Assessment of Beaver (*Castor canadensis*) Herbivory on a Bottomland Forest in Central Oklahoma

Marco Donoso
Agricultural Research Service, University of Nevada-Reno, Reno, NV 89557

Victoria L. Jackson
Department of Biology, University of Central Oklahoma, Edmond, OK 73034

Chad B. King*
Department of Biology, University of Central Oklahoma, Edmond, OK 73034

Abstract: North American beaver (*Castor canadensis*) play a key role in engineering ecosystems by altering hydrology, forest structure, and plant species composition. We investigated beaver foraging in a bottomland forest at a human-made lake in central Oklahoma to understand if beaver were preferentially feeding on certain tree species. Beaver fed on four of the nine tree species present in the forest. Approximately 60% of trees had signs of beaver herbivory. We found a significant relationship between the degree of beaver herbivory and tree species. A significant difference was found in diameter between tree species, and a significant difference in diameter between beaver herbivory categories. We conclude that beaver were feeding more frequently on green ash due to their high density and smaller mean diameter to maximize their optimal foraging strategy.

Introduction

North American beaver (*Castor canadensis*) are recognized as ecosystem engineers that increase landscape heterogeneity and species richness (Wright et al. 2002), modify lotic functioning (Smith et al. 1991), and alter riparian forest stand density and basal area (Johnston and Naiman 1990). Beaver forage on aquatic vegetation and woody plant species in adjacent riparian and bottomland habitats (Jenkins and Busher 1979; Rosell et al. 2005).

Beaver foraging behavior affects riparian and bottomland forest succession. Previous research has shown that beaver can alter forest understory structure and species richness (Guillermo et al. 2006) and reduce the density and basal area of preferred tree species (Johnston and Naiman 1990; Barnes and Dibble 1988). Beaver selection for preferred tree species has the potential of shifting forest structure and species composition (Rosell et al. 2005). Changes in forest communities can also be driven by a combination of ungulate and beaver herbivory (Hood and Bayley 2009).

Several studies have indicated that beaver are selective foragers of woody plants. Jenkins (1979) indicated a temporal shift in foraging as beaver altered between feeding on pine (*Pinus*) to birch (*Betula*), oak (*Quercus*), and witch hazel (*Hamamelis*) over the course of two years. In one of the earliest studies of beaver herbivory, Shadle et al. (1943) found that members of the Genus *Populus* accounted for 33.8% of all tree cuttings in New York. Pinkowski (1983) showed that beaver used approximately 21% of *Populus* and 21% of *Fraxinus* that were available at the study site in North Dakota. Crisler and Russell (2010) reported that beaver girdled a greater proportion

***corresponding author: cking24@uco.edu**

of *Celtis occidentalis*, *Morus rubra*, and *Salix* sp. than other species across multiple sites in south-central Kansas. In Nevada, Harper (2001) found that beaver preferentially fed on *Populus*, *Salix*, and *Fraxinus* along a 38 km stretch of riparian habitat. At sites in Georgia and Louisiana in the southeastern United States, beaver showed a preference for sweetgum (*Liquidambar styraciflua*) relative to species composition but had little overall effect on altering forest stand density (Chabreck 1958; Brzyski and Schulte 2009).

Most components of a tree (leaves, twigs, bark) are used as a food source (Allen 1983; Jenkins and Busher 1979) and for dam and lodge construction (Allen 1983). Tree diameters that had signs of beaver herbivory vary tremendously, ranging from 1.1 cm to 31 cm (Crisler and Russell 2010; Jenkins 1980; Brzyski and Schulte 2009; Pinkowski 1983; Barnes and Dibble 1983). While there is a wide range of tree diameters that beaver feed on, the frequency of feeding is often skewed towards trees < 10 cm diameter. Often the greatest amount of foraging occurs within 25-30 m from shoreline (Barnes and Dibble 1983; Jenkins 1980).

