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Beaver

Castor canadensis

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NOMENCLATURE

COMMON NAMES. Beaver, North American beaver, Canadian beaver, American beaver, el Castor
SCIENTIFIC NAME. *Castor canadensis*
SUBSPECIES. *C. c. acadicus, C. c. baileyi, C. c. belugae, C. c. caecator, C. c. canadensis, C. c. carolinensis, C. c. concisor, C. c. duchesnei, C. c. frondator, C. c. idoneus, C. c. labradorensis, C. c. leucodontus, C. c. mexicanus, C. c. michiganensis, C. c. missouriensis, C. c. pallidus, C. c. phaeus, C. c. repentinus, C. c. rostralis, C. c. sagittatus, C. c. shastensis, C. c. subauratus, C. c. taylori,* and *C. c. texensis* (Hall 1981)

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 *C. 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 *Casteroides,* 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, initiating a continent-wide recovery of beaver populations. To supplement natural recovery, during the mid-1900s beaver were livetrapped 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 km^2 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 subsist 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).

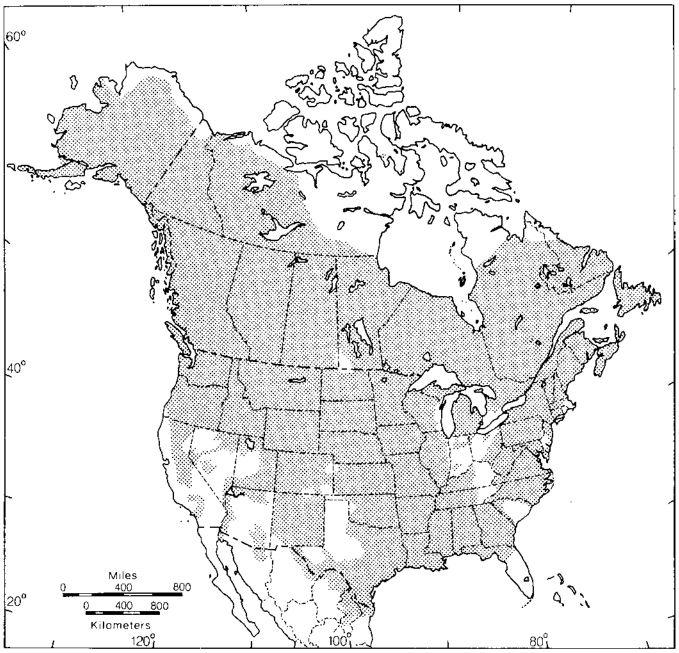

FIGURE 15.1. Distribution of the beaver (*Castor canadensis*). Modifications of the range map by Deems and Pursley (1978) include populations in Mexico, southern California, west-central Florida, and Delaware and the absence of beaver in the North Slope of Alaska.

Introductions of beaver in Finland (Lahti and Helminen 1974), Asian Kamchatka (Safonov 1979), Argentina (Lizarralde 1993), and other locations have resulted in the establishment of viable populations beyond their original range in North America. For example, 25 mated pairs of beaver were introduced (as a captive population) to Tierra del Fuego, Argentina, in 1946 to establish a fur industry. Animals that later escaped or were intentionally released resulted in a viable wild population. This population rapidly expanded in the absence of predators and other natural population controls, causing a substantial impact on native southern beech (*Nothofagus*) forests (Lizarralde 1993).

DESCRIPTION

Beaver are the largest rodents in North America. Most adults weigh 16–31.5 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 dorsoventrally 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) containing a few scattered, coarse hairs. The caudal vertebrae are dorsoventrally flattened, with a complex arrangement of muscles and tendons to support the flat tail (Mahoney and Rosenburg 1981). Incisors are generally orangish in color, with the anterior surface in adults >5 mm wide, a feature that helps distinguish beaver damage from other rodent damage on the basis of toothmark width.

Beaver move with an awkward waddle on land, but can gallop if frightened. Adult beaver can walk upright in a bipedal fashion (partially supported by the tail) while carrying mud or sticks held against the chest with their chin and front legs. In water, they swim by alternate kicks of the hind legs, appearing graceful and efficient, though slow and deliberate. Beaver are shaped more like marine mammals than like other terrestrial mammals, with a fineness ratio (a hydrodynamic index of streamlining) of 4.8, a value similar to that for phocid seals (Reynolds 1993). In addition, the surface area of unfurred extremities (hind feet and scaly tail) is 30% of the total, perhaps a compromise between the need for propulsion and minimization of the area for heat exchange. Webbed toes on large hind feet (up to 200 mm long) facilitate swimming, and short, heavily clawed front feet facilitate digging. Great forepaw dexterity enables beaver to fold individual leaves into their mouth and to rotate small, pencil-sized stems as they gnaw off bark. 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.

The two inside (medial) toes of each hind foot have movable, split nails, which beaver use as combs to groom their fur (Wilsson 1971). Beaver have closable nostrils, valvular ears, nictitating eye membranes, and lips that close behind large incisors, adaptions important to their semiaquatic existence. During periods of active lactation and when parturition is near, four pectoral mammae 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 trappers's lures.

Beaver skeletons are massive when compared to those of other mammals of similar length. The skull and the 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 (Friley 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 I 1/1, C 0/0, P 1/1, M 3/3. Incisors grow continuously and the chiseled edge is sharpened by grinding the uppers against the lowers (Wilsson 1971). The hard enameled front surface of incisors serves as the cutting edge to fell trees and peel bark. Cheek teeth are hypsodont 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.

