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Food Habits and Ecology of Beavers in Southeastern Virginia

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BEAVERS IN SOUTHEASTERN VIRGINIA

by

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ABSTRACT

FOOD HABITS AND ECOLOGY OF
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The food habits and ecology of three beaver colonies in James City County, Virginia were studied. Vegetation surrounding the colonies was characterized as southern mixed hardwood forest or lowland swamp forest. Stream flow values ranged from 0.013 to 0.369 m^3/sec. Water depth ranged from 0.5 to 4.0 m. Caloric value of 13 heavily used woody species ranged from 3305 to 6204 cal/g. Considerable seasonal variation was noted in most species with the lowest caloric values noted in summer. No relationship was found between caloric value and frequency of use. Fresh cutting was monitored on a weekly basis and a tally was made of all cut stumps. Chi-square analysis was used to determine food preferences. Alder, tulip poplar, red maple, willow, white oak, bayberry, dogwood, pine, ironwood, viburnum, beech, and spicebush were heavily used. The latter three species have not been previously reported in the literature as food for beavers. Beavers were found to be active year-round, building an extensive food cache but using it only lightly.

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INTRODUCTION

The beaver is a member of the Order Rodentia, the gnawing mammals. It belongs to the family Castoridae, which is represented in North America by a single species, Castor canadensis. Beavers were formerly common over much of the United States and Canada. They have much the same distribution today but their numbers are much reduced due to trapping. Being semi-aquatic, they are always found along waterways. Beavers are best recognized by large gnawing incisors, a broad, flat, hairless tail, and webbed feet. Beavers reach a body length of 62 to 75 cm and weigh 13 to 27 kg as adults (Hammond, 1943).

Beavers are probably best known for their tree-felling and dam-building activities. Although they often build lodges of sticks and mud in a pond, in some areas they may dig burrows into the bank of a stream or lake. Beavers eat the bark, cambium, and small twigs of the trees they cut. Certain tree species may be cut preferentially for food. In summer, they may feed more heavily on herbaceous growth such as cattails (Typha spp.), arrowhead (Sagittaria spp.), and water lily (Nuphar spp.). At most latitudes, beavers construct caches of branches in their ponds each fall and remain active throughout the winter, feeding from these caches. Beavers are mostly nocturnal, becoming active soon after sundown and ceasing activity before dawn in most cases. They are occasionally seen during the day, especially during the fall when they are gathering branches for the winter food cache (Slough, 1978).

The most common type of beaver colony consists of a mated pair, young of the year (kits), and yearlings (their young of the previous year) (Hammond, 1943). The two year olds either leave or are driven out of the colony in mating season. Females usually breed at two and a half years of age. The mating season usually begins at the end of January and extends through February. A single litter of two to four kits is born during April or May (Brenner, 1964). Beavers are long-lived, living up to 11 years in the wild. They are also highly mobile, sometimes moving 1.6 to 9.6 km from their birthplace.

The beaver, an important fur animal, was extirpated over large parts of its range due to over-trapping. By 1911, the beaver was largely absent from Virginia. In 1932, a re-introduction program was started. Beavers from the northern states were successfully re-introduced into several locations (Augusta, Chesterfield, Craig, Cumberland, Dinwiddie, Giles, Goochland, and Prince George counties) in Virginia and served as nucleus populations for later introductions into other parts of the state. Beavers are presently found in almost all parts of Virginia, with their highest density being in the piedmont area (Virginia Game Commission, unpublished).

The food habits of beavers have been the subject of numerous studies throughout most of North America. The major results of these studies are summarized in Table 1.

The most common type of study has focused on counts of cut stumps to determine food preference. Examples of this type of study include Atwood (1938), Aldous (1938), Hammerstrom and Blake (1939), Shandle and Austin (1939), Shandle, et al. (1943), Jahoda (1948), Townsend (1953), Hay (1958), Hall (1960), Brenner (1962) and Plocher

Table 1. Literature review of beaver food habits in North America.

* = light use by beavers, ** = moderate use, *** = heavy use.

Author (Date) and Location	Alnus sp.	Populus sp.	Betula papyrifera	Salix sp.	Liriodendron tulipifera	Fraxinus pennsylvanica	Quercus alba	Acer rubrum	Prunus serotina	Cornus sp.	Carpinus caroliniana	Quercus rubra	Pinus sp.	Persea borbonia	Rhus typhina	Liquidambar styraciflua	Nyssa sylvatica
Jahoda (1948) New Hampshire							*					*					
Jenkins (1979) Massachusetts			***				***				***		**				
Shandle and Austin (1939); Shandle, et. al. (1943) New York		***	***	***				***	***		***		***				
Brenner (1962) Pennsylvania	***	***						***									
Svendsen (1980) Ohio					***			***			***						
Hammerstrom and Blake (1939) Wisconsin	**	***	***	***			**		**			**					
Aldous (1938) Minnesota	***	***	***	***						***							
Hammond (1943) North Dakota				***		***	**		**	***							
Townsend (1953) Montana	***	***		***						***							
Alekaluk (1970) British Columbia	***	***		***													
Slough (1978) British Columbia	**	***		***													
Atwood (1938) Missouri	***	***	***	***			**	**	***	**		**					
Hay (1958) Colorado		***		***													
Hall (1960) California	**	**											*				
Flocher (1979) Virginia				***				***						***	***		
Chabreck (1958) Louisiana											***		***			***	***

(1979, unpublished data).

Other studies have focused on the contents of the food cache to determine food preferences. Studies of this type include Hammond (1943), and Slough (1978). Slough (1978) also observed that the placement of sticks in the cache can reveal food preference. Alder (Alnus sp.) often was used to construct a raft to secure the food cache underneath. Preferred foods may be used in place of alder to construct the raft, if they exist in abundance.

Several studies have taken an important step by comparing the availability of a tree species with the number cut. This is done in fixed plots surrounding the beaver colony. Studies of this type include Chabreck (1958), Aleksiuk (1970), and Jenkins (1979). Chabreck (1958) also noted that beavers de-barked rather than cut 24 percent of all woody plants over one inch in diameter. This was rarely observed to kill the plant. He also observed that the beavers were active throughout the winter in the mild climate of Louisiana. Perhaps because of this prolonged activity, a food cache was not constructed for winter.

In a study based on extensive observation, Svendsen (1980) observed that bark was heavily used for food in spring and fall. In summer the beavers switched and made heavy use of aquatic and herbaceous growth. Aleksiuk (1970) observed that leaves and growing tips of willow (Salix sp.) were the beavers' main summer food.

Aleksiuk (1970) also noted a strong correlation between the caloric and protein content of woody foods and the extent to which they were utilized. Willow bark was found to be higher in protein and calories than aspen or alder.

From the above studies, it is clear that aspen (Populus sp.) is a favored food of northern beavers. However, the status of species such as willow (Salix nigra), green ash (Fraxinus pennsylvanicus), tulip poplar (Liriodendron tulipifera), ironwood (Carpinus caroliniana), and others commonly found in southeastern Virginia is unknown and should be investigated. Overall, there seem to be few studies of beaver food habits and ecology in the southeastern United States.

