WOODY PLANT USE AND PREFERENCES BY THE AMERICAN BEAVER (*Castor canadensis*) IN CENTRAL TEXAS

THESIS

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INTRODUCTION

The American beaver (*Castor canadensis*) is the largest rodent in North America. Adults range in weight from 16 to 31.5 kg and reach a maximum length of 120 cm (Hill 1982). The species has semi-aquatic adaptations of fine dense underfur, valvular ears and nostrils, webbed hind feet, small eyes with nictitating membranes, and a dorsoventrally flattened tail used for propulsion and as a rudder. The beaver belongs to the suborder Sciuromorpha, which is characterized by an advanced zygo-masseteric muscle arrangement, where the infraorbital canal is very small and is not a conduit for any branches of the large masseter muscles (Hill 1982). The beaver skull is massive, an adaptation for withstanding extreme forces while gnawing on woody tissues. The incisors, which grow continuously, are sharpened by grinding the upper and lower teeth against one another, creating beveled edges (Vaughan 1986). Hypsodont cheek teeth with parallel sides and flattened grinding surfaces with numerous infoldings of enamel separated by dentine (Lawlor 1979) are characteristics of the species.

The American beaver has been described as a keystone species in aquatic and adjacent riparian ecosystems. Through dam building and feeding activities, beavers modify the hydrology, channel morphology, biogeochemical pathways, biotic composition and heterogeneity of stream and riparian ecosystems (Naiman *et al.* 1986, Duncan 1984). Because beaver activities affect many levels of ecological organization, a better understanding of how beavers function in environments will assist in the management of these ecosystems.

Beavers modify their habitat by constructing dams across low-volume streams and in marshes to impound water for food and protection. This has an immediate effect on the ecology of the stream and adjacent systems because runoff velocity decreases, nutrient-rich suspended sediments settle out and become trapped behind the dams, and the water table increases locally such that surrounding soils become flooded. These factors interact to further influence the functioning of the ecosystem by regulating nutrient cycles, primary production, biotic succession, hydrological characteristics, and sediment loading (Naiman *et al.* 1988).

Beavers inhabiting mountainous valleys and marshes where relief is relatively gentle often drastically alter the flood plain. This type of environment allows multiple colonies to form "beaver complexes" (Naiman *et al.* 1988). As beaver populations increase, colonizers often turn marginal habitat into suitable habitat by flooding additional tributaries and backwater areas surrounding streams (Hill 1982). Interconnecting canals to transport foods and building materials between the individual ponds may be built (Ives 1942). Naiman (1988) described this as a "beaver mosaic landscape." Dams often form a stair-stepping series of ponds on a stream which effectively dampens runoff flow rates. If dams are numerous and distributed evenly, much of the precipitation which falls or melts in the watershed above the mosaic will remain in the complex (Hill 1982). It was estimated that during droughts as much as 30% of the surface water in Oregon and 60% in Colorado is impounded in beaver ponds (Duncan 1984).

Naiman *et al.* (1986) suggested that North American streams and rivers have changed drastically with the decline of beaver populations over the last two centuries. The larger rivers had more extensive floodplains and better developed backwaters with numerous woody snags and low turbidity. The low order streams were well-terraced by beaver dams such that sequestering of nutrients occurred higher in the watershed. Extensive spatial and temporal beaver-induced landscape alterations have been described by previous investigators (Ives 1942, Naiman *et al.* 1988).

Beavers essentially have the same geographic distribution today as prior to the arrival of European immigrants. The species is characteristic of boreal and montane environments. However it exists in almost every conceivable aquatic habitat in North America except for southern Florida, areas in the southwest lacking sufficient overland water flow, and most regions above tree line (Naiman *et al.* 1988, Vaughan 1986). Permanent streams and lakes surrounded by growths of mixed deciduous trees and shrubs, or streams with pure stands of willow, aspen, or alder are preferred habitats (Jenkins 1981).

Prior to European settlement in North America, the estimated beaver population was 60 to 400 million (Seton 1929). By the 20th century, over-exploitation had placed the beaver on the brink of extinction across North America (Naiman *et al.* 1988). Today, beaver populations are increasing throughout most of the species' range. This increase is attributed to depressed fur prices, laws regulating their harvest, and a lack of natural predators (Novak 1987). The present beaver population in North America is small (between 6 and 12 million) relative to the historical population and will probably remain lower due to the loss of over 2.5×10^5 km^2 of wetland habitat during the last 150 years (Duncan 1984). However, unexploited beaver populations currently influence between 20 and 55% of the total length of second through fifth order streams in North America (Naiman and Melillo 1984).

Stream gradient is a major determinant in habitat selection by beavers (Slough and Sadlier 1977). Sixty-eight percent of all beaver colonies in Colorado were located on stretches with gradients of less than 6%, and no beaver colonies inhabited stretches with gradients over 15% (Retzer *et al.* 1956). Optimum densities occurred in areas with flat terrain and fertile valleys, where preferred woody species thrive (Hill 1982). Boyce (1981) suggested the density of colonies in an area is related to stream bifurcation, biomass of available winter foods and the degree of spatial heterogeneity of vegetation types.

The beaver lodge or burrow supplies the colony with escape, resting, thermal, and reproductive cover (Jenkins and Busher 1979). Lodges are constructed of debarked wood, herbaceous vegetation, mud, rock and sod. Both the central chamber of lodges and the main chamber of bank burrows are located above the water table and lined with dry grasses and other vegetation (Hill 1982). If channel substrates are unstable or not suitable for burrowing, beavers must find an appropriate site to build a lodge. If neither alternative is favorable, colonization of these areas may be inhibited (Henderson 1960).

Beavers in central Texas are often referred to as bank beavers by trappers and landowners because of their habit of burrowing into the bank and building a lodge (Ray Drumm 1990, pers. comm.). However, beavers may build dams and lodges in this area across first through third order streams, especially if water discharge is too low to provide the colony with food and protection, or if banks are not suitable for burrowing.

Beavers have been described as "choosy generalists" with respect to diet (Harper 1969). They utilize a wide variety of plant parts such as bark, shoots, foliage, nuts, and roots, but they exhibit distinct preferences for particular species, size classes, and nutritional quality within these categories (Jenkins 1981). Beavers rely heavily on herbaceous vegetation during the spring and summer (Jenkins 1979). In fact, beavers prefer herbaceous vegetation over woody plants during all seasons, when available (Jenkins 1981). However, an adequate supply of woody plants is the limiting dietary factor for the presence of beavers (Slough and Sattlier 1977).

Aquatic plants, such as duck potato (*Sagittaria* sp.), duckweed (*Lemna* spp.), pondweeds (*Potamogeton* spp.), water lilies (*Nymphaea* spp. and *Nuphar* spp.), and water weed (*Elodea* sp.), are preferred and utilized consistently through the spring, summer, and early fall. Beavers forage on a wide variety of terrestrial forbs and grasses throughout the year. Some of the more common species include smartweeds (*Polygonum* spp.), giant ragweeds (*Ambrosia* spp.), marshpurslanes (*Ludwigia* spp.), pigweed (*Amaranthus* sp.), sunflowers (*Helianthus* spp.), cat-tail (*Typha* sp.), panic grasses (*Panicum* spp.), giant reed (*Arundo donax*), bulrushes (*Scirpus* spp.), corn (*Zea* sp.), sorghum (*Sorghum* sp.), sedges (*Carex* spp.), and poison ivy (*Toxicodendron radicans*) (Henderson 1960, Svendsen 1980, Roberts and Arner 1984). Svendsen (1980) observed a beaver grazing on all species in its path, with no apparent selectivity, while feeding in dense grass and forb growth in southeastern Ohio.

Studies have addressed the physical and biological consequences of beaver impoundments (Naiman *et al.* 1986, Smith *et al.* 1989). However, there is a paucity of information on specific forage preferences and the effects of selective foraging on the structure and composition of aquatic and riparian vegetation. Also, relative food preferences are known for a few areas in northeastern and western North America, but dietary preferences of beaver in most regions remain unknown (Jenkins 1981).

Beavers select for forage resources at different levels of resolution, but little is known of the mechanisms involved at the various levels (Jenkins 1981). Initially, beavers select a suitable foraging site. Factors controlling forage site selection may be stream gradient, woody plant composition and species abundance, substrate quality and structure, and the amount of cover in the foraging area (Allen 1983). Next, the beavers select for particular life forms such as herb, shrub, or tree. The third level is selection for various species within these groups. Finally, there is intraspecific selection for specific size classes or nutritional states. Jenkins (1980) suggested preferences varied both spatially and temporally at each level, and future investigations of these topics should develop theoretical and applied perspectives of beaver selection patterns.

Beavers have a very high dependence on woody vegetation from October through April (Svendsen 1980, Hill 1982, Roberts and Arner 1984). This resource is extremely important during this period because the beaver's reproductive cycle begins when the availability of herbaceous foods is limited (Hill 1982).

The woody plant diet of beavers is well documented, but diet varies geographically with the availability of plant species. Svendsen (1980) reported the most frequently used woody species in southeastern Ohio were yellow poplar (*Liriodendron tulipifera*), American hornbeam (*Carpinus caroliniana*), red maple (*Acer rubrum*), and sugar maple (*A. saccharinum*). Aleksiuk (1970) suggested beavers in an arctic habitat in the Northwest Territories, Canada, relied on willow (*Salix* sp.), poplar (*Populus* *balsamifera*), and alder (*Alnus crispa*). A summary of woody plant preferences by beavers throughout North America was presented by Denney (1952). He reported beavers selected, in order of preference, aspen (*Populus* sp.), willow (*Salix* sp.), cottonwood (*Populus* sp.), and alder (*Alnus* sp.). However, Jenkins (1981) warned that numerous literature reports of extensive use of these species did not imply preference over other deciduous species. When a greater diversity of woody species is present, food selection patterns are often more complex. While the present information on woody plant use by beavers is important, it has limited application to beaver management in central Texas.

This study compared relative preferences for woody species and intraspecific selection for size classes of woody species after beaver colonies had selected forage sites. The specific objectives of this study were: (1) to identify and compare woody vegetation use by beaver populations on the San Marcos, Blanco, and San Gabriel Rivers in central Texas, (2) to determine relative preferences for species and size classes of woody vegetation, and (3) to investigate niche breadth with respect to the forage resource.

METHODS

Description of Study Sites—The study was conducted along 8 km stretches of the San Marcos, Blanco, and San Gabriel Rivers in central Texas. These rivers originate on the eastern perimeter of the Edward's Plateau (Fig. 1) and flow southeasterly through the Blackland Prairie (Gould 1960). The study sites along the San Marcos and Blanco Rivers are located in southern Hays County, and the San Gabriel site is situated in eastern Williamson County (Fig. 2). A list of the plants ecountered in the study area is presented in Appendix 1.

