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Patterns in Beaver Herbivory in South-Central Kansas Riparian Woodlands

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Abstract

Beaver (*Castor canadensis*) herbivory can strongly affect the physiognomy and successional dynamics of forests and woodlands near bodies of water. In the central and southern Great Plains, the riparian zones that occur in a grassland / cropland matrix are foci of biodiversity and beaver activity, but little is known about patterns of beaver damage in these areas. We conducted a regional survey of beaver girdling of trees in riparian woodlands in south-central Kansas to determine 1) how the frequency of girdling was related to distance from streams, 2) whether there were differences among tree species in the frequency of girdling and, if so, which species were damaged most and 3) how the probability of beaver girdling varied with tree diameter. The frequency of girdling of trees declined more rapidly with distance from water (< 10 m) than in most northern ecosystems where beaver foraging patterns often have been quantified. Damage occurred significantly more frequently on *Celtis occidentalis*, *Morus rubra* and *Salix* sp. than on *Maclura pomifera*, *Catalpa speciosa* and *Ulmus* sp. Beavers avoided very small- and large-diameter stems, but within the range of stem diameters that beavers gnawed, the probability of girdling decreased with increasing stem diameter. Distance to the stream did not alter the distribution of girdling among tree species nor did it change the relationship between girdling probability and stem diameter. In south-central Kansas riparian woodlands, beavers have the potential to alter woodland physiognomy by reducing the density of the sapling-small adult tree layer. Further, their strong preferences among tree species suggest the potential to alter tree species composition by affecting regeneration patterns. However, at most sites these effects will be weak >10 m from streams.

Introduction

Beaver (*Castor canadensis*) gnawing is a form of herbivory that is likely to have rapid and far-reaching effects upon riparian plant community composition. By killing adult trees and altering tree morphology, beavers can increase light availability to understory vegetation (Naiman, Johnston and Kelley 1988, Donkor and Fryxell 2000). These changes can occur very quickly compared to effects of herbivores that only consume tree seedlings and small saplings. Further, beavers often show pronounced species-specific gnawing preferences (Jenkins 1980, Pinkowski 1983, Lesica and Miles 2004). Differential damage among tree species can alter community composition by changing inter-specific differences in mortality or reproductive rates (Naiman, Johnston and Kelley 1988, Donkor and Fryxell 2000, Lesica and Miles 2004). In boreal ecosystems, for example, beaver gnawing drives changes in the relative abundances of preferred vs. non-preferred species along gradients away from water (Donkor and Fryxell 2000, Barnes and Mallik 2001). Given beavers' strong dietary preferences and their potentially large impact on individual tree performance, changes in beaver population sizes might be expected to profoundly affect riparian plant communities.

Beavers often have been used to test central place foraging theory. Therefore, central place foraging theory may provide a basis for predicting how effects of beavers upon riparian tree communities vary with distance from water. Specifically, theory predicts that central place foragers will become increasingly selective in their choice of food items at longer distances from the home base (Schoener 1979, Orians and Pearson 1979). Beavers often narrow the range of stem diameters (Jenkins 1980, Pinkowski 1983, Haarberg and Rosell 2006, Raffel et al. 2009) and, in some ecosystems, narrow the range

of tree species (Pinkowski 1983, Raffel et al. 2009) that they cut (meaning “girdle, fell and remove the stem”) at longer distances from water. Therefore, not only the magnitude, but also the direction of beavers’ effects on the riparian plant community may vary with distance from the stream.

Historically, beavers were abundant throughout North America as far south as northern Mexico (Naiman, Johnston and Kelley 1988). After being nearly extirpated from the United States by intense commercial hunting and wetland destruction in the 19th century, beaver populations throughout their former range have increased since the early- to mid-20th century (Cockrum 1952, Naiman, Johnston and Kelley 1988). Because canopy trees in many riparian woodlands may have recruited during periods when beavers were rare, renewed species-specific gnawing damage may cause changes to the current composition of these woodlands. While ecologists have explored the impacts of beavers on tree species composition near lakes or rivers in boreal (Belovsky 1984, Donkor and Fryxell 2000), montane (McGinley and Whitham 1985) and eastern deciduous forest (Jenkins 1980, Raffel et al. 2009) regions of North America, little research has addressed the role of beaver herbivory in affecting riparian community composition on the central or southern Great Plains. In Great Plains ecosystems, where cropland and grassland are the predominant land cover types, riparian woodlands add habitat complexity and enhance biodiversity (Magill, Smith and Ray 2003, Hall et al. 2006).