The overall objective of this study was to investigate the ecology of beavers in southeastern Virginia. The overall objective was divided into the following primary and secondary objectives.

The primary objectives were to:

1) Determine the food habits of beavers, both in winter and summer, and to rank foods in order of preference.
2) Analyze the vegetation, including the tree and shrub understory, of different habitats to compare what is available to what is taken as food or for construction materials.
3) Analyze stream flow and water depth in different habitats for comparison and contrast.
4) Determine the caloric content of different woody foods.
5) Monitor activity of beavers on a year-round basis.

The secondary objectives were to:

1) Separate those species cut for food from those used only in construction.
2) Observe colonies located in study areas for data on population structure and movements.

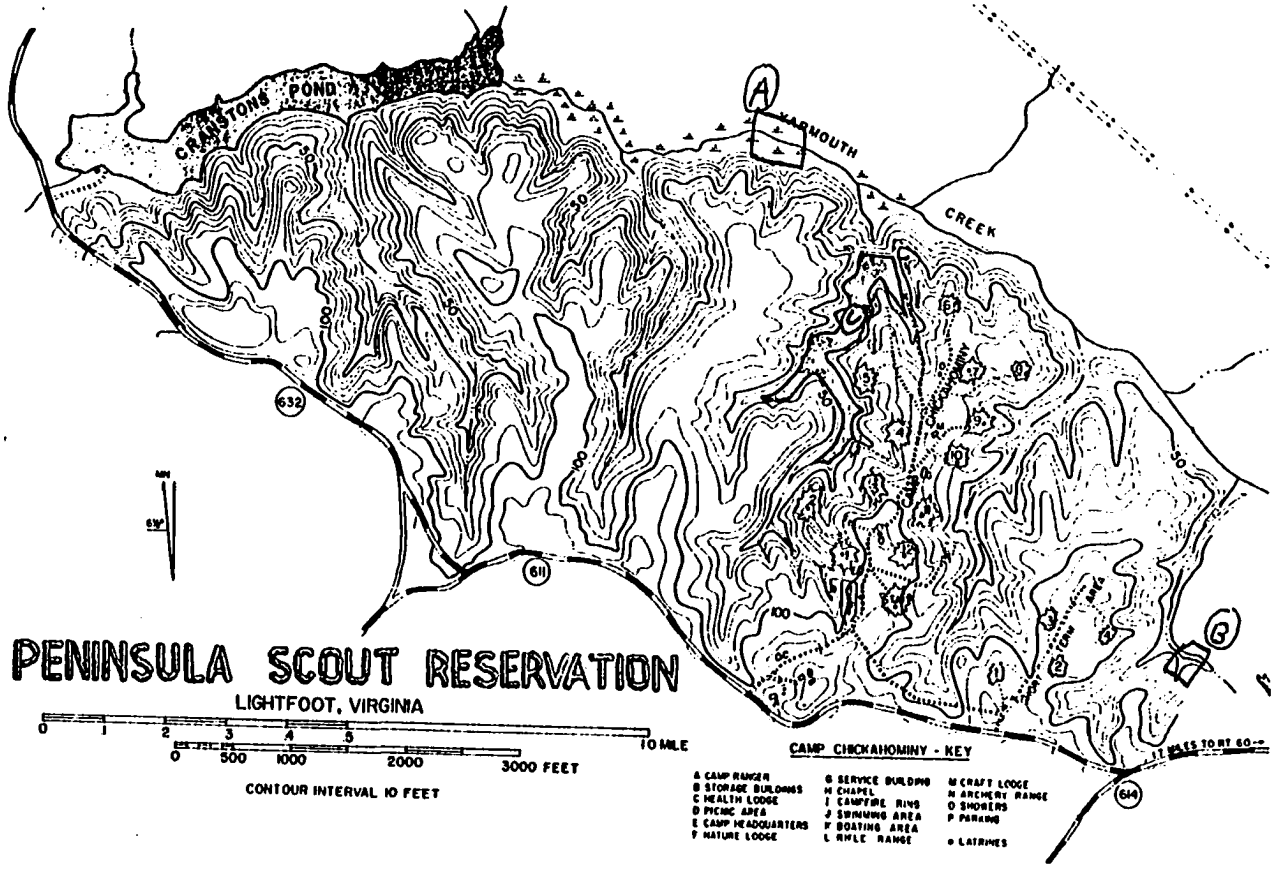
STUDY AREA

The study sites are located on the Peninsula Scout Reservation (Camp Chickahominy) in the town of Lightfoot, James City County, Virginia. The camp entrance is located on State Route 611, approximately 800 m from the intersection of Routes 611 and 614. Three beaver colonies were studied, all located on Yarmouth Creek or its tributaries. In addition, five other colonies in the area were visited regularly. Field work began in January 1980 and ended in March 1981. See Fig. 1 for the location of all study areas.

The first colony (hereafter referred to as "the swamp") is located 400 m downstream from the lake on Yarmouth Creek. The creek runs in a broad, flat-bottomed ravine roughly 100 m wide. The hills on either side slope gently. The beavers have built a dam across the ravine which raised the water level to 0.5 to 1.5 m deep for 100 m behind the dam. The base of the ravine supports a forest of green ash and red maple (Acer rubrum) with an understory of alder (Alnus serrulata), viburnum (Viburnum nudum), spicebush (Lindera benzoin), and green ash and maple seedlings. The hillsides support a mixed hardwood forest with an understory of mountain laurel (Kalmia latifolia) and hardwood saplings. In winter this area freezes over for one to two weeks at a time, generally longer than the other areas because it lies just north of a steep hill and consequently is shaded by the hill.

The second colony (referred to as "the pond") is located on a

Figure 1. Location of Peninsula Scout Reservation and study sites. A = swamp, B = pond, C = lake.



tributary of Yarmouth Creek approximately 800 m downstream from Campsite Two, in the short-term camping area. The pond was formed at the junction of two small streams when a logging road was built across the deep ravine, blocking it off. Beavers later moved into the area and built a dam atop the road, raising the water level to four m deep. The pond has roughly 300 m of shoreline. The predominant shrub is mountain laurel with an overstory of mixed hardwoods. Beech (Fagus grandifolia) and maple saplings are also important in the understory. One area of a quarter hectare was cleared and planted in pine (Pinus virginiana and P. taeda). In winter the pond freezes over for periods of one week or more.

The third colony (referred to as "the lake") is located in a man-made lake in the main camp. The lake has approximately five hectares of surface area and about 1.5 km of shoreline. The lake is surrounded by a mixed hardwood forest. In some areas, mountain laurel is the dominant understory plant. Other areas have a mix of hardwood saplings and dogwood (Cornus florida). Alder and willow are most common in small swampy areas along streams feeding the lake. Clumps of bayberry (Myrica cerifera), alder, and willow grow along the water's edge. There are also extensive patches of cattails (Typha latifolia). The lake had been inhabited by muskrats but none was observed during the study. The lake has heavy recreational use (swimming and boating) during the daytime in summer, but receives only light use in other seasons. In winter, the lake surface freezes solid for periods up to one week, but otherwise is relatively ice free.