The San Marcos River is a spring-fed perennial river with a relatively constant flow and temperature. The study site extends from Spring Lake in San Marcos to the confluence with the Blanco River. This entire stretch of the river has moderate recreational use throughout the year, and portions within the San Marcos city limits are heavily used, especially in the spring and summer months. Outside the city, land adjacent to the river is used primarily for livestock grazing and mixed cultivation. The floodplain is slightly rolling; river banks are relatively steep.

Dominant woody species along the river included bald cypress (*Taxodium distichum*), black willow (*Salix nigra*), American and cedar elm (*Ulmus americana, U. crassifolia*), pecan (*Carya illinoensis*), chinaberry (*Melia azedarach*), hackberry (*Celtis* sp.), eastern cottonwood (*Populus deltoides*), boxelder (*Acer negundo*), and sycamore (*Platanus occidentalis*). The understory woody vegetation consists primarily of boxelder, privet (*Ligustrum* sp.), elderberry (*Sambucus canadensis*),

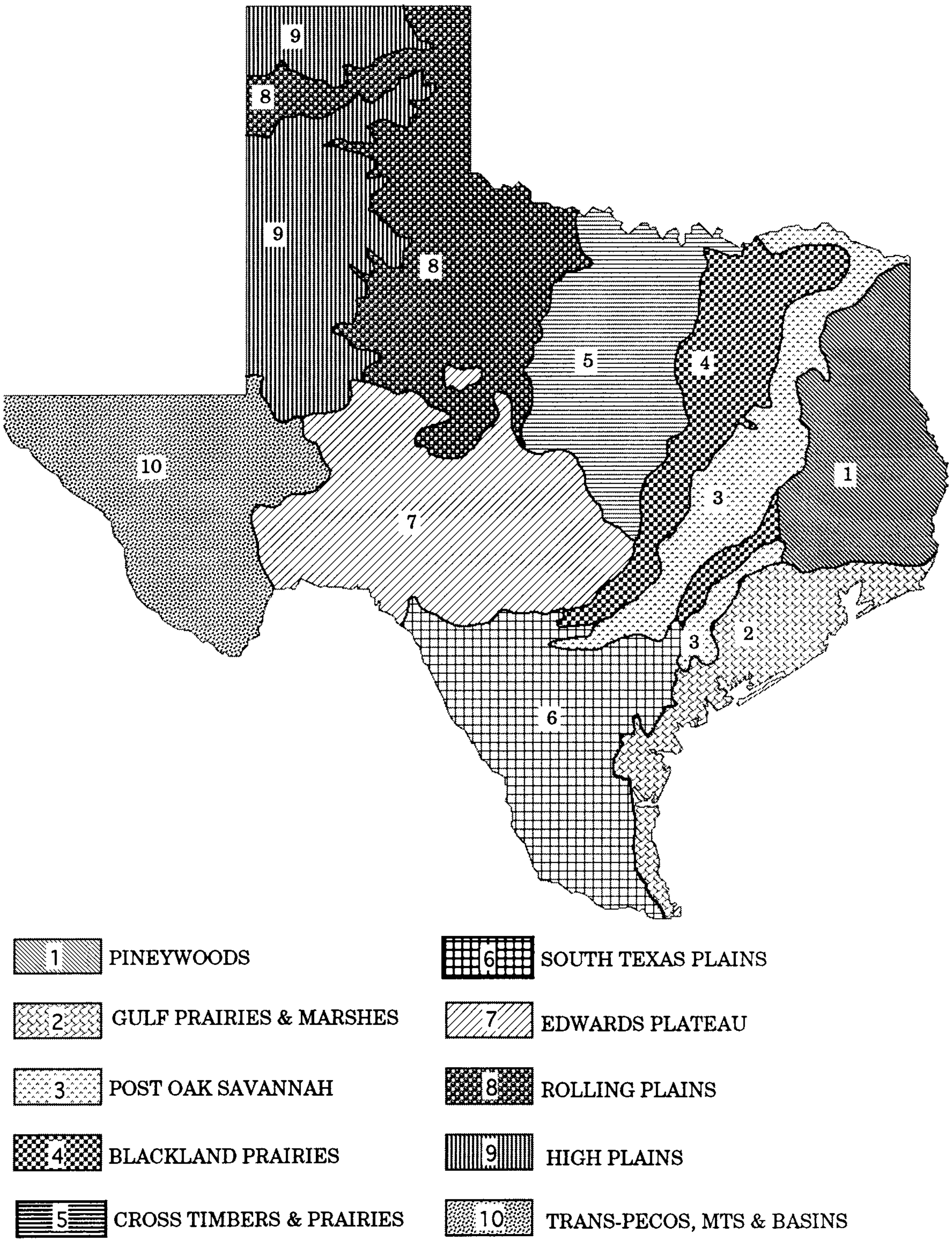

Figure 1. Ecological areas of Texas (after Gould *et al.* 1960).

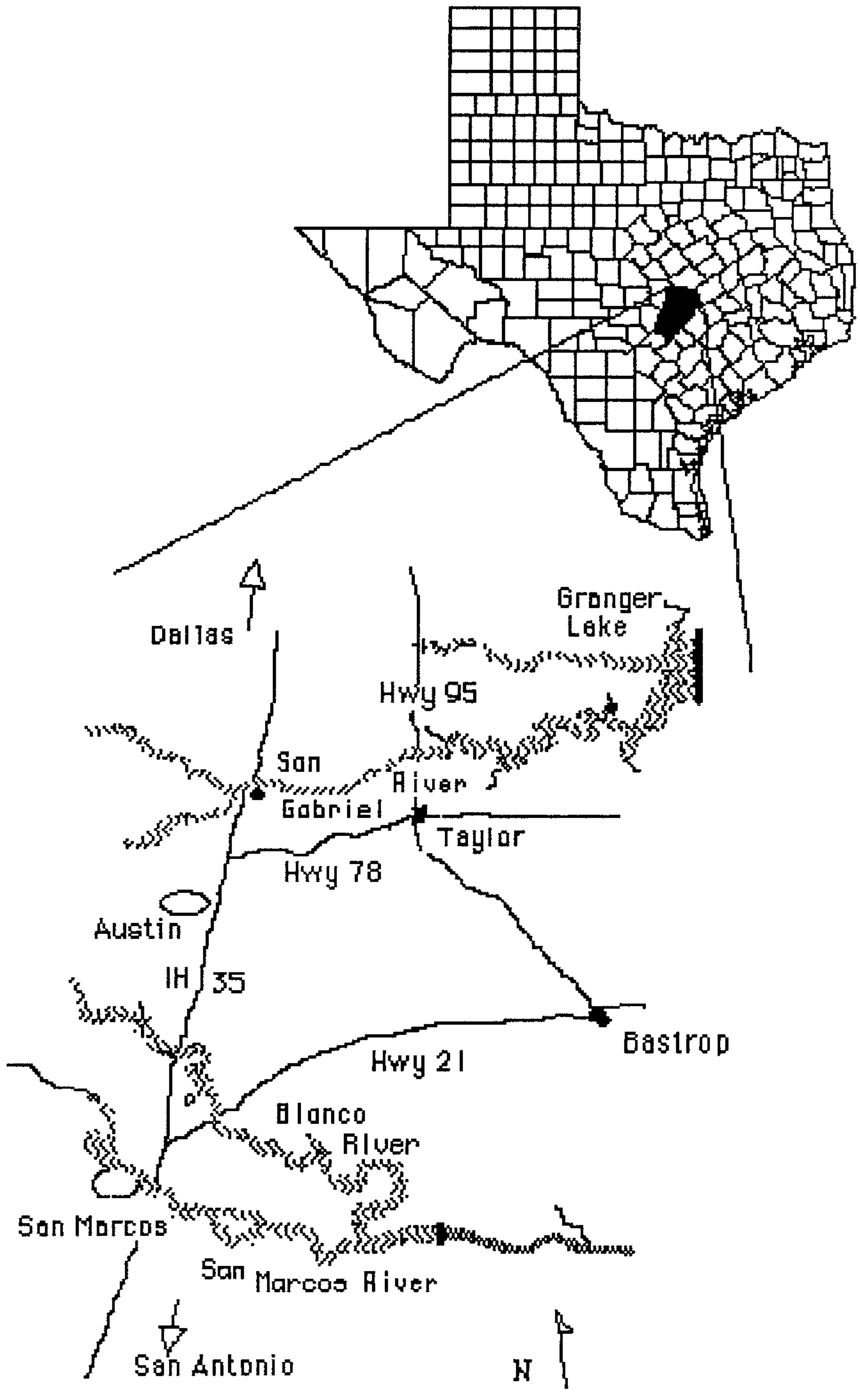

Figure 2. Map of the study area in central Texas.

hackberry, rough-leaf dogwood (*Cornus drummondii*), Chinese tallow (*Sapium sebiferum*), and black willow stands. Other woody species composing the understory include Mexican buckeye (*Ungnadia speciosa*), red buckeye (*Aesculus pavia*), anacua (*Ehretia anacua*), bur oak (*Quercus macrocarpa*), white and red mulberry (*Morus alba, m. rubra*), honey mesquite (*Prosopis glandulosa*), Texas persimmon (*Diospyros texana*), poison ivy (*Toxicodendron radicans*), mustang grape (*Vitis mustangensis*), and Virginia creeper (*Parthenocissus quinquefolia*).

The Blanco River study site starts where IH-35 crosses the river and ends at the confluence of the San Marcos River. Periodic and intense floods have produced eroded, steep cliffs adjacent to the river on meandering curves, while relatively straight stretches have well developed floodplains. This stretch of the river is perennial, but base flow is much lower, and fluctuations in discharge are greater than on the San Marcos or San Gabriel Rivers. Land use is largely livestock grazing and cultivation, and recreational use is minimal. There are several backwater areas along this stretch of the river, found primarily behind point bars. These depressions are the remnants of gravel mining operations, and provide alternative habitat for beaver and other wildlife.

The structure of the riparian plant community along the Blanco River is generally similar to the San Marcos River flora. However, areas adjacent to the Blanco River have a greater abundance of small and large sycamore, green ash (*Fraxinus pensylvanica*), and black willow trees, and a decreased abundance of understory species such as rough-leaf dogwood, privet, and Mexican buckeye.

The San Gabriel River study site is located along the west side of the San Gabriel Wildlife Unit of the Granger Wildlife Management Area. The site extends from the river at the Texas Highway 95 Bridge to a point approximately 8 km downstream where the river flows into Granger Lake. Surrounding the lake and riparian zone are 2,671 ha of wildlife management units operated by the Texas Parks and Wildlife Department. The area has been used for wildlife habitat conservation and as a public-use facility for controlled hunting, fishing and non-consumptive recreational uses. The topography along the river is similar to the Blanco River in that steep banks cut by previous periodic flooding are interspersed with well developed floodplains.