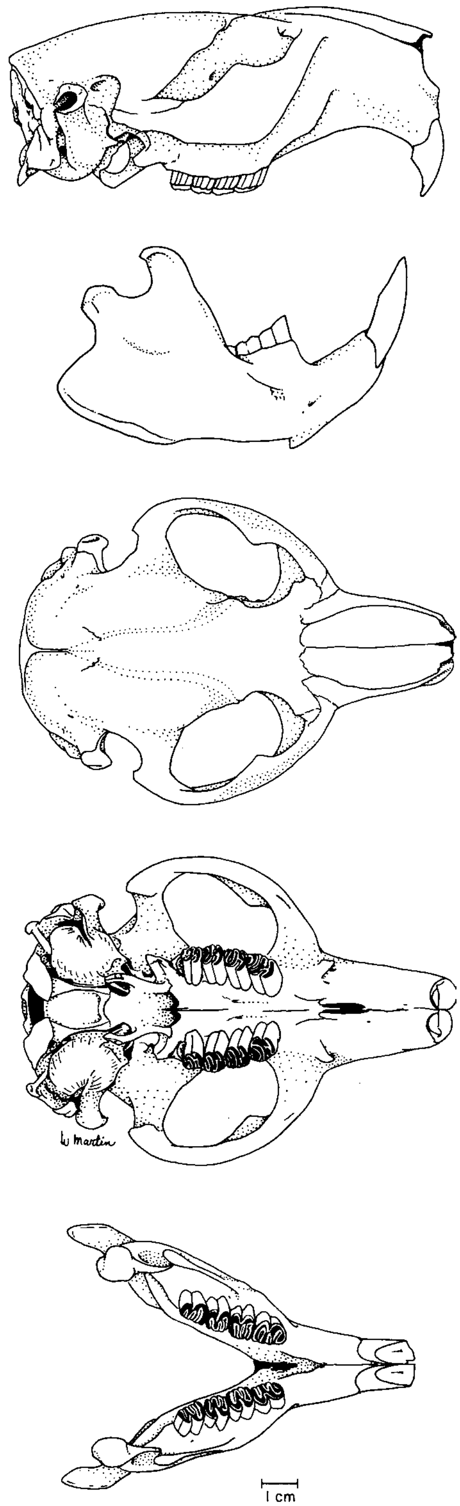

FIGURE 15.2. Skull of the beaver (*Castor canadensis*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

PHYSIOLOGY

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 torpor. 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 cardiogastric 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 (Buech 1984). In contrast, lagomorphs reingest and swallow mucous-covered entire pellets.

Circulation. Beaver heart weight averages 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 mammalian and resemble those of both terrestrial and aquatic mammals (Bisaillon 1981). Beaver have no unusual oxygen storage capacity, but certain changes in blood parameters, heart rhythm, and circulation enable them to make dives lasting up to 15 min without asphyxiation (review by Hill 1982). Aleksiuk (1970a:145) noted that "minute blood vessels permeate the entire tail, and a countercurrent heat exchange system is present at the base." This specialized circulatory feature helps conserve heat energy in extremely cold water and radiate heat during hot weather.

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-old beaver produced young, and believed that early sexual maturity in Saskatchewan beaver was enhanced by high-quality habitat. Reproduction in yearlings may cease where >40% of suitable beaver habitat is occupied by established colonies. In Newfoundland, 24% of yearling females had bred (Payne 1975). In northern Canada, Novakowski (1965) found first pregnancies in 3 of 21 females that were approaching their third birthday, but no indications of conception in females that were almost 2 years old. In Alabama, in 2.5- to 3-year-old females, only 16 of 65 had ovulated, and there were no indications of ovulation or pregnancy in 50 yearlings. However, in Tennessee, Lizotte (1994) found sexual maturity occurred at 1.5–2.0 years of age, with a 25% pregnancy rate in this age class.

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, which is generally shorter in colder climates and longer in warmer climates (Hill 1982; Wigley et al. 1983). Breeding takes place in water (Kowalski 1976), bank dens, or lodges. Wilsson (1971) reported that *C. fiber* remains in estrus 10–12 hr and has a second estrus in 14 days if not fertilized. A gestation period of 100 days is typical for *C. canadensis* (Wigley et al. 1983), with a range of 98–111 days (review by Hill 1982).

Sex Ratios. Sex ratios in monogamous species are important because they can influence pregnancy rates. When averaged across age class, region, and harvest level, the sex ratio of beaver may be nearly even, but substantial variation among populations suggests caution in making this assumption. Sex ratios of trapped populations may reflect bias inherent in trapping methods, although results of different studies are inconsistent. For example, some studies found no difference in susceptibility of sexes to baited Conibear traps set under ice, but others suggested trapping was selective for adult females. Others have noted higher mortality from trapping and other causes for adult males (review by Hill 1982). In a review of 15 studies, Woodward (1977) found an average sex ratio of 98.5 males:100 females, but a ratio of 90.7:100 for adults and 111.4:100 for subadults. The combined average from studies in Saskatchewan, Newfoundland, Vermont, and Alabama was 105:100 ($N = 4867$) (review by Hill 1982).

Pregnancy Rates. Knowledge of pregnancy rates among age groups in monogamous species increases accuracy in computing estimates of reproductive performance. Pregnancy rates usually increase from 1.5 years of age until about age 4 years, remain high until old age, and then decrease (Lizotte 1994). Where populations are not exploited and suitable habitat is fully occupied, there likely is less dispersal and therefore less breeding among young adults, which remain in colonies containing older dominant pairs. Thus, both habitat quality and extent of exploitation should be considered when using pregnancy rates to calculate reproductive performance.

Reproductive Performance. Placental scar counts (Hodgdon 1949), counts of developing embryos, and, with some limitations, counts of corpora lutea and corpora albicantia are useful indices of reproductive performance in beaver (Provost 1958). In Mississippi, counts of fetuses, placental scars, and corpora lutea all yielded statistically similar estimates of litter size, despite pre- or postimplantation losses (Wigley et al. 1984). Preimplantation losses from unfertilized ova or failure of fertilized ova to implant and postimplantation losses resulting in resorptions account for differences between ovulation rates and litter size. Intrauterine mortality was 16% in 48 beaver from Ohio and almost 19% in 40 beaver from western Massachusetts (review by Hill 1982). Where rates of prenatal loss are high, correction factors should be developed to obtain more precise estimates of litter size and annual productivity (Wigley et al. 1984).