METHODS

Food Habits - A tally of all stumps and de-barked trees was made in each area. The tally included the diameter of the cut stump and identification to species. Stumps were identified by bark and wood characters and by any buds or sprouts present. Stems per hectare, calculated for each species from habitat analysis (see below) were then added to the number cut per hectare to provide the total number of stems of each species available per hectare. The number cut per hectare was compared to the number of stems per hectare to determine a percent utilization for each species. This percent utilization was used to rank foods in order of preference. Chi-square analysis was done on the species cut in each study area. The observed value for each species was the number of stems cut per hectare. The expected values were derived as follows: The total number of stems cut per hectare was divided by the total number of stems available to yield a percent use. The number available per hectare of each species was multiplied by this figure to yield the expected value for each species. Chi-square analysis was also done by seasons on the species cut in each study area. The observed value was the number of fresh cut stumps of a species in a season. The expected value was derived from the total number of fresh cuts in a season divided by the number of species cut in that season, assuming proportional use or no preference.

Observations on the materials used to construct the dam and food

cache were made to help determine the uses of different species. The amount of cutting per unit time was determined by marking cut stumps with paint and checking at regular intervals (Brenner, 1962). This method allowed cutting activity to be monitored on a year-round basis.

Habitat Analysis - The vegetation surrounding active beaver colonies was sampled to determine density and importance values (Curtis, 1959) for each species. The methods were selected for time-efficiency, ease of use by one person, and accuracy of results for the vegetation type sampled. It was realized that a single sampling method used in all three areas would have made comparisons of the results more valid. However, because of the physical differences at each of the three sites, it was not felt that any single sampling method could be used by one investigator without significantly hampering either efficiency or accuracy. Therefore, a different sampling method was used in each area. In data evaluations of all areas, all oaks of the red oak group were lumped, as were Virginia and loblolly pines.

The swamp (Area A) was sampled using the point-centered quarter method (Cottam and Curtis, 1956). A baseline, which marked the farthest extent of beaver activity (cuttings) from the dam, was laid out across one end of the ravine and extended up the hillsides for approximately 30 m on each side. A series of parallel lines, extending to the beaver dam, ran from the baseline at right angles, with a minimum of 15 m between lines. The location of sampling points, a minimum of 10 m apart, was determined on these lines by drawing random numbers from a table. At each sampling point, four quarters were laid out (90^{o}). Distances to the nearest tree and shrub or

sapling were measured in each quarter. Diameter at breast height (DBH) was recorded for all trees. These data were used to calculate relative importance values and stems per hectare for each species (Curtis, 1959). Relative importance values for trees were calculated as the sum of the relative density, dominance, and frequency, divided by three. Relative importance values for saplings and shrubs were calculated using the sum of the relative density and frequency divided by two.

The pond (Area B) was sampled using 2 by 50 m strip plots set 10 m apart. These plots started at the shore and extended up the hill 50 m or further, to the farthest extent of beaver activity. In each plot, the presence, number of individuals, and diameter (for trees) were recorded for each species. These data were used to calculate relative importance values and stems per hectare for each species (Curtis, 1959).

The area around the lake (Area C) was sampled using 100 m^2 circular plots. Initially, the lake subjectively was divided into different vegetation types, for example, mixed hardwoods with mountain laurel. The approximate area (in m^2) of each type was determined by measuring the shoreline and the distance from shore to beaver activity. Using this estimated area, the number of plots needed for a ten percent sample was determined. The number of plots used was usually doubled to increase confidence in the results. The plots were laid out in pairs at regular intervals, the interval depending on the length of shoreline sampled. The center of the first plot was 6 m from shore, the center of the second plot was 10 m from the center of the first. The center of each plot was on a line running at right angles to the

shore. Trees were sampled in a circular plot of 5.6 m radius and saplings and shrubs were sampled in a nested plot of 2.5 m radius. In each plot, the presence, number of individuals, and diameter (for trees over 10 cm in diameter) were recorded for each species. This allowed the calculation of relative importance values for each species (Curtis, 1959). The number of stems per hectare for each species was also calculated.

In all methods, all lines were laid out with a liquid-filled, hand-held compass (Silva brand). All distances were measured with a rangefinder (Ranging brand) and all tree diameters were measured with a metric diameter tape.

Stream Analysis - Stream flow was measured by the method described by Robins and Crawford (1954). The volume of the stream bed was determined and flow was measured with a stopwatch. Measurements were made upstream from beaver colonies. Water depth was measured with a meter stick, and a permanent stake was left in each area to record changes in water depth.

Bomb Calorimetry - The caloric value of 13 species of trees and shrubs believed to represent the main foods of beavers in the study areas was determined. A full set of samples was collected in each season and analyzed for seasonal variation in the caloric value of stems. For each species, a composite sample was made by pooling the bark and cambium from five individuals. Bark and cambium were removed from the lower portion of the plants since this part of the stem was more commonly eaten by the beavers than the bark on the branches and twigs. The woody plants were selected at random from the three study areas and represented the range of diameters most commonly

used by beavers. All samples were oven-dried at 70° C for 48 hours, then ground in a Wiley mill using #60 mesh screen and then pressed into pellets. Pellets were oven-dried for one hour at 70° C and desiccated prior to bombing. Samples were bombed in a non-adiabatic Parr bomb calorimeter. A benzoic acid standard was bombed prior to the bombing of each day's set of samples. Caloric values were compared to utilization percentages to see whether caloric value had any relationship to the use of a species as food. Special attention was paid to seasonal variation in caloric value compared to seasonal food preferences.

Food Cache Analysis - Dams, lodges, and food caches constructed by beavers were dismantled and analyzed to determine the species of woody plants that were used in their construction. Food caches were of primary interest in reflecting food preferences.

Observations - Direct observations were made to determine activity times and foraging behavior. Observation was also the primary census method since live-trapping was unsuccessful. On the average, two days each week were spent in the field during the course of this study. This amounted to 120 days total, or 30 days in each season. Many of the daylight hours were spent in indirect evaluation of food habits and behavior through stump counts, food cache analysis, and other means. Two evenings each month (30 nights or 180 hours) were devoted to observations of the beavers in the study sites. The bulk of the observations were made at the lake site, from the shore or by canoe. Observations were made from twilight until midnight. Initially, observations were also made at dawn (5:00 a.m. until full light; five mornings or 20 hours), but this was discontinued since

no beavers were ever seen at that time of day.

The number of beavers consistently observed at a site was considered to be the population size. After population size was determined, it was monitored by the amount of fresh cutting. Any change in the amount of fresh cuttings was assumed to represent a potential change in the beaver population size, later verified by direct observation.

RESULTS

Habitat Analysis - In the swamp site (Table 2), the most important (based on Relative Importance Value--RIV) tree species (in order, greatest to least) were green ash, red maple, and sweet gum (Liquidambar styraciflua). The most important shrubs and saplings in the swamp were alder, spicebush, green ash, viburnum, red maple, and ironwood.

The swamp is bordered by a mixed hardwood forest. The most important trees were hickory (Carya tomentosa), white oak (Quercus alba), beech, red oak (Quercus coccinea, Q. falcata, Q. rubra), and tulip poplar. The most important shrubs and saplings were mountain laurel, ironwood, holly (Ilex opaca), highbush blueberry (Vaccinium corymbosum), and white oak.