Woody dominants along the river are bald cypress, American and cedar elm, eastern cottonwood, hackberry, pecan, sycamore, green ash, black willow, osage-orange (*Maclura pomifera*), and mustang grape. The understory consists primarily of boxelder and green ash stands with a lesser number of willow, hackberry, and cedar elm saplings. Other common woody species include white and red mulberry, western soapberry (*Sapindus saponaria)*, anacua, bur oak, American elm, live oak (*Quercus virginiana*), and Texas sophora (*Sophora affinis*).

Field Methods—During the springs of 1990 and 1991, all active forage stretches within the study sites were identified. To obtain the maximum amount of data relative to woody species availability and use, a forage stretch was defined as the area within a width of 5 m inland from the shoreline, and a length equal to recognized beaver foraging activity. Although beavers in this study foraged up to 110 m from the shoreline in a few instances, I could not determine if all plants within this distance of the rivers were actually available. The decision to limit the width of the forage stretch to 5 m was made in order to reduce the likelihood of contaminating availability data with plants that were not actually available.

All available and utilized (felled or girdled) tree and shrub trunks greater than 1 cm in diameter were identified, analyzed for beaver use, and assigned to one of six 4 cm size classes for each stretch. Size classes were based on the diameter of the vegetation at 50 cm above the ground to provide comparability between felled and standing stems, and to compensate for some of the interspecific variation of basal trunk spread.

Woody plants with main stem diameters less than 1 cm were excluded because nutria (*Myocastor coypus*) and swamp rabbits (*Sylvilagus aquaticus*), which occurred in the study sites, have been documented to forage on small saplings (Blair and Lauglinais 1960, Conner and Toliver 1990). All woody tree and shrub trunks > 1 cm which had been felled and those with over 25% of the trunk girdled were considered utilized, and were assigned to appropriate size classes. The decision to limit positive data to stems with greater than 25% girdling was again based on observations of other rodents gnawing on trees within the study sites. Multiple-trunk plants within the beaver foraging areas were deemed separate individuals for both usage and availability counts. Data for the San Marcos, Blanco, and San Gabriel Rivers for 1990, 1991, and combined 90-91 are presented in Appendices 2, 3, and 4 respectively.

A preliminary study was conducted during the winter of 1988-89 to determine woody species use by beavers at the three study sites and to evaluate where most of the use occurred with respect to distance from the shoreline. Active forage areas were well-spaced, associated with beaver den sites, and represented distinct colonies. Boyce (1981) observed beavers were clearly "central place" foragers with the den, lodge, or food cache forming the central place. An assumption that forage stretches within the study sites represented the woody plant use of discrete colonies was made. Ninety-five percent of 18 woody species used by beavers within the study sites during the preliminary study grew within 5 m distance from the shoreline. It was surmised that beavers had actively selected these areas, and so individual woody plants of the 18 species growing within these areas were deemed available.

Quantitative Methods—Woody resource use and preferences were analyzed by four calculations. Hurlbert's standardized niche breadth index was chosen for the evaluation of woody resource use because differences in availability of resource states affect the index (Hurlbert 1978). Patterns in relative preferences for different woody species and for size classes within each species with respect to the rivers were evaluated by a chi-square contingency analysis (Zar 1984). Relative preferences for utilized species for each river were calculated by the rank-preference index (Johnson 1980). Relative preferences for size classes within each species were determined by Ivlev's Electivity Index (Krebs 1989).

Hurlbert's standardized niche index is a modified version of Levin's measure of niche breadth. The latter index estimates the uniformity of the distribution of individuals among the resource states (Krebs 1989). Hurlbert (1978) suggested resources should be scaled to their availability when evaluating niche breadth so that the resource matrix includes a measure of the proportion of each available species. Hurlbert's standardized niche breadth is calculated by the following equations:

$$B' = \frac{1}{\sum \left(p_j^2 / a_j \right)},$$

and

$$B'_A = \frac{B' - a_{\min}}{1 - a_{\min}},$$

where: B' = Hurlbert's niche breadth,

p_j = Proportion of individuals found in resource j,

a_j = Proportion of total available resources consisting of resource j,

$a_{\min}$ = The smallest observed proportion of all the resources, and

B'_A = Hurlbert's standardized niche breadth (B' expressed as a proportion).

Temporal variation in woody species use for all three rivers was determined by niche breadth. The usage and availability data from 1990 and 1991 were combined for each river. Niche breadth values were used to determine if any spatial variation in woody species usage could be detected among the rivers. Woody species with usage greater than 10% with respect to the total number of utilized plants for each river were identified as "frequently used species." Actual percentages were calculated for all frequently used species (Fig. 3, 4, and 5).

A 3 × 16 chi-square contingency table was constructed to test the null hypothesis that patterns in relative species preferences by beavers were independent of the rivers. The table consisted of three columns representing the rivers and 16 rows representing the utilized woody species common to all three sites. The proportion of utilized individuals to available individuals for each woody species was pooled from both years on each river and transformed to count data. These data were then entered into the respective cells for observed frequency of occurrence. The expected frequency for each cell was obtained by the following expression (Zar 1984):

$$\hat{f} = \frac{R_i C_j}{n},$$

where: $\hat{f}$ = expected frequency for each cell,

R_i = total frequency for each row,

C_j = total frequency for each column, and

$n = \sum R_i + \sum C_j$.

The chi-square statistic was calculated by the following equation (Zar 1984):

$$\chi^2 = \sum \sum \frac{\left(f_{ij} - \hat{f}_{ij}\right)^2}{\hat{f}_{ij}},$$

where: χ^2 = chi-square statistic,

f_{ij} = observed frequency of each observation, and

$\hat{f}_{ij}$ = expected frequency of each observation.

The $\sum \chi^2$ for each row (representing species relative use by beavers for all rivers) was considered to represent the species which contributed most to the observed differences in the relative preference patterns among the rivers.

The null hypothesis for this test was that patterns in relative preferences for size classes were independent of rivers, and was tested by chi-square contingency analyses. In this procedure, a 6×3 table was constructed with the six rows representing size classes and three columns representing rivers.

Relative preferences for woody species within each river were determined using the rank preference index (Johnson 1980). Previous investigators of resource preferences have reported that when a common but seldom-used species is included or excluded in other preference indices, an aberrant reversal of preference or avoidance may occur (Krebs 1989). The rank preference index avoids this problem by ranking both the utilization and availability of the resources. The difference in ranks is a measure of preference. Negative rank-preference values indicate preference for a resource, while positive rank preference values show avoidance.

The rank-preference index has been applied by numerous investigators evaluating relative preferences for habitat types (Bodurtha *et al.* 1989, Carey *et al.* 1990, Finch 1989). For this study, beaver colonies were considered to represent individual subjects (Douglas Johnson, pers. comm. 1991), and the various species of woody plants used by beavers within the study sites were the resource states. The rank-preference index was calculated by the following expression:

$$t_i = r_i - j_i,$$

where: t_i = rank difference for species i (measure of preference),

r_i = rank of usage of resource i, and

s_i = rank of availability of resource i.

The final index value generated for statistical comparison was the mean difference in ranks for each resource. This value was calculated by combining the ranks of all subjects for each river by the following expression:

$$\bar{t}_i = \bar{r}_i - \bar{s}_i,$$

where: $\bar{t}_i$ = mean difference in ranks for species i,

$\bar{r}_i$ = mean usage rank for species i, and

$\bar{s}_i$ = mean availability rank for species i.

The lower the value of mean difference in ranks, the greater the degree of selection for the resource; higher positive mean difference in rank values indicate greater degrees of avoidance.

The null hypothesis that all species are equally preferred by beavers on each river was tested by the Waller-Duncan procedure (Johnson 1980). In this test, an F-statistic was generated by multiple comparisons between the species using the following equation:

$$F_{ik} = \frac{J(J-1+1)}{(J-1)(I-1)} \sum_{i=1}^{I-1} \sum_{k=1}^{I-1} \bar{t}_i \bar{t}_k U_{ik},$$

where: F_{ik} = the calculated F statistic,

J = number of individual subjects,

I = number of woody species,

$\bar{t}_i$ = mean difference in ranks for species i,

$\bar{t}_k$ = mean difference in ranks for species k, and

U_{ik} = designated element of the inverse matrix of the covariance between species i and species k.

This analysis is one-tailed with $(i-1)$ and $(j-1+1)$ degrees of freedom.

The proportion of utilized to available individuals of each size class were evaluated by Ivlev's index of electivity to determine relative preferences for size classes within the utilized species. This index was chosen because it is well suited for proportional data and it takes into consideration the availability of the various categories (Krebs 1989). Ivlev's electivity is given by the following expression:

$$E_i = \frac{r_i - n_i}{r_i + n_i} ,$$

where: E_i = Ivlev's index of electivity measure for category i,

r_i = percent utilization of category i and,

n_i = percent availability of category i.

RESULTS

General—Beavers utilized 25% of 26,244 available stems of 18 woody species within 40 active forage stretches. The number of forage stretches and their respective lengths varied spatially and temporally. Length of forage stretches ranged from 117 to 263 m. The number of forage stretches along the San Marcos River site increased from six in 1990 to seven in 1991. The number of Blanco River forage stretches also increased from seven in 1990 to eight in 1991, while the number on the San Gabriel River site remained at 6 stretches for both years (Tables 1 and 2).

Niche Breadth—Woody resource niche breadth was similar among the rivers in two respects. Hurlbert's niche breadth varied only slightly among the rivers when compared temporally for each river and among the three rivers by comparison of the combined data from both years. The San Gabriel River had both the smallest and largest Hurlbert's niche values with 0.813 for 1990 and 0.902 for 1991, but overall the results showed striking similarities in the equitability of woody species usage by beavers, both from year to year and among the rivers (Table 3). Secondly, the number of frequently used species (those used in quantities >10% with respect to the total number of used individuals) was four on each river. However, the species included as "frequently used" varied among the rivers, but remained constant for each river for both years.

White mulberry (*Morus alba*) and boxelder (*Acer negundo*) were among the most frequently used woody species on all rivers. Black willow (*Salix nigra*) use was high on the Blanco and San Gabriel Rivers. Rough-leaf dogwood (*Cornus drummondii*) and privet (*Ligustrum* sp.) were frequently

Table 1. Number and length (m) of active beaver forage stretches along 8 km study sites on the San Marcos, Blanco, and San Gabriel Rivers, 1990.

	Forage Stretch Lengths		
Forage stretch #	San Marcos	Blanco	San Gabriel
1	193	162	132
2	186	123	121
3	161	217	202
4	263	112	154
5	169	205	193
6	117	125	149
7	—	138	—

Table 2. Number and length (m) of active beaver forage stretches along 8 km study sites on the San Marcos, Blanco, and San Gabriel Rivers, 1991.