Here we present results of a survey of patterns in beaver girdling of trees in south-central Kansas riparian zones. “Girdling” refers to stripping bark around the entire circumference of a stem. We consider “cutting,” which involves beavers girdling a stem, felling the stem and removing the stem to be a sub-set of “girdling.” We focused upon

“girdling”, rather than “cutting” only, because bark removal around the entire circumference will kill a stem regardless of whether the stem is felled. Although beavers can strongly affect riparian zones by altering stream hydrology, we focus only upon patterns and potential direct effects of girdling. In this study, we asked 1) how far from streams do beavers girdle trees? 2) which tree species have the highest probability of being girdled? and 3) how does girdling probability vary with stem diameter? In addition, we ask whether the distribution of beaver girdling among tree species and the diameter of stems girdled depend upon distance to streams. Our goal is to present observational data that can be used to formulate hypotheses for direct effects of beavers on central Great Plains riparian tree communities. Ultimately, testing hypotheses that may arise from our data will require experimental manipulations, such as beaver exclusion experiments.

Methods

We surveyed beaver girdling of trees in nine riparian woodlands along free-flowing reaches of streams between September 2007 and December 2009 (Fig. 1, 2 (for stream names)). Criteria for selecting a site were 1) the riparian woodland was >35 m wide on at least one side of the stream and 2) girdling had occurred sufficiently recently that stems that were cut could be identified from bark at the stem base if there were no re-sprouts.

At each site, we sampled trees along three transects that were perpendicular to the stream using the point-quarter sampling method (Cottam and Curtis 1956). The starting point for each transect was chosen by walking along the stream until beaver gnawing on trees or shrubs on the bank was observed. Adjacent transects were separated by ≥ 10 m. Along each transect, we began sampling 5 m from the stream edge and sampled at 5 m

intervals up to 40 m from the stream. At the Miller site we sampled only up to 35 m from the stream where we reached the woodland edge. No individual tree was sampled more than once along a transect or in neighboring transects. We only sampled species that achieve a tree life-form at maturity.

At each sampling point (5 m – 40 m from the stream), the presence / absence of beaver girdling on the nearest tree in each quadrant was noted. For sampling points between 5 m and 20 m from the stream, but not sampling points ≥ 25 m, the nearest tree in each quadrant also was identified to species and its diameter at breast height (hereafter, “dbh”) was measured, regardless of whether the stem was girdled or not. If the tree had been felled and the upper trunk removed, we used species-specific regression relationships to estimate dbh from stem diameter at 30 cm height (hereafter, “basal diameter”). We developed these regressions from data collected at four sites (Harvey East, Harvey West, Chaplin and Miller) where we measured both dbh and basal diameter on all trees for which the stem was not removed.

Data Analysis

Our goal was to identify general patterns in beaver damage rather than to explain site-to-site differences, so we pooled data from all nine sites. In all statistical analyses, the dependent variable was categorical reflecting whether the stem was girdled or not. SAS version 9.1 was used for statistical analyses.

We analyzed a 6 (distance classes) x 2 (girdling classes) contingency table with a chi-square test to evaluate whether the probability that beavers girdled a tree depended on distance from the stream. Distances were 5 m, 10 m, 15 m, 20 m, 25 m and ≥ 30 m. Data

from sampling points ≥ 30 m were pooled because damage was rare at these distances. Upon finding that the frequency of beaver damage did vary with distance, we analyzed 2 X 2 contingency tables with chi-square tests to identify a distance threshold at which the frequency of girdling differed significantly from at 5 m. According to Benjamini and Hochberg (1995)'s procedure for controlling the false discovery rate in multiple comparisons, these pair-wise distance comparisons did not require lowering the significance threshold from $p < 0.05$.