At the pond site (Table 3), the most important trees were

Table 2. Relative importance values (RIV) for species of trees, saplings, and shrubs found in the swamp study site. The letters (A-D) refer to: A) trees, and B) saplings and shrubs in the swamp, C) trees, and D) saplings and shrubs on the hillsides bordering the swamp.

Species	A RIV	B RIV	C RIV	D RIV
Fraxinus pennsylvanica	47.5	15.3	---	1.1
Acer rubrum	28.5	12.5	---	1.1
Liquidambar styraciflua	12.4	---	6.6	---
Ulmus americana	7.0	---	---	---
Carpinus caroliniana	3.0	12.5	2.6	17.3
Alnus serrulata	---	21.4	---	---
Lindera benzoin	---	20.4	---	---
Viburnum nudum	---	13.3	---	---
Viburnum rafidulum	---	4.6	---	---
Carya tomentosa	---	---	23.6	2.5
Quercus alba	---	---	16.1	9.3
Fagus grandifolia	---	---	15.4	---
Quercus rubra, *Q. falcata*, *Q. coccinea*	---	---	13.2	2.5
Liriodendron tulipifera	---	---	11.0	---
Ilex opaca	---	---	7.8	17.0
Pinus virginiana, *P. taeda*	---	---	1.6	---
Cornus florida	---	---	0.7	1.1
Kalmia latifolia	---	---	---	27.8
Vaccinium corymbosum	---	---	---	10.2

Table 3. Relative importance values (RIV) for species of trees, saplings, and shrubs found in the pond study site. The letters (A-B) refer to: A) trees, and B) saplings and shrubs.

Species	A RIV	B RIV
Quercus alba	24.2	2.5
Fagus grandifolia	22.3	10.8
Pinus virginiana, *P. taeda*	13.8	4.3
Quercus rubra, *Q. falcata*, *Q. coccinea*	12.2	3.2
Carya tomentosa	10.5	3.2
Liriodendron tulipifera	6.5	4.4
Acer rubrum	5.9	12.8
Fraxinus pennsylvanica	1.4	<1.0
Ilex opaca	0.9	9.1
Platanus occidentalis	0.6	<1.0
Salix nigra	0.6	---
Kalmia latifolia	---	26.2
Myrica cerifera	---	4.5
Cornus florida	---	4.0
Sassafras albidum	---	3.6
Nyssa sylvatica	---	3.2
Liquidambar styraciflua	---	1.4
Castanea pumila	---	1.0
Cercis canadensis	---	<1.0
Oxydendron arboreum	---	<1.0
Asimina triloba	---	<1.0
Diospyros virginiana	---	<1.0
Prunus serotina	---	<1.0
Juniperus virginiana	---	<1.0
Aralia spinosa	---	<1.0
Carpinus caroliniana	---	<1.0

white oak, beech, pine, red oak, and hickory. The most important saplings and shrubs were mountain laurel, red maple, and beech.

The vegetation at the lake site (Table 4) was divided into five different areas, which were then compared using Jaccard's Index of similarity (Mueller-Dumbois and Ellenberg, 1974). The results, presented in Table 5, indicate that Area One was distinct from all other areas, being 15 percent similar or less. Areas Three, Four, and Five were 75 percent similar in tree species and could be grouped as having a common overstory makeup. Area Two was only 55 percent similar in tree species to Areas Three, Four, and Five. Area Two had the same dominant tree species as Areas Three, Four, and Five but had more species present, causing the lower similarity value. Area Two probably could be grouped with Areas Three, Four, and Five in overstory makeup. Areas Two, Three, Four, and Five supported somewhat different shrub and sapling communities with similarity values of 50 to 62 percent.

Area One covered the small swamps along feeder creeks and consisted of sapling and shrub growth only. The most important saplings and shrubs were willow, tulip poplar, and alder. A common overstory for Areas Two, Three, Four, and Five would include white oak, beech, pine, hickory, red maple, and red oak. A common sapling and shrub understory would include mountain laurel, red maple, holly, hickory, white oak, and beech.

In calculating the number of stems per hectare from the lake site, an average density was calculated for species in Areas Two through Five. This average density was used to determine stems per hectare. Densities of species in Area One were used to calculate

Table 4. Relative importance values (RIV) for species of trees, saplings and shrubs found at the lake study site. The letters (A-I) refer to: A) saplings and shrubs in area 1, B) trees, and C) saplings and shrubs in area 2, D) trees, and E) saplings and shrubs in area 3, F) trees, and G) saplings and shrubs in area 4, H) trees, and I) saplings and shrubs in area 5.

Species	A RIV	B RIV	C RIV	D RIV	E RIV	F RIV	G RIV	H RIV	I RIV
Salix nigra	38.2	---	7.5	---	---	---	---	---	---
Liriodendron tulipifera	21.0	4.6	---	---	---	---	6.5	---	---
Alnus serrulata	16.6	---	---	---	---	---	---	---	---
Myrica cerifera	6.0	---	---	---	---	---	---	---	1.9
Rhus copallina	5.9	---	---	---	---	---	2.3	---	---
Lindera benzoin	4.5	---	---	---	---	---	2.3	---	---
Carpinus caroliniana	3.4	1.0	5.1	---	---	---	3.2	---	---
Viburnum rafidulum	2.0	---	---	---	---	---	---	---	---
Fraxinus pennsylvanica	2.0	---	---	---	---	---	---	---	---
Quercus alba	---	33.4	15.7	14.8	---	40.3	---	31.0	---
Carya tomentosa	---	20.3	8.0	13.2	7.3	14.3	8.0	5.1	3.9
Pinus virginiana, *P. taeda*	---	11.7	5.4	4.4	6.8	11.9	4.6	21.5	1.9
Acer rubrum	---	9.7	15.2	14.5	9.6	3.2	23.5	10.2	16.3
Quercus rubra, *Q. falcata*, *Q. coccinea*	---	9.2	5.6	13.0	2.3	---	2.3	12.2	---
Fagus grandifolia	---	3.7	4.5	35.4	1.9	23.5	9.8	12.4	6.4
Nyssa sylvatica	---	3.5	1.6	---	---	---	5.5	---	1.9
Ilex opaca	---	1.9	11.6	---	7.8	3.1	8.5	3.1	7.9
Liquidambar styraciflua	---	---	7.6	3.8	1.9	3.1	---	2.2	---
Cornus florida	---	---	4.9	---	3.8	---	5.5	---	---
Sassafras albidum	---	---	3.1	---	2.3	---	4.6	---	2.4
Kalmia latifolia	---	---	---	---	49.8	---	6.5	---	52.9
Cercis canadensis	---	---	---	---	5.9	---	5.5	---	1.9
Juniperus virginiana	---	---	---	---	---	---	---	1.5	1.9

Table 5. Per cent similarity (From Jaccard's Index of Similarity) of vegetation areas at the lake study site.

Per cent Similarity (Tree species)

AREA NUMBER	1	2	3	4	5
1	--	--	--	--	--
2		--	54	54	58
3			--	75	77
4				--	77
5					--

Per cent Similarity (Sapling and shrub species)

AREA NUMBER	1	2	3	4	5
1	--	15	0	14	5
2		--	56	61	38
3			--	62	57
4				--	50
5					--

stems per hectare for those species.