	Forage Stretch Lengths		
Forage stretch #	San Marcos	Blanco	San Gabriel
1	187	135	166
2	164	122	241
3	142	194	188
4	129	182	112
5	121	161	118
6	138	219	129
7	208	147	—
8	—	115	—

Table 3. Hurlbert's niche breadth values for woody plant use by beavers on the San Marcos, Blanco, and San Gabriel Rivers during 1990, 1991, and combined 1990-91.

	Hurlbert's niche breadth values for the rivers		
Year	San Marcos	Blanco	San Gabriel
(1990)	0.833	0.814	0.813
(1991)	0.895	0.863	0.902
(1990-1991)	0.881	0.835	0.862

used on the San Marcos River (18% and 21%, respectively), only slightly used on the Blanco (1% and 2%, respectively) and unused on the San Gabriel River. Green ash was frequently used on the San Gabriel River (24%), but only minimally foraged on the San Marcos (0.02%) and Blanco (6%) Rivers. Sycamore (*Platanus occidentalis*) accounted for 24% of the foraged individuals on the Blanco River, but only 1% on the San Marcos River, and 3% on the San Gabriel River.

Rough-leaf dogwood, willow, boxelder, privet, and white mulberry comprised 77% of the utilized species on the San Marcos River. Willow, boxelder, sycamore, and white mulberry represented 80% of woody plants used on the Blanco River, and willow, boxelder, green ash, and white mulberry accounted for 90% of woody species utilized on the San Gabriel River. A summary of the percentages for the most frequently used woody species on each river is presented in Figures 3, 4, and 5.

The proportions of frequently used woody species were also combined for all rivers for both years. Black willow, boxelder, and white mulberry accounted for 55% of woody species use by beavers on all rivers during the study. Boxelder accounted for 25% of the total number of utilized individuals, followed by willow and white mulberry each at 15% (Fig. 6).

Chi-square Contingency Analyses—The overall pattern for relative species preferences by beavers was significantly different among the rivers $\left[P\left(\chi^2_{(1)30} \geq 84.34\right) < 0.001\right]$. Beaver use of rough-leaf dogwood accounted for the greatest departure from expected use frequencies with a chi-square value of 28.7. Other species used which contributed most to the heterogeneity included bur oak (*Quercus macrocarpa*), chinaberry (*Melia azedarach*), eastern cottonwood (*Populus deltoides*), and privet with chi-square values of 17.4, 8.99, 6.77, and 6.08, respectively (Table 4).

The pattern of relative preferences for size class use by beavers among the rivers was not significant $\left[P\left(\chi^2_{(1)10} \geq 7.12\right) >> 0.05\right]$. The 13 to 17 cm and 17 to 21 cm size classes showed the greatest use differences with χ^2 values of 2.46 and 2.36, respectively (Table 5).

Rank-Preference Index—There were significant differences in relative species preferences by beavers on all rivers with $\left[0.025 < P\left(F_{(1)4,9} \geq 4.400\right) < 0.05\right]$ for the San Marcos River, $\left[0.025 < P\left(F_{(1)6,9} \geq 3.550\right) < 0.05\right]$ for the Blanco River, and $\left[0.025 < P\left(F_{(1)3,9} < 4.331\right) < 0.05\right]$ for the San Gabriel River.

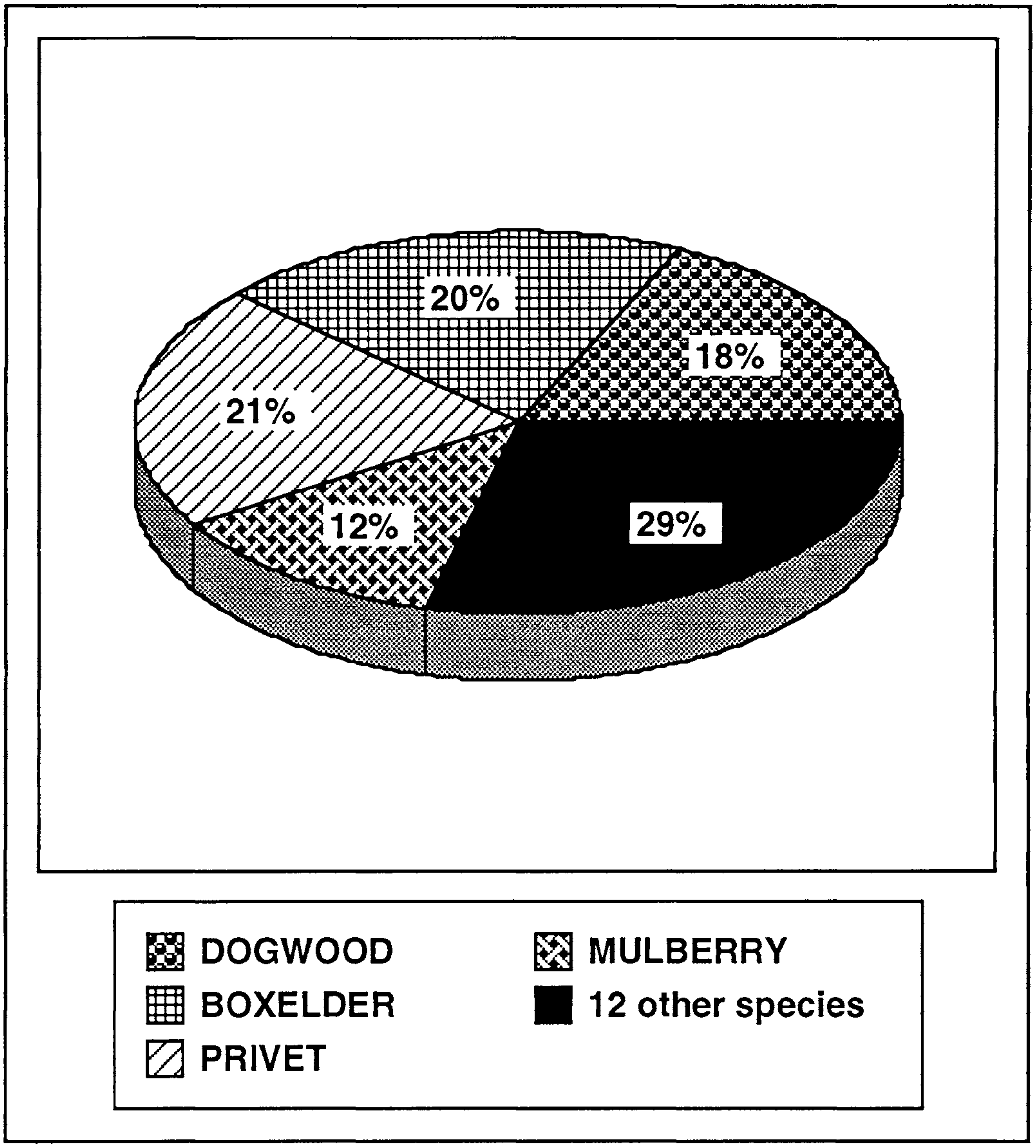

Figure 3. Percent utilization of the major components of woody vegetation by beavers on the San Marcos River during 1990-1991.

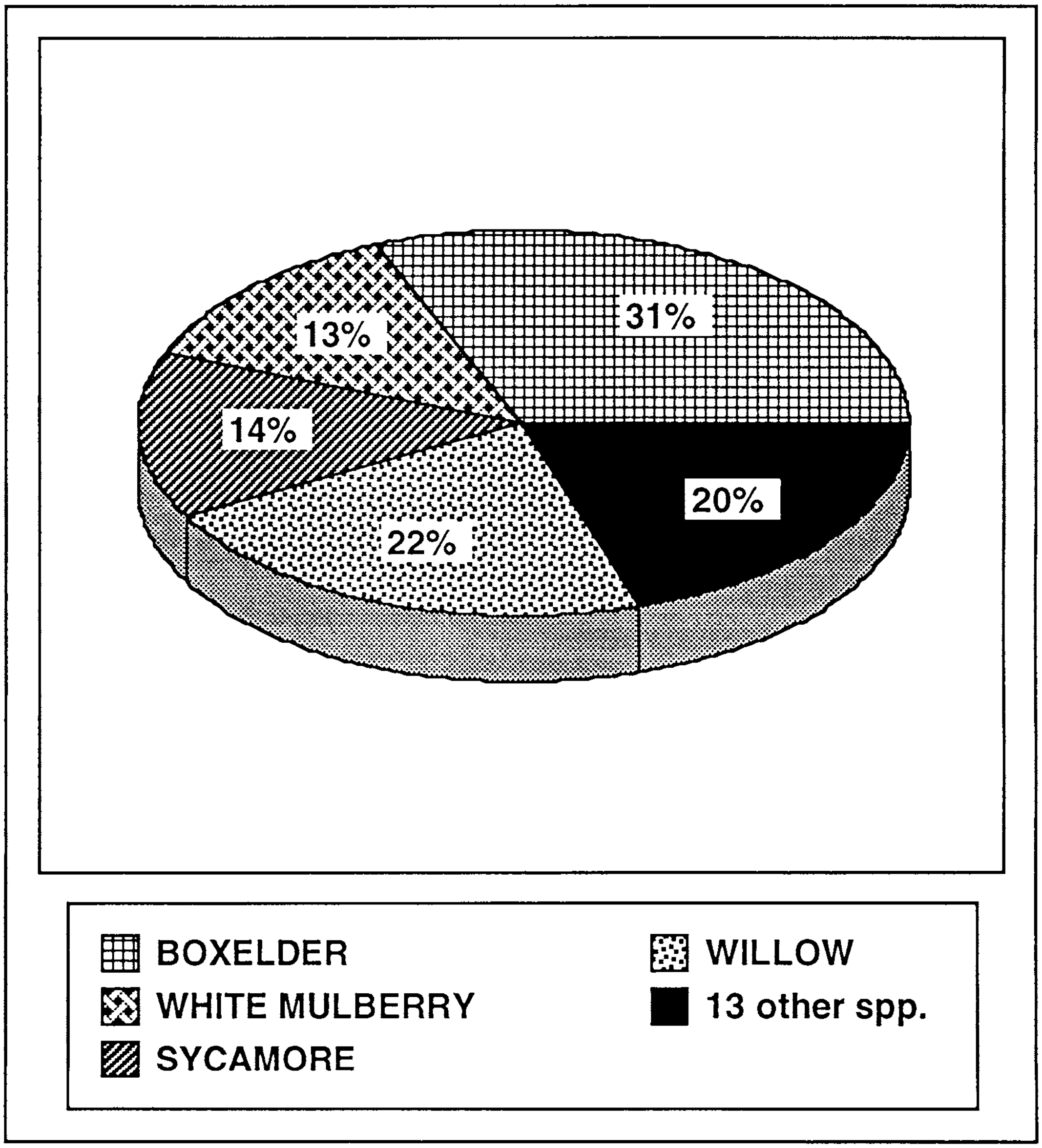

Figure 4. Percent utilization of the major components of woody vegetation by beavers on the Blanco River during 1990-1991.

