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Castor canadensis.

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Castor canadensis Kuhl, 1820

North American Beaver

Castor canadensis Kuhl, 1820:64. Type locality Hudson Bay, Canada.
Castor subauratus Taylor (1912:167). Type locality Grayson, San Joaquin River, Stanislaus Co., California.
Castor caecator Bangs (1913:513). Type locality near Bay St. George, Newfoundland.

CONTEXT AND CONTENT. Order Rodentia, Family Castoridae. The family contains one genus with two species, *C. canadensis* and *C. fiber*, the European beaver. The following 24 subspecies of *C. canadensis* are recognized by Hall and Kelson (1959):

C. c. acadicus V. Bailey and Doutt, 1942:87. Type locality Nepisiquit River, New Brunswick.
C. c. baileyi Nelson, 1927:125. Type locality Humboldt River, 4 mi. above Winnemucca, Humboldt Co:, Nevada.
C. c. belugae Taylor, 1916:429. Type locality Beluga River, Cook Inlet region, Alaska.
C. c. caecator Bangs (1913:513). See above.
C. c. canadensis Kuhl, 1820:64. See above.
C. c. carolinensis Rhoads, 1898:420. Type locality Dan River, near Danbury, Stokes Co., North Carolina.
C. c. concisor Warren and Hall, 1939:358. Type locality Monument Creek, SW of Monument, El Paso Co., Colorado.
C. c. duchesnei Durrant and Crane, 1948:413. Type locality Duchesne River, 5600 ft., 10 mi. NW Duchesne, Duchesne Co., Utah.
C. c. frondator Mearns, 1897:502. Type locality Río San Pedro, Sonora, near Mon. 98, Mexican boundary.
C. c. idoneus Jewett and Hall, 1940:87. Type locality Foley Creek, tributary to Nehalem River, Tillamook Co., Oregon.
C. c. labradorensis V. Bailey and Doutt, 1942:86. Type locality 5 mi. above Grand Falls, Hamilton River, Labrador.
C. c. leucodontus Gray, 1869:293. Type locality Vancouver Island, British Columbia (*pacificus* Rhoads a synonym).
C. c. mexicanus V. Bailey, 1913:191. Type locality Ruidoso Creek, 6 mi. below Ruidoso, Lincoln Co., New Mexico.
C. c. michiganensis V. Bailey, 1913:192. Type locality Tahquamenaw River, 5 mi. above falls, Luce Co., Michigan.
C. c. missouriensis V. Bailey, 1919:32. Type locality Apple Creek, 7 mi. E Bismarck, Burleigh Co., North Dakota.
C. c. pallidus Durrant and Crane, 1948:409. Type locality Lynn Canyon, 7500 ft., Boxelder Co., Utah.
C. c. phaeus Heller, 1909:250. Type locality Pleasant Bay, Admiralty Island, Alaska.
C. c. repentinus Goldman, 1932:266. Type locality Bright Angel Creek, 4000 ft., Grand Canyon, Arizona.
C. c. rostralis Durrant and Crane, 1948:411. Type locality Red Butte Canyon, 5000 ft., Fort Douglas, Utah.
C. c. sagittatus Benson, 1933:320. Type locality Indianpoint Creek, 3200 ft., 16 mi. NE Barkerville, British Columbia.
C. c. shastensis Taylor (1916:433). Type locality Cassel, Hot Creek, near Pit River, Shasta Co., California.
C. c. subauratus Taylor (1912:167). See above.
C. c. taylori Davis, 1939:273. Type locality Big Wood River, near Bellevue, Idaho.
C. c. texensis V. Bailey, 1905:122. Type locality Cummings Creek, Texas.

C. caecator and *C. subauratus* were relegated to subspecific rank by Allen (1942) and Grinnell (1933), respectively.

DIAGNOSIS. *C. canadensis* closely resembles *C. fiber* of Eurasia in external appearance. They differ in chromosome number: *C. canadensis*, 2N = 40; *C. fiber*, 2N = 48 (Lavrov and Orlov, 1973). There are also consistent differences in cranial morphology (Lavrov and Orlov, 1973; Troszyński, 1975).

