The Beaver

Natural History of a Wetlands Engineer

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Food Selection

chapter 9

> Their food chiefly consists of a large root, something resembling a cabbage-stalk, which grows at the bottom of the lakes and rivers. They eat also the bark of trees, particularly that of the poplar, birch, and willow; but the ice preventing them from getting to the land in Winter, they have not any barks to feed upon during that season, except that of such sticks as they cut down in Summer, and throw into the water opposite the doors of their houses; . . . the roots above mentioned constitute a chief part of their food during the Winter. In summer, they vary their diet, by eating various kinds of herbage, and such berries as grow near their haunts during that season.
>
> *Samuel Hearne, 1795*

Range of Plants Eaten

Beavers fell trees. They shock us by cutting down a specimen tree in our backyard, or make national news by destroying cherry trees at the Tidal Basin in Washington, D.C. At the very least, many of us have seen stumps left by beavers or pruned willows along a stream. Indeed, many professional studies of food habits have focused on stumps, severed tree trunks or limbs on the ground or in the water, and food caches, which are piles of branches from various trees that beavers conveniently place near their lodge for the winter. This woody material is literally hard evidence of the beavers' foraging and feasting.

Direct observation of the beavers' feeding behavior teaches us that they consume much nonwoody vegetation that leaves little trace. Besides trees, beavers eat grasses and forbs on land and aquatic vegetation in the pond or at the lake bottom. Of these three categories of plant food, beavers in southeastern Ohio spent 60%–90% of their feeding time on tree bark in March/April and October/November. In May they abruptly switched to grasses, and later in summer to aquatic plants. During the summer months, they fed on nonwoody vegetation 90% or more of the time.[1] From March to November (including summer), one Ohio colony spent only 40.2% of feeding time on woody vegetation, another one even only 31.4%, and the remainder was spent eating grasses and forbs.[1] These beavers may have chewed additional bark while inside their lodge. In Pennsylvania, the ratio between woody and nonwoody foods was 25:6.2 kg/month in winter, but 2:30 kg in summer.[2] Therefore, to appreciate the needs and impact of beavers, it is imperative to consider all types of food plants. Indeed, where available, beavers prefer herbaceous vegetation, such as water lily rhizomes, to woody vegetation in all seasons.[3]

In agricultural areas beavers consume corn, and they readily accept other foods such as apples when offered by well-meaning people.

Where Beavers Harvest Trees

Beavers are "central place foragers": from the lodge where they live, they venture out in all directions to cut plants. They forage at greater distances upstream from their main lodge than downstream.[4] Obviously, it is easier to float logs downstream. On the slopes near their site, beavers forage the less the greater the distance. This way they minimize not only energy expenditure but also risk of predation. However, once areas close to the pond become depleted of preferred tree species, beavers have to go farther afield.[5]

Beavers clear-cut at distances of up to 300–500 feet (92–152 m) from their pond. This distance affords tolerable risk and energy expenditure. For a stand of aspen they may go as far as 200 m from their main pond, and up steep slopes at that.[6] Generally speaking, beavers forage more selectively at increasing distances from their "central place."[7] In one study in Michigan, beavers used 21,313 m² of terrestrial area around the pond for cutting woody vegetation.[8]

Tree Preferences

North American beavers prefer aspen and other species of the genus *Populus*. Indeed, a look at the distribution maps of beavers and quaking aspen (*P. tremuloides*) confirms that the ranges of the two species are almost identical. Beavers are also fond of willows.[9] Where aspen have been depleted locally near beaver sites, willow becomes the main food. This is the case in Rocky Mountain National Park and at some sites at Allegany State Park in New York, to name two examples. The first beaver family to establish itself at Allegany State Park in 1937 found plenty of choice among various tree species. They cut 199 quaking and bigtooth aspen trees (71% of all trees harvested) but only 3 small willows (1.1%).[10] Similarly, beavers on a willow-dominated site (36.6% of all trees) in Ohio preferred aspen and alder. Willow constituted only 5.9% of their diet.[11] At their northern distribution limit, such as in Alaska and Labrador, beavers subsist on willow, for lack of other tree species.