We report the results of a study that assessed characteristics of trees that had signs of beaver herbivory at a man-made lake in central Oklahoma. Previous research has described the structure of the bottomland forest at the lake (King and Buck 2018). The bottomland forest floods frequently following periods of precipitation. Observations at the bottomland forest since 2016 suggest increased beaver herbivory during periods of flooding. The bottomland forest overstory is dominated by *Salix nigra* (black willow) and *Fraxinus pennsylvanica* (green ash). However, black willow dominates basal area while green ash dominates density (King and Buck 2018). Given this difference between these two tree species, we tested whether beaver at the man-made lake have a selection preference. Green ash are, on average, smaller diameter and higher density relative to black willow. We expect that beaver would maximize their foraging by preferentially feeding on and collecting the smaller diameter and higher density green ash. The objectives of this study were: 1) categorize the degree of beaver herbivory on black willow and green ash; and 2) assess beaver preference for tree species.

Methods

Study Area

This study occurred in a section of bottomland forest at Arcadia Lake, Oklahoma County, Oklahoma (35˚38'54"N, 97˚24'03"W). The lake is a man-made water source that covers 736.5 ha (1820 ac) when the lake is at its standard pool elevation (306.6 m; 1006 ft). Construction of the lake began in the early 1980s, and the lake reach conservation pool status in 1987 (U.S. Army Corps of Engineers 2020, https://www.swt.usace.army.mil/Locations/Tulsa-District-Lakes/Oklahoma/Arcadia-Lake/).

Regional climate (Oklahoma Climate Division 5) is warm-temperate with mean annual temperature of 15.7˚C (60.2˚F). The warmest months include July and August and the coldest months are December and January. Mean annual precipitation is 87.4 cm (34.41 in) (NOAA National Centers for Environmental Information 2020, https://www.ncdc.noaa.gov/cag/).

Our study site is 4.7 ha and is located in the northwest section of Arcadia Lake. The site was previously defined as a black willow-green ash (*Salix nigra-Fraxinus pennsylvanica)* bottomland forest (King and Buck 2018). Cottonwood (*Populus deltoides*), silver maple (*Acer saccharinum*), Osage orange (*Maclura pomifera*), and honey locust (*Gleditsia triacanthos*) are minor components of the forest overstory.

Data Collection

We established three belt transects that were 150 m in length and 10 m wide. Transects were oriented southeast-northwest based on the shape of the study site. Distance between belt transects was exactly 50 m. All trees (diameter at breast height (DBH) > 8 cm) and saplings (height > 1.3 m; DBH < 8 cm) were identified to species. Diameter of trees and saplings were measured at breast height (1.3 m above ground level) using a DBH tape measure and assessed for beaver herbivory. All data collection occurred during September-October 2019.

Beaver herbivory was categorized in the field during sampling. We classified the degree of beaver herbivory into five categories based on visual observations at the study site: 0 = no evidence of beaver herbivory; 1 = bark removed, < 50% circumference of tree; 2 = bark removed, > 50% circumference of tree; 3 = gnawing, < 50% through tree, tree standing; 4 = gnawing, > 50% through tree, tree standing; 5 = felled tree. For statistical analysis, we pooled data into two categories based on the presence or absence of beaver herbivory (1 = no herbivory, 2 = herbivory).

Data Analysis

We analyzed the effect of beaver herbivory on the two most common tree species in our sampling, green ash and black willow, due to sample sizes. We tested for effects of tree species and beaver herbivory category on tree diameter using a two-factor analysis of variance (ANOVA). We used a chi-square (χ^2) contingency test to determine if there was a relationship between the category of tree damage and the species of tree. All analyses were conducted at $\alpha = 0.05$.

Results

Table 1. Descriptive statistics of trees sampled and tree characteristics that exhibited beaver herbivory at Arcadia Lake, Oklahoma.