GENERAL CHARACTERS. Figure 1 shows external appearance, and figure 2 the tail. Typical adult sizes are: total length, 1000 to 1200 mm; tail length, 258 to 325 mm; tail width, 90 to 200 mm; hind foot length, 156 to 205 mm; ear length, 23 to 29 mm; greatest length of skull, 121 to 146 mm; zygomatic width, 87 to 108 mm (Grinnell *et al.*, 1937; Osborn, 1953); weight, 11 to 26 kg (Grinnell *et al.*, 1937; Leege and Williams, 1967; Novakowski, 1967; Aleksiuk and Cowan, 1969*a*). Maximum reported weights are 37 to 39 kg, but these occur rarely (Grinnell *et al.*, 1937; Schorger, 1953). There is a prominent depression in the basioccipital. Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20. The eyes have a nictitating membrane, ears and nose are valvular, and lips close behind incisors. Each limb has five digits. Hind feet are webbed between digits and the second digit of each is split. Front feet are small and all digits are clawed. Underfur is dense and lead-gray in color. Guard hair is long and coarse. Color may range from yellowish-brown to black, with reddish-brown being most common. Tail is flattened dorsoventrally, scaled, and relatively hairless. It is black in young animals but becomes lighter with age.

DISTRIBUTION. *Castor canadensis* occurs naturally in streams, ponds, and the margins of large lakes (Shelton, 1966) throughout North America, except for the arctic tundra, peninsular Florida, and southwestern deserts (figure 3). Boundaries between subspecies are uncertain because of large-scale transplanting and restocking operations, and so are not shown in figure 3. *C. canadensis* has been introduced into Eurasia, and may even be out-competing *C. fiber* in some areas (Lahti and Helminen, 1974).

FOSSIL RECORD. The earliest known representative of the family Castoridae is from the early Oligocene of Natrona County, Wyoming (Emry, 1972). The evolutionary relationships of the Castoridae with other extant families of rodents are not

FIGURE 1. External view of *Castor canadensis*. Photo from American Museum of Natural History photo files.

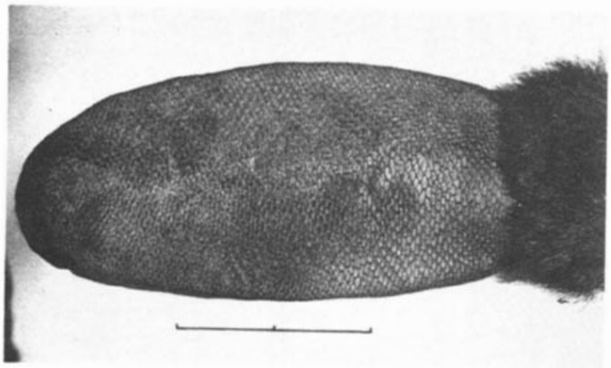

FIGURE 2. Tail of beaver. American Museum of Natural History photo files. Scale represents about 100 mm.

FIGURE 3. Distribution of *Castor canadensis* in North America. Modified after Hall and Kelson (1959) by extension into the drainages of the east slopes of the Sierra Nevada mountains of central California and extreme western Nevada (Richardson, 1954; personal observations), and into the Alaska Peninsula (M. S. Boyce, personal communication). Isolated populations in peninsular Florida (J. N. Layne, personal communication) and San Diego County, California (Bond, 1977) are not shown.

known (Wood, 1959; Wahlert, 1977), although Fischer (1971) showed that the placenta of *C. canadensis* is generally sciuromorph in form. The genus *Castor* apparently arose in the Pliocene, and is first represented by fossils from Bohnerze von Melchingen, Germany; Fresno Co., California; and perhaps Shansi, China (Stirton, 1935). Speciation within the genus during the Pleistocene is not fully understood (Fichter, 1972), but these medium-sized beavers coexisted with much larger forms (*Castoroides* in North America, *Trogontherium* in Eurasia) until about 10,000 years B.P. (Martin, 1967).

FORM. Female beavers have four pectoral mammae. Except during lactation, there is no external sexual dimorphism. Osborn (1953) pictured the baculum, and Osborn (1953) and Bond (1956) gave bacular measurements. The skull is robust, with a distinct pit in the basioccipital, a small slit-like infraorbital canal, a dorsoventrally broadened jugal, and a tubular extension of the bulla enclosing the long external auditory meatus (figure 4). Bond (1956) found no sexual dimorphism in cranial measurements. The cheek teeth are strongly hypsodont, with molariform premolars. The incisors are evergrowing and prominent. Osborn (1969) described their structure in detail. Robertson and Shadle (1954) described skeletal changes with age, particularly epiphyseal consolidation and ankylosis. Carlson and Welker (1976) characterized the tail, with emphasis on musculature and innervation.