Beavers need a mixed diet. Kept on a strict diet of quaking and bigtooth aspen for several weeks, American beavers lost weight at the rate of 0.1%/day. Fed only red maple, paper birch, or alder, the animals lost even more weight (0.3%–0.6%

of body mass/day). One beaver actually died on such an extremely restricted, one-species diet.[12]

What tree species beavers choose depends on the locally available mix. As "choosy generalists," they are highly flexible at any one locale and over their entire geographical range. However, just as aspen and willow usually rank at the top, their last choices predictably are conifers such as spruce, fir, and pine, although on occasion these are eaten to some extent too. Among the deciduous trees, red maple (*Acer rubrum*) scores very low, right along with the conifers.[13,14] Many of the other forest trees, such as beech, ash, maples, hornbeam, and cherries, fall somewhere in the middle. The preference order varies, depending on local abundance of the various trees. For instance, on Isle Royale in Lake Superior, beavers preferred sugar maple and yellow birch, while they tended to avoid paper birch, baked hazelnut, honeysuckle, balsam fir, northern white cedar (arborvitae), spruce, and elder.[8]

Where introduced into new areas with tree species entirely "exotic" to them, beavers have no problem living on food that does not occur in their natural range. Transplants to Tierra del Fuego use several species of southern beech (genus *Nothofagus*) as food and building material (see Plate 44). Thriving on this, they have colonized many rivers and today live in a high-density population.

Different beaver families in the same population may prefer different food plants. For example, of two colonies on Isle Royale that were offered food experimentally, only one accepted white clover readily, while only the other ate yellow pond lily stems and leaves. Each chose the plant that grew naturally at their site and ignored the species that was absent.[15]

Food Choice and Feeding Behavior

First, beavers sample trees. Careful observation near beaver ponds reveals saplings and trees beavers have bitten into but left alone (Fig. 9.1). They appear to assess nutritional value. In a study in Massachusetts, beavers switched from birch to oak and witch hazel in two subsequent fall seasons. During the second season they sampled many birch trees without utilizing them further.[16]

How do beavers choose one species over another? In an ingenious experiment, Doucet and coauthors combined aspen stems and "canopies" of red maple and then red maple stems and aspen canopies.[17] After this switching of canopies, beavers judged these "hybrid plants" by their stems: they cut more aspen stems with maple canopies than the other way around. Covering the stems with paper bags did not alter their response. This shows that odor, rather than visual cues, is important in beaver food selection.

Distance from the water also plays an important role: the greater the distance from the pond, the more selective the beavers are in terms of species chosen (they go far for aspen), and the smaller the diameter of the trees the beavers cut.[18]

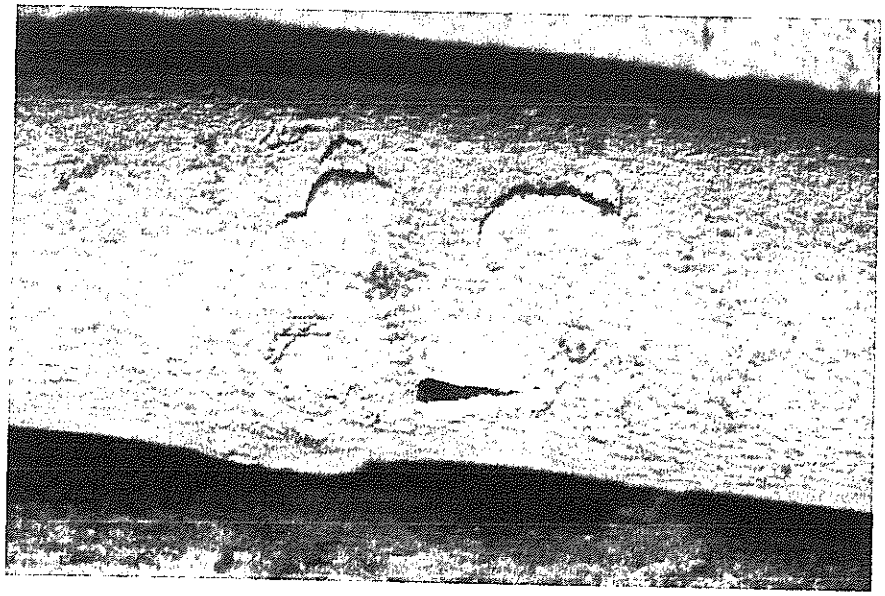

Figure 9.1 | Red maple sampled by beavers (tooth marks).