Species	Number of Stems	Overall Mean Diameter (cm) (±SD)	Beaver Herbivory Tree Diameter (cm) (±SD)	Percentage of Trees with Beaver Herbivory (# stems)
Black willow	83	25.4 (7.55)	26.5 (6.82)	28% (23)
Green ash	170	12.5 (5.23)	13.2 (4.69)	78% (132)
Silver maple	6	17.9 (8.23)	[a]7.30	17% (1)
Boxelder	3	5.97 (6.70)	8.05 (7.99)	67% (2)
Total	262			

[a]The value represents the diameter at breast height (cm) of a single silver maple.

We collected data on 262 trees across four species. Green ash was the most common tree species encountered within the belt transects (n = 170) followed by black willow (n = 83), silver maple (n = 6), and boxelder (n = 3). The tree species with the largest diameter (cm) was black willow (¯ = 25.4 cm ± 7.55 SD). Green ash had the highest proportion of trees that exhibited signs of beaver herbivory (78%, n = 132) (Table 1).

Beaver herbivory was greater on the two most common tree species, green ash and black willow. The largest diameter black willow and green ash that had beaver herbivory were 37.9 cm and 26.2 cm, respectively. Black willow had a greater number of trees that did not have herbivory compared to green ash (Table 2). Smaller diameter size classes (< 20 cm DBH) of green ash accounted for approximately 70.6% of beaver herbivory (Figure 1). This is in contrast to black willow in which approximately 21.7% of trees in the larger size classes (> 20 cm DBH) exhibited evidence of beaver herbivory. There was also a difference in total proportion of trees that exhibited beaver herbivory (green ash = 77.7%; black willow = 27.7%).

Table 2. Categories of beaver herbivory and number of green ash and black willow trees that exhibited the degree of beaver herbivory. 0 = no sign of beaver herbivory; 1 to 2 = bark removed; 3 to 4 = bark removed and evidence of gnawing; 5 = a completely felled tree.

	0	1 to 2	3 to 4	5
Green ash	38	48	48	36
Black willow	60	17	6	0
Total	98	65	54	36

There was a significant relationship between the degree of beaver herbivory and tree species based on chi-square contingency test results ($\chi^2_{3, 253} = 66.315$, $P < 0.0001$). Approximately 72.2% of black willow sampled at the study site did not have any sign of beaver herbivory while only 22.4% of green ash did not have beaver herbivory (Figure 1). There was a greater number of green ash that had been felled by beaver compared to black willow. Statistical analysis indicated a significant difference in diameter between tree species ($F_{1, 249} = 241.233$, $p < 0.0001$) and a significant difference in diameter between herbivory categories ($F_{1, 249} = 7.254$, $P = 0.008$). There was no significant interaction between tree species and herbivory category ($F_{1, 249} = 1.268$, $P = 0.261$). Approximately 61.3% (n = 155) of trees among green ash and black willow had evidence of beaver herbivory (Figure 1).

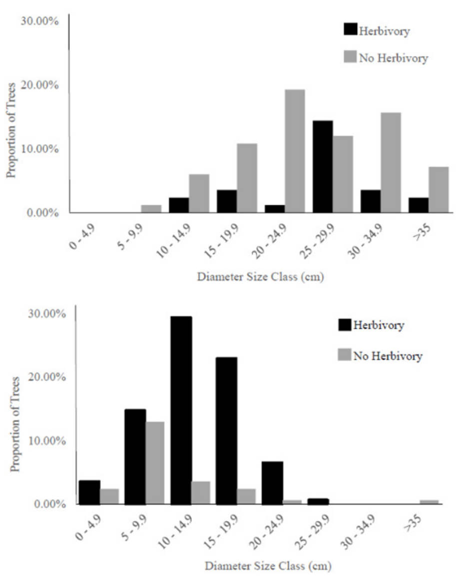

Figure 1. Proportion of black willow (top) and green ash (bottom) that had evidence of beaver herbivory or no herbivory based on tree size classes (cm).

Discussion

Our study at Arcadia Lake in Oklahoma County, Oklahoma indicates that beaver herbivory occurred on four tree species. The most common tree species that were fed on at the study site were black willow and green ash. Analysis of beaver herbivory on the two most common tree species indicates a significant relationship between beaver herbivory category and tree species.