Central nervous system and brain structure were described by Pilleri (1959*a*) and Carlson and Welker (1976). Pilleri (1959*b*) described the anatomy of the hypothalamus. Since the epiglottis is intranarial, the trachea opens only into the nares (Coles, 1970). Except during swallowing, passage of material to the pharynx is blocked by a raised section of the back of the tongue which fits snugly against the palate (Coles, 1970). The digestive system is similar to that of other rodents except for the large cardiac gland in the stomach. The caecum is large, but not as large in relation to body size as in guinea pigs and rabbits (Currier *et al.*, 1960). Aleksiuk and Cowan (1969*a*) gave heart and kidney weights for 0–3 year-old beavers. McKean and Carlton (1977) reported a mean heart weight/body weight ratio for adult-sized beavers of 0.22%, an unusually low value for a mammal.

There is great variation in size and shape of beaver ovaries during anestrus as well as during estrus or pregnancy (Provost, 1962). The maximum size reported by Provost (1962) was 15 by 25 mm. Corpora lutea are 6 to 8 mm in diameter and prominent; corpora albicantia are also prominent and remain visible for at least one year after they are formed (Provost, 1962). Fischer (1971) described the structure and development of the placenta, and noted the existence of an endometrial papilla which forms on the mesometrial wall of the uterus just before chorioallantoic contact. This structure is apparently unique to beavers. Osborn (1953) and Conaway (1958) gave testes and seminal vesicle weights of males of various ages at various stages in the reproductive cycle. Conaway (1958) described the histology of the uterus masculinus, which is quite variable in shape and size but not as large as that of *C. fiber*. The urogenital system opens into a common pouch (cloaca) with the scent glands and rectum. Svendsen (1978) described anal and castor glands, which are present in both sexes.

FUNCTION. Lactation and milk composition were described by Zurowski *et al.* (1974) for *C. fiber*. The lower pair of nipples yield more milk than the upper pair. Duration of lactation is at least 90 days, and milk composition remains the same from day 10 to day 90.

Carlson and Welker (1976) found that somatic sensory cerebral neocortex projections from the upper lip and hands of beavers are more prominent than in other rodents, whereas projections from the tail and vibrissae are similar in relative size to those of other rodents. Miller (1967, 1970) described aspects of nerve function which are adaptive for cold temperatures. In particular, he showed that peripheral nerves function at lower temperatures than interior nerves and that caudal nerves continue to conduct impulses at −5.0°C in some animals (five of his nine subjects).

Kitts *et al.* (1958) and Stevenson *et al.* (1959) gave data on normal blood chemistry. Clausen and Ersland (1968, 1970) described in detail the effects of diving on the blood chemistry of *C. fiber*. Beavers can remain underwater for at least 15 minutes, though 1 to 2 minutes is more usual (Irving and Orr, 1935). Irving (1937) found that cessation of respiration for 1 to 2 minutes follows inflation of the lungs. During this period, blood pressure drops, muscle blood flow drops, and blood flow in the brain increases. These responses also occur in terrestrial mammals during asphyxiation, but are more pronounced in beavers and other diving mammals (Irving, 1937). Interestingly, total oxygen storage capacity in beavers is about the same relative to body weight as in human beings, and much less than in harbor seals (McKean and Carlton, 1977).

Postgastric fermentation by caecal microorganisms enables beavers to assimilate about 30% of the cellulose in their diet (Currier *et al.*, 1960; Hoover and Clarke, 1972). Efficiency of digestion is further increased by caecotrophy, the periodic ingestion of material produced in the caecum. This fecal material is quite different in color and form from the usual feces (Wilsson, 1971). Food passage time for the beaver gut is at least 60 hours (Currier *et al.*, 1960).