Stream Flow and Water Depth - Stream flow and water depth measurements were taken in April, 1980 (Table 6). Stream flow into the swamp study site was 0.369 m^3/sec, and no dramatic changes in stream flow were observed during the study. Water depth in the swamp varied from 0.5 m to 1.5 m over the study area, with extensive areas of deep water (1 m or more) close to the dam and lodge. Water depth fluctuated from 2 to 10 cm (+ or -) when the area was occupied by beavers, but when the beavers left the area, water depth dropped by 70 cm, suggesting that continued maintenance of the dam is required.

Stream flow into the pond study site was 0.013 m^3/sec, and no major changes in stream flow were observed during the study. Water depth in the pond was 0.5 m to 1 m close to shore, and 2 to 4 m in the center. Water depth varied from 2 to 6 cm (+ or -) when the area was occupied by beavers, but when beavers left the area, water depth dropped by 70 cm.

By definition, the lake study site had no stream flow. Streams feeding into the lake were comparable in flow to those at the pond. Water depth at the lake varied from 0.5 m to 1 m near shore, to 15 m in the center. Also, a small beaver dam was built on one stream feeding the lake. The water depth behind the dam was 0.5 m to 1.5 m. The stream flow into the dammed area was comparable to stream flow at the pond.

Composition of Colonies - The swamp was inhabited by beavers for at least one year prior to the study, based on the presence of an old food cache (Slough, 1978). One beaver inhabited the area from the

Table 6. Stream flow and water depth at swamp, pond, and lake study sites.

Study site	Stream flow (m^3/sec)	Water depth (m)
Swamp	0.369	0.5 to 1.5
Pond	0.013	0.5 to 4.0
Lake	Not measured	0.5 to 15.0
Lake (small dam)	≅0.013	0.5 to 1.5

start of the study until April, 1980. The area was unoccupied over the summer and early fall, 1980. A single beaver moved into the area in October, 1980 and remained until the end of the study (March, 1981).

The pond was occupied by beavers for at least one year prior to the study based on the presence of old food caches (Slough, 1978). The area had been inhabited by a mated pair. However, the female was removed by fur trappers at the start of the study. The male remained until May, 1980, when he left, leaving the area unoccupied over the summer and early fall. The area was briefly occupied by a single beaver in November and December, 1980, but afterwards, it was unoccupied until the end of the study.

The lake was occupied by beavers for at least two years prior to the study, based on the presence of old food caches (Slough, 1978). Three adult beavers were taken by trappers in the summer of 1979. In this study, three adult beavers were observed initially (March, 1980). After November 1980, only two adults were observed. A single young beaver was observed once, in September, 1980.

Woody Foods - In the swamp, a total of 2219 woody plants was cut by beavers for food. Of the total, 98.9 percent were saplings and shrubs; the remaining 1.1 percent were trees. Eight different species were cut by beavers. Of these, three species, viburnum, alder, and spicebush, made up the bulk of the beavers' diet. All sapling and shrub species cut were given a utilization rank based on the number cut per hectare divided by the number available per hectare. Utilization percentages are given in Table 7. Based on Chi-square analysis (Table 8), viburnum and alder were preferred foods in the swamp.

At the pond, a total of 1536 woody plants was cut by beavers for

Table 7. Utilization of sapling and shrub species at the swamp, pond, and lake study sites.

C = No. of stems cut/ha, A = No. of stems available/ha, U = Utilization percent

	Swamp			Pond			Lake		
Species	C	A	U	C	A	U	C	A	U
Viburnum nudum	674	1079	62	---	---	---	---	---	---
Alnus serrulata	614	1338	45	---	---	---	249	379	65
Acer rubrum	118	376	31	174	814	7	233	333	69
Carpinus caroliniana	134	452	29	10	13	76	192	224	85
Lindera benzoin	220	828	26	---	---	---	15	34	44
Quercus falcata, Q. coccinea, Q. rubra	19	85	22	40	128	31	118	137	86
Fraxinus pennsylvanica	97	502	19	25	40	62	4	12	33
Quercus alba	18	299	6	26	91	28	289	410	70
Cercis canadensis	---	---	---	11	18	61	---	---	---
Liquidambar styraciflua	---	---	---	44	74	59	80	125	64
Myrica cerifera	---	---	---	103	233	44	11	36	30
Liriodendron tulipifera	---	---	---	102	252	40	281	383	73
Cornus florida	---	---	---	74	194	38	134	157	85
Oxydendron arboreum	---	---	---	6	21	28	---	---	---
Pinus virginiana, P. taeda	---	---	---	99	349	28	90	118	76
Fagus grandifolia	---	---	---	146	626	23	117	143	81
Castanea pumila	---	---	---	---	---	---	33	44	75
Salix nigra	---	---	---	---	---	---	575	850	67
Carya tomentosa	---	---	---	---	---	---	81	122	66
Nyssa sylvatica	---	---	---	---	---	---	20	34	58
Sassafras albidum	---	---	---	---	---	---	16	31	51
Rhus copalina	---	---	---	---	---	---	41	114	35
Juniperus virginiana	---	---	---	---	---	---	1	9	11

Table 8. Chi-square analysis of sapling and shrub species cut at the swamp, pond, and lake study sites. O = Observed number of stems cut/HA, E = Expected number of stems cut/HA, P = Probability value, * = species which were preferred, i.e., the observed value was significantly greater than the expected value, NS = not significant.

Species	Swamp			Pond			Lake		
	O	E	P	O	E	P	O	E	P
Viburnum nudum	*674	410	<.005	---	---	---	---	---	---
Alnus serrulata	*614	508	<.005	---	---	---	249	261	NS
Acer rubrum	118	143	<.05	174	244	.005	233	229	NS
Carpinus caroliniana	134	171	<.005	* 10	4	<.005	*192	154	<.005
Lindera benzoin	220	314	<.005	---	---	---	15	23	NS
Quercus falcata, Q. coccinea, Q. rubra	19	32	<.01	40	38	NS	*118	94	<.01
Fraxinus pennsylvanica	97	190	<.005	* 25	12	<.005	4	8	NS
Quercus alba	18	113	<.005	26	27	NS	289	282	NS
Cercis canadensis	---	---	---	* 11	5	.01	---	---	---
Liquidambar styraciflua	---	---	---	* 44	22	<.005	80	86	NS
Myrica cerifera	---	---	---	*103	70	<.005	11	24	.01
Liriodendron tulipifera	---	---	---	*102	75	<.005	281	264	NS
Cornus florida	---	---	---	* 74	58	<.05	*134	108	.025
Oxydendron arboreum	---	---	---	6	6	NS	---	---	---
Pinus virginiana, P. taeda	---	---	---	99	104	NS	90	81	NS
Fagus grandifolia	---	---	---	146	188	.005	117	99	NS
Castanea pumila	---	---	---	---	---	---	33	30	NS
Salix nigra	---	---	---	---	---	---	575	586	NS
Carya tomentosa	---	---	---	---	---	---	81	84	NS
Nyssa sylvatica	---	---	---	---	---	---	20	23	NS
Sassafras albidum	---	---	---	---	---	---	16	21	NS
Rhus copallina	---	---	---	---	---	---	41	78	<.005
Juniperus virginiana	---	---	---	---	---	---	1	6	.05

food. Of the total, 97.6 percent were saplings and shrubs and only 2.3 percent were trees. Fifteen species were cut, seven of which made up the bulk of the beavers' diets. These were red maple, beech, bayberry, pine, tulip poplar, and dogwood (Table 7). Based on Chi-square analysis (Table 8), ironwood, redbud (Cercis canadensis), green ash, sweet gum, bayberry, tulip poplar, and dogwood were preferred foods at the pond.