For analyses of differences among tree species in the proportion of individuals girdled, and for analyses of the relationship between stem diameter and the probability of being girdled, we used data collected ≤ 20 m from streams only. We analyzed a 9 (tree species) X 2 (girdling classes) contingency table with a chi-square test to evaluate whether the proportion of individuals girdled differed significantly among tree species. We then analyzed 2 X 2 contingency tables with Fisher's exact tests to identify pairs of tree species that differed significantly in their frequency of girdling. We controlled the false discovery rate at $p = 0.05$ for these comparisons among species pairs using Benjamini and Hochberg (1995)'s significance level adjustment. Using this adjustment, the threshold for significance in the species pair-wise comparisons was set at $p \leq 0.023$. Although we sampled 14 tree species, five were too rare (< 15 individuals) for analysis. A sample size of 15 individuals allows us to detect a 50% difference between two species in the proportion of individuals girdled (e.g. 75% girdled vs. 25% girdled) at $p < 0.0236$ with a power of ≥ 0.71 . In fact, the smallest sample sizes used in the pair-wise species comparisons were 16 (*Catalpa*) and 18 (*Salix*).

We used logistic regression to determine whether the probability that a tree suffered beaver girdling was related to the tree's dbh. When a tree had been "cut," we estimated dbh from basal diameter. Because Raffel et al. (2009) found a quadratic relationship between stem diameter and probability of being "cut," we used deviance values to evaluate the fit of a logistic regression model for girdling probability in which the independent variable was dbh vs. fit of a logistic regression model that included both dbh and dbh^2 as independent variables. Lower deviance values indicate better fit.

Central place foragers are predicted to become increasingly selective at greater distances from the home base (Schoener 1979, Orians and Pearson 1979). To evaluate whether the distribution of beaver girdling among tree species depended on distance to the stream, we used a chi-square test to analyze 2 X 2 X 4 contingency tables that included girdling category, distance to the stream and tree species. We used two distance categories; ≤ 10 m vs. > 10 m-20 m. We used data for four tree species that we showed to be either of high or intermediate preference to beavers and that were represented by ≥ 15 individuals both ≤ 10 m and > 10 m from streams. We did not include tree species that were strongly discriminated against by beavers in this analysis because increases in selectivity with distance are most likely to be manifest among relatively preferred species. To evaluate whether the distribution of girdling among different size trees depended upon distance, we conducted logistic regression with distance category, dbh, dbh^2 and the interaction between dbh X distance in the model.

In testing predictions of central place foraging theory we used distance from the stream edge as a surrogate for distance from the bank den. Therefore, our measure of distance from the "home base" does not include the distance that beavers traveled through

water to the shore where they foraged. Although the den is the “home base,” distance from the stream edge has been used by all previous studies of beaver foraging from streams that we found (McGinley and Whitham 1985, Lesica and Miles 2004, Haarberg and Rossell 2006, Bryzski and Schulte 2009) and, hence, facilitates cross-system comparisons.

Distance traveled through water may have less impact on beaver foraging decisions than distance traveled on land because predation risk for beavers in water is less (Basey and Jenkins 1995) and buoyancy provided by water is hypothesized to reduce the energetic costs of carrying food (Raffel et al. 2009). Raffel et al. (2009) showed that, for beaver colonies in an Ohio reservoir, the distance through the water from the lodge to trees had a much weaker, although statistically significant, effect than distance from the shore to trees in explaining beaver foraging preferences even though distances through water were 10X greater than the distances traveled on land.

To evaluate whether differences among tree species in girdling probability result from differences in the species’ stem diameters, we used a likelihood ratio test to compare the fit of a logistic regression model that included both dbh, dbh^2 and tree species as independent variables with the fit of a model that included only dbh and dbh^2 . If the more complex model did not explain more of the variability in probability of girdling then we could attribute differences among tree species in girdling frequency to differences in stem diameters. Similarly, to evaluate whether including stem diameter improved explanatory ability over logistic regression models that included only tree species, we compared the fit of a model that included tree species only with the fit of a model that included stem diameter (both dbh and dbh^2) using a likelihood ratio test.

Results

Tree species composition and beaver damage in south-central Kansas riparian zones.