Maintenance metabolism of beavers is reported to be about 64 kcal/kg/day (Pearson, 1960). The tail functions in thermoregulation (Coles, 1966), fat storage (Aleksiuk, 1970*a*), and communication (see Behavior section). Aleksiuk and Cowan (1969*b*) investigated seasonal changes in hormonal status, metabolism, and growth. In beavers from the arctic (Mackenzie Delta) there was a marked depression in thyroid activity and growth during winter; these changes were less apparent in beavers from a tem-

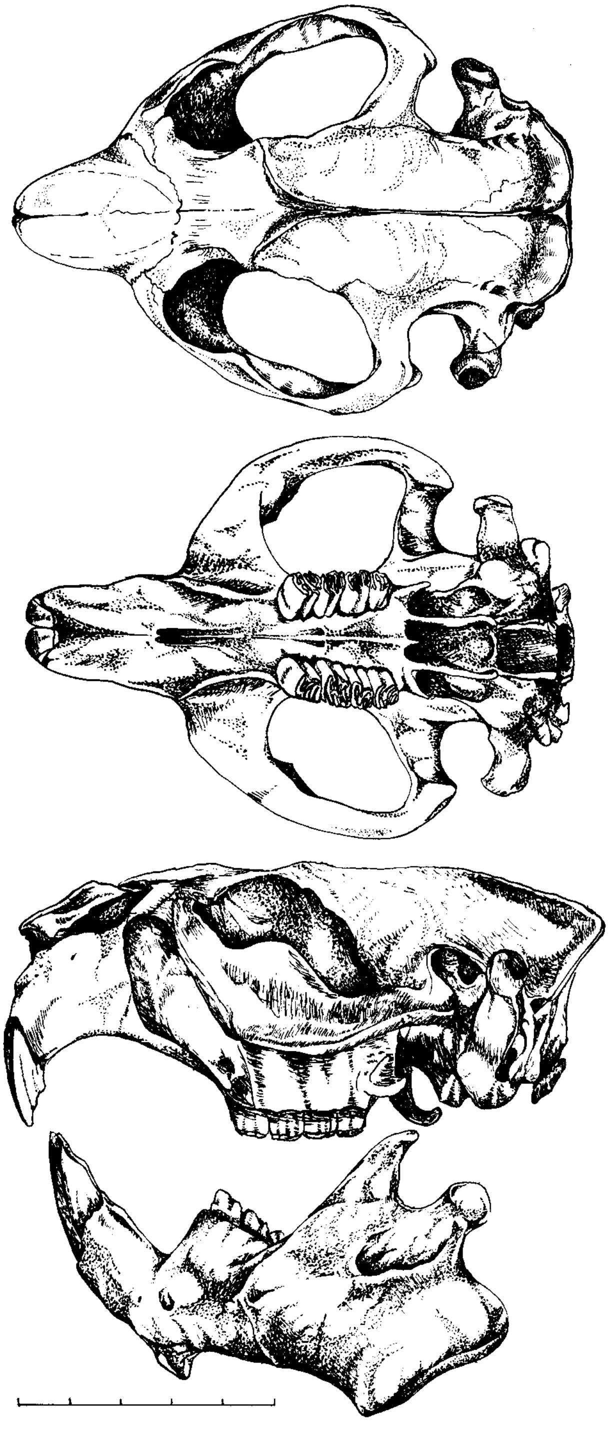

FIGURE 4. Skull of *Castor canadensis*, Univ. of Nevada Museum of Biology no. T165. Drawn by C. Hewitt. Scale represents 50 mm.

perate climate (California) held under the same environmental conditions in the lab in British Columbia.

ONTOGENY AND REPRODUCTION. Beavers reproduce once a year, generally in January or February (Hodgdon and Hunt, 1953; Bergerud and Miller, 1977). The gestation period is about 107 days (Wilsson, 1971). Birth usually occurs in May or June (Shadle, 1930; Bradt, 1939; Hodgdon and Hunt, 1953; Osborn, 1953; Bergerud and Miller, 1977), but occasionally as early as February (Miller, 1948) or as late as November (Thomas, 1943; Cook and Maunton, 1954). Osborn (1953) found no evidence that young females breed later than older ones, though earlier workers (Grinnell *et al.*, 1937) had suggested this. Limited data suggest that timing and duration of the breeding season may vary with latitude or habitat (Thomason and Jacobson, 1978).