At the lake, 7087 woody plants were cut by beavers for food. Of this total, 99.0 percent were saplings and shrubs and one percent were trees. A total of 20 species were cut. Of these, five species, willow, white oak, tulip poplar, alder, and red maple, made up the bulk of the beavers' diet. Ironwood and dogwood were preferred foods at the lake site, based on Chi-square analysis (Table 8).

Food Cache Analysis - Three food caches were taken apart in the spring and their contents were analyzed. Two food caches were from the lake site and one was from the swamp site (Table 9). In the swamp cache, the main component was red maple (60%) with smaller amounts of white oak (13%), alder (9%), and green ash (8%). At the lake, the first food cache was primarily willow (56%) with smaller amounts of tulip poplar (28%), and red maple (7%). The other food cache from the lake was primarily alder (56%) with smaller amounts of tulip poplar (9%), red maple (5%), sweet gum (4%), red oak (5%), and hickory (5%).

Herbaceous and Other Foods - During the summer, some use of herbaceous foods was observed. Several clumps of cinnamon fern (Osmunda cinnamomea) were cut, foliage stripped off and eaten, leaving only the central stalk (rachis). On several occasions, the growing tips or buds of willow were observed to have been nipped off and

Table 9. Food cache contents from swamp site and lake site (Nos. 1 and 2).

A = Number of stems in cache B = Percent of total stems in cache

	Swamp		Lake (No. 1)		Lake (No. 2)	
Species	A	B	A	B	A	B
Acer rubrum	70	60	15	7	8	5
Quercus alba	16	13	---	---	4	3
Alnus serrulata	11	9	5	2	72	53
Fraxinus pennsylvanica	10	8	---	---	2	1
Viburnum nudum	4	3	---	---	---	---
Quercus coccinea, *Q. falcata*, *Q. rubra*	2	1	---	---	7	5
Fagus grandifolia	1	0.8	1	0.5	3	2
Carpinus caroliniana	1	0.8	---	---	7	5
Salix nigra	---	---	111	56	---	---
Liriodendron tulipifera	---	---	55	28	13	9
Carya tomentosa	---	---	4	2	8	4
Cornus florida	---	---	2	1	---	---
Liquidambar styraciflua	---	---	1	0.5	---	---
Prunus serotina	---	---	1	0.5	---	---
Myrica cerifera	---	---	1	0.5	4	3
Pinus virginiana, *P. taeda*	---	---	---	---	2	1
TOTAL	115		196		135	

eaten. Lizard's tail (Saururus cernuus) was also utilized on occasion. Beavers were also observed to consume various grasses at the water's edge. On one occasion, beavers ate the leaves of a devil's walking stick (Aralia spinosa) which had been blown down by the wind. Soft stem rush (Juncus effusus) and spike grass (Juncus roemarianus) were occasionally eaten. Cattail roots were observed to be dug up and partly eaten on several occasions at the lake site. This could be attributed to beavers as muskrats were not known to inhabit the area.

Seasonal Food Preferences - In the swamp study site, there was a definite preference shown by beavers for green ash in the spring (March through May) (Table 10). The 31 de-barked and two felled green ash trees accounted for most of the cutting in this season ($P = .005$). In winter (December through February), there was an increase in the number cut of all species, primarily due to the construction of food caches. Red maple make up a large part (50%, $P < .005$) of the cutting in this season. Red maple also made up a large part of the same food cache. Viburnum was also important (2%, $P < .005$) in the winter cutting, but was a minor part of the cache.

At the lake, beech and alder made up a large part (21% and 19%, respectively, $P < .005$) of the cutting in spring. In fall (September through November), the amount of cutting of all species was higher due to construction of the food cache. Alder accounted for a large part (16%, $P = .005$) of the cutting in this season and made up a large part of the lake food cache. Willow also made up a large part (21%, $P < .005$) of the fall cutting but did not appear in the food

Table 10. Seasonal use of woody species at the swamp and lake sites. Values are the number of stems cut in that season. Values in parentheses are p values from chi-square analysis. Seasons are defined as follows: Spring = March through May, Summer = June through August, Fall = September through November, Winter = December through February.

	Swamp				Lake			
Species	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Fraxinus pennsylvanica	33(<.005)	--	7	47	--	--	--	--
Viburnum nudum	11	--	1	81(<.005)	--	--	--	--
Acer rubrum	4	--	8	97(<.005)	--	6	21	23
Alnus serrulata	2	--	1	41	32(<.005)	3	192(<.005)	210(<.005)
Carpinus caroliniana	2	--	1	24	13	20	74	28
Quercus rubra, *Q. falcata*, *Q. coccinea*	--	--	--	13	14	1	129	102
Quercus alba	--	--	--	15	4	3	190(<.005)	168(<.005)
Fagus grandifolia	--	--	--	3	36(<.005)	1	11	123(<.005)
Pinus virginiana, *P. taeda*	--	--	--	--	13	3	21	74
Liriodendron tulipifera	--	--	--	--	25	17	145	77
Carya tomentosa	--	--	--	--	13	6	39	88
Rhus copallina	--	--	--	--	13	2	52	39
Liquidambar styraciflua	--	--	--	--	4	--	--	--
Salix nigra	--	--	--	--	--	9	253(<.005)	--
Cornus florida	--	--	--	--	--	7	62	12

cache. There was a definite preference shown for sumac in the fall. Half of all the sumac cut at the lake was cut in the fall. In winter, white oak, beech, and alder made up a large part (16%, 16%, and 17%, respectively, $P < .005$) of the cutting in this season. There was again a definite preference shown for sumac with 37 percent of all sumac cut at the lake cut in this season.

Data were not available from the swamp site for the summer season as it was unoccupied by beavers. Chi-square analysis was not done on the summer season from the lake site as it represented only the later part of the summer (circumstances preventing data collection during early summer). Data from the pond site were not presented because the beavers intermittently occupied the site and were never present through an entire season of data collection.

Activity Patterns - Beavers were observed to be active throughout the year in this study. Moderate amounts of cutting were noted in the spring and summer when beavers were observed to eat herbaceous and woody foods. The amount of cutting increased in fall as the availability of herbaceous foods decreased. At the lake site, construction of a food cache was begun November 15 and continued until December 6, 1980. In the swamp, a food cache was constructed during the first two weeks of December. Food cache construction was followed by a cold snap of approximately four weeks, ending in mid-January. During this period, the lake and swamp were covered with ice (two to ten cm thick) more or less continually. Cutting dropped to a very low level during this period, with the beavers using the food cache heavily. Whenever possible, beavers used openings in the ice to come out and feed on land. As soon as the areas were ice-free, the amount of cutting

increased to a moderate level and remained so until spring.