In areas where carcasses are available from fall or early winter trapping, counts of placental scars and persisting corpora albicantia, corrected for current resorption rates and prenatal loss, respectively, provide an index of litter size from the previous spring. Sources of error, such as regression or discoloration of implantation sites by some preservatives and degeneration of corpora albicantia with the onset of the breeding season (Provost 1962), make estimates of reproductive performance in fall less accurate than those made at other times. Where trapping seasons overlap the breeding season, a combination of placental scar counts corrected for the past season resorption rates and corpora lutea counts corrected for current resorption rates can provide information on litter size. However, early in gestation, it is difficult to distinguish between corpora lutea of ovulation and corpora lutea of pregnancy, which introduces a potential source of error in estimates of reproductive performance (Provost 1962). Also, embryo counts and ovulation rates of females trapped in January and February may not provide precise estimates of current-year breeding among yearlings and subadults. These age groups may breed later than adults (Grinnell et al. 1937), particularly at southern latitudes or if they had dispersed during the summer. Thus, winter samples may not reflect reproductive performance as well as those from May or June.

Where trapping seasons occur after the breeding season, counts of developing embryos, corrected for current resorption rates, provide an accurate index of litter size among age groups. Resorption is negligible if embryos are in an advanced stage of development. Where possible, delaying the trapping season until breeding has occurred may lower the incidence of unbred females whose mates were trapped from the population before breeding (Hodgdon and Hunt 1953). Such delay also facilitates measurement of current litter size through embryo counts.

The litter size of beaver is typically two to four, although local averages may be as high as six, and the number can vary from one to nine (reviews by Hill 1982; Wigley et al. 1983). These reviews suggest that beaver in the southeastern United States tend to have smaller litters, whereas northern and perhaps western beaver tend to have larger litters. Large litters may be associated with better quality habitats and increased weight of the mother. In Mississippi, age of mother was only weakly correlated with litter size, but weight of mother was strongly correlated. Litter size can also be reduced by lack of food (e.g., due to ice on ponds) or quality of food (e.g., limited supply of preferred plants) (Rutherford 1955). Because fewer yearlings breed in relatively dense populations and litter size may be inversely related to the number of beaver in the family, reproduction in beaver may be density dependent (Payne 1984). Some evidence also suggests that beaver may breed only during alternate years in very poor quality habitat, although this hypothesis needs further investigation (D. W. Smith, pers. commun., 2001).

Development of Young. Growth curves of the fetus 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. Zurowski 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 coterie 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 (Patenaude 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 (Hodgdon and Lancia 1983). The whine is the most frequent vocalization and can be repeated in rapid succession. Beaver of all ages whine, 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, either separately or in combination. The response of 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 beaver. Kits are least likely to move or to elicit a 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 secretions 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 reoccupy 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 castor fluid among family members, neighbors, and nonneighbors (beaver from beyond adjacent territories). They "overmark" the scents from strangers more often than scents from family members (Schulte 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 Schulte (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 Heckman 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 (Aleksuik 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 in winter limits movements (Van Deelen and Pletscher 1996). Movements 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 Pletscher 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 summer, 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 radiotelemetry 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 contribute to variation in 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/km^2 (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-Schwarze 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, after beaver returned to 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 (Busher 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 understand extrinsic factors affecting beaver populations, such as trapping, anthropogenic habitat alteration, and competition with other species.

Construction of Dams, Ponds, and Canals. Beaver are unique in their ability to create favorable aquatic habitat by building dams to restrict the flow of moving water, a behavior richly described in early literature on beaver and in many popular texts (Hilfiker 1991). The widely recognized beaver dam and beaver pond have made this seldom seen nocturnal rodent a familiar and well-studied mammal in North America.

Dams may be initiated by pushing sediment, rocks, or sticks into a ridge formed perpendicular to the flow of moving water or by locating sites to take advantage of existing substrate (Hodgdon and Lancia 1983). 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.

Beaver 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, corncobs, cornstalks, 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 overflows the channel as it develops behind the dam, then beaver will often extend the dam laterally by adding shallow wings. Often several dams 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 breach in the dam (Aeschbacher and Pilleri 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; Busher 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.

Beaver 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 they will build or extend canals to access 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 in summer and 8 mg/cal 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 herbaceous component of the diet (Novak 1987). Its edible rhizomes remain succulent after cutting and are often stored in a food cache for winter use (Jenkins 1981). A variety of grasses, sedges (*Carex*), rushes (*Scirpus*), and cattails (*Typha*) is important in the West and Southwest.

Deciduous woody plants are usually the most important component of the diet of beaver and often are the primary limiting factor where ice forces subsistence on a winter food cache. Beaver eat the leaves, buds, twigs, noncorky bark, roots, and fruits of deciduous woody 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 1970), 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.

Conifers also are cut or gnawed by beaver and used for food or building material, although their value varies greatly by region and availability of preferred deciduous species. In the eastern United States, loblolly pine (*Pinus taeda*) and Virginia pine (*P. virginiana*) may make up over half of the woody material cut by beaver (Novak 1987). They may repeatedly gnaw the bark of pine trees to obtain sap (Svendsen 1980b) or sweetgum (*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 often 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 (Jenkins 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 aspen 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 food preference and retention time are 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 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-Schwarze 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-Schwarze 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).

The size–distance relation in food selection by beaver also may be affected by species preferences. For example, Jenkins (1980) found that beaver cut larger stems of preferred species, such as oak and cherry (*Prunus*), further from the central place than less-preferred species. In contrast, although Belovsky (1984) did find that beaver had strong food preferences, preferences did not change relative to distance from beaver ponds. In many cases, the interaction of species preferences with stem size and distance from the central place has been difficult to document in the field because depth to water and other plant-growing conditions preclude equal availability of stems to beaver. Modeling the diet of beaver is one way to overcome limitations of field experiments. For example, Belovsky (1984:220) found that beaver at Isle Royale selected their diet "consistent with an energy-maximizing solution to a linear-programming model." This energy maximization model was further confirmed by Fryxell (1992) with a second line of evidence, which found both density and distance were important predictors of food selection by beaver.

Chemical factors and stem size may also influence stem selection by beaver. If aspen responds to repeated beaver cutting by producing a juvenile growth form, then higher concentrations of phenolic compounds (secondary metabolites) may inhibit further cutting by beaver and influence the predictive value of optimal foraging models for beaver. Basey et al. (1988) found beaver avoided aspen stems <4.5 cm in diameter in favor of those >19.5 cm in diameter near a 20-year-old beaver pond where 51% of stems had been previously cut by beaver and the remaining 49% of stems were in juvenile form. In contrast, beaver at a newly occupied site selected smaller aspen stems and against larger ones. Taken together, these results suggest that phenolic compounds, or other factors in addition to size of stem, may influence selection by beaver.