The number of tree species encountered along transects within 20 m of streams varied between four (Harvey West) and ten (Chaplin) per site (Fig. 2). *Celtis occidentalis* was the most abundant tree species among individuals taller than breast height at five sites and *Fraxinus pennsylvanica*, *Ulmus* sp., *Cornus drummondii* and *Morus rubra* were each the most abundant species at a single site. Although *Populus deltoides* individuals were relatively rare, at three sites they accounted for the largest fraction of total stem area (mm^2), estimated from dbh. We did not distinguish between *Salix amygdaloides* and *Salix nigra* because the species hybridize (Little 1979).

The frequency of girdling of trees within 40 m of streams varied from 1.0% at Harvey East to 20.8% at Kaw (mean across all sites: $11.1\% \pm 2.17$). A large proportion of girdled stems were not “cut.” Only 58.1% of girdled stems were felled and removed.

Beaver damage in relation to distance to the stream

The probability that a tree was girdled by beavers depended upon distance to streams (Fig. 3; $\chi^2_5 = 72.21$, $p < 0.0001$). At all distances >5 m, the proportion of stems girdled was significantly less than at 5 m (p -values < 0.05). The median distance of girdled trees from the stream was 5 m at two sites, 10 m at six sites and 20 m at one site. The maximum distance of girdled trees was 5 m at one site, 10 m at two sites, 15 m at two sites, 20 m at two sites, 25 m at one site and 35 m at one site.

Beaver damage in relation to tree species

The proportion of individuals girdled varied among tree species (Fig. 4; $\chi^2_8 = 48.21$, $p < 0.0001$). In pair-wise comparisons, *Celtis occidentalis*, *Morus rubra* and *Salix* sp. had a significantly higher proportion of individuals girdled than *Catalpa speciosa*, *Maclura pomifera*, *Populus deltoides* and *Ulmus* sp. (Table 1). Within these two groups of species, there were no significant differences in the frequency of girdling. The probabilities of girdling for *Cornus drummondii* and *Fraxinus pennsylvanica* relative to other species were either intermediate between the “*Celtis*, *Morus*, *Salix*” group and the “*Catalpa*, *Maclura*, *Populus*, *Ulmus*” group or were not as clearly resolved. *Cornus drummondii* was girdled more frequently than *M. pomifera*, but did not differ from any other species. *Fraxinus pennsylvanica* was girdled more frequently than *M. pomifera*, *P. deltoides* and *Ulmus* sp., but not *C. speciosa*, and it was girdled less frequently than *Salix* sp.

Among the species that were frequently girdled (*Celtis occidentalis*, *Morus rubra*) or girdled at intermediate frequency (*Fraxinus pennsylvanica*, *Cornus drummondii*) and had ≥ 15 stems both ≤ 10 m from water and > 10 from water, the relative probabilities of suffering girdling damage did not depend on distance ($\chi^2_3 = 5.29$, $p = .152$). In other words, there was no indication that the distribution of girdling among these tree species depended on distance to water.

Beaver damage in relation to tree size—For the probability that a stem was girdled, logistic regression models with dbh and dbh² as explanatory variables fit better than models with dbh only (dbh and dbh²: deviance = 215.08; dbh: deviance = 231.9), indicating a quadratic effect of stem diameter on girdling. This effect of dbh² on probability of girdling was significant ($\chi^2_1 = 9.73$, $p = 0.002$). The quadratic effect likely arose because only stems between 10.7 mm and 310 mm dbh were girdled; none of the 37

stems <10.7 mm dbh were girdled nor were any of the 28 stems >310 mm dbh girdled.

Within the diameter range in which stems were gnawed (10.7 mm to 328mm), the probability of girdling was significantly, negatively related to dbh ($\chi^2_1 = 16.29$, $p < 0.0001$). We found no indication that the relationship between stem diameter and the probability of girdling depended on distance from the stream (dbh X distance: $\chi^2_1 = 1.4$, $p = 0.237$).

Logistic regression models that included both stem diameter and tree species explained significantly more of the variation in the probability that a stem would be girdled (-2Log Likelihood = 37.98, $p < 0.001$) than did models that included only stem diameter. The improvement in logistic regression models that included species and stem diameter (both dbh and dbh²) over models that included only tree species was marginally significant (-2Log Likelihood = 5.34, $p=0.069$).