The beavers were observed to be active only at night. In spring, summer, and early fall, they became active at twilight and were observed feeding until midnight. In late fall and winter, they were rarely observed before 8:30 or 9:00 p.m. Beavers were active nearly every night of observation in spring, summer, and early fall. In late fall and winter, this was not the case: no activity was noted for two or three consecutive nights on some occasions.

Caloric Content of Woody Foods - Caloric content of woody foods was found to vary with the seasons (Table 11). Generally, caloric content was lowest in summer for the species tested. This corresponded to the time of greatest utilization of herbaceous foods. No relationship was found between the species highest in caloric value for a given season and seasonal food preferences. Green ash was second highest in caloric value in spring and was heavily used in the swamp site in that season. Viburnum, which ranked sixth in caloric value during the winter, was heavily used in the swamp during that season. At the lake site, alder and poplar were heavily used in the spring; they ranked first and sixth, respectively, in caloric value for that season. Also, alder was heavily used at the lake site in fall, and was ranked third in caloric value for that season. By taking an average caloric value for each species (sum of all four seasons caloric values divided by four), the top five species in caloric value were alder, pine, spicebush, viburnum, and green ash.

Table 11. Caloric values of woody species used by beaver (All values in cal/g).

Species	$\bar{X}$ caloric value	$S_{\bar{x}}$	Spring	Summer	Fall	Winter
Alnus serrulata	5424	2.645	6204	4991	5253	5251
Pinus virginiana, P. taeda	5043	3.58	4841	4639	5353	5339
Lindera benzoin	4957	99.5	5110	4727	4822	5171
Viburnum nudum	4880	175.0	4511	4742	5365	4903
Fraxinus pennsylvanica	4800	269.6	5366	4057	4967	4812
Quercus alba	4786	354.1	---	4086	5134	5146
Myrica cerifera	4742	211.1	5137	4169	5003	4660
Salix nigra	4625	165.8	4648	4139	4796	4918
Carpinus caroliniana	4599	117.1	4949	4451	4470	4527
Fagus grandifolia	4571	112.2	4673	4414	4640	4559
Liriodendron tulipifera	4550	187.5	4872	3998	4734	4598
Acer rubrum	4230	202.0	4175	3667	4522	4558
Cornus florida	4152	284.0	4555	4202	3305	4489

DISCUSSION

The beaver is a valuable fur-bearer and its food habits and ecology have been the subject of a number of investigations in the northeastern and western United States (Table 1). However, relatively few studies on beaver ecology have been done in the southern United States. The two that have been done (Chabreck, 1958; Plocher, 1979) revealed the use of woody species not reported from other regions. The purpose of this study was to contribute to the body of knowledge on beaver ecology in the southeastern United States, with the hope that such information will prove useful in management.

The primary focus of the study was on the food habits of beavers, including food preferences and food cache analysis. Other ecological factors investigated include habitat characteristics (vegetation and stream flow), colony composition, and activity patterns. The results obtained in this study are compared to reports in the literature.

Woody Foods - The selection of small diameter woody foods was evident in this study. At the swamp site, 98 per cent of the cutting was of stems less than 10 cm in diameter. At the pond site, this figure was 97 per cent, and at the lake site, 99 per cent. Chabreck (1958), Shandle *et al.* (1943), and Jenkins (1979), have also reported the use of small diameter trees and shrubs. The small diameter woody plants are easy to cut and transport back to water. Also, as trees

increase in diameter, the bark of the lower trunk becomes thicker and less palatable to beavers, and is harder to transport back to water, so only the upper branches are easily transportable, palatable food. Thus, cutting a tree greater than ten cm in diameter involves considerable time and effort for only a moderate amount of food (Stegman, 1954). Aldous (1938) and Stegman (1954) also found much lower utilization of trees over ten cm in diameter.

At this point, several terms must be defined. 'Preference' or 'selection' for a species will refer to Chi-square analysis. Thus, a preferred or selected species is one in which the number of stems cut per hectare was significantly greater than expected. In describing a species or group of species as 'heavily used', it is meant that they made up a large part (over 60 per cent) of the number of stems cut in an area. Thus, some species may be preferred but may be cut in such small numbers that they are unimportant foods in the beavers' diets. Also, some species may be classified as heavily used but not be preferred.

Tables 7 and 8 reveal a group of 13 species which were heavily used by beavers in this area. This group includes alder (lake and swamp sites), tulip poplar (lake and pond sites), red maple (lake and pond sites), willow (lake site), white oak (lake site), viburnum (swamp site), spicebush (swamp site), bayberry (pond site), dogwood (pond site), pine (pond site), beech (pond site), and ironwood (lake and swamp sites).

Most of these species have been noted as beaver foods in previous studies (Table 1). However, no references were found describing spicebush, viburnum, or beech as beaver foods, although all three were

important to beavers in this study.

Of the 13 species, several were designated as preferred foods based on Chi-square analysis. These were viburnum, alder, ironwood, tulip poplar, and dogwood. In addition, willow and pine were felt to be preferred species based on field observations. All the preferred species were usually the first to receive heavy use in an area. As these species were depleted, the beavers would shift to other species. Most species resprout after being cut by beavers, but willow appeared to be most important in this respect. Willow stumps sprout vigorously for two to three years and provide food in the form of coppice vegetation.

The remaining five species, red maple, white oak, beech, spicebush, and bayberry, were considered low preference foods based on field observations. Use of these species increased as beavers depleted the numbers of high preference foods. Shandle and Austin (1939) found that in the presence of more highly preferred foods, red maple is not used heavily. After the preferred foods were depleted, the beavers shifted to red maple. This shift is sometimes dramatic, as was seen in the case of bayberry in this study. As other foods were depleted at the pond, the beavers shifted to bayberry, previously untouched. Within a short period, much of the available bayberry was cut.

Heavy use of spicebush was recorded in the initial tally. However, most of the spicebush in the swamp was killed by the standing water impounded behind the beaver dam. Consequently, very little fresh cutting of spicebush was noted.

Several woody plant species were avoided by beavers. One such

species was mountain laurel. This species was never observed to be cut by beavers. Muenscher (1970) stated that mountain laurel is poisonous and is avoided by herbivores. Sycamore and persimmon were also avoided by beavers. At the study sites and other colonies observed on Yarmouth Creek and at York River State Park, these three species were conspicuous in that they alone remained among the newly cut stumps of the other species of trees and shrubs.

Finally, beavers were observed to de-bark standing trees of 30 cm or greater diameter in some areas. De-barking consisted of gnawing off the bark and cambium for as high as the beaver could reach. De-barking was most extensive in the swamp where 62 trees were partially or completely de-barked. Eighteen trees were de-barked at the lake and 11 trees were de-barked at the pond. No particular species was singled out for this treatment. Trees that were completely girdled were dead by the next growing season. Partial girdling by de-barking did not visibly affect the trees' vitality. Chabreck (1958) observed that trees completely girdled by de-barking did not die. Possibly he did not follow the study long enough, for forestry studies indicate that trees are invariably killed by complete girdling. It is not known if the trees were de-barked for food in Chabreck's study. Other possibilities include killing of less desirable species (not likely) and killing overstory species to promote understory growth for use as food (a good possibility in the swamp).