Food Consumption and Production. Estimates of daily forage consumption rates (wet woody biomass) for beaver vary from 0.5 kg/day (Dyck and MacArthur 1993) to 2.0 kg/day (review by Stegeman 1954). ln an interesting account of a Colorado beaver colony fed by a Forest Service contractor in the 1920s, it was estimated that each beaver consumed (although possible use in dams was not described) an average of about 900 kg of green aspen/year (Warren 1940). 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.

Estimates of beaver food (twigs and bark) produced by trees and shrubs may be useful for predicting the carrying capacity of beaver where woody biomass limits population density. Beaver food estimates are derived from graphs or equations that model annual production (current annual growth) and total biomass based on measures of basal stem diameter. Estimates have been derived for aspen (Aldous 1938; Stegeman 1954), willow (Baker and Cade 1995), and five species of riparian shrubs in Minnesota (Buech and Rugg 1995). The maximum diameter of twigs that are entirely consumed by beaver is a critical consideration in deriving estimates of beaver food. The diameter used is often based on assumptions made from observing the size of peeled stems, but may vary greatly by species and region. For example, Aldous (1938) assumed beaver ate all stem portions <12.7 mm in diameter for aspen, Buech and Rugg (1995) assumed <5 mm for Minnesota shrubs, and Baker and Cade (1995) assumed <3 mm for coyote willow (*S. exigua*). Application of results among studies and different woody species requires caution. In addition, intense ungulate or livestock herbivory of the terminal leaders on shrubs may strongly reduce the biomass of beaver food relative to unbrowsed stems of equal diameter (B. W. Baker, pers. obs.).

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 above 3400 m (reviews by Hill 1982; Novak 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 quantified habitat requirements and created a framework for making and testing predictions. Slough and Sadleir (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 km of stream or 1.3 km^2 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 riverine lodge-site locations in areas that had thick, concealing vegetation cover (which was often left uncut) and steep shoreline banks (Dieter and McCabe 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., *Alnus*) 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 riverine habitat quality for beaver in the central United States (Robel 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, territoriality, 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: 55% of wolf scats had beaver remains (Voigt et al. 1976). In an experimental study in Quebec, density of beaver colonies increased 20% after 3 years of wolf control and then declined again after wolf control ceased, indicating wolf predation may have suppressed populations below the carrying capacity of the habitat (Potvin et al. 1992). Habitat conditions that force beaver to forage farther from water may increase predation rates by wolves. On Isle Royale, beaver foraged further (>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.), wolverines (*Gulo gulo*), 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 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* biovar *palaearctica* (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 (Morner 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 epizootics. 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 (Gunson 1970; Bergerud and Miller 1977). Sudden snowmelts 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 overall and disproportionately large relative to its abundance (Power et al. 1996). 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 annual stream discharge rate by retaining precipitation runoff during high flows and slowly releasing it during low flows, alter stream gradients by creating a stair-step 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 (Ruedemann and Schoonmaker 1938). They suggested that during the 25,000 years since the last glaciation, layer on layer of sediment-filled beaver ponds caused the "complete aggrading of valley floors, originally in small descending steps, which disappear in time and leave a gently graded, even valley plain horizontal from bank to bank" (Ruedemann 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 (Meentemeyer and Butler 1999). Thus, unless dams fail, 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 sediment-loaded 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 (Meentemeyer 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 runoffs. In 1994, a beaver dam in central Alberta failed and released 7500 m^3 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 dams 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, sodium hydroxide-extractable phosphorus (biologically available P), and total Kjeldahl nitrogen were reduced in water flowing through beaver ponds during high spring runoff (Maret et al. 1987). The effect of beaver ponds on these parameters continued during summer low flows, but was of lower magnitude. Effects disappeared at about 1.6 km below the beaver dams, likely due to inputs from bank erosion (Parker et al. 1985; Maret et al. 1987). Beaver ponds may also influence water quality by affecting the number and composition of bacteria in the stream. In Wyoming, some 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 Ecological Processes. In addition to geological affects, 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 browse zone concentric 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 process. Effects are greatest where contrast is greatest. Beaver that create dams in existing wetlands have less effect than those that dam streams in upland forest or desert shrubland. Basin geomorphology and length of occupancy also affect the magnitude of influence. Beaver typically select the best pond sites first and move to less desirable sites as populations grow or as resources are depleted. Ponds built in better sites have greater longevity and affect the disturbance dynamics in the system. In a Minnesota study, a series of aerial photographs between 1940 and 1986 showed the rate of patch formation was much greater during the first two decades following colonization than during the second two decades, which suggests that geomorphology eventually limited the availability of pond sites after the initial better sites were occupied (Johnston and Naiman 1990a).

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 anerobic conditions, slow flows, and increase oxygen demand by retaining organic matter. In Quebec, a beaver-modified section of stream "accumulated 10^3 times more nitrogen than before alteration" (Naiman and Melillo 1984:150). Anerobic 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 vegetative 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 m^3 of wood retained 2000–6500 m^3 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, 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 confluens*) 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 nonresprout 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.

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 freezing in winter (often capped with ice and snow, 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 Wyoming, 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 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 coho fry 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 "source" 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 (Snodgrass 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 hydrological and ecological conditions within 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 below 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 the following season (Kindschy 1985). 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 that 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 Naiman 1990b). In contrast to many other herbivores, beaver foraging is restricted to a central place within riparian communities where their habit of felling much more woody material than they actually consume dramatically increases the magnitude of their effects relative to other woody-plant foragers. In a Minnesota study, intense foraging by beaver decreased tree density and basal area by up to 43% near ponds, where individual beaver harvested an average of 1400 kg/ha/year of woody biomass over a 6-year period (Johnston and Naiman 1990b). Selective foraging decreased aspen and increased alder and conifer, with long-term effects on forest succession. In Wisconsin, beaver substantially reduced the density of preferred understory tree species (W. J. Barnes and Dibble 1988). Because understory species normally replace overstory species in areas without beaver, it was predicted that selective foraging by beaver strongly altered riparian forest succession. Donkor and Fryxell (1999) also found that the foraging activity of beaver altered forest succession by replacing deciduous species with conifers. They suggested this detracted from the keystone role of the beaver because the already dominant conifer community was increased.

