed or punched to individually mark beaver. Subcutaneously placed passive integrated transponder tags can positively identify recaptured beaver as well as beaver tails of various sizes (kits, adults) and allow telemetry. Beavers are nocturnal and difficult to observe, so telemetry is often valuable in studies of their behavior and movements. However, transmitter attachment has been problematic. Neck collars often slip off because beaver have a thick neck relative to head size, and tail collars slip off if tail size decreases following release (B. W. Baker, pers. obs.). Free-floating intraoral transmitter implants have proven successful in several studies, although their range can be relatively short (ground-to-ground signal of 0.1 km for beaver inside burrows and 2 km for active beaver; Davis et al. 1984). Implanted transmitters tend to become tightly encapsulated with necrotic fibrous tissue and may be well tolerated by beaver (Guyrn et al. 1987). Implants have been performed via dorsal (Davis et al. 1984) and ventrolateral (Whately 1997d) incisions. Although both techniques have been successful, the ventrolateral method appears to involve less risk to the animal.

Tail-mounted transmitters have shown variable success in Wyoming (Bothmeier et al. 2002), Massachusetts (C. Henner, pers. commun., 2001), and Colorado (B. W. Baker, pers. obs.). This method uses a livestock ear tag transmitter attached to the dorsal surface of a beaver’s tail. Dimensions and weight of tail-mounted transmitters can be designed to fit beaver tails of various sizes (kits, adults) and allow for variation in tail thickness. Durability and attachment effects (e.g., tearing the tail) of tail-mounted transmitters have yet to be determined, although preliminary evidence suggests short retention time for a relatively high percentage of individuals (B. W. Baker, pers. obs.).

Reintroduction. The first step in any reintroduction program should be to determine the purpose and feasibility of attempting to establish new
beaver populations. This includes an understanding of why beaver are absent from the site, why they are important to the site, justification for relocation rather than natural dispersal, likelihood of movement beyond the intended relocation site, and potential conflicts or interactions with other resources or landowners. Relocation decisions and expectations are usually based on professional judgment after considering all available information. Techniques need further refinement to stay at specific release sites by providing aspen or other preferred species as food and building material or creating a base for a beaver dam by placing posts, wire fencing, silt-retaining fabric, rock, or other material (Apple et al. 1985; B. W. Baker, pers. obs.).

Survival of relocated beaver can depend on suitability of available habitat, timing of release (late summer in areas that freeze allows time to establish ponds and food cache), sex, age, composition, and number released (entire family units may improve establishment success), predation, and disease. In a study of 57 released Eurasian beaver in the Netherlands, 19 animals were found dead within the first year and 50% of these had died of infectious diseases (Vereinia pseudobehrholodis, Y. enterococli, Leptopiosis, and others) (Nolet et al. 1997). Stress during handling may increase risk of disease following release. Vac-cinate data, but also may be based on anti-attenuation vaccination records before release may reduce mortality. Holding beaver in a cool, damp environment, providing adequate food and water, and minimizing length of captivity should improve survival following release (Novak 1987).

RESEARCH NEEDS

Beaver research has evolved from descriptions of beaver and their habi-tat to attempts to better understand mechanisms that explain behavior, population structure, and their keystone role in ecosystem structure and function. New knowledge about beaver will likely come from cross-discipline studies that stretch the boundaries of our already rich litera-ture base on beaver. For example, a better understanding of the role of beaver as geological agents in the formation of alluvial woodplain valleys begs for the integration of the ecological sciences with new methods of dating sedimentary layers. This is also true for understanding beaver s ability to absorb their impact. The human dimensions of the proposed reintroduction of Eurasian beaver to Scotland. Their model evaluated the potential dispersal and abandonment that make up the life history of a beaver pond ecosystem. In South America and Europe, beaver are an important resource or landowner for the intended relocation site, and potential conflicts or interactions with other resources or landowners. Relocation decisions and expectations are usually based on professional judgment after considering all available information. Techniques need further refinement to stay at specific release sites by providing aspen or other preferred species as food and building material or creating a base for a beaver dam by placing posts, wire fencing, silt-retaining fabric, rock, or other material (Apple et al. 1985; B. W. Baker, pers. obs.).

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ACKNOWLEDGMENTS

We are grateful to David Mitchell for compiling relevant literature, Dale Crawford for the preparing the artwork in Figures 15.3 and 15.4, and Stewart Breck, Doug Smith, and Butch Roelle for reviewing the manuscript. Funding was provided by the U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado.

LITERATURE CITED


Barnes, D. M., and A. U. Mallik. 1997. Use of woody plants in construction of beaver dams and pond sediments. An important research need is to develop independent lines of evidence about how beaver affect ecosystem structure and function over the full range of ecolog­ical conditions inhabited by beaver, especially in the less well-known communities such as southeastern forests, western shrub-steppe, and desert grasslands. These studies should include the sequential events of development and abandonment that make up the life history of a beaver pond ecosystem. In South America and Europe, beaver are an invasive species with an ecological role that likely will require a differ­ent level of understanding than in their native North American habitat. The economic values of beaver wetlands in storing water, improving water quality, restoring wetland function, and mitigating development will be of critical importance as human populations expand and strain the land’s ability to absorb their impact. The human dimensions of beaver management and control methods need improved understand­ing to better educate a public that is becoming more removed from the land and more inclined to use legislative or judicial means rather than the judgment of wildlife professionals to manage wildlife popula­tions. Techniques need further refinement to more effectively estimate beaver populations, determine sex and age of live beaver in the field, and better use advanced telemetry as a research and management tool. For example, no radio-attachment technique has simultaneously solved problems of minimal effects to the animal, long retention time, long signal range, and long battery life. The information presented in this chapter was based primarily on literature published since 1982. Readers are referred to the first edition of Wild Mammals of North America for a more thorough coverage of earlier work, and the following reviews and annotated bibliographies: Denney (1952), Yeager and Hay (1955), Jenkins and Busher (1979), Hodgdon and Larson (1980), Novak (1987), Medin and Torquemada (1988), and Olson and Hubert (1994).


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