What Do Beaver Eat?

A literature review prepared for the Grand Canyon Trust

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This literature review found an abundance of studies investigating the dietary preferences of American beaver (*Castor canadensis*, hereafter "beaver"), conducted across the North American continent and spanning eight decades. All studies agreed that beaver are "fastidious generalists" (Olson & Hubert 1994), capable of consuming a wide array of vegetal species yet demonstrating preference for some species over others, depending on what is available in their habitat. For ease of reference, discussion of this vast body of literature is hereby arranged as answers to the following five questions:

- What are beavers' preferred species of woody and herbaceous vegetation?
- Do their diets fluctuate seasonally, and in what ways?
- From where do they gather their consumables, and at what rate?
- How much food does a beaver require each year, and how was that measured?
- How might beaver diets change over time, or influence their habitats?

Dietary Species Preferences

Beaver will sample just about any herbaceous or woody plant found in their habitats. Through analysis of stomach contents, Roberts and Arner (1984) identified 16 genera of herbaceous plants, 4 woody vines, and 15 tree species consumed by beaver in Mississippi. Usage of woody or herbaceous species is not proportionate to availability, however, but shows clear preferences, although the makeup of each "list of favorites" is a function of habitat (Fitzgerald et al. 1994, Jungwirth 2005).

Where they exist, aspen (*Populus tremuloides*) and cottonwood (multiple species) are favored more than any other woody species (e.g., Allen 1983, Busher 1996, Olson & Hubert 1994, among others). Beaver can thrive in the absence of these two species, however (Jenkins &

Busher 1979). Willow (*Salix spp*.), and alder (*Alnus spp*.) are also commonly favored, while birch (*Betula spp*.) maple (*Acer spp*.) and ash (*Fraxinus spp*.) receive only infrequent mention in the literature (Howard & Larson 1985). When preferred foods are less abundant, beaver broaden their diets to include higher percentages of less preferred foods (Fryxell & Doucet 1993). Jenkins (1979, 1980) found that beaver at his study sites in Massachusetts consumed an abundance of witch hazel (*Liquidambar spp*.), while Roberts and Arner (1984) documented substantial consumption of oak leaves (*Quercus spp*.), buttonbrush (*Cephalanthus occidentalis*), dogwood (*Cornus florida*), and grasses (particularly *Arundinaria tecta*) at his study sites in east-central Mississippi. Several studies found that conifers were cut by beaver and used to construct the surface "raft" for winter food caches (beneath which food was stored) but never showed signs of feeding (Northcott 1971, Allen 1983, Slough 1978). It is possible they are cut without the intent of ingestion, but merely for their value as durable construction material.

Hall (1960) found that, among beaver in Sagehen Creek, NV, the amount of both willow and aspen utilized was determined by aspen's availability. This pattern shows a preference for aspen over willow, but also highlights the importance of willow as a second-tier food source. Hall suggests that willow may be easier to get during twilight periods – since it grows at water's edge - before it is dark enough to safely venture forth to procure aspen. This could explain beavers' use of willow even where aspen is abundant.

When several species of a preferred genus are present, some may be selected more than others. A cafeteria-style study in central Oregon showed that beaver there prefer cottonwood (*P. trichocarpa*) over all willow species, and prefer some willows (*Salix lucida* spp. *lasiandra* and *S. monochroma*) over others available locally (*S. geyeriana*, *S. exigua*, and *S. prolixa*) (Kate

Martin, Bridge Creek Restoration Coordinator, Oregon Natural Desert Association, kate.h.martin@gmail.com, personal communication).

Beaver also consume a diverse list of aquatic vegetation. Plants most commonly mentioned in the literature include sword-fern (*Polystichum*), pondweed (*Potamogeton*), waterweed (*Elodea*) and water-lily (*Nuphar spp.*). Algae that grow in the mats of floating species may also be eaten, as well as horsetail (*Equisetum*) that grows along the water's edge (Svendsen 1980). A study in Ohio showed a greater reliance on aquatic vegetation among subadults (Svendsen 1980), while another found no significant difference in food usage by either sex or age (Roberts & Arner 1984).