Most studies report mean litter sizes between three and four. Of 215 pregnant or recently post-partum females examined by Hodgdon and Hunt (1953), Osborn (1953), and Brenner (1964), 51% contained three or four embryos or placental scars and 96% contained six or less (see Hodgdon, 1949, for methods). Litter size varies markedly with habitat, even within a limited geographic area (Yeager and Rutherford, 1957; Pearson, 1960; Rutherford, 1964). The most important proximate factors influencing litter size appear to be quantity and quality of available food and severity of winter weather. Litter size is also positively correlated with weight of the mother (Pearson, 1960; Boyce, 1974). Of the few studies in which age was estimated by degree of dental development rather than weight (Novakowski, 1965; Henry and Bookhout, 1969; Boyce, 1974), only Henry and Bookhout's showed a consistent increase of litter size with age. *C. fiber* has smaller litters than *C. canadensis* where the two species are sympatric in Finland (Wilsson, 1971; Lahti and Helminen, 1974).

Bergerud and Miller (1977) reported data on prenatal growth. Beavers are born fully furred, with eyes at least partially open and incisors erupted (Bradt, 1939; Guenther, 1948). Individual birth weights are inversely related to litter size, and average 340 to 630 g (range of within-litter means of one litter reported by Shadle, 1930, and three reported by Bradt, 1939).

Bailey (1927) stated that beavers are weaned at about 6 weeks to 2 months, although they begin to eat solid food somewhat earlier. Zurowski *et al.* (1974) showed that lactation lasts at least 3 months in *C. fiber*, and suggested that the same may be true for *C. canadensis*. Aleksiuk and Cowan (1969*a*, 1969*b*) studied growth of beavers in the wild and in captivity. Beavers from the Mackenzie Delta grew only during summer; beavers from California grew year-round. In their sample of arctic beavers, growth essentially stopped at age 3.5. However, duration of growth may vary between populations in the same geographic area (Boyce, 1974), so broad generalizations about growth patterns are not possible at present.

There are no reliable reports of beavers becoming sexually mature in the first winter after birth, but both sexes may be mature in their second winter, at age 1.5 (Larson, 1967; Henry and Bookhout, 1969). Henry and Bookhout (1969) found that 40% of 1.5-year-old females and 89% of older females trapped in northeastern Ohio during early February had ovaries with corpora lutea. In interior Alaska and northern Canada, sexual maturity may be delayed until age 2.5 or even later for virtually all females and most males (Novakowski, 1965; Boyce, 1974). Age of sexual maturity depends on colony composition; in his study in Wood Buffalo National Park, Novakowski (1965) found that the only pregnant 2.5-year-old females (3 of 21) were trapped in colonies lacking older females.

Larson (1967), Henry and Bookhout (1969), and Boyce (1974), working in Maryland, Ohio, and Alaska, respectively, collected data on the age structure of beaver populations. Age was determined according to degree of dental development of trapped specimens (van Nostrand and Stephenson, 1964; Larson and van Nostrand, 1968). There were marked differences among the population samples; for example, frequency of kits (0.5 to 1 year old at the time samples were taken) varied from 14% to 42%, and of kits plus yearlings from 40% to 58%. Some of these differences can be attributed to differences in intensity of exploitation of the populations by trappers. This relationship was most clearly demonstrated by Boyce (1974), who compared trapped and untrapped populations on two nearby river systems in interior Alaska. Bergerud and Miller (1977) presented a survivorship curve for a population in Newfoundland which they presumed was stationary; annual mortality rate was approximately 30% for all age classes. The longevity record for a wild beaver is 20.5 to 21 years, but few animals live beyond 10 years (Larson, 1967).

ECOLOGY. Like many rodents, beavers build elaborate nests and burrows, and store food for winter use. Their ability to cut trees is unique, and enables them to build mud and wood "lodges" surrounded by open water and watertight dams even in fast-flowing streams. Lodges usually have two or more underwater entrances and a chamber a few inches above water level (Grinnell *et al.*, 1937). Stephenson (1969) found that temperatures inside an Ontario beaver lodge in winter were both higher and less variable than external air temperatures. Temperatures in the lodge decreased when beavers left. Dams may be very long and cause large areas of land to be flooded. Wilsson (1971) and Hartman (1975) showed that beavers are stimulated to build dams by the sound of running water. Berry (1923) gave a detailed description of beaver-made canals, a less familiar example of their alteration of habitat than dams or lodges. Warren (1927) presented numerous examples of the variety of sizes and shapes of beaver dams, lodges, and canals.