Discussion

The frequency of girdling by beavers differs greatly among tree species and size classes in south-central Kansas riparian zones. These species- and diameter-related differences in girdling frequency create the possibility that beavers could affect riparian woodland tree species composition and physiognomy. Strong effects of beavers on riparian woodlands in our region, however, will be confined to the immediate vicinity of streams because girdling frequency declines rapidly with distance.

What is the likely affect of beaver girdling upon physiognomy, tree species composition and succession in south-central Kansas riparian woodlands? The immediate effects of beavers upon riparian woodland physiognomy will be determined by the sizes of

stems that they kill. As Raffel et al. (2009) showed for beavers foraging in eastern deciduous forest adjacent to a reservoir, our data indicate that beavers avoid both large and very small stems. The threshold stem diameter below which girdling did not occur was very similar in our study and in Raffel et al. (2009); we found no trees <10.7 mm dbh that were girdled and Raffel et al. (2009) found that stems <20 mm basal diameter were avoided. Within the range of diameters used by beavers, however, we found that smaller diameter stems are girdled at a higher rate than larger stems. Therefore, the short-term effects of beaver girdling on south-central Kansas woodland physiognomy are to reduce the density of the sapling-small adult layer. Effects upon canopy density will occur if high rates of girdling persist for decades, suppressing recruitment to canopy size classes as overstory trees die. Reductions in understory and canopy densities, however, depend upon no compensatory recruitment by tree species that are not heavily used by beavers.

Tree species in south-central Kansas riparian woodlands differ greatly in their frequency of girdling by beavers. In other regions, beavers prefer *Populus* species (McGinley and Whitham 1985, Donkor and Fryxell 2000, Lesica and Miles 2004), but *Populus deltoides* may have avoided girdling at our study sites because stems were large (all ≥ 276 mm dbh). With the exception of *P. deltoides*, tree species that experienced the lowest rates of girdling in south-central Kansas riparian zones are not indigenous. *Maclura pomifera* is native to Texas and extreme southern Oklahoma (Little 1979) and *Catalpa speciosa* is native to the mid-lower Mississippi River valley (Little 1979). Elms were either *Ulmus pumila*, native to central Asia (Little 1979), or, based on their intermediate leaf morphology, hybrids between *U. pumila* and native *U. americana*. Lesica and Miles (2004) suggest that beaver avoidance of the exotics Russian olive

(*Elaeagnus angustifolia*) and tamarisk (*Tamarix* spp.) and high rates of damage to native cottonwoods in eastern Montana may result from a lack of evolutionary history between beaver and these exotic trees, an example of the exotic species experiencing “enemy release” in their invaded range. In south-central Kansas, uncertainty concerning the origins of beaver populations makes it difficult to attribute differences among tree species in girdling frequencies to local adaptation in beaver populations to the native tree community. Although Cockrum (1952) suggests that modern Kansas beaver populations are descended from isolated colonies that escaped extirpation in north-central and northwestern Kansas, in general, the recovery of North American beaver populations during the 20th century involved extensive re-locations (Jenkins and Busher 1979). Therefore, indigenous south-central Kansas riparian tree species also may be evolutionarily novel to our beavers. Regardless of the mechanism that underlies lower rates of girdling to the non-indigenous trees, beaver gnawing may provide some advantage to these species over indigenous tree species in close proximity to streams. While cases of direct effects of beaver gnawing favoring non-indigenous trees over natives must be considered in plans to re-introduce beavers, in many circumstances the benefits for native plants that arise indirectly through beavers’ alteration of hydrology are substantial (Albert and Trimble 2000).

Effects of beavers upon the rate of succession in riparian woodland will depend upon whether 1) beavers differentially damage early vs. late successional species and 2) whether the net effect of early successional species on late successional species is inhibitory or facilitative. For example, in boreal forests, beaver gnawing is hypothesized to speed succession because beavers cut early successional hardwoods, creating low competition environments for establishment of late successional conifers (Donkor and

Fryxell 2000). In south-central Kansas riparian woodlands, tree species' successional niche and frequency of beaver girdling are not strongly correlated. *Salix* sp., which are colonizers of sand bars and mud flats in the Great Plains (Bellah and Hulbert 1974) are frequently girdled by beavers, but so are *Morus rubra* and *Celtis occidentalis*, which Bellah and Hulbert (1974) identify as mid- and late-successional, respectively. The critical role, however, of pioneer *Salix* sp. in building-up organic matter and increasing elevation above the stream (Ware and Penfound 1949, Wilson 1970) may mean that any reduction in their cover by beavers will slow the rate of succession by reducing this facilitative effect. Effects of beavers upon succession rate in Great Plains riparian zones are likely to be more complex than that hypothesized for boreal forest and only long-term experimental manipulation of beaver densities can quantify this effect.