Size of trees and palatability are interrelated: beavers cut only smaller specimens of less preferred trees, while they take all size classes of the more preferred trees. This has been interpreted as the result of the smaller nonpreferred trees ("best" sizes of nutritionally poorer species) being nutritionally equivalent to the "worst" sizes of the preferred species.[19]

Beavers often eat bark of thicker trees directly on site, without felling the tree itself. Of those they cut down, they gnaw thicker branches into pieces that can be easily hauled or floated to the water area near the lodge (Fig. 9.2). They chew the bark off while holding the stick or log in their front paws (Plate 21). Where beavers continue to consume the bark of twigs and logs in shallow water over several days, a "feeding bed" results (Fig. 9.3). The sticks in various stages of being peeled provide evidence of what species are preferred at that site and time. Also, very thin sticks as leftovers indicate that kits might be present.

How long does it take a beaver to cut down a tree? For all woody plants, the overall average time per plant was 1.24 minutes, according to one study.[8] Trees up to 15 cm in diameter can be felled in less than 50 minutes. But the time needed for larger trees increases exponentially: trunks 25 cm and larger require over 250 minutes.[8] After all this effort, many trees become hung up in neighboring trees. How often this happens depends on the density of the stand of trees. In Europe, 12.5%–15.0% of beaver-cut trees end up not being available for this reason.

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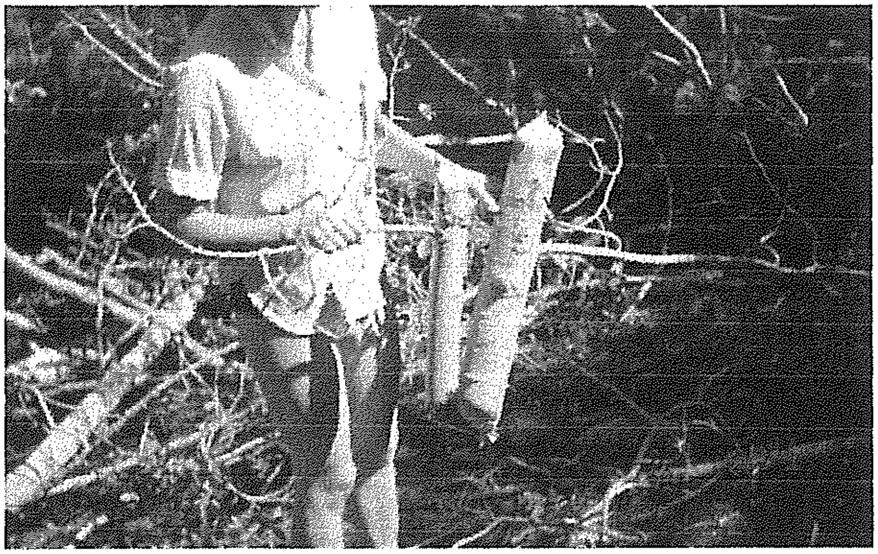

Figure 9.2 | Aspen logs, cut into typical length for transport.

Figure 9.3 | A "feeding bed" in a beaver pond.