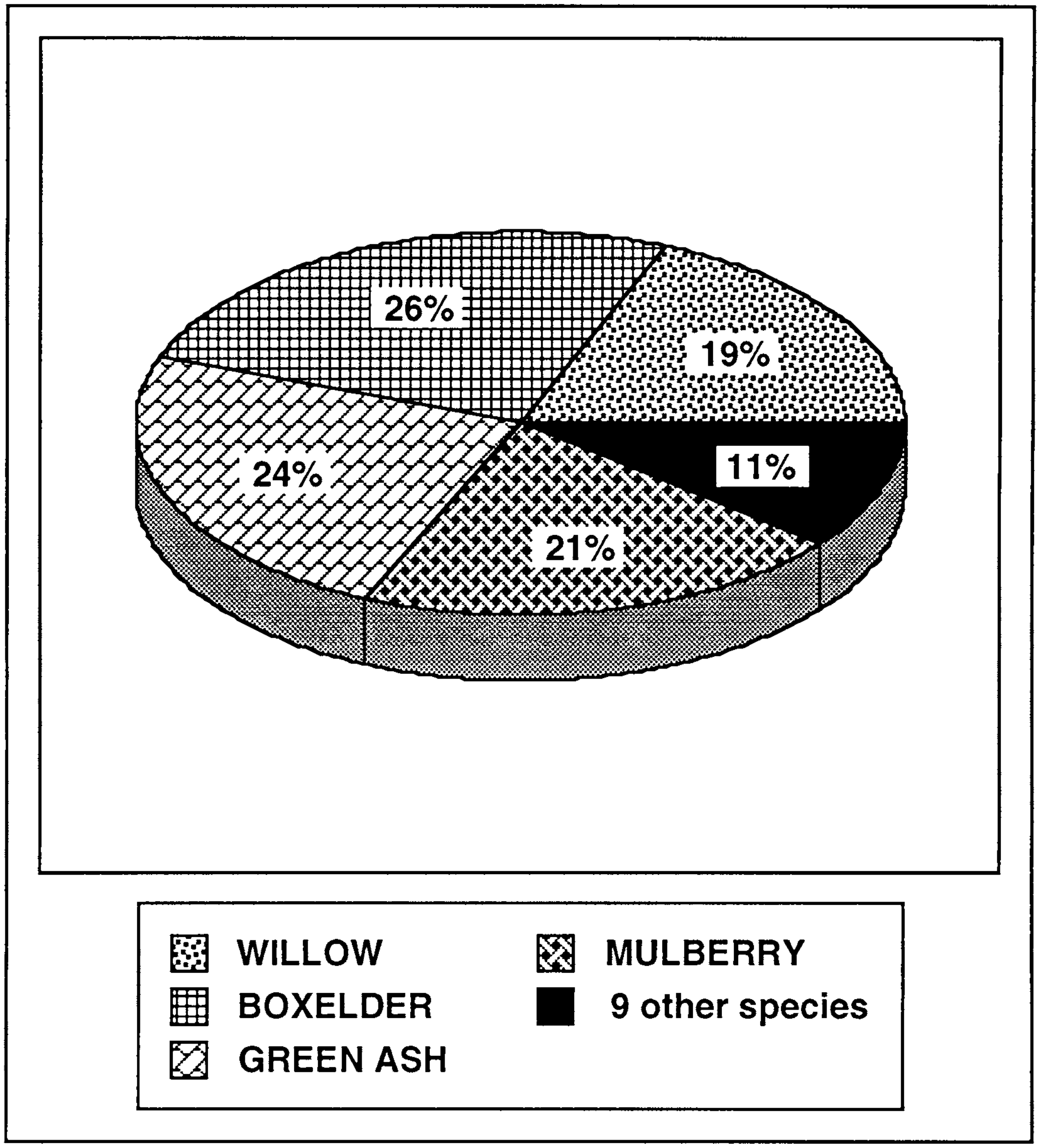

Figure 5. Percent utilization of the major components of woody vegetation by beavers on the San Gabriel River during 1990-1991.

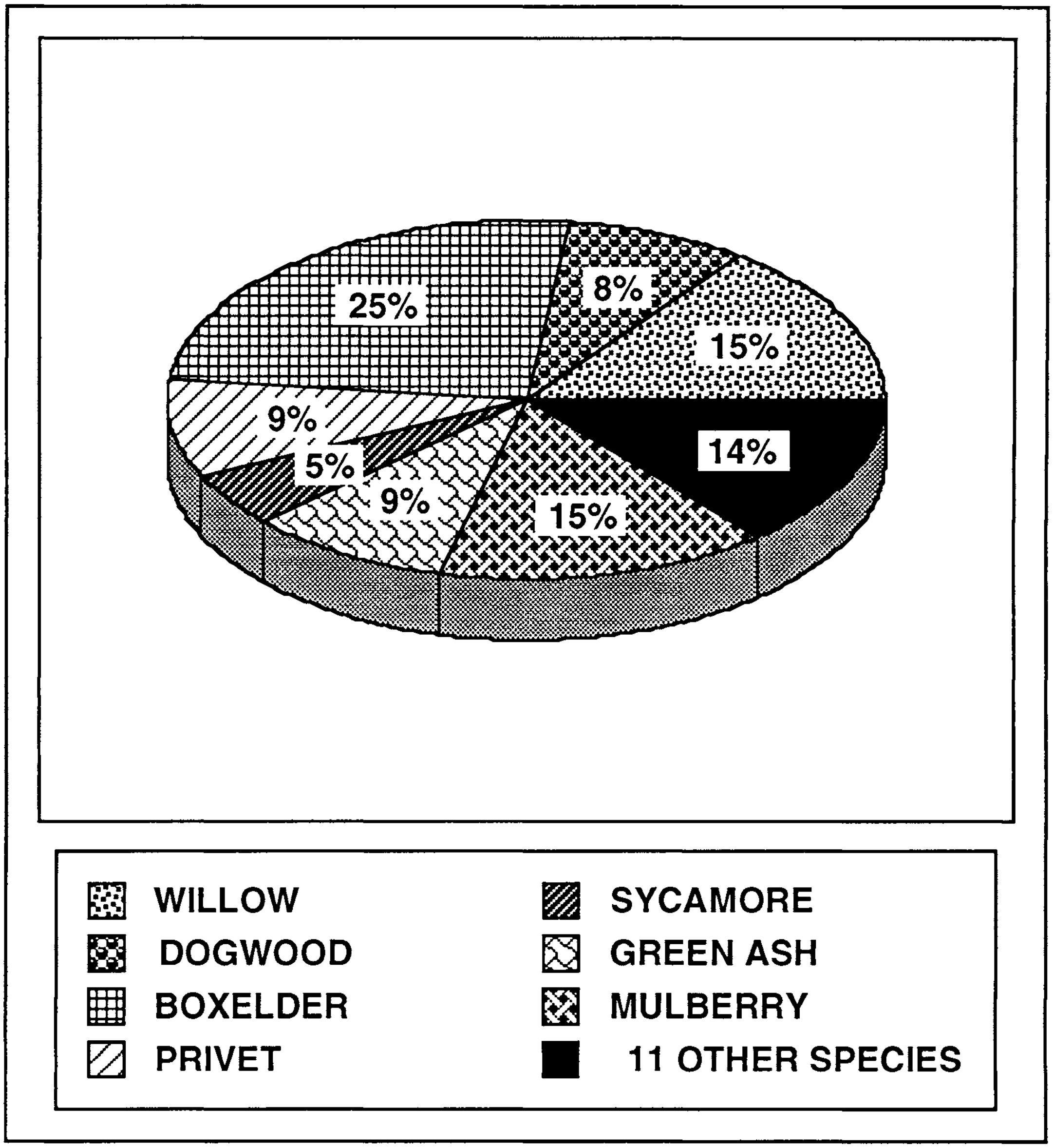

Figure 6. Percent utilization of the major components of woody vegetation by beavers on the San Marcos, Blanco, and San Gabriel Rivers during 1990–1991.

Table 4. Chi-square contingency table comparing relative species preference patterns by beavers among the San Marcos, Blanco, and San Gabriel Rivers. Observed frequency (f_i) is shown in each cell, with the expected frequency if H_0 is true in parentheses.

species	f_i & $(\hat{f}_i)$ for each river San Marcos	Blanco	San Gabriel	Row sum R	row χ^2
cottonwood	64 (61.2050)	41 (55.4532)	59 (47.3417)	164	6.77
willow	37 (39.182)	33 (3505086)	35 (30.3103)	105	1.02
boxelder	25 (26.4973)	24 (24.0072)	22 (20.4955)	71	0.20
hackberry	13 (8.5836)	4 (7.7770)	6 (6.6394)	23	4.17
pecan	12 (9.7034)	5 (8.7914)	9 (7.5054)	26	2.48
sycamore	23 (22.0189)	19 (19.9496)	17 (17.0315)	59	0.09
dogwood	27 (34.7077)	55 (31.4460)	11 (26.8426)	93	28.7
privet	30 (24.6313)	26 (22.3165)	10 (19.0521)	66	6.08
mulberry	52 (51.1286)	47 (46.3237)	38 (39.5477)	137	0.08
green ash	18 (23.5117)	26 (21.3022)	19 (18.1862)	63	2.36
Mx. buckeye	39 (38.0665)	38 (34.4892)	25 (29.4442)	102	0.73
bald cypress	19 (18.6600)	16 (16.9065)	15 (14.4335)	50	0.08
Amer. elm	10 (13.0620)	14 (11.8345)	11 (10.1034)	35	1.20
cedar elm	3 (4.3957)	3 (4.3957)	7 (3.7527)	13	4.00
bur oak	25 (26.4973)	11 (24.0072)	35 (20.4955)	71	17.4
chinaberry	18 (12.6888)	14 (11.4964)	2 (9.8147)	34	8.99
Column sum C_k	C = 415	C = 376	C = 321	N= $\sum$C = 1112	χ^2 = 84.35

Table 5. Chi-square contingency table comparing patterns in relative size class preferences by beavers among the San Marcos, Blanco, and San Gabriel Rivers. Observed frequency (f_i) is shown in each cell, with the expected frequency if H_0 is true in parentheses.