The prevalence and type of herbaceous vegetation available may influence beavers' reliance on woody species. Jenkins (1981) compared the rate of tree cutting in two adjacent ponds: one dominated by yellow and white water lily (*Nymphaea variegatum* and *N. ororata*), which have thick rhizomes, versus a pond dominated by water shield (*Bassenia schreberi*), which lacks thick rhizomes. Trees adjacent to the water lily pond experienced a low and constant rate of cutting throughout the fall (which suggests sustained consumption of the aquatic rhizomes), while the other pond showed increased tree cutting once the water shield leaves died (indicating seasonal use of the leaves only).

Busher (1996) conducted cafeteria-style experiments during the food caching season (October-December) of a beaver colony in Ontario. He found that beaver cached branches of all six species offered (not just the most desirable of the selection, *Acer rubrum*), though not at the same rate. They selectively cached far more witch hazel than they ate immediately (106/122 branches cached vs. 11/122 eaten) while they ate more red oak than they cached 23/40 vs. 9/40). Also, there was a significant difference in the species selected for caching in October but not in

November or December, showing that beaver are "choosier" early in the season than later. Beaver appear to be balancing the total energy content of the food cache with its nutritional diversity, emphasizing volume growth over diversity as the season advances and time for preparation diminishes. Vander Wall (1990, cited in Busher 1996) and Busher (1996) suggest that diversity of diet may be sufficiently important to long-term food cachers, like beaver, to outweigh the energy expenditure of foraging for less abundant species.

Overall, it may be concluded that beaver can and do subsist on a wide variety of foods, so the species of food plants present at a site may not be a strong determinant of suitable habitat (Jenkins 1981, cited in Beier & Barret 1987). The presence of sufficient winter food supplies may be, however. (Allen 1983).

Seasonal Patterns

Beaver are known for their consumption of the bark and twigs of woody vegetation. However, they appear to prefer herbaceous vegetation over woody vegetation during all seasons of the year, if it is available (Jenkins 1981 cited in Allen 1983). Forbs and grasses are important diet constituents in spring and summer (Fitzgerald et al. 1994, Collins 1976 cited in Olson & Hubert 1994) while rhizomes and aquatic roots or tubers are important additions to winter food supplies. In one Pennsylvania study, the ratio of woody : nonwoody materials consumed by beaver shifted from 25:6.2 in winter to 2:30 in summer (Brenner 1962). Woody vegetation may be desired primarily for its ability to be preserved and consumed over a long, icy winter when other resources become unavailable.

The main activities of beaver during summer are dam maintenance and feeding (Lew Pence, retired Natural Resources Conservation Service Ranger and Soil Conservationist, pence5302@msn.com, personal communication). Beavers' summer diet is varied, and may include the bark and twigs of deciduous trees and shrubs, aquatic plants, grasses, sedges, rushes, and water lilies (Grasse & Putnum 1955, Northcott 1971, Belovsky 1984). Aquatic plants play a particularly important role, comprising up to 50% of food consumed in summer (Jenkins & Busher 1979, Svendsen 1980). Gurnell (1998) documented beaver spending 90% of summer feeding time consuming grass, forbs, and aquatic vegetation. All studies agree that beaver show a strong reliance on herbaceous and aquatic vegetation during the summer season.

Construction of a winter food cache begins in late summer/early fall, unless the winter climate is warm enough to suppress this behavior (Lew Pence, personal communication, and Collins 1976 cited in Olson & Hubert 1994). Edible, woody species are primarily used for the cache, though Slough (1978) relates an observation of beaver in Canada constructing food caches made entirely of pond lilies (*Nuphar variegatum*) topped with unpalatable black spruce (*Picea mariana*). Cached material comprises the primary food source throughout winter, though beaver will surface to collect herbaceous vegetation available in winter: beaver in Ohio eat Christmas fern (*Polystichum acrostichoides*), for which they travel up to 50m from the water (Svendsen 1980). Overall decreased intensity of feeding in winter (rarely exceeding 2 hours/day) suggests a seasonal metabolic depression for northern beaver (Svendsen 1980).