Woody plant communities along major river systems can also be affected by the foraging behavior of beaver. In rivers too large for beaver to dam, bank-dwelling beaver can have significant effects on the structure of woody riparian vegetation. Regulation of rivers by major dams can modify the effects of beaver as peak flows are decreased and base flows are increased, which affects growth of woody vegetation and its use by beaver. In a comparative study of the unregulated Yampa River and the regulated Green River in northwestern Colorado, Breck (2001) found that beaver harvested a higher percentage of willow and cottonwood on the regulated river, where the constant flow regime caused vegetation patches to be more uniformly available to beaver. In the unregulated river, shifting channels constantly changed access to shoreline vegetation.

Abandonment of beaver ponds creates new habitat for plant establishment. Beaver meadows dominated by grasses and sedges often develop on the rich sediment that settles in beaver ponds. Meadows may eventually be replaced by forests, but in some cases succession is slower than expected. In northern forests, beaver meadows may resist invasion by conifers and persist for many decades as graminoid meadows (Terwilliger and Pastor 1999). Successful conifer (*Abies, Picea*) invasion requires the presence of ectomycorrhizal fungi, which form an obligate association with tree roots. Because past flooding would have killed these necessary fungi, beaver meadows require dispersal of fungi from nearby forest soils before conifers can invade. One possible mechanism of ectomycorrhizal fungi dispersal is via small-mammal feces. However, an evaluation of the red-backed vole (*Clethrionomys gapperi*) as a vector showed only about one third of plants grown in beaver meadow soils inoculated with vole feces had ectomycorrhizae present, compared to 100% of plants grown in forest soil. In addition, the potential of red-backed voles to facilitate dispersal of fungi is limited by their general avoidance of beaver meadows (Terwilliger and Pastor 1999). Thus, persistence of beaver meadows in forest communities may be controlled by complex ecological mechanisms.

Effects of Beaver on Mammals. A variety of mammals use the lush vegetation around beaver ponds as food and cover or rely on beaver to provide aquatic habitat (review by Olson and Hubert 1994). Beaver ponds are often important habitat for moose (*Alces alces*) because they increase production of woody plants and aquatic vegetation, which can contribute substantially to their total diet. In some cases, moose may compete with beaver for limited food supplies; however, the extent of their interaction and its effect on riparian vegetation are not well understood. Elk and deer can also be attracted to the increased abundance, palatability, or availability of woody and herbaceous forage at beaver ponds. Beaver ponds also create habitat for other semiaquatic mammals, such as river otter, mink, and muskrat, some of which may occur in a large percentage of active or abandoned ponds. In Idaho, the density and standing crop biomass of small-mammal populations was two to three times higher in willow-dominated beaver pond habitat than in adjacent riparian habitat (Medin and Clary 1991). Montane voles (*M. montanus*) and shrews (*Sorex* spp.) were the most abundant small mammals in the beaver pond habitat, and their populations accounted for most of the differences. However, neither species richness nor species diversity of small mammals was influenced by beaver in this study.

Effects of Beaver on Reptiles and Amphibians. Beaver ponds and associated riparian habitat likely alter the species composition and abundance of regional herpetofauna throughout the range of beaver. However, few studies have quantified these effects and some conclusions have been equivocal. For example, Russell et al. (1999) compared new (<5 years) and old (>10 years) beaver ponds to unimpounded streams in South Carolina. They found that richness and abundance did not differ among sites for amphibians, but both were higher for reptiles at the older beaver ponds than at new ponds or unimpounded streams. Reptile species diversity was highest at old ponds, intermediate at new ponds, and lowest at unimpounded sites. They suggested that beaver have generally benefited herpetofauna in the Piedmont of South Carolina, as the range of several species, such as common musk turtle (*Sternotherus odoratus*) and eastern mud turtle (*Kinosternon subrubrum*), has increased concurrent with the range expansion of beaver.

Effects of Beaver on Birds. Waterfowl use beaver ponds for nesting and brood-rearing habitat and as stopover sites during migration. Beaver ponds enhance vegetation growth, which improves dense nesting cover and enhances interspersion of cover and water, improving nest isolation for territorial waterfowl pairs and increasing nest density (review by McCall et al. 1996). When beaver ponds flood timber, dead trees provide nesting sites for waterfowl (cavity nesters) that are relatively safe from predators. Beaver ponds increase the production of invertebrates and aquatic vegetation, which improves brood-rearing habitat. The benefits of beaver ponds to waterfowl may be expressed by increased production of waterfowl as regional beaver populations increase. For example, when beaver populations in south-central Maine increased in the 3–4 years following a trapping closure, density of Canada geese (*Branta canadensis*), hooded mergansers (*Lophodytes cucullatus*), and mallards (*Anas platyrhynchos*) also increased, as did the number of wetlands used by these species (McCall et al. 1996). Waterfowl in Finland also responded positively to increasing beaver populations, but response varied by species. Teal (*Anas crecca,* the European race of the green-winged teal) increased to become the dominant species during the first 2 years following flooding by beaver, but populations of mallards and wigeon (*Anas penelope*) did not respond (Nummi and Poysa 1997).

Beaver ponds can be preferred to similar open-water wetlands by breeding waterfowl. In Ontario, open-water lakes made up 47% of the study area, but were avoided by blue-winged teal (*Anas discors*), mallards, and wood duck (*Aix sponsa*). However, beaver ponds constituted only 25% of the area and were preferred by wood ducks (Merendino et al. 1995). Preference for beaver ponds may be due to their increased production of invertebrates important to waterfowl broods. For example, populations of water fleas (*Cladocera* spp.), a small invertebrate preferred by young ducklings, were abundant in first-year beaver ponds, with populations of larger invertebrates more important in 2- and 3-year-old ponds (Nummi 1992). Beaver ponds substantially enhance waterfowl habitat in the western United States, where riparian areas constitute <2% of the landscape. Breeding waterfowl surveys in Wyoming found that streams with beaver ponds had 7.5 ducks/km, but similar streams without beaver ponds had only 0.1 duck/km (McKinstry et al. 2001). A survey of 125 land managers found that beaver had been removed from 23% of 28,297 km of Wyoming streams and that >3500 km of streams without beaver had potential for beaver reintroduction to improve waterfowl nesting habitat (McKinstry et al. 2001). Finally, beaver ponds can be highly important for migrating waterfowl throughout North America and for wintering waterfowl in ice-free southern regions (Ringelman 1991).