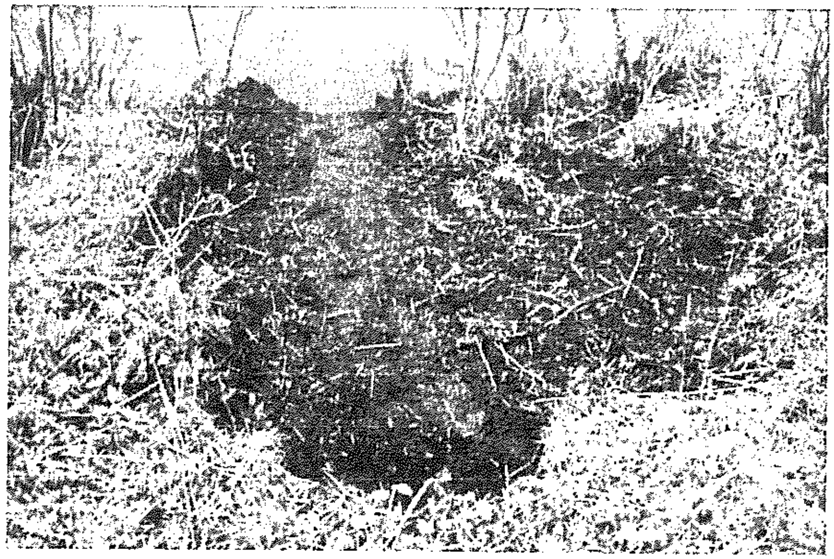

Figure 9.4 | Beavers have dug up the ground near their pond to feed on bracken rhizomes. Pond in background.

Seasonal Changes of Food Preferences

In addition to the alternation between trees in winter and grasses, forbs, and aquatics in summer, beavers prefer different tree species during different seasons. Conifers such as pine are accepted primarily in late winter and spring[1,3] (our own observations) (Plate 22). Presumably, lack of other vegetation, combined with renewed sugar flow in the pines, renders them attractive for a short period of time. In fact, we found a colony that used Scots pine in April. In a choice experiment, this family preferred Scots pine to aspen! Also, beavers might need compounds from pine bark for forming castoreum, which they use for scent marking in spring.[3] In early spring our beavers at Allegany State Park, and also in the Adirondacks, dig up the rhizomes of bracken fern at the edges of their ponds (Fig. 9.4). Beavers intensify tree cutting in the fall. In Massachusetts, the number of trees cut by one colony increased drastically from mid-October to late November.[18]

Nutrients

Proteins, carbohydrates, and fats form the foundation of an adequate diet. While animals choose vegetation of high quality, many plant species contain little of one or more of the essential nutrients. This forces herbivores to subsist on a varied diet. The beaver exemplifies such a generalist feeder.

Nutritionally, tree species differ. For instance, the often-rejected red maple has less energy content[20] (see Digestion and Digestibility).

In addition to these basic nutrients, vitamins and trace elements are important. Deficiencies can lead to disease and death. The famous captive beaver "Nicky" at Beaversprite in New York died of goiter in September 1987. Three other beavers had died of goiter before. It is well known that captive wildlife such as deer and felines develop goiter, an iodine deficiency. In a study in Michigan, the iodine content of deer foods ranged from a minimum of 0.008 part per million (ppm) in fruits, nuts, and grains to 3.1 ppm in aquatic plants.[21] Now we can see how important those aquatics must be to beavers. Water plants also can provide beavers and deer with sodium in areas with sodium-deficient terrestrial vegetation. However, beavers in Algonquin Provincial Park in Canada[12] and on Isle Royale National Park in the United States[14] do not seem to suffer a sodium constraint.

Secondary Plant Compounds

In addition to nutrients and trace compounds and elements, plant secondary compounds also affect the beavers' feeding, often in a negative way. Phenolic-laden trees such as red maple and witch hazel are avoided (Plate 23). Especially young trees can be chemically defended.