A seasonal cycle of dietary preference is evident, and has been documented by at least two year-long studies. Svendsen (1980) found that beaver in Southeastern Ohio consume mostly bark/twigs in spring (Mar-Apr 70% of diet), fall (Oct-Nov 50%) and winter (Dec-Feb 70-90%), while their summer time woody consumption is much lower (June-Aug 10-20%.) A major shift occurs in May when grasses & forbs become popular (May-Jun 50-70% of diet, July-Aug 40%), while aquatics are most popular from summer through early fall (Jun-Oct 40-50%).

Roberts and Arner (1984) found a similar pattern evidenced by the stomach contents of beaver in east-central Mississippi. Woody material averaged 85.5% of dry weight stomach contents for Dec-Mar and declined to 31.7% in May, 16.7% in August, and rose to 56% in Nov. While 80% of beaver examined had woody material in their stomachs in winter, only 42% had any in May, 33% in August, and 60% in November. Grasses were found in 25% of samples between July-Sep, though grass consumption was highest (20% of dry weight total) in October.

At least one study suggests that seasonal and year-to-year variation in dietary preferences may be related to temporal variation in the relative nutritional value of certain species. Jenkins (1979) found that beaver increased their reliance on *Pinus spp.* in spring, which is the same period when deciduous trees' carbohydrate reserves decrease sharply due to spring growth. Also, oaks were cut more often in years they didn't produce acorns (and, thus, would have more stored nutrients) than in years they did. Water lily (*Nupha*) is lower in calories than woody matter (aspen, etc.) but is high in crude protein and sodium – either of which might be a reason for beavers' preference for them (Doucet & Fryxell 1993).

Location and Size

Beaver are most vulnerable to predation when out of the water and prefer to remain within proximity to its banks. Jenkins (1980) and Hall (1960) found that up to 90% of cutting of woody material occurred within 30m of the water's edge. Olson & Hubert (1984) agree, though they documented occasional forays up to 600 feet, while others (Allen 1983, Fitzgerald et al. 1994) restrict the likely feeding corridor to 100m, or 328 feet.

Many studies of beaver diet have sought to construct predictive models of their feeding behavior based on central-place foraging theory. Central place foragers acquire their "prey" while afield, and then bring it back to a central place for consumption. They should be more selective in their targets and, in order to maximize their energy gain, should select larger prey when further from their central location. However, some have suggested that the relationship between size and distance should be inverted when the prey is larger than the predator (Jenkins 1980). It is also possible that size-selection is only manifested at relatively large distances from shore for highly preferred woody species, such as aspen, but will manifest at short distances for less preferred species (Jenkins 1980).

A positive correlation between distance and selectivity has been documented by many studies, in which beaver consumed larger numbers of preferred species than non-preferred species at greater distances from their central place (Pinkowski 1983, Raffel et al. 2009). Results are contradictory, however, regarding whether distance correlates with overall selection for larger or smaller prey. Jenkins (1979, 1980, 1981) and Busher (1996) consistently documented beaver selecting smaller diameter trees farther from shore, while others (Fryxell & Doucet 1993, Pinkowski 1983) have shown the opposite.

It is possible that both are correct. Schoener (1979) proposed a relationship between provisioning time and the size of food items that leads to two alternative foraging strategies. When provisioning time is independent of size, larger food items that are more energetically profitable should be preferred at all distances from the central place. When provisioning time increases with item size (such as with larger diameter mature trees), the profitability of large food items relates inversely to distance from place, resulting in their being selected against at greater distances.

Either of these feeding strategies may be demonstrated by beaver where food items of different diameters are prevalent. McGinley & Whitham (1985) studied beaver food consumption along the San Juan River in SE Utah, where aspen branch diameters are very small (1.5-30.0mm). Their results upheld Schoener's first prediction: larger branches were preferred at all distances because the influence of size on provisioning time was negligible. Jenkins (1980) and Belovsky (1984) found that the diameter of trees their beaver cut decreased with increasing distance from shore. The trees in these studies ranged from 5-25cm, however – ten times the size of branches in McGinley's study – and, therefore, offer evidence of Schoener's second prediction. Jenkins also found that witch hazel, which was uniformly small in size (all <6cm), was cut at the same high rate at all distances, indicating that it is a strongly preferred species and further enforcing the notion of the independence of distance and size of prey when provisioning time is constant.