In addition to waterfowl, a variety of other bird species benefit from beaver activity. Beaver ponds can increase the area of open water, length of the shoreline, density of dead standing trees, and biomass, height, and canopy cover of shrubs. The abundance and diversity of terrestrial insects important to foraging birds are enhanced by changes in 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 Hair 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.

Native Americans valued beaver 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 pelt prices have caused the economic importance of trapping beaver (numbers marketed and value of pelts) to decline relative to furbearers 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.

Strict 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 furbearers. 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 prevalent, severe, 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; Woodward 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 the 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 strychnine 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 benefit 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 immigrants from June to September, or until dispersal rates are relatively low (Houston et al. 1995). In some cases, trees may tolerate relatively high levels of beaver damage without any major effect on the forest. In a study of beaver damage to bald cypress (*Taxodium distichum*) trees in Texas, 85% of the trees near lodges had their bark peeled by beaver with only minimal effects on tree survival (King et al. 1998). Thus, managing timber damage requires understanding the response of the particular tree species to foraging and flooding by beaver, gaining cooperation of all landowners within the affected area, and evaluating costs and benefits of beaver control relative to timber production.

Livetrapping and relocation of problem beaver is more acceptable to the general public and has become fairly popular in urban areas. However, this can be cost prohibitive without volunteer labor and is not an option if suitable relocation sites are not available (Hammerson 1994). Moreover, released beaver may suffer high mortality from predation or from their inability to successfully assimilate into established populations. Hancock traps are usually preferred to Bailey traps for removing problem beaver, although properly used snares may be more effective and less costly than either trap type (Hill 1982; Novak 1987; Hammerson 1994; McKinstry and Anderson 1998). In some situations, hand-held nets can help capture beaver on land or in shallow water from boats (Rosell and Hovde 2001). Chemosterilents and surgical sterilization also have been evaluated for beaver control, but remain impractical for treating wild populations (reviews by Hill 1982; Hammerson 1994).

Beaver repellents or wire fencing may be an effective means of protecting plants from cutting or discouraging beaver occupancy of selected sites. Tree trunks can be protected by hardware cloth, chain link, or similar wire mesh connected at the ends (leaving room to allow tree growth) and extending about 1 m above the ground (Hammerson 1994). A solution of 10% creosote and 90% diesel fuel sprayed or painted on tree trunks reduces gnawing damage by beaver, as does a mixture of acrylic paint and sand, which acts as an unpalatable abrasive. Commercial deer repellents (Thiram, Magic Circle) may also be effective chemical repellents (Hammerson 1994). Chemical extracts from native tree species that beaver avoid (Jeffery pine) also may be effective as a beaver repellent (Basey 1999). Marking areas with beaver scent (artificial scent mounds) may discourage occupancy in the short term, but this method is likely an ineffective long-term solution. Scent marking by beaver more likely acts as a form of territoriality rather than as a scent fence (Welsh and Muller-Schwarze 1989; Sun and Muller-Schwarze 1998; Schulte and Muller-Schwarze 1999).

Flooding by beaver can often be prevented or managed by installation of beaver-proof road culverts and other water control structures or by installation of flow control devices in existing beaver dams (Fig. 15.3). Damage occurs when beavers plug culverts or impound water against the beds of roads or railroads, causing flooding or washouts. Techniques for minimizing or preventing beaver from plugging road culverts include using oversized pipe-arch culverts (Fig. 15.3A), low-profile box culverts (Fig. 15.3B), and various designs of beaver exclosure fencing (Fig. 15.3C) which prevent beaver from building a dam at the upstream end of a road culvert (Buech 1985; Hammerson 1994; Olson and Hubert 1994; Jensen et al. 1999; S. Lisle, oral communication, Beaver and Common-Sense Conflict Solutions Conference, 1999). In most cases, preventing damage with proper culvert design is far more cost-effective than the repeated, labor-intensive unplugging of dammed culverts or removing unwanted beaver (Jensen et al. 1999). Flow control devices installed in existing beaver dams have been very effective at mitigating damage to roads or other developments while maintaining the ecological and esthetic values of beaver presence. For example, the Clemson beaver pond leveler (Fig. 15.3D) can control the water level in beaver ponds by using tubes or similar structures laid perpendicular to the dam with the upstream end porous and protected from plugging by beaver (Buech 1985; Hammerson 1994; Olson and Hubert 1994). The most widely used method to control flooding is to dynamite 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 special 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 instream 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 individuals, communities, regions, and type of land tenure. Rural residents, especially in agricultural areas, may have less opposition to lethal control than urban residents. People who experience beaver problems 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, girdled 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 saturated 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 conditions, beaver populations in optimum habitat may become saturated or self-limiting below habitat-based carrying capacity. Beaver typically maintain intercolony distances and body weight regardless of population density. In some areas, forage near the central place may become temporarily depleted or ponds may become silted-in, causing colonies to periodically move to former beaver habitat that has