Food Cache Analysis - Of particular interest in food cache analysis is a study by Slough (1978), who suggested that low preference foods were used to construct a cap on the food cache, thereby submerging the more highly preferred foods below it.

In the swamp, red maple made up the cap of the food cache. This could indicate that maple is a low preference food, but it also reflects the abundance of red maple in the immediate area of the cache.

At the lake, the cap of one cache was willow while the cap of the other was alder. The use of these two species is primarily a reflection of their abundance in the immediate area of the respective caches. Overall, it was observed in this study that the beavers concentrated their cutting for the food cache in a very small area close to where the cache was constructed. So the position of different species in the cache can reveal their preference level, but the abundance of species in the immediate area must also be considered.

The most remarkable thing about the food caches in this study was their size relative to the amount of use they received. Caches were extensive, being built in two or three weeks of heavy cutting by the beavers. The caches were used intermittently during winter (four weeks in January and February), whenever ice conditions prevented feeding on land. When caches were analyzed in the spring, the bulk of them remained unused. No subsequent use of the caches was observed.

Herbaceous Foods - Svendsen (1980) reported that beavers made a major shift to herbaceous and aquatic vegetation in spring and summer. Bradt (1938) and Townsend (1953) also noted a similar shift. In this study, beavers also were observed to use herbaceous foods during spring and summer. Light use of cattail roots was noted year round. It was difficult to measure the amount of herbaceous food used, but it is felt that woody foods made up the bulk of the

diet year round.

Seasonal Preferences - Significant seasonal preferences were observed for several species. Most fall and winter preferences were associated with food cache construction and included alder, tulip poplar, and red maple. Significant preferences in fall and winter were noted for willow, white oak, viburnum, and sumac, which were all used for food. Svendsen (1980) also observed a preference for sumac in the fall. He theorized that the red leaves served to attract beavers. Significant preferences in spring were observed for alder, tulip poplar, beech, and green ash.

Overall, the preference for species used in the food cache is mostly a reflection of their abundance in the immediate vicinity of the cache. The preference for species as food is probably a combination of availability, caloric and nutrient content, and distance from water.

Caloric Content of Woody Foods - Some relationship was found between seasonal preferences and high caloric value for a species in that season (Table 11). However, beavers did not consistently prefer those species highest in caloric value for a given season. Therefore, the question of food selection cannot be answered by caloric value alone, but probably depends upon a combination of factors, including protein content of the food, density or availability (number of stems/unit area), and the distance of the food from water.

The low caloric values found in summer are probably due to the movement of stored food from the stems to areas of growth at the branch tips (Koslowski and Keller, 1966).

Activity Patterns - Beavers were found to be active year round in this study. Beaver activity was restricted primarily by ice conditions which prevented them from feeding on land. Severe ice conditions were only observed for a four week period in mid-January and February, 1981. During this period the food cache was used. Much of the food cache, however, remained unused at the end of the winter. In Ohio, Svendsen (1980) also found that beavers were restricted by periods of ice in January and February. They fed from the food cache during these periods but much of the cache remained unused after the winter. Chabreck (1958) observed that beavers in Louisiana were active year round due to the mild weather and did not build a food cache. By contrast, Aleksiuk (1970) found that beavers in British Columbia reduced both food intake and metabolism in winter. In addition, they sometimes depleted the food cache before the spring thaw. Ice conditions are the main restriction on beaver activity in Southeastern Virginia, and beavers here are probably on the threshold for requiring a food cache in order to get through the winter. A well-built food cache is constructed but the amount of use it receives varies with the severity of the winter.

Composition of Colonies - It was interesting to note that none of the three colonies studied were as large as a "typical" colony of six to ten beavers (Hammond, 1943). Of the other five colonies visited, only two were comparable to a "typical" colony. This suggests that single beaver and mated pair colonies may be more common than the larger colonies. However, the smaller colonies may be a result of trapping.

Also, during the course of this study two sites were unoccupied

by beavers for periods of at least three months. The reasons beavers leave an area are not known. The pond may have been deserted because of diminishing food supplies (small diameter saplings) but this was not the case in the swamp, where ample food was available. Also of interest was the beavers' tolerance for human activity. The large number of people (200 - 300) camping around the lake and using it for swimming, fishing, and boating (daytime only) did not appear to affect the beavers in any way.

Habitat Requirements - Some general habitat requirements for beavers can be noted. The most obvious is a source of water. Beavers will readily inhabit most artificial lakes. Otherwise, a stream or river is the usual water source. In this study, beavers were not found on streams of less than 0.36 m^3/ sec flow. (The pond is a special case, initially being created by man.) The area dammed up must be able to provide a water depth of at least 0.5 to 1.0 m. In the swamp, several channels dug by beavers were noted. These were in shallow areas of water and probably made these areas more accessable to feeding.

The vegetation in the study area can be divided into two types, a southern mixed hardwood forest as described by Ware (1970), and a lowland swamp forest of green ash, red maple, alder, viburnum, ironwood, and willow. The southern mixed hardwood forest surrounded the lake and pond sites, while the lowland swamp forest was found at the swamp site. In this study, beavers required an area of 1.2 to 2.6 hectares for feeding. The size of the area needed depended primarily on the available vegetation. A usable area of 1.0 to 1.5 hectares seems to be a minimum. Some factors that might make an area unusable

by beavers include extremely steep slopes (beavers avoided climbing slopes greater than 40° in this study) and heavy growth of non-food plants such as mountain laurel. Furthermore, some of the species used heavily by beavers should be present. An overall sapling and shrub density of 2000 to 3000 stems per hectare is probably a base-line requirement. If non-food species make up a significant part of the vegetation (25 to 30 per cent), this sapling and shrub baseline should probably be increased to 3000 to 4000 per hectare.

It is also interesting to note that the small bodies of water formed by beaver activity at the pond and swamp sites provided habitat for several species of wildlife. The most notable of these was the wood duck; groups of three to four birds were frequently observed in fall and winter. There was also a large amount of deer and raccoon signs at these sites. Mink sign was noted several times at another beaver colony on Yarmouth Creek.

Conclusions - Based on a study of three locations in Virginia's coastal plain, it would appear that beavers heavily use and show a preference for viburnum, alder, ironwood, bayberry, tulip poplar, and dogwood. In addition, red oaks, green ash, red bud, and sweet gum received light use by beavers. Also, beavers heavily used but showed no significant preference for pine, beech, red maple, spice-bush, and willow.

This study is the first report of the use of viburnum, beech, and spicebush as food for beavers. Also important is the apparent avoid-ance of mountain laurel, persimmon, and sycamore by beavers. Also of interest is the building of well-stocked food caches that are only lightly used in the winter season, which is only about one month long

in eastern Virginia.

Overall, Virginia beavers behave differently from beavers in other locations in at least two important ways. They use a different group of woody species for food, compared to beavers further north which use primarily aspen, and those further south which use a different group of species, primarily pine. Beavers in southeastern Virginia are on a threshold of winter conditions which make a well-constructed food cache necessary but which may mean that it is only partially used.

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