Basey et al. (1988) compared tree selection of beaver at two study sites in Nevada: one that had been occupied for over 20 years (Sagehen Creek) and another only recently occupied (Little Valley). Beaver at Little Valley showed a preference for aspen less than 7.5cm diameter. Beaver at the Sagehen Creek site, however, preferred aspen of either less than 4.5 diameter or greater than 19.5cm in diameter. They suggest that aspen respond to sustained browsing pressure by producing chemical defenses in their suckers, causing beaver to shift their preferences to more mature trees (which lack these chemicals.) (Under intense browsing pressure, aspen produce a high number of "juvenile form" suckers, which contain high amounts of a phenolic compound that is lacking in the adult-form suckers.) The authors offer this as evidence that predictive, energy-maximizing foraging models have limited value unless they account for such inducible plant responses. In their summary, the two hypotheses are not mutually exclusive, but are differentially applicable over the course of a colony's residence at a site: beaver might maximize energy intake until a time when chemical defenses make such food items unpalatable.

Quantity and Method

Estimates of beavers' caloric intake vary widely, and come from a variety of experimental designs. Aldous (1938) fed piles of aspen bark and twigs to 2 caged beavers for a month to determine average daily consumption. Svendsen (1980) directly observed six beaver colonies to document feeding behavior during daylight and nighttime hours, through 52 weeks of the year. Northcott (1971) conducted fixed-wing flyovers to map available vegetation, and then inspected colony sites to determine percentages of vegetation use. Summer foods were documented by noting chewed pieces of aquatic vegetation floating at each colony, while winter foods were documented by marking recently cut trees, and by noting leftovers evident in summer. Jenkins (1979) measured availability of tree species at a location in central Massachusetts in a series of non-overlapping circular plots, and monitored species, stump diameter, and location of fresh cuts – analyzed in four time periods (fall and spring). Roberts and Arner (1984) conducted analysis of stomach contents of 165 beaver caught by traps in Mississippi. Lastly, Jungwirth (2005) defined strip transects 3m wide stretching from water's edge to woody habitat, and documented all trees marked by beaver as well as actual and relative density.

Brenner (1967) offers a comprehensive review of the many studies in the early 20th century that assessed the daily caloric requirements of beaver. His own study in 1962 estimated 1.5-2.2 lb/beaver/day, which is close to Aldous' (1938) "feeding experiment" results of 1.3-2.1 lb/beaver/day. Others claim as high as 4.5 lb/day (Warren 1940, Grasse & Putnam 1955 cited in

Olson & Hubert 1994). Cowan et al. (1950, cited in Brenner 1967) calculated fresh aspen contains 1156 kcal/pound, and studies assessing beavers' ability to digest cellulose estimate a digestibility of between 28-50%. Therefore, one pound of aspen could yield as much as 580 useable calories to a beaver. Stephensen (1956, cited in Brenner 1967) claimed a 28-lb beaver requires 850 kcal daily, which would correlate nicely with Brenner's observations made in the field. However, Belovsky (1984) estimated that adult beaver in Isle Royale National Park require 1213 kcal/day, and Dyck & MacArthur (1998) found that beaver in Ontario consumed an average of 0.52 kg/day of woody forage, representing an estimated gross energy intake of 6547 kJ/day.

There are many dangers in comparing dietary requirement assessments between studies. Climate assuredly plays a role in beavers' relative activity and rates of consumption, as well as the animals' size. Slough (1978) highlights the pitfalls of relying solely on a measure of cut stumps to reveal food preference, for some trees (such as pine or alder) may be cut merely to give structure to the food cache pile without intended use as a food source. Also, beaver rarely eat their entire winter food cache, so any study using that volume as a baseline will err on the high side. (Lew Pence, personal communication.)

One of the most frequently cited estimates of beaver dietary needs is Macdonald (1956, cited in Vore 1993). By extrapolating from observed tree-felling activity of beaver in North Park, CO, MacDonald determined the acreage of pure stands of willow or aspen that could support a colony of 6 beaver for a year. In his estimation, 6 acres of 30' aspen or 18 acres of mature willow would provide sufficient food supplies for such a colony (in the absence of competition from livestock or game). This study was cited by three state agencies as the basis for their management plans (Blackwell & Pederson 1993, Vore 1993, and Saldi-Caromile et al. 2004), despite broad geographic difference.