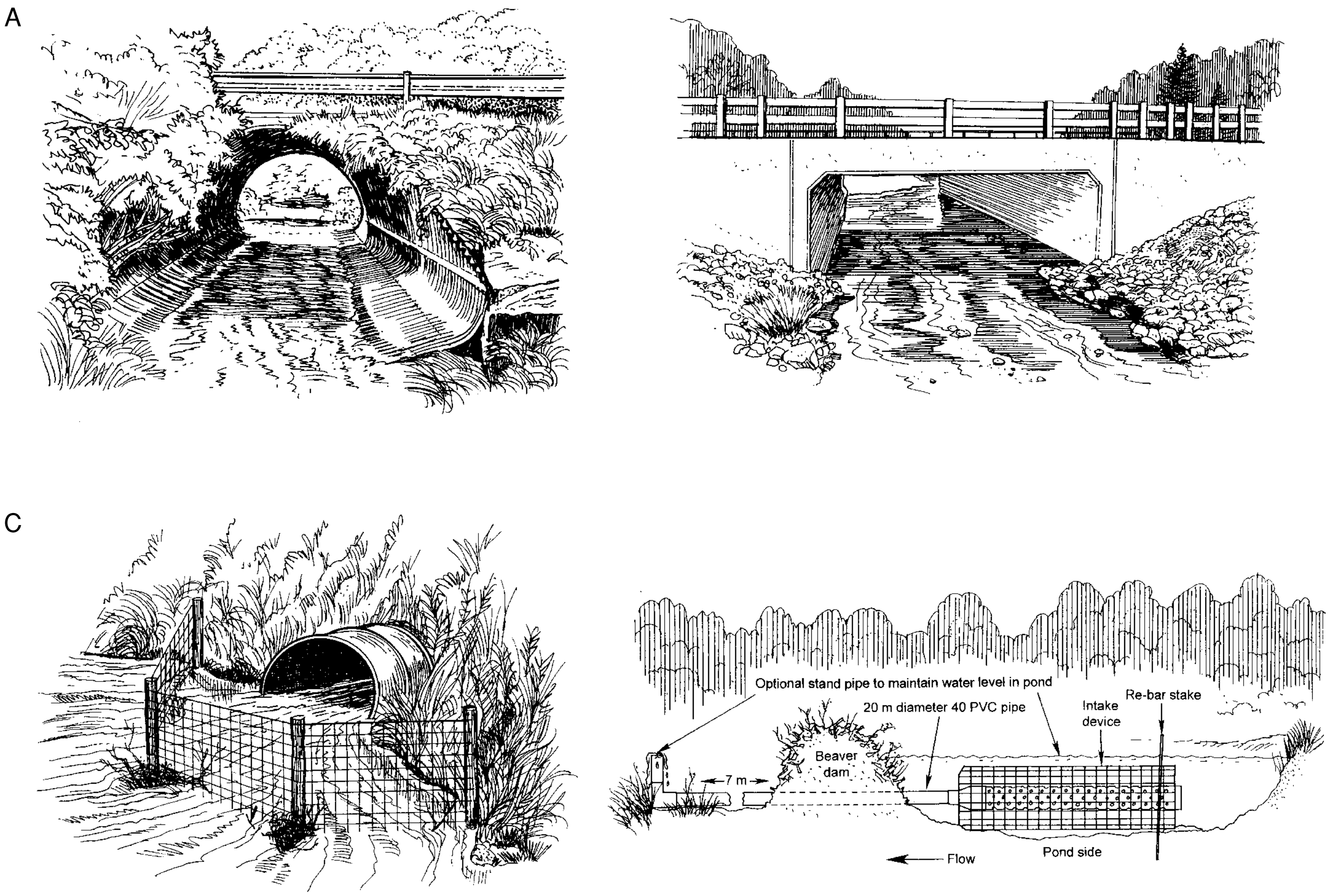

FIGURE 15.3. Examples of water control structures used to manage beaver (*Castor canadensis*) impacts. SOURCE: Adapted in part from Jensen et al. (1999).

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 unsuccessful. Thus, natural restoration of riparian systems can be an attractive alternative.

Reintroduction of beaver into degraded riparian systems has shown promise 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 woody vegetation suitable as 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.

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. exigua*) relative to tamarisk (B. W. Baker, unpublished data). A similar response was observed on the Zuni Indian Reservation in New Mexico following the relocation of 23 beaver to seven restoration sites (Albert and Trimble 2000). As beaver selectively cut vegetation and impound water and sediment behind dams, they alter conditions driving establishment and survival in riparian plant communities. Thus, beaver may create a competitive advantage for willow relative to tamarisk in some riparian systems, although specific mechanisms need further study at various spatial and temporal scales (B. W. Baker, unpublished data).

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 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 dismantling 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 were a significant predictor of colony size in a Montana study (Easter-Pilcher 1990). This was not the case in a Wyoming study, however, perhaps due to variation in cache-building behavior among different age cohorts (Osmundson and Buskirk 1993).

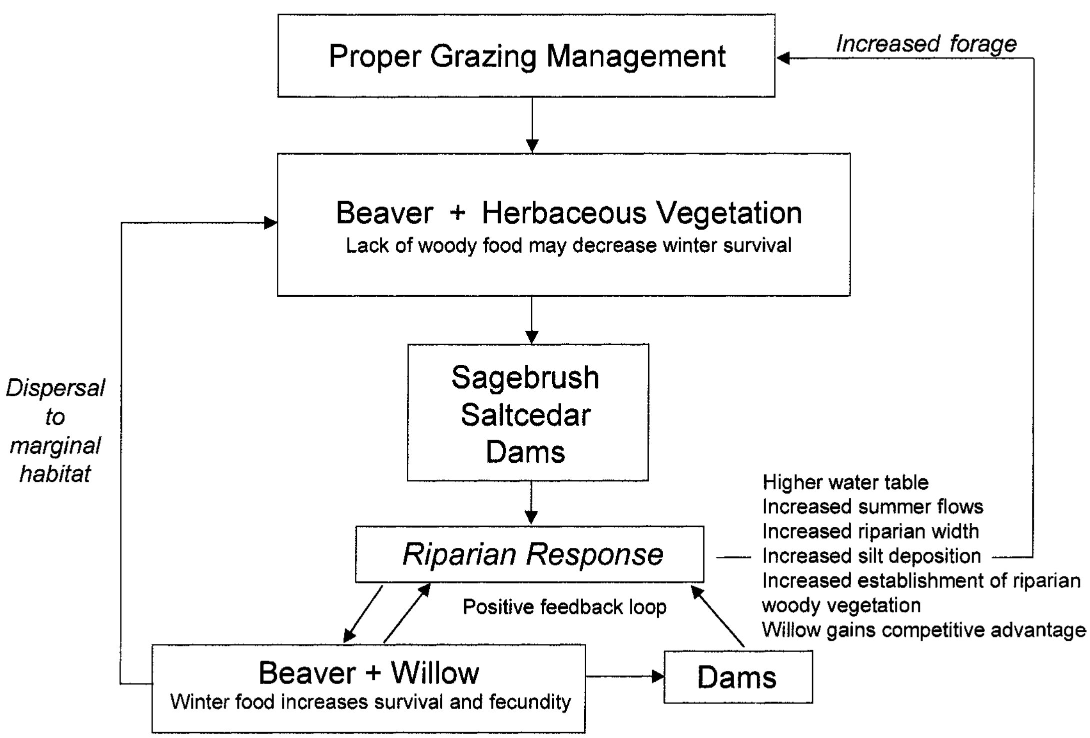

FIGURE 15.4. A conceptual model of the use of the beaver (*Castor canadensis*) activity as a possible mechanism for riparian restoration in shrub–steppe ecosystems.