size class in cm dia.	f_i & $(\hat{f}_i)$ for each river			Row sum R	row χ^2
	San Marcos	Blanco	San Gabriel		
1–5	31 (34.1649)	31 (30.3333)	29 (21.8421)	91	0.60
5–9	28 (28.1579)	24 (25.0000)	23 (21.8421)	75	0.10
9–13	16 (13.1404)	10 (11.6667)	9 (10.1930)	35	1.01
13–17	5 (4.1298)	5 (3.6667)	1 (3.2035)	11	2.46
17–21	5 (8.2596)	8 (7.3334)	9 (6.4070)	22	2.36
> 21	22 (19.1474)	17 (17.0000)	12 (14.8526)	51	0.59
Column sum C_k	C = 107	C = 95	C = 83	N = ∑C = 285	χ^2 = 7.12

When data were combined for both years, cottonwood, white mulberry, Mexican buckeye (*Ungnadia speciosa*), willow, and bur oak were preferred by beavers on all rivers, while, chinaberry, hackberry (*Celtis* sp.), pecan (*Carya illinoensis*), cedar elm (*Ulmus crassifolia*), and boxelder had negative preference values on all rivers. Bald cypress (*Taxodium distichum*) was preferred on the San Gabriel River with a rank-preference value of -0.625, while the species was avoided on the Blanco and San Marcos Rivers with values of 0.033 and 0.538, respectively. Sycamore was a preferred species on the San Marcos River (-0.192), but beavers showed negative preference for it on the Blanco and San Gabriel Rivers (1.100 and 0.375, respectively). Beavers preferred green ash on the Blanco River (-0.667), but it was avoided on the San Marcos and San Gabriel Rivers with rank-preference values of 0.154 and 0.375, respectively. Rough-leaf dogwood was preferred on the Blanco River (-1.467), avoided on the San Marcos River (0.077) and not encountered on the San Gabriel River. Eastern cottonwood was the most preferred species on all rivers with rank-preference values of -3.125, -2.933 and -1.629 for the the San Gabriel, Blanco, and San Marcos Rivers, respectively. Table 6 presents a summary of preferred woody species by beavers among the rivers in order of preference values, and Table 7 summarizes the rank preference values for those woody plants used by beavers with negative selection in order of avoidance.

Table 6. Mean difference in ranks for preferred species by beavers on the San Marcos, Blanco and San Gabriel Rivers. Species are presented in order of preference for each river.

San Marcos River		Blanco River		San Gabriel River	
Species	X diff in ranks	Species	X diff in ranks	Species	X diff in ranks
cottonwood	-1.692	cottonwood	-2.933	cottonwood	-3.125
Mx. buckeye	-1.346	mulberry	-1.567	bur oak	-1.958
mulberry	-1.154	buttonbush	-1.500	Mx. buckeye	-1.500
red buckeye	-0.808	Mx. buckeye	-1.467	mulberry	-1.292
willow	-0.731	dogwood	-1.467	bald cypress	-0.625
bur oak	-0.538	bur oak	-0.833	willow	-0.292
privet	-0.308	green ash	-0.667	Amer. elm	-0.167
sycamore	-0.192	privet	-0.400		
		willow	-0.200		

Table 7. Mean difference in ranks for avoided species by beavers among the San Marcos, Blanco and San Gabriel Rivers. Species are presented in order of avoidance for each river.

San Marcos River		Blanco River		San Gabriel River	
Species	X diff in ranks	Species	X diff in ranks	Species	X diff in ranks
pecan	2.192	hackberry	4.067	hackberry	3.458
hackberry	1.846	pecan	2.967	chinaberry	1.625
cedar elm	0.692	cedar elm	1.533	pecan	1.333
Amer. elm	0.692	sycamore	1.100	boxelder	.0917
bald cypress	0.538	Amer. elm	0.900	cedar elm	0.875
boxelder	0.308	boxelder	0.433	green ash	0.375
chinaberry	0.269	bald cypress	0.033	sycamore	0.375
green ash	0.154	chinaberry	0.000		
dogwood	0.077				

Ivlev's Index of Electivity—Since patterns of relative preferences for size classes by beavers were not found to be different among rivers, data from all rivers for both years were pooled for the description of relative preferences for these resource states. Unlike the rank-preference index, Ivlev's electivity values greater than zero indicate relative preference for the resource. The 1–5 cm diameter size-class was the most preferred class in all plant species except rough-leaf dogwood, eastern cottonwood and bald cypress. Beavers preferred the 5–9 cm size-class of Rough-leaf dogwood slightly over the 1–5 cm size-class (Ivlev's electivities of 0.028 and -0.005, respectively). Relative preferences for the > 21 cm size-class were evident for bald cypress and cottonwood. A summary of relative preference values for size classes for each species using Ivlev's index of electivity is presented in Table 8. General trends in size class preferences among the most frequently utilized species by beavers are shown in Figure 7.

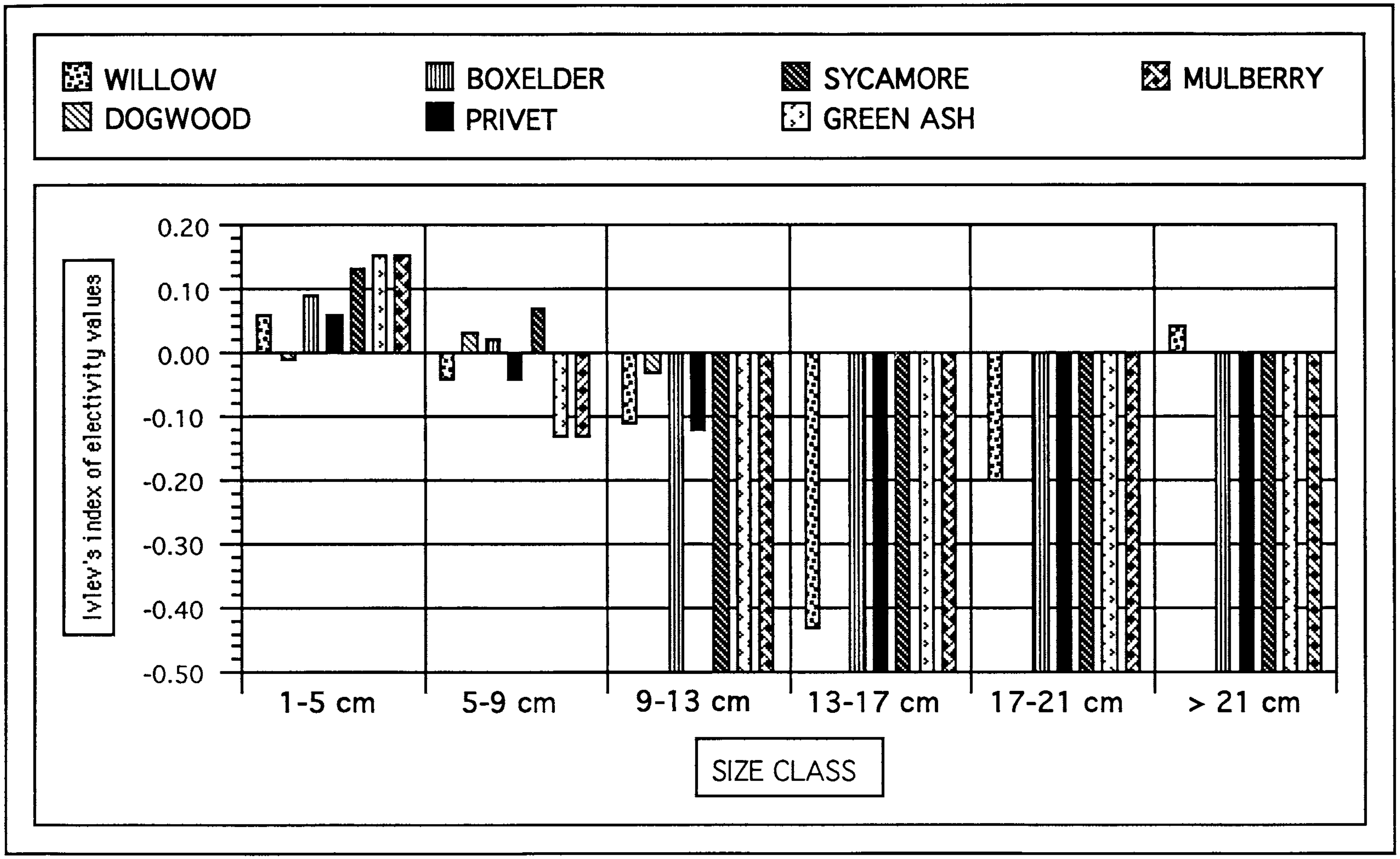

Figure 7. Ivlev's Electivity Index values for size classes among the seven most frequently used species by beavers. Values > 0 represent selection for the resource, while values < 0 show avoidance.

Table 8. Ivlev's Index of Electivity values among size classes (cm) for all utilized species by beavers. Values > 0 indicate relative preference, while values < 0 show avoidance.

species	1–5	5–9	9–13	13–17	17–21	> 21
cottonwood	0.147	-0.335	-1.000	-0.164	0.033	0.252
willow	0.052	-0.030	-0.120	-0.430	-0.200	0.003
boxelder	0.094	0.004	-0.636	-0.953	-1.000	-1.000
hackberry	0.232	-0.114	-1.000	-1.000	-1.000	-1.000
pecan	0.261	0.225	0.173	-0.272	-0.126	-0.413
sycamore	0.128	0.072	-1.000	-0.873	-0.782	-0.515
dogwood	-0.005	0.028	-0.028	—	—	—
privet	0.063	-0.044	-0.121	-0.538	-0.704	—
mulberry	0.057	0.030	-0.277	-0.636	-0.845	-0.355
green. ash	0.154	-0.131	-0.842	-0.787	-1.000	-0.858
Mx. buckeye	-0.017	0.085	0.061	—	—	—
bald cypress	-0.573	-0.488	-1.000	-0.431	-0.035	0.204
Amer. elm	0.088	-0.289	-0.242	-1.000	-0.062	0.115
cedar elm	0.283	-0.407	-1.000	-1.000	-0.153	-0.554
bur oak	0.119	-0.335	-1.000	-1.000	-1.000	-0.069
chinaberry	0.122	0.063	-1.000	-1.000	-1.000	-1.000
buttonbush	0.107	-0.225	—	—	—	—
red buckeye	0.051	-0.024	-1.000	—	—	—

DISCUSSION

Of the woody plant genera deemed utilized by beavers in this study, *Salix, Populus, Morus, Quercus, Fraxinus, Acer, Ligustrum, Ungnadia,* and *Cornus* have been reported as important winter foods of beavers in other parts of North America (Svendsen 1980, Hill 1982, Roberts and Arner 1984, Kindschy 1985, Beier and Barrett 1987). Although the availability of woody species varies geographically, these genera have consistently been reported as preferred or important resources of beavers. This generalization may be of major importance to management schemes where beavers exist, but little or no information is available concerning their local resource requirements.