The fundamental unit of a beaver population is the colony, which typically consists of four to eight related individuals (Bradt, 1938; Bergerud and Miller, 1977) occupying a pond or section of stream more (Bergerud and Miller, 1977) or less (Warner, 1976) exclusively. Adult females appear to be more sedentary than adult males (Townsend, 1953; Leege, 1968; Bergerud and Miller, 1977). Beavers disperse at about two years of age (Bradt, 1938; Townsend, 1953; Aleksiuk, 1968), or later in some populations (Novakowski, 1965; Bergerud and Miller, 1977). Dispersal movements are usually less than 16 airline km (Beer, 1955; Libby, 1957; Hibbard, 1958; Leege, 1968), with 110 km being the maximum distance reported (Hibbard, 1958). The density (of colonies) may reach 3/km^2 (Voigt *et al.*, 1976), but more typical values in favorable habitat are 0.4 to 0.8/km^2 (Aleksiuk, 1968; Voigt *et al.*, 1976; Bergerud and Miller, 1977).

Beavers are "choosy generalist" herbivores (terminology of Harper, 1969). They eat the leaves, twigs, and bark of most species of woody plants which grow near water, as well as many different kinds of herbaceous plants, especially aquatics. Despite this generality, beavers are usually quite selective. For example, Jenkins (1974) found that 16 of 17 tree genera present at a beaver pond in central Massachusetts were cut over a two-year period, but 6 genera accounted for more than 90% of all trees cut. Where aspen (*Populus* spp.), willows (*Salix* spp.), and conifers (especially *Pinus* spp.) are the only woody species present in their habitat, beavers strongly prefer aspen and willow. Hall (1960) suggested that aspen is preferred to willow, although willow more closely approximates a renewable resource for beavers than aspen. However, beavers thrive even in the absence of aspen and willow (Chabreck, 1958; Jenkins, 1975).

During summer, beavers rely largely on herbaceous vegetation (Chabreck, 1958; Northcott, 1971) or willow leaves and twigs (Aleksiuk, 1970*b*). In northern populations, tree-cutting occurs primarily during fall, when a food cache of branches and logs is built in the water near a lodge or bank burrow. Materials from this cache are eaten throughout the winter, although beavers will continue to go ashore to cut fresh trees as long as they can break through the ice at the edge of their pond. There is some evidence that branches of certain tree species are added to caches not for future food use but simply to hold the cache in place (Slough, 1978). Slough's study emphasized the pitfalls of relying solely on a survey of cut stumps as a measure of food preference. Where available, the fleshy roots, rhizomes, and runners of water lilies (*Nuphar* and *Nymphaea*) may be an important source of winter food (Nash, 1951; Hakala, 1952; Gibson, 1957; Shelton, 1966).

Most work indicates that beavers either prefer small trees (Nixon and Ely, 1969; Kienzler, 1971) or show no selectivity by size (Gibson, 1957; Henry, 1967). Jenkins (1974) demonstrated greater selectivity by size at greater distances from shore. Trees larger than about 10 cm in diameter are sometimes debarked at the base without being felled (Chabreck, 1958), or felled and the trunks debarked in place, with only the branches carried back to the pond for addition to the food cache (personal observation).

Availability of food, particularly aspen trees, is an important determinant of habitat suitability for beavers (Lawrence, 1954; Rutherford, 1955). Aspen is an early successional species in most habitat types within the beaver's geographic range, so fire and other disturbances which initiate secondary succession may ultimately lead to increased beaver populations (Lawrence, 1954). Numerous physical features of lakes and streams also influence their suitability for occupation by beavers (Yeager and Rutherford, 1957; Slough and Sadleir, 1977). Certain sites with special topographic or edaphic conditions may permit continuous occupation by beavers. These sites provide a source of colonists for temporary occupation of patches of early successional deciduous trees, especially aspen, created by fire or other disturbance (Slough and Sadleir, 1977).