In spite of the potential for beavers to influence tree species composition in south-central Kansas riparian woodlands, these effects will be restricted to the immediate vicinity of streams. Beaver girdling frequency decreased much more rapidly with distance from streams at our study sites than has been shown in more northern regions of the beaver's range. For example, in boreal forest (Donkor and Fryxell 2000, Barnes and Mallik 2001), northeastern deciduous forest (Jenkins 1980) and northern Great Plains prairies (Pinkowski 1983, Lesica and Miles 2004) cut trees occurred 50 m – 100 m from water. The short distances from streams over which beavers girdled trees at our study sites probably does not reflect avoidance of edge habitats between woodlands and grasslands/croplands because beavers in Kansas use irrigation ditches and farm ponds with little tree cover (Robel, Fox and Kemp 1993).

Bryzski and Schulte (2009) hypothesize that distance from streams over which beavers gnaw trees decreases with decreasing latitude. They suggest that a latitudinal pattern may occur because longer growing seasons at southern sites provide herbaceous foods over more of the year and beavers need to rely less on woody plants for large over-winter caches. Similar to our finding and those of Bryzski and Schulte (2009), Lacki et al. (2001) showed that beaver damage was largely confined to within 5 m of a reservoir in Kentucky. Testing Bryzski and Schulte (2009)'s hypothesis of a positive correlation between latitude and distance over which beavers gnaw trees requires more studies of beaver-vegetation interactions in ecosystems of the southern United States.

The lack of interactions between the 1) species of trees that were girdled and distance from the stream and 2) the diameter of trees that were girdled and distance suggest that the direction of beavers' effects on the composition and physiognomy of the riparian tree community does not change with distance. Beavers have often been used to test central-place foraging theory and, hence, we hypothesized that the predictions of central place foraging theory could inform predictions for spatial variation in beavers' effects on the riparian tree community. However, the predictions of increased selectivity by beavers at greater distances from the stream (Schoener 1979, Orians and Pearson 1979) were not borne out in our study.

Central place foraging theory may not be easily translated into effects on the riparian tree community in regions where much of the stem mortality caused by beavers occurs through girdling without cutting the stem. Under these conditions, much beaver-caused stem mortality occurs when beavers are not acting as central place foragers because they are not returning to the home base to eat the food, store the food or provision off-

spring (Orians and Pearson 1979). Almost 42% of girdled stems at our study sites were not removed and, hence, were not cut. Chabreck (1958) suggested that feeding by peeling bark without felling the tree is common in southern parts of the beavers' range where streams do not freeze over for as extended periods as in northern regions. If Chabreck (1958)'s hypothesis is true then central foraging theory may be more useful for predicting beavers' effects on riparian tree communities in northern than in southern communities.

Beaver population sizes throughout much of the species' range have undergone dramatic changes during the 19th and 20th centuries as beaver were first hunted to near extirpation and now have partially recovered (Naiman, Johnston and Kelley 1988). Our results suggest that in south-central Kansas riparian woodlands such fluctuations in beaver populations have the potential to alter regeneration dynamics of tree communities in the immediate vicinity of streams. Further, the interactions between beaver and the tree community at the south-central Kansas riparian woodlands that we sampled differed from beaver-vegetation interactions often shown in more northern regions of the beaver's range in that 1) damage that caused stem mortality occurred over shorter distances from streams and 2) a large proportion of girdled trees were not cut. Systematic differences between ecosystems in northern and southern portions of the beaver's range, including length of growing season and open water availability during winter, suggest that a comprehensive understanding of the consequences of variation in beaver population sizes in North America requires more studies of beaver-vegetation interactions in southern portions of the beaver's range.