We found that black willow and green ash accounted for 98% of trees with evidence of beaver herbivory (Table 1). Shadle et al. (1943) found that seven tree genera across six beaver colonies accounted for 93% of beaver cuttings with *Populus* and *Carpinus* accounting for 56.9% of total beaver cuttings. Crisler and Russell (2010) in Kansas found that the most abundant tree species, northern hackberry and red mulberry, were also the most frequently girdled at their study sites. Gerwing et al. (2013) suggest that beaver selection of certain plant species is a function of the site, distance of plant species from water, and the plant species, themselves.

Previous research at our study site indicated that black willow and green ash are the two most important overstory tree species (King and Buck 2018). This suggests that beavers at Arcadia Lake are utilizing more often what is available to them. The previous literature (Shadle et al. 1943, Crisler and Russell 2010) and others at sites across North America (Brenner 1962, Pinkowski 1983, Johnston and Naiman 1990, Harper 2001) all indicate the most common tree species at their study sites and beaver selection for those common species. This suggests a flexibility in the beaver's generalist herbivory.

We found a discrepancy in beaver herbivory when assessing tree diameter. Black willow were the largest diameter trees while green ash were smaller diameter (Table 1). Beaver did feed on larger diameter black willow and smaller diameter green ash (Figure 1). King and Buck (2018) have previously demonstrated that black willow dominated basal area while green ash dominated tree density at our study site. Allen (1983) based on a review of early 20th century beaver research reported that beaver selected trees less than 11 cm DBH. However, Jenkins (1980), and Raffel et al. (2009), report that beaver selected a range of tree size classes and that the selection of trees changed with an increasing distance from water. While we did not assess changes in beaver selection with distance from lake edge, we do note that most herbivory on black willow occurred along the edge of the lake while herbivory on green ash occurred at a greater distance from the lake edge. The feeding on large diameter black willow and small diameter green ash may be an artifact of the study site given the current size classes of trees that are available to the beaver.

There was evidence of different feeding behavior by beaver at the study site. This is highlighted by the beaver herbivory categories (Table 2). We show a significant relationship between beaver herbivory category and tree species (black willow and green ash). Collectively, 38.7% of black willow and green ash had no signs of beaver herbivory (Table 2). Based on our categories of beaver herbivory, green ash had similar number of trees that had bark removed only (categories 1-2), gnawing (categories 3-4), and completely felled (category 5). There were fewer black willow with signs of herbivory, but bark removal was the most common sign of beaver herbivory (categories 1-2). Bark is an important woody food source for beaver, and Svendsen (1980) reported that beaver in southeast Ohio fed on bark during early spring and fall months often when terrestrial and aquatic herbaceous vegetation was limiting. We found that bark removal was the most common type of damage to black willow and green ash, accounting for 41.9% of trees that were damaged. Similar to our results from Oklahoma, King et al. (1998) found that bark removal was the most common type of beaver damage to trees at Caddo Lake, Texas.

All felled (beaver herbivory category 5) trees were green ash (Table 2). Green ash at the study site have the highest tree density but a lower basal area relative to black willow (King and Buck 2018). While we did not directly assess the number of ash trees removed by beaver at the site, most ash trees remained lying next to the stump. This likely indicates the felling of ash trees was to access canopy leaves and branches either for food or for caching (Jenkins and Busher 1979). Additionally, Busher (1996) found that beaver in western Massachusetts cached or immediately consumed branches of the most common tree species. We found a significant difference between tree diameter and beaver herbivory category which may indicate that beaver are maximizing their energy consumption (Gallant et al. 2016) by selecting for a resource that is a higher density but smaller in size. Selecting for a smaller size resource requires less time and energy to fell but maximize the energy intake by felling multiple ash trees relative to larger black willow at the study site. This would also minimize predation risk (Pinkowski 1983). Nolet et al. (1994) also found that Eurasian beaver (*Castor fiber*) selected for shrub willows, which are smaller in diameter, than tree willows.