In a comparative study, beavers selected smaller-diameter aspen at Little Valley, Nevada, but preferred larger diameters at Sagehen Creek, California (Fig. 9.5). The two sites differed in that beavers had colonized Little Valley only recently, whereas beavers had cut aspen at Sagehen Creek for over 20 years (as described in Hall's study[9]). Sagehen Creek experienced considerable juvenile regrowth of as-

Figure 9.5 | Aspen cut at Sagehen Creek, California.

pen, which is characterized by high levels of a phenolic compound.[22] Feeding experiments showed that beavers avoid the root sprouts of aspen that have juvenile characteristics, including large leaves, and no lateral branching. A phenolic factor with a molecular weight of 426 occurs at high levels in juvenile sprouts, but it is not one of the known compounds salicin, salicortin, tremuloidin, and tremulacin. These four compounds occur at approximately the same levels in adult-form and juvenile-form sprouts.[23] The phenolic factor may be responsible for the discrimination of these two growth types by beavers.

Beavers cope with one class of phenolics, the tannins, in an evolutionarily ingenious way. As generalist feeders, they encounter many different phenolics. However, they employ physiological coping mechanisms for only the most characteristic tannins of their diet. These are *condensed* (as opposed to *hydrolyzable*) tannins. Condensed tannins, in turn, can be linear molecules or have a branched structure. Beavers prefer tree species with linear, and not branched, condensed tannins. Correlated with this, beaver saliva contains proteins that bind only to the linear and not to the branched condensed tannins and hydrolyzable tannins.[24]

Herbivores in general may feed on willow because this way they avoid the chemical defenses, mostly resins, of other deciduous trees such as birches and alder.[25]

Food Conditioning

Beavers leave twigs and sections of tree limbs in the water before they consume the bark. In the winter food caches, branches also sit in the water for weeks or months. The beaver is in an excellent position to utilize streams and its ponds for leaching out undesirable compounds from the bark before eating it. The first experiments to test whether beavers process their food in this way suggested that they do, but we are far from knowing for sure. In Upstate New York, beavers tend to leave sticks of the less palatable red maple and witch hazel in the water for 1–3 days before they consume the bark.[26]

Digestion and Digestibility

Aspen passes through the digestive tract of beavers in about 10–20 (mostly 16–18) hours, while red maple takes 30–50, even as long 84 hours.[12,20] The faster the food passes through the beaver's system, the higher the rate of nutrient absorption. This explains why beavers accept red maple very reluctantly, and only when they have to. Because of the limitations on how much of each food can pass through the gut each day, Fryxell and Doucet[20] calculated that the beavers could never meet their energy requirement were they to eat red maple exclusively.

Since some plants are more digestible than others to the beaver, we can determine the digestibility by measuring how much the beaver eats and comparing this with the fiber or nitrogen content of the droppings. The difference is the digested portion of the food. The ratio of the amount of matter or energy digested to what is eaten is termed *apparent digestibility.*

However, some material excreted in the feces does not stem from food but rather from the animal's body itself. If such "endogenous losses" are taken into account, "true digestibility" can be determined. This measure is more useful than apparent digestibility.[27] True digestibility can be determined by plotting the ingested daily amounts of, say protein for each animal on the abscissa, versus the digested amount per day on the ordinate of a graph. Such a graph shows that red maple, for instance, is eaten in smaller amounts than aspen or alder, and for the amount eaten, less of the protein is digested.[27]

These studies show that several different factors affect how beavers select trees. Size, distance, species, nutritional value, and palatability all play a role.

Beavers do not seem to possess cellulases, the enzymes to digest cellulose. And yet they are able to digest about 30% of the cellulose they ingest, most likely by the action of microorganisms.[28] It is not clear whether the cardiac gland along the lesser curvature of the stomach plays a role in cellulose digestion. Although they consume more woody material than most other mammals, beavers have no special adaptations for cellulose digestion beyond what we find in ruminants.[28]

Caecal microbes may turn cellulose into nutrients that the beavers take up from their "cloaca" and eat a second time. This reingestion of "coecotrophe" is neither rumination nor coprophagy, as the caecal material is blackish and soft and therefore quite different from regular feces. During this second passage, the small intestine will absorb the recovered nutrients. The smaller particles of this reingested coecotrophe travel faster on their second passage through the gastrointestinal tract. When labeled with magnetic, fluorescent microtaggant, 55% of these smaller particles passed after 10–14 hours, and 88% passed after 40 hours. By comparison, only 6% of eaten bark was digested after 11 hours (first defecation after a meal), but 88% was digested by the second defecation on the second day. In summary, passage time for 100% of both original food and reingested material is about 60 hours. But the mean passage time for the microtaggant was only 36 hours. This is a turnover rate of 70% of eaten material in 24 hours for a beaver on an aspen bark diet.[29] Compare this with some extremes in birds and mammals: seeds can pass through songbirds in only 12 minutes but will take up to 60 days in a horse.