Major predators on beavers are wolves, *Canis lupus* (Voigt *et al.*, 1976), and coyotes, *Canis latrans* (Young and Jackson, 1951). Wolverines, *Gulo luscus* (Rausch and Pearson, 1972), and bears, *Ursus americanus* (Hakala, 1952), may occasionally prey on adults; and mink, *Mustela vison* (Swank, 1949), on kits. Beavers comprise a highly variable fraction of the diet of wolves, with a maximum of 75% reported by Voigt *et al.* (1976) for a population in central Ontario. Major ectoparasites include *Platypsyllus castoris*, *Prolabidocarpus canadensis*, *Schizocarpus mingaudi*, *Leptinillus vallidus*, and *Ixodes banksi* (Erickson, 1944; Lawrence *et al.*, 1961; Janzen, 1963). Relatively few species of helminths parasitize beaver intestinal tracts, the most common being the trematode *Stichorchis subtriquetrus* and the nematodes *Travassosius americanus* and *Castorstrongylus castoris* (Erickson, 1944; Brenner, 1970). Ernst *et al.* (1970) described two species of coccidians obtained from beaver feces. Epidemics of tularemia, spread directly by water (Jellison *et al.*, 1942) or by the tick *Ixodes banksi* (Lawrence *et al.*, 1956), have been recorded in beaver populations (also see Stenlund, 1953).

Other browsing mammals, especially moose and snowshoe hares (Northcott, 1964; Shelton, 1966), are potential competitors of beavers. Damming of streams by beavers affects fish populations in many ways, often beneficially (Neff, 1957; Gard, 1961; Hanson and Campbell, 1963), but sometimes harmfully (Rupp, 1954; Knudsen, 1962). Waterfowl populations may be greatly enhanced by the presence of beaver ponds (Rutherford, 1955). Beavers influence vegetation not only by their selective cutting of certain tree species, but also by producing elevated water tables and associated changes in soil chemistry (Ives, 1942; Wilde *et al.*, 1950). They may hasten or impede forest succession adjacent to occupied ponds or streams, depending on local conditions (Lawrence, 1954; Rutherford, 1955; Slough and Sadleir, 1977). Ives (1942) argued that beavers had an important role in landscape evolution in North America.

Some important methodological papers are those of Whitelaw and Pengelley (1954) on handling live-trapped beavers, Miller (1964) on marking beavers for individual identification, Osborn (1955) and Larson and Knapp (1971) on sexing live beavers, van Nostrand and Stephenson (1964) on age determination, and Busher (1975) and Lancia and Dodge (1977) on radio-telemetry. Bailey (1927) and Wilsson (1971) discussed various aspects of keeping beavers in captivity. Transplanting beavers has been spectacularly successful in establishing new populations (Harris and Aldous, 1946; Knudson and Hale, 1965). Patric and Webb (1953), Yeager and Hill (1954), Yeager and Rutherford (1957), and others have discussed stocking, harvesting, and other aspects of beaver management.

BEHAVIOR. General descriptions of beaver behavior were presented by Morgan (1868), Mills (1913), Dugmore (1914), Warren (1927), and Seton (1929). More recent field studies emphasizing behavior include those of Tevis (1950), Schramm (1968), and Hodgdon and Larson (1973). Wilsson (1971) conducted extensive experimental studies, both in the laboratory and in the field, of *C. fiber* behavior.

Most workers consider beavers to be monogamous. Novak (1977) presented evidence that almost all colonies in his study area in Ontario contained only one pregnant female. The few cases reported by others in which two pregnant females were present in some colonies (for example, Hammond, 1943; Warner, 1976) occurred in high density populations. Reproductive behavior was described by Roth (1938), Bradt (1939, 1940), and Hediger (1970). Copulation usually takes place in the water, but may occur in a lodge or burrow (Wilsson, 1971). Wilsson (1971:214) diagramed a copulatory position of captive *C. canadensis* observed by Hediger (1970). Aggression is characterized by hissing, grunting, and tooth-sharpening (Leighton, 1933; Novakowski, 1969; Wilsson, 1971). Nearly all aggressive interactions observed by Tevis (1950) in a New York colony were associated with competition for food. Tevis (1950) considered the adult male and female to be co-dominant, but Hodgdon and Larson (1973) reported strong dominance by the adult female over other colony members in their observations of a Massachusetts colony. In both studies there were indications that young animals were dominated by older ones. Other known social behaviors are mutual grooming, nose touching, and wrestling or dancing (Tevis, 1950; Schramm, 1968; Wilsson, 1971). Some instances of these latter behaviors can reasonably be interpreted as play. It is important to note that social interactions among beavers, even among members of the same colony, are relatively rarely observed, at least outside the lodge.