While black willow and green ash were most commonly fed on by beaver, other tree species are present at the study site. We documented beaver herbivory on silver maple and boxelder, but that was rare. King and Buck (2018) documented nine tree species that were in the forest overstory or understory. Cottonwood is the third most important overstory species at the study site (King and Buck 2018), but we did not document beaver herbivory on cottonwood within the belt transects. One possible explanation for the lack of herbivory on cottonwood is that the majority of cottonwood are furthest from the lake edge that would require beaver traveling overland. This is also the case for the other tree species at the study site. Most black willow and green ash are at or near the lake edge.

Another possible explanation for higher beaver herbivory on black willow and green ash are higher nutrient availability and lower secondary compounds in the wood and bark of these tree species. Nolet et al. (1994) argue that selection for willow may be an avoidance of plant defenses like resins, which are generally lower in willow species. Multiple ash species are known to have secondary defense compounds that are associated with plant-herbivore interactions (Eyles et al. 2007). Our data on beaver herbivory suggests that secondary compounds likely have a minimal influence on tree selection by beaver given that a greater proportion of green ash exhibited evidence of beaver herbivory compared to black willow. Nutritional value of bark and wood may be an explanation of beaver selection for black willow and green ash at our study site. Hill et al. (2012) assessed the concentrations of multiple nutrients in four ash species and found that green ash was intermediate in nutrition relative to other ash species. Five and ten-year-old cultivar willows in New Zealand were found to have similar protein levels (Kemp et al. 2001) compared to eight-year-old green ash in Hill et al. (2012). In a cafeteria-style study, Doucet and Fryxell (1993) found that while beaver had a preference for trembling aspen (*Populus tremuloides*), they consumed all five species that were presented. They found that each plant species had different nutrient concentrations and concentrations changed throughout the study period. Jenkins (1979) argued that seasonal and annual shifts in beaver herbivory may be related to changes in nutrient concentrations in bark and wood. While we did not assess temporal patterns in tree selection, it is possible that beaver at Arcadia Lake are foraging black willow and green ash at particular times during the year that is associated with changing nutrient availability.

Our study indicates that beavers at Arcadia Lake, Oklahoma County, Oklahoma are using the most common tree species available to them. Evidence indicates that the beavers are foraging green ash more frequently than black willow, the two most common tree species at the study site. Foraging on green ash is likely due to their smaller diameter and higher density. As beaver densities continue to increase, we encourage further studies of beaver herbivory in southern states where beaver have the ability to be active year-round due to less long-term freezing temperatures during the winter.

Acknowledgments

This project was partially funded through the University of Central Oklahoma Office of High Impact Practices RCSA Grant Program. We thank the City of Edmond for continued support to study the Arcadia Lake ecosystem and permission to access the site. We thank T. Dawkins, W. Babb, and E. Rodgers for their assistance in the field. We thank the reviewers of this manuscript for helpful recommendations.

References

Allen, A. W.(1983). Habitat suitability index models: beaver. U.S. Fish and Wildlife Service FWS/OBS-82/10.30. 20pp.

Brenner, F. J. (1962). Foods consumed by beavers in Crawford County, Pennsylvania. The Journal of Wildlife Management 26:104-107.

Brzyski, J. R. & Schulte, B. A. (2009). Beaver (*Castor canadensis*) impacts on herbaceous and woody vegetation in southeastern Georgia. American Midland Naturalist 162:74-86.

Busher, P. E. (1996). Food caching behavior of beavers (*Castor canadensis*) selection and use of woody species. The American Midland Naturalist 135:343-348.

Chabreck, R. H. (1958). Beaver-forest relationships in St. Tammany Parish, Louisiana. Journal of Wildlife Management 22:179-183.

Crisler, J. D. & Russell, F. L. (2010). Patterns of beaver herbivory in south-central Kansas riparian woodlands. Transactions of the Kansas Academy of Science 113:161-176.

Doucet, C. M. & Fryxell, J. M. (1993). The effect of nutritional quality on forage preference by beavers. Oikos 67:201-208.