Estimates of Food Supply

Wildlife managers and property owners often want to know whether an area harbors an adequate food base for beavers. For proper estimates we need to know not only the food preferences of the beavers but also how flexible beavers are in terms of making do with less preferred species. To derive an estimate of available beaver forage from a count of aspen or willow specimens, one has to consider how much of the total biomass is edible. For instance, 93.6% of the stem weight of first-year shoots (2.5 mm in diameter or less) of coyote willow (*Salix exigua*) is beaver food. By contrast, the edible bark of the largest investigated willow stems (40–60 mm in diameter) comprised only 12.2% of their total biomass.[30]

Edible biomass, consisting of leaves, twigs, and bark, has been calculated for trembling and bigtooth aspen of different sizes. Trees with a breast-high diameter (bhd) of 2.5 cm (1 inch) provide 1.3 kg (2.85 lb) of beaver food on average; those with a bhd of 7.5 cm (5 inches), 21.3 kg (46.9 lb); and trees with a bhd of 25 cm (10 inches), 101.2 kg (223 lb).[31]

Food Caches

In northern areas, beavers store food for the winter in a cache or "raft" (see Plate 4). In fall (October/November) they drag branches and saplings to their pond and pile them up in the water close to the lodge. This way the food can be reached easily from the lodge and eaten or removed under the ice. The time of cache construction varies with latitude. A beaver population on the Mackenzie Delta (latitude 69° north) in the Northwest Territories, Canada, close to the northern limit of the species' distribution, collected their food caches in late August and early September. They stored mostly willow (76% of the cache) but also poplar (*Populus balsaminifera;* 14%) and alder (*Alnus crispa;* 10%). Willow was preferred, while alder was taken much less than its abundance would suggest.[32]

In another study in Wood Buffalo National Park (latitude 58° north) in Alberta, Canada, beavers also stored mostly willow, specifically sand-bar willow (*Salix interior*). Here the beavers are icebound during the winter for about 164 days, almost half a year. The butt diameter of the stored branches rarely exceeded 5 cm. The available amount of food in five caches was estimated to range from 39.5 to 56.0 kg (87–143 lb). Willow, alder, aspen, and red osier were analyzed for protein, fat, fiber, and nitrogen-free contents, and the digestible energy in each cache was calculated. The five food caches contained from 30,000 to 70,000 kcal. Compared to the needs of the beaver in winter, this does not suffice. The older age groups run a deficit of 57,000 to 150,000 kcal/colony during the 150 days they are icebound.[33]

In the northern interior of British Columbia (lat # 54°N to 55° 30'N) white spruce and subalpine fir form the forest, with trembling aspen stands interspersed. Along the waterways willow and alder are common. In fall, before consumption, 83% of the food caches contained aspen; 50%, willow; and 44%, alder. Aspen and willow were placed throughout the cache, while alder occurred only in the raft, that is, on top of the cache. Low-preference or nonfood species are also often found in the raft covering the cache. These include white birch (*Betula papyrifera*), subalpine fir (*Abies lasiocarpa*), and white spruce (*Picea glauca*). After use of the stored food (in spring), 78% of the caches contained unbrowsed alder;

28%, aspen; and 18%, willow. Thus, beavers first select aspen from the cache. The uneaten alder was later used as construction material. These findings show that the stumps of trees cut by beavers or the composition of the food cache do not necessarily indicate what the beavers actually eat.[34]