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 survey; to map locations of dams, 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 colony 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 lodges and dens, 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 meandering riparian systems that are difficult to observe from low-level, fixed-winged aircraft (B. W. Baker, pers. obs.). Video has the advantage of instant availability on return from the flight and can be integrated with on-board 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 characteristics 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 pectoral mammae in pregnant females (after 2 months), by giving beaver the anesthetic combelen (which causes the penis to lapse into the cloaca), by detecting Barr bodies in blood smears, and by using radiographs that reveal the presence of the baculum (review by Novak 1987). Each of these methods has some level of uncertainty or practical constraints for adult beaver and is especially difficult for young (reviews by Novak 1987; Schulte et al. 1995). A recently developed technique uses the color and viscosity of anal gland secretion to determine the sex of adult and juvenile beaver. This method produced relatively accurate and consistent results from three different regions in New York, which suggests it may have general field application for sex identification in beaver (Schulte et al. 1995).

Age Estimation. Characteristics of tooth eruption and annual cementum layers have been in standard use for age determination since the 1960s (reviews by Hill 1982; Novak 1987). A refinement in the cementum layer method used the independent variables cementum length and noncementum length to fairly accurately predict ages for a sample of 28 beaver ($\geq$4 years old) with an exponential model, suggesting practical application in cases where more exact data are not necessary (Houston and Pelton 1995). Techniques for estimating age of live beaver are generally less accurate than the cementum method used for carcasses. The most common methods have used weight and skull measures, despite large error rates (Novak 1987; Hartman 1992). A refinement using regression models to estimate the age of live beaver based on live weight, tail width, and tail length was useful in identifying three age classes: kits, yearlings, and $\geq$ 2-year olds (Van Deelen 1994). A technique using dental radiographs to observe tooth root closure and annual deposition of cementum and dentine layers appears useful for estimating age of either live or dead beaver (Hartman 1992).

Livetrapping. Beaver can be captured alive using Hancock traps, Bailey traps, box traps, snares, or nets. Hancock traps are set on the sides of steep banks and Bailey traps are set in shallow water. Both are suitcase-type traps, which hold the beaver in a wire cage above water until released. Hancock traps are usually more effective than Bailey traps and are preferred in most situations (Novak 1987). Snares are cheap, light, and easy to set. They permit trappers to increase capture rates by saturating an area with traps, but have a greater mortality rate than Hancock traps due to increased risk of predation, entanglement leading to suffocation, and drowning (Hill 1982; McKinstry and Anderson 1998). Box traps baited with aspen and scent lure were effective for all age classes in spring and early summer when set along shoreline travel lanes in Massachusetts (C. Henner, pers. commun., 2001). In all cases, multiple traps per trapnight percolony will increase the likelihood of trapping all colony members or specific targeted individuals before colony members become trap shy. In some cases, beaver can be captured by nets or by hand after being flushed from lodges or dens by dogs or other means (Hill 1982; Rosell and Hovde 2001). In large river systems or lakes, surface-swimming beaver can be captured using a dip net. A dive net can be pushed down over the top of swimming beaver in shallow water, after locating them with the aid of spotlights and headlights from a motorboat (Rosell and Hovde 2001).

Tagging. Beaver can be individually marked with ear tags, neck collars, tail tags, and other methods (Novak 1987). Beaver may retain ear tags for several years, but retention rates have varied greatly among studies (review by Novak 1987). The tail can be marked with holes, notches, rivets, waterproof paint, branding, cryobranding with liquid nitrogen, and cattle ear tags (B. W. Baker, pers. obs.), and the fur can 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 free-ranging beaver, which can be scanned with a tag reader as they enter or exit burrows or lodges (although this method has not been field tested). These techniques all vary in their effectiveness and in trauma caused to beaver during and after marking, important considerations when selecting an appropriate marking technique.

Telemetry. Beaver 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 intraperitoneal 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 become tightly encapsulated with necrotic fibrous tissue and may be well tolerated by beaver (Guynn et al. 1987). Implants have been performed via dorsal (Davis et al. 1984) and ventrolateral (Wheatley 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 (Bothmeyer 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 interaction with other resources or landowners. Relocation decisions and expectations are usually based on professional judgment after considering all available data, but also may be based on mathematical simulation models. South et al. (2000) developed a spatially explicit model to evaluate the proposed reintroduction of Eurasian beaver to Scotland. Their model simulated births and deaths of individuals and dispersal between habitat patches based on a land cover map and predicted that a reintroduction of 20 beaver would be sufficient to establish an initial population that would eventually expand and fill suitable habitat.

Most beaver do not stay at release sites and may move great distances following release. Average dispersal distances were 14.6 km in a North Dakota study, 16.7 km in a Colorado study, 11.7 km in a Maine study, 18 km in a Quebec study, and 7.4 km for beaver transplanted to streams and 3.2 km for beaver transplanted to lakes in a Wisconsin study (review by Novak 1987). Beaver can sometimes be encouraged 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 (*Yersinia pseudotuberculosis, Y. enterocolitica,* Leptospirosis, and others) (Nolet et al. 1997). Stress during handling may increase risk of disease following release. Vaccination against likely disease agents and attention to animal hygiene 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 habitat 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 literature base on beaver. For example, a better understanding of the role of beaver as geological agents in the formation of alluvial floodplain valleys begs for the integration of the ecological sciences with new methods in geology and geomorphology, such as dating of buried organic layers that represent 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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