Eyles, A., Jones, W., Riedl, K., Cipollini, D., Schwartz, S., Chan, K., Herms, D. A. & P. Bonello, P. (2007). Comparative phloem chemistry of Manchurian (*Fraxinus mandshurica*) and two North Amerian ash species (*Fraxinus americana* and *Fraxinus pennsylvanica*). Journal of Chemistry Ecology 33:1430-1448.

Gallant, D., Leger, L., Tremblay, E., Berteaux, D., Lecomte, N. & Vasseur, L. (2016). Linking time budgets to habitat quality suggests that beavers (*Castor canadensis*) are energy maximizers. Canadian Journal of Zoology 94:671-676.

Gerwing, T. G., Johnson, C. J., & Alstrom-Rapaport, C. (2013). Factors influencing forage selection by the North American beaver. Mammalian Biology 78:79-86.

Guillermo, M. P., Lencinas, M. V., Escobar, J., Quiroga, P., Malmierca, L., & Lizarralde, M. (2006). Understory succession in *Nothofagus* forests in Tierra del Fuego (Argentina) affected by *Castor canadensis*. Applied Vegetation Science 9:143-154.

Harper, B. J. (2001). The ecological role of beavers (*Castor canadensis*) in a southwestern desert stream. M.S. Thesis. University of Nevada-Las Vegas, Las Vegas, NV. 64pp.

Hill, A. L., Whitehill, J. G. A., Opiyo, S. O., Phelan, P. L., & Bonello, P. (2012). Nutritional attributes of ash (*Fraxinus* spp.) outer bark and phloem and their relationships to resistance against the emerald ash borer. Tree Physiology 32:1522-1532.

Hood, G. A., & Bayley, S. E. (2009). A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. Forest Ecology and Management 258:1979-1989.

Jenkins, S. H. (1979). Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112-116.

Jenkins, S. H. (1980). A size-distance relation in food selection by beavers. Ecology 61: 740-746.

Jenkins, S. H. & Busher, P. E. (1979). *Castor canadensis*. Mammalian species no. 120. American Society of Mammalogists 1-8.

Johnston, C. A. & Naiman, R. J. (1990). Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Research 20:1036-1043.

Kemp, P. D., Mackay, A. D., Matheson, L. A., & Timmins, M. E. (2001). The forage value of poplars and willows. Proceedings of the New Zealand Grassland Association 63:115-119.

King, C. B. & Buck, J. (2018). Characteristics of a bottomland hardwood forest at Arcadia Lake with special emphasis on green ash (*Fraxinus pennsylvanica*, Marshall). Oklahoma Native Plant Record 18:4-18.

King, S. L., Keeland, B. D., & Moore, J. L. (1998). Beaver lodge distributions and damage assessments in a forested wetland ecosystem in the southern United States. Forest Ecology and Management 108:1-7.

Nolet, B. A., Hoekstra, A., & Ottenheim, M. M. (1994). Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. Biological Conservation 70:117-128.

Pinkowski, B. (1983). Foraging of beavers (*Castor canadensis*) in North Dakota. Journal of Mammalogy 64:312-314.

Raffel, T. R., Smith, N., Cortright, C., & Gatz, A. J. (2009). Central place foraging by beavers (*Castor canadensis*) in a complex lake habitat. The American Midland Naturalist 162:62-73.

Rosell, F., Bozser, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review 35:248-276.

Shadle, A. R., Nauth, A. M., Gese, E. C., & Austin, T. S. (1943). Comparison of tree cuttings of six beaver colonies at Allegany State Park, New York. Journal of Mammalogy 24:32-39.

Smith, M. E., Driscoll, C. T., Wyskowski, B. J., Brooks, C. M., & Cosentini, C. C. (1991). Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. Canadian Journal of Zoology 69:55-61.

Svendsen, G. E. (1980). Seasonal change in feeding patterns of beaver in southeastern Ohio. The Journal of Wildlife Management 44:285-290.

Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape level. Oecologia 132:96-101.

Submitted July 8, 2024 Accepted November 10, 2024