An animal's niche is not completely defined by its preferred foods, but certainly the diet is of major importance when discussing niche concepts. Data from this study showed similarities in woody resource niche breadth among the rivers (Table 1). Four woody species were used by beavers in quantities greater than 10% on each river, and the composition of these remained constant for both years on all rivers. However, the four most frequently used species varied among the rivers. In most cases this variation can be explained by differences in the availabilities of woody species within forage stretches among the rivers. Boxelder was among the most frequently used woody species on all rivers, and it accounted for approximately 22%, 30%, and 27% of the total available individuals on the San Marcos, Blanco, and San Gabriel Rivers, respectively. Similar trends were observed in the use and availability of privet and rough-leaf dogwood on the San Marcos River and with sycamore and willow on the Blanco River. Green ash was among the most frequently used woody species on the San Gabriel River and represented

29% of the available woody plants. These data suggest beavers are opportunistic foragers. They consume large quantities of woody species which are abundant, even though these species were consistently "avoided" with respect to their availabilities. It appears that many of the frequently used woody species in the beaver's diet, such as boxelder, are staple foods. These staples are important with respect to frequency, but are taken in much lower quantities than expected relative to their availability.

Willow was among the most frequently used woody species on the San Gabriel River despite the fact that it accounted for less than 13% of the available woody plants within the forage stretches. White mulberry only accounted for 12% of the available individuals on the San Gabriel River and less than 7% on the San Marcos and Blanco Rivers, but it was among the four most frequently used woody species on all rivers. Some frequently used woody species such as white mulberry appear to have been selected in proportions greater than expected. Beavers foraged on white mulberry up to 110 m from the shoreline and the species was consistently preferred on all rivers.

Freeland and Janzen (1974) suggested that beavers may have an innate desire to use a variety of plants to avoid high levels of secondary compounds in any single species. The implications of niche breadth data from this study are that beavers rely on numerous woody plants, but they do utilize a small number of species in large quantities. They used a wide variety of woody species, but used only four species in quantities > 10%.

The significant difference in patterns of relative preferences for woody species among the rivers was consistent with previous investigations concerning spatial variation of preferences for woody resources (Henry and Bookout 1970, Jenkins 1981). Although differences in spatial selection patterns have been reported, little is known of the mechanisms involved. Data from this study suggest that beavers have a greater preference for certain species such as sycamore, green ash, and rough-leaf dogwood, only when their availability relative to the other species present is low. This implies that beavers may require certain compounds from these species, and show a greater preference for them only when thier availabilities are low. If this is true, the mechanisms for relative preferences are non-linear, while the index assumes linear relationships.

Sycamore was preferred on the San Marcos River, but the species only accounted for 1% of the total available individual woody plants within the forage stretches. Beavers had a strong negative selection for the species on the Blanco River where sycamore stems constituted 17% of the total available woody plants. Green ash was preferred on the Blanco River where it accounted for only 7% of the total available woody stems, but was avoided on the San Gabriel River where its availability exceeded 28% of the total available woody plants. A similar pattern exists for rough-leaf dogwood. On the San Marcos River, where availability of dogwood is roughly 18%, it is negatively selected by beavers, while on the Blanco River, where availability is less than 1%, beavers show a strong preference for dogwood (Tables 6 and 7, Appendices 1, 2, and 3). Jenkins (1980) suggested use of a particular woody species may be more dependent on the abundances of other species with different nutritional qualities than on the absolute abundance of the species in question.

Jenkins (1978) observed beavers in central Massachusetts frequently removed the bark of trees without felling them and without using the plants further after they had inspected it. This implies beavers have a means of assessing relative nutritional values prior to usage. Data from this study supports this hypothesis because although relative species preference patterns by beavers varied among the rivers, many woody plants were consistently preferred while others were generally avoided across all sites. Eastern cottonwood, Mexican buckeye, white mulberry, bur oak, and willow were preferred by beavers on all rivers; however, chinaberry, hackberry, pecan, cedar elm, and boxelder were avoided (Tables 6 and 7).

Patterns in relative preferences for size classes by beavers were independent of the rivers. Beavers consistently selected smaller stems in 15 of the 18 species utilized during the study (Table 8). This trend was also documented by Nixon and Ely (1969). Jenkins (1980) suggested that lower provisioning costs may be the reason beavers generally selected smaller size classes of woody species. More energy is required to transport larger stems back to the central place. Fryxell and Doucet (1991) stated that provisioning time was an important determinant of resource exploitation by beavers only in certain species. Nutritional value may also be of considerable importance, but little information is available to test this prediction and this study was not designed to address the subject. Relative preferences by beavers for the 5–9 cm diameter size class for rough-leaf dogwood was probably due to the large number of available plants within this size class. The same explanation can be applied to the preferences for the > 21 cm size class in eastern cottonwood and bald cypress (Appendices 2, 3, and 4).

Several studies have addressed the question of whether beaver food habits and foraging strategies conform to the central place foraging theory. Recent studies have shown that beavers selected a lower number of species with increasing distance from the central place (Jenkins 1980, McGinley and

Whitham 1985). The ability to "sample" resources, such as the behavior observed in beaver foraging by Jenkins (1978), seems likely to be an important mechanism in central-place foraging. As suggested by Jenkins, (1981) studies concerning variations in the nutritional states of forage resources might allow the development of optimum foraging models.

While it is generally accepted that beavers act as central place foragers with respect to resource selection, little is known of the dynamics involved in the selection of the central place. Boyce (1981) suggested the density of colonies in an area was positively correlated to the biomass of available winter foods. As expected by this model he found that colonies chose central places within or near large quantities of preferred winter forage species. Another interesting result of his study was that beavers selected central places which had a high diversity of vegetation types, but a low equitability of species within them. Boyce (1981) concluded that beavers selected sites which had abundant winter foods and a low number of other species and areas with relatively high spatial heterogeneity of vegetation types.

Data from my study suggest similar patterns of site selection. Although not analyzed, it appears that the woody plant communities of localities containing forage stretches shared one of two important structural characteristics. They either had relatively low equitabilities of woody species, or were situated in areas with diverse vegetation types. Beavers also selected sites with abundant small (1–5 cm) woody plants. It would be interesting to compare characteristics of the foraged areas with adjacent non-foraged surrounding areas.

Because beavers are mid-size herbivores, they have a significant impact on the riparian community structure and composition. The local extinction of black cottonwood (*Populus trichocarpa*) and quaking aspen along 4 to 5% of the Truckee River Basin, California, was attributed to depletion by beavers (Beier and Barrett 1987). Naiman *et al.* (1988) and Ives (1942) reported that although beaver did cause localized extinctions of aspen, the perpetuation of that forage species was maintained in the habitat because clearcutting stands of aspen by beavers inhibited succession. The resulting mid-successional stage community increased the overall productivity of the ecosystem by supporting forbs, sedges, grasses, and shrubs which beaver and other wildlife utilize. Not only was the composition of riparian communities altered, the growth forms of willow, alder, and many other woody plants were changed from trees to shrubs by the pruning action of the beaver (Naiman *et al.* 1988).

Kindschy (1985) found heavy extended use of red willow (*Salix laevigata*) did not cause deterioration or local extinction of the species in southeastern Oregon. McGinley and Whitham (1985) suggested selective foraging by beavers affects the growth forms of certain species. They associated intensity of foraging upon black cottonwoods with a shrubbier growth form. The result was that many trees along the shores, where beavers most actively foraged, were kept in a shrub growth form and juvenile state; thus reproduction was primarily by vegetative means. In contrast, trees growing away from the river reached sexual maturity earlier, reproduced sexually, and developed a canopy growth form. These characteristics were frequently observed in plants within the forage stretches of the study sites.

The management implications of selective foraging by beavers on the availability and structure of future woody resources are significant based on the fact that beavers showed distinct preferences for certain resources. It is likely that the effects of selective foraging on vegetation observed in other animals such as mule deer (*Odocoileus hemionus*) can be applied to beaver management strategies. Jewell and Holt (1981) suggested high mule deer densities and selective foraging have caused adverse changes in the community structure and composition of vegetation within certain portions of their range. Species diversity decreased markedly in areas inhabited by large numbers of deer because preferred plants were consistently utilized and subsequently replaced by less desirable species.

Beaver populations are increasing throughout most of their range in response to reduced trapping pressure, lack of natural predators and laws restricting their harvest (Novak 1987). Land managers may face similar problems as seen in other herbivorous species which become over-populated. Barnes and Dibble (1988) studied the effects of selective foraging by beavers on the succession of riparian forests in west central Wisconsin. Preferred species such as green ash (*Fraxinus pensylvanica*) and yellowbud hickory (*Carya cordiformis*) showed greatly reduced abundance in areas inhabited by beavers when compared to surrounding riparian forests. They predicted a continued decline in populations of preferred beaver foods and an increase in undesirable species.

In order to effectively manage beavers and the environment they inhabitat, it will be necessary to understand the dynamics of beaver foraging. This study may assist in developing an understanding of factors involved in woody resource use and selection by beavers, especially in central Texas where few data are available on this subject. Diamond *et al.* (1987) suggested the management of stream floodplains as wildlife corridors for the migration of native vegetation may help slow the rate of species extinction caused by habitat fragmentation. If this is to be a viable strategy, it is imperative that the ecology of herbivorous organisms, especially those which are prone to over-populate and thus cause extensive damage, is fully understood.

CONCLUSIONS

The American beaver has been described as a "choosy generalist" because it uses a wide variety of plant organs from numerous woody and herbaceous species, but often exhibits distinct preferences for any category (Harper 1969). Results from this study suggest that woody resource niche breadth was similar among the colonies, but there were differences in usage related to the composition of the utilized species. There was spatial variation in the patterns of relative preferences for species among the rivers, but size-class preferences were not significantly different among rivers. The differences observed in foraging patterns were attributed to variations in the availability of preferred woody species. Although patterns in relative preferences varied among the rivers, beavers consistently exhibited distinct preferences for certain species on all rivers.

To elucidate some of the subtleties involved in beaver foraging patterns in central Texas, several questions should be investigated. First, what are the mechanisms involved in colony site selection? Is there a significant difference in the woody plant community structure of forage stretches as compared to stretches of the rivers unoccupied by beavers? Is stream gradient as important to beaver site selection on higher order streams as it is on lower order streams? Is stream gradient as important to beaver colony selection in central Texas as it is in northern latitudes? Secondly, what are the differences in nutritional values of available woody forage? Does the nutritional value of a woody species vary seasonally? Does herbivory result in higher concentrations of secondary compounds in woody species?