Changes over Time

There remains in popular thought a notion that aspen and cottonwood are non-sustainable food sources for beaver that will, when given the opportunity, "eat themselves out of house and home." While some older studies supported this idea (such as Beier & Barrett 1987, Northcott 1971), many others have shown that beaver do not permanently decimate their food sources in an area they inhabit.

If beaver do consume the available woody species at a site, they will relocate to another site to allow the vegetation to regrow in their absence. An 18-year study of beaver colonization in Finland found that the mean colony duration length was 2.6 years, and that old sites were recolonized an average of 9 years after abandonment – most likely due to regrowth of food supply (Hyvönen & Nummi 2008). Demmer and Beschta (2008) saw the same pattern among beaver colonies in Central Oregon. During their 17 year study, they noted episodic colony abandonment triggered by heavy utilization of riparian vegetation, followed by a regrowth of woody plants to a higher density than prior to the beaver colonization (and, thus, more than capable of supporting their return.) Masslich et al. (1988) assessed density of stump classes in Strawberry Valley, Utah, to determine that beaver regularly return to previously cut-over aspen stands once sprouts approach 5cm in diameter, or an age of 20 years.

During their occupation, however, beaver inarguably impact the vegetation stands in their habitat. McGinley & Whitham (1985) noted that trees subjected to herbivory show changes in their architecture and sexual development. Cottonwoods adjacent to the river (where beaver forage young, small diameter branches) are kept small and in a perpetually juvenile state, showing much higher numbers of basal branches (vegetative reproduction). Trees farther from shore (where beaver select against small diameter trunks and, thus allowed young trees to grow) are taller with single trunks and reproduce sexually. Masslich et al. (1988) noted a similar pattern, in which heavily cut stands responded with a rate of root sprouting akin to that following clear-cutting.

Willow are more tolerant of beaver use and are better than aspen for sustaining stable populations at one site (Hall 1960 and Kindschy 1985). Beavers may harvest 82% of available willow stems annually, but they cut them when they are dormant, which promotes suckering and rapid regrowth (Kindschy 1985). Kindshey notes that red willow used by beaver maintains a high growth rate and increasing basal diameter similar to unused willow, and suggests that periodic migrations among recovered willow patches could sustain a colony in a localized area for a long time. In his assessment, cattle grazing and not beaver foraging is responsible for willow denudation in SE Oregon, for cattle crop willow sprouts during the growing season. Masslich et al. (1988) suggest that downed but unused trees lying on the ground in an active beaver cutting area may produce an effective barrier to grazing animals, thus protecting their food source from browse competition.

Lastly, beavers' dietary makeup changes over time as a result of their own influence on their habitats. A study in Minnesota noted the persistence of a colony long after aspen were depleted, indicating that switching of diet to less preferred foods may sometimes be preferable to finding a new residence (Wilkinson 2003). If beaver are relocated onto marginal habitat, they'll "scrounge a little bit", eating the best of what's available – even sagebrush, grass, or nearby agricultural products, such as alfalfa or cornstalks (Kate Martin and Lew Pence, personal communications) until the ecological changes caused by their dams and ponds (raising the water table, stemming sediment loss, increasing biodiversity of flora and fauna, etc.) improves their habitat, and so their diets improve in response. Thus, it may be difficult to accurately assess preference without a sustained period of observation over which such habitat changes occur.

Land managers, conservationists, and advocates for forest health would do well to study the dietary needs of beaver. Beck & Staley (2005) offer a wise caution, however, to those who base management decisions on wide-ranging reviews such as this. "It is crucial to evaluate important predictors of habitat suitability relative to habitat components available on a respective forest. In other words, context is important and we should not expect the same criteria to function in cottonwood (*Populus* spp.) gallery forests of the national grasslands as in high elevation glaciated streams in a conifer landscape on national forests." Despite regional differences in certain parameters, such as rank of food species preference or total caloric requirement, it is widely accepted that these "choosy generalists" are keystone species of many riparian habitats, and the beneficial impacts they have on the ecology of such systems warrants our attentive care and feeding.

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