Farther to the south, in west central Massachusetts, the numbers of branches in the food cache reflected the relative abundance of the various tree species at the two investigated colonies. At one colony, sugar maple (*Acer saccharinum*) and alder (*Alnus rugosa*) comprised 61.2% of the total available trees and 79% of the branches in the food caches. Black birch (*Betula lenta*) and alder were preferred, and ironwood was avoided. At the other colony, sugar and red maple made up 68.5% of the trees present and 91.8% of all branches stored. Sugar maple was significantly preferred, and white pine (*Pinus strobus*) selected against. Shrubs (winterberry, *Ilex verticillata*, and blueberry, *Vaccinium* spp.) were also collected. They made up 52% of all branches.[35]

In a cafeteria-style experiment, Busher[35] offered five tree and one shrub species to beavers from mid-October to early December while the beavers were constructing food caches. He followed the fate of the branches that beavers removed from the experimental piles on the bank of the pond. The beavers stored more than 50% of the branches of yellow birch, white pine, red maple, and the shrub witch hazel. They ate immediately more than 50% of the red oak branches and divided the black cherry branches about equally between storage and immediate consumption. Early in the season (mid-October), beavers were more selective in caching different tree species than later (late November), when they cached almost everything offered. Several tree species were not incorporated into the cache when beavers foraged for themselves, but were stored when offered experimentally. These were black cherry, yellow birch, and white pine. Busher[36] pointed out that diversity of food plants in the cache may be adaptive.

Beavers venture farther from the pond from September to November when they construct food caches. In Pennsylvania, they traveled up to an unusual 600 m from the pond to get food for storage.[37]

Captive beavers construct food piles with whatever is available to them. One particularly interesting case was about two young beavers that were raised without an opportunity to learn from older beavers. They severed the branches from supplied aspen and cut the remaining stems into pieces about 1 m long. These pieces floated. The beavers lashed them together with smaller branches. The animals cut up other branches, dove under the raft, and left them beneath the raft. They did this for several days and nights until a compact pile had accumulated. Eventually, the raft became waterlogged and sank below the surface, holding the food pile in place where the ice would entangle it under normal circumstances. However, the water in their concrete basin did not freeze during the winter because a steam pipe ran along one wall, unknown to the experimenters. The fol-

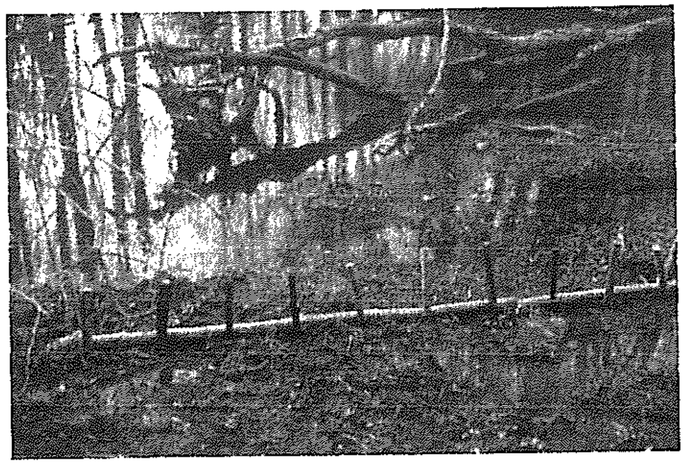

Figure 9.6 | Array of experimental sticks nailed to a long pole before contact with beavers.

lowing fall, the beavers did not build a food cache, nor did they ever in any of the 6 subsequent years.[38]

Cafeteria-Style Food Choice Experiments

Beavers readily respond to food provided at their pond's edge. This has permitted many experiments with standard sizes and numbers of sticks or twigs. Such experiments vary in their presentation: the food can be laid on the ground, stuck into the soil, fastened to some base, or placed in the water. With luck, it is possible to directly observe the beavers' choices. Plates 24 and 25 show a beaver sniffing, selecting, and then carrying away a bundle of experimental sticks that had been laid on the pond's bank. When the natural foraging behavior of beavers is mimicked by fastening the experimental sticks to a holder, the animals will bite off desirable samples. Figure 9.6 and Plate 26 show arrays of sticks before and after the beavers made their choices.

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