A third area of research involving beavers as central place foragers is needed to determine how provisioning costs may vary with size-class of forage and distance from the "central place." Is central place foraging a learned or innate behavior? Finally, and probably most importantly, is the question of how foraging by beavers impacts the riparian community structure Is selective foraging by beavers detrimental to the diversity of riparian communities? This is certainly a density dependent question. What is the carrying capacity of central Texas Rivers for beaver populations. Does foraging alter the growth habits of certain plants? If so, are these alterations cumulative? Second do beavers have a positive or negative impact on the community? There are many questions concerning beaver foraging patterns which must be answered in order to effectively manage beavers and the riparian communities in which they reside.

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APPENDICES

Appendix 1. A list of riparian plants encountered within the study area along the San Marcos, Blanco, or San Gabriel Rivers, 1989-91.

Family	Scientific Name	Common Name
Taxodiaceae		
	Taxodium distichum	Bald cypress
Cyperaceae		
	Cyperus esculentus	Yellow-nut grass
	Cyperus odoratus	Fragrant flatsedge
	Cyperus uniflorus	Oneflower flatsedge
Gramineae		
	Arundo donax	Giant reed
	Paspalum dilatatum	Dallisgrass
	Panicum texanum	Texas panicum
	Cynodon dactylon	Bermudagrass
	Sorghum halepense	Johnson grass
	Cenchrus incertus	Sandbur
	Stipa leucotricha	Texas wintergrass
	Chloris cucullata	Hooded windmillgrass
	Aristida purpurea	Purple threeawn
Commelinaceae		
	Commelinantia anomala	False day flower
Liliaceae		
	Smilax bona-nox	Saw greenbriar
Amaryllidaceae		
	Cooperia pedunculata	Rain-lily

Appendix 1. continued.

Family	Scientific Name	Common Name
Iridaceae		
	Sisyrinchium ensigerum	Blue-eyed grass
Salicaceae		
	Populus deltoides	Eastern cottonwood
	Salix nigra	Black willow
Juglandaceae		
	Juglans microcarpa	Texas black walnut
	Carya illinoensis	Pecan
Fagaceae		
	Quercus macrocarpa	Bur oak
	Quercus virginiana	Live oak
	Quercus buckleyi	Texas oak
Ulmaceae		
	Celtis reticulata	Netleaf hackberry
	Celtis laevigata	Sugar hackberry
	Ulmus americanus	American elm
	Ulmus crassifolia	Cedar elm
Rhamnaceae		
	Condalia hookeri	Brasil
Ranunculaceae		
	Clematis pitcheri	Purple leatherflower
	Clematis drummondii	Old man's beard
Moraceae		
	Morus rubra	Red mulberry
	Morus alba	White mulberry
	Broussonetia papyrifera	Paper mulberry
	Maclura pomifera	Osage-orange

Appendix 1. continued.

Family	Scientific Name	Common Name
Loranthaceae		
	Phoradendron tomentosum	Mistletoe
Berberidaceae		
	Berberis trifololiata	Agarito
Papaveraceae		
	Argemone albiflora	White prickly poppy
Platanaceae		
	Platanus occidentalis	American sycamore
Rosaceae		
	Rubus trivialis	Southern dewberry
	Prunus mexicana	Mexican plum
	Prunus serotina	Black cherry
Leguminosae		
	Acacia smallii	Huisache
	Prosopis glandulosa	Honey mesquite
	Sesbania drummondii	Rattlebush
	Cercis canadensis	Redbud
	Parkinsonia aculeata	Retama
	Amorpha fruticosa	False indigo
	Sophora affinis	Texas sophora
	Sophora secundiflora	Texas mountain laurel
	Lupinus texensis	Texas bluebonnet
	Petalostemum pulcherrimum	Purple prairie clover
Krameriaceae		
	Vicia ludoviciana	Deer pea vetch

Appendix 1. continued.

Family	Scientific Name	Common Name
Oxalidaceae		
	Oxalis dillenii	Yellow wood-sorrel
Meliaceae		
	Melia azedarach	Chinaberry
Euphorbiaceae		
	Sapium sebiferum	Chinese tallow
	Cnidoscolus texanus	Bull nettle
	Euphorbia marginata	Snow-on-the-mountain
Anacardiaceae		
	Rhus lanceolata	Flame-leaf sumac
	Toxicodendron radicans	Poison ivy
Aquifoliaceae		
	Ilex decidua	Possumhaw
	Ilex vomitoria	Yaupon holly
Aceraceae		
	Acer negundo	Boxelder
Hippocastanaceae		
	Aesculus pavia	Red buckeye
Convolvulaceae		
	Ipomoea trichocarpa	Morning glory
	Convolvulus equitans	Texas bindweed
Sapindaceae		
	Sapindus saponaria	Western soapberry
	Ungnadia speciosa	Mexican buckeye
Vitaceae		
	Ampelopsis cordata	Heart-leaf ampelopsis

Appendix 1. continued.

Family	Scientific Name	Common Name
Vitaceae		
	Parthnocissus quinquefolia	Virginia creeper
	Parthnocissus heptaphylla	Seven-leaf creeper
	Vitis mustangensis	Mustang grape
	Vitis berlanderii	Spanish grape
Malvaceae		
	Malvaviscus drummondii	Turk's cap
Passifloraceae		
	Passifloria lutea	Yellow passionflower
Cactaceae		
	Opuntia lindheimeri	Texas prickly pear
Onagraceae		
	Calylophus drummondianus	Square-bud primrose
	Oenothera speciosa	Pink evening primrose
Umbelliferae		
	Torilis arvensis	Hedge-parsley
Cornaceae		
	Cornus drummondii	Rough-leaf dogwood
Ebenaceae		
	Diospyros texana	Texas persimmon
Oleaceae		
	Foresteria pubescens	Elbow-bush
	Fraxinus pensylvanica	Green ash
	Ligustrum sp.	Privet
Asclepiadaceae		
	Asclepias tuberosa	Butterfly weed

Appendix 1. continued.

Family	Scientific Name	Common Name
Boraginaceae		
	Ehretia anacua	Anacua
Rubiaceae		
	Cephalanthus occidentalis	Common buttonbush
Verbenaceae		
	Verbena bipinnatifida	Prairie verbena
	Caliicarpa americana	American beautyberry
Labiatae		
	Scutellera drummondii	Drummond skullcap
	Physostegia intermedia	Obedient-plant
	Salvia roemeriana	Cedar sage
	Salvia coccinea	Tropical sage
	Marrubium vulgare	Common horehound
	Mentha spicata	Spearmint
Solanaceae	*Solanum elaeagnifolium*	Silver-leaf nightshade
	Datura inoxia	Jimson-weed
	Solanum dimidiatum	Western horse-nettle
Scrophulariaceae		
	Verbascum thapsus	Common mullein
	Penstemon cobaea	Fox-glove
	Agalinis heterophylla	Prairie agalinis
	Buchnera floridana	Bluehearts
Caprifoliaceae		
	Sambucus canadensis	Elderberry
Cucurbitaceae		
	Cucurbita foetidissima	Buffalo gourd

Appendix 1. continued.

Family	Scientific Name	Common Name
Campanulaceae		
	Lobelia cardinalis	Cardinal flower
Compositae		
	Vernonia lindheimeri	Woolly ironweed
	Baccharis neglecta	Roosevelt weed
	Solidago altissima	Tall goldenrod
	Aster texanus	Texas aster
	Rudbeckia hirta	Brown-eyed susan
	Ratibida columnaris	Mexican hat
	Helianthus annuus	Common sunflower
	Verbesina virginica	Frostweed
	Calyptocarpus vialis	Straggler daisy
	Gaillardia pulchella	Indian blanket
	Helenium quadridentatum	Sneezeweed
	Taraxacum officinale	Dandelion
	Ambrosia psilostachya	Western ragweed
	Ambrosia trifida	Giant ragweed

Appendix 2. Frequency of individual stem usage by beavers, and plant availability within forage stretches along the San Marcos River during 1990, 1991, and combined for both years.

	1990		1991		Pooled	
species	usage	avail.	usage	avail	usage	avail
willow	89	250	61	156	150	406
cottonwood	15	21	20	34	35	55
dogwood	101	326	410	1548	511	1874
boxelder	301	1310	267	1001	568	2311
hackberry	48	528	86	537	134	1065
pecan	9	96	18	129	27	225
privet	262	791	309	1098	571	1889
red buckeye	7	47	44	111	51	158
Mx. buckeye	39	64	93	274	132	338
bur oak	30	91	34	162	64	253
Amer. elm	6	51	3	41	9	92
sycamore	10	68	25	81	35	149
green ash	5	32	2	7	7	39
chinaberry	33	190	84	447	117	637
mulberry	146	303	189	340	335	643
bald cypress	8	43	3	16	11	59
ceder elm	0	24	2	44	2	68
Totals	1109	4235	1650	6026	2759	10,261

Appendix 3. Frequency of individual stem usage by beavers and plant availability within forage stretches along the Blanco River during 1990, 1991, and combined for both years.

	1990		1991		Pooled	
species	**usage**	**avail.**	**usage**	**avail**	**usage**	**avail**
cottonwood	12	31	18	42	30	73
cedar elm	3	54	0	50	3	104
boxelder	295	1179	254	1064	549	2243
hackberry	7	233	15	329	22	562
pecan	4	70	3	75	7	145
privet	5	43	31	97	36	140
Mx. buckeye	7	17	11	31	18	48
bur oak	3	11	0	17	3	28
Amer. elm	2	40	10	47	12	87
sycamore	103	599	140	691	243	1290
green ash	51	174	80	332	131	506
bald cypress	19	130	26	156	45	286
mulberry	138	289	90	198	228	487
buttonbush	20	45	0	0	20	43
chinaberry	1	34	12	59	13	93
dogwood	22	40	0	0	22	40
Totals	901	3616	872	3758	1773	7374

Appendix 4. Frequency of individual stem usage by beavers and plant availability within forage stretches along the San Gabriel River during 1990, 1991, and combined for both years.

	1990		1991		Pooled	
species	**usage**	**avail.**	**usage**	**avail**	**usage**	**avail**
cottonwood	10	18	9	14	19	32
boxelder	342	1522	169	776	516	2298
hackberry	19	221	5	162	24	383
pecan	2	51	8	55	10	106
cedar elm	3	70	12	135	15	205
chinaberry	2	88	0	33	2	121
bur oak	14	37	22	65	36	102
Amer. elm	5	43	3	28	8	71
sycamore	37	218	41	241	78	459
green ash	196	1358	272	1114	473	2472
bald cypress	6	34	3	25	9	59
mulberry	265	629	152	472	417	1101
Mx. buckeye	0	0	5	20	5	20
dogwood	3	26	0	0	3	26
privet	5	52	0	0	5	52
Totals	1228	5206	762	3403	1990	8609