Beavers communicate by postures, vocalization, tail-slapping, and scent-mounding. Leighton (1933) described seven different sounds made by captive beavers, although only two or three of these have been reported in field studies (Schramm, 1968; Hodgdon and Larson, 1973). Novakowski (1969) presented sound spectrographs of normal beaver vocalizations, and discussed the behaviors accompanying vocalizations of a laboratory colony. Hodgdon and Larson (1973) showed that kits vocalized more than adults, but that most vocalizations were directed toward adults rather than other kits or yearlings. Tail-slapping, particularly its effects on other members of a colony, was studied in detail by Hodgdon and Larson (1973). In the colony they studied, the adult female tail-slapped most often. Males and females of all ages were more likely to respond (by swimming to deep water) to a tail-slap by a female than to one by a male. The possibility of substantial variation between colonies in tail-slapping and other social behaviors remains to be explored. There is fairly good evidence that tail-slapping functions to warn other beavers of danger (Tevis, 1950), but additional functions, such as frightening a potential predator, are also possible. Scent-mounding, in which castoreum (washed out of the castor glands by urine) and possibly also anal gland secretions (Svendsen, 1978) are deposited on piles of mud within a colony's home range, appears to function primarily to mark territorial boundaries (Aleksiuk, 1968; Wilsson, 1971).

Locomotion in the water is powered primarily by the webbed hind feet; the front feet are held tight against the body. Transverse motions of the tail are used intermittently, especially when swimming rapidly (Wilsson, 1971). On land beavers usually walk, but they can gallop if frightened. Tevis (1950) described various types of dives.

Beavers feed on shrubs such as willow by grasping a branch with a forelimb, pulling it to the mouth, and cutting it off with the teeth. When cutting trees they stand on their hind feet and gnaw with their incisors.

Construction behavior was described by Warren (1927) and Shadle (1956). Hodgdon and Larson (1973) presented data on age and sex differences in amount of time spent on lodge maintenance, food cache building, and dam maintenance. Wilsson (1971) described the ontogeny of these (and other) behaviors in *C. fiber*. Though complex behaviors, lodge and dam maintenance appear to be largely innate. The former is released by rising water levels and appearance of holes in the sides or roof of the lodge, and the latter is released by the sound of running water (Wilsson, 1971).

Beavers are active for about 12 hours a day during spring, summer, and fall, from about 1600 or 1800 hours until 0600 or 0700 hours (Busher, 1975). During the day, all members of a colony rest together in a single lodge (Tevis, 1950) or in several subgroups, each in a different lodge or bank burrow (Busher, 1975). At northern latitudes during winter beavers exhibit a "free-running circadian rhythm of period length 26.25 to 28.0 h, with or without relative coordination, depending on available light intensity, which in turn depends on ice and snow cover conditions" (Potvin and Bovet, 1975).

GENETICS. *C. canadensis* has 2N = 40 chromosomes, with a fundamental number of 80 chromosomal arms (Lavrov and Orlov, 1973). Larson and Knapp (1971) described sexual dimorphism in polymorphonuclear neutrophil leucocytes, apparently resulting from inactivation of one member of the pair of X-chromosomes present in cells of females. Lavrov and Orlov (1973) obtained copulations of *C. canadensis* and *C. fiber* in captivity, but no hybrid offspring were born.

REMARKS. An enormous number of books and papers have been written about beavers. Yeager and Hay (1955) listed early works. Much useful but hard-to-obtain information is in theses, dissertations, and reports of various governmental agencies concerned with wildlife management.

Beavers were historically important as a primary stimulus for exploration of western North America (Cline, 1974). They were reduced to low numbers throughout much of North America by 1900, but have been reintroduced and become re-established in most of their former range and are quite abundant in many areas (Anderson, 1964). We thank C. Hewitt for drawing figure 4, M. Boyce for comments on the manuscript, and S. Anderson for assistance above and beyond his duties as editor.

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