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LITERATURE CITED

Albert, S. and Trimble, T. 2000. Beavers are partners in riparian restoration on the Zuni Indian Reservation. *Ecological Restoration* 18: 87-92.

Basey, J.M. and S.H. Jenkins. 1995. Influences of predation risk and energy maximization on food selection by beavers (*Castor canadensis*). *Canadian Journal of Zoology* 73: 2197-2208.

Barnes, D.M. and Mallik, A.U. 2001. Effects of beaver (*Castor canadensis*) herbivory on streamside vegetation in a northern Ontario watershed. *Canadian Field Naturalist* 115: 9-21.

Bellah, R.G. and Hulbert, L.C. 1974. Forest succession on the Republican River floodplain in Clay County, Kansas. *Southwestern Naturalist* 19: 155-166.

Belovsky, G.E. 1984. Diet optimization by beaver. *American Midland Naturalist* 111: 209-222.

Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B (Methodological)* 57: 289-300.

Bryzski, J.R. and Schulte, B.A. 2009. Beaver impacts on herbaceous and woody vegetation in southeastern Georgia. *American Midland Naturalist* 162: 74-86.

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

Cockrum, E.L. 1952. Mammals of Kansas. pp 1-303. in Hall, E.R., Leonard, A.B., Taylor, E.H., and Wilson, R.W. (eds). *University of Kansas Publications Museum of Natural History*. Vol. 7. Lawrence KS.

Cottam, G. and Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.

Donkor, N.T. and Fryxell, J.M. 2000. Lowland boreal forests characterization in Algonquin Provincial Park relative to beaver (*Castor canadensis*) foraging and edaphic factors. *Plant Ecology* 148: 1-12.

Haarberg O. and Rosell, F. 2006. Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. *Journal of Zoology* 270: 201-208.

Hall, G.I., Wallace, M.C., Ballard, W.B., Ruthven, D.C., Butler, M.J. and Houchin, R.L. 2006. Rio Grande wild turkey habitat selection in the southern Great Plains. *Journal of Wildlife Management* 71: 2583-2591.

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

Jenkins, S.H. and Busher, P.E. 1979. *Castor canadensis*. *Mammalian Species* 120: 1-8.

Lacki, M.J., Wilson, T.C., Bouland, J.R., Guess, G.W. and Mueller, C.A. 2001. Impact of feeding behavior of beavers (*Castor Canadensis*) on woody plants at Owsley Fork Reservoir in eastern Kentucky. *Journal of the Kentucky Academy of Sciences* 62:96-99.

Lesica, P. and Miles, S. 2004. Beavers indirectly enhance the growth of Russian Olive and Tamarisk along eastern Montana rivers. *Western North American Naturalist* 64: 93-100.

Little, E.L. 1979. Checklist of United States trees (native and naturalized). United States Department of Agriculture handbook no. 541. Forest Service. United States Department of Agriculture. Washington D.C.

Magill, R.T., Smith, L.M. and Ray, J.D. 2003. Nest box use by cavity nesting birds in riparian zones of the southern Great Plains. *Texas Journal of Science* 55: 235-246.

McGinley, M.A. and Whitham, T.G. 1985 Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). *Oecologia* 66: 558-562.

Naiman, R.J., Johnston, C.A. and Kelley, J.C. 1988. Alteration of North American streams by beaver. *Bioscience* 38:753-762.

Orians, G.H. and N.E. Pearson. 1979. On the theory of central place foraging. in is something missing here?

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

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

Robel, R.J., Fox, L.B. and Kemp, K.E. 1993. Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. *Wildlife Society Bulletin* 21: 415-421.

Schoener, T.W. 1979. Generality of the size-distance relation in models of optimal feeding. *American Naturalist* 114: 902-914.

Ware, G.H. and W.T. Penfound. 1949. The vegetation of the lower levels of the floodplain of the South Canadian River in Central Oklahoma. *Ecology* 30: 478-484.

Wilson, R.E. 1970. Succession in stands of *Populus deltoides* along the Missouri River in southeastern South Dakota. American Midland Naturalist 83: 330-342.

TABLE 1-- Beaver damage to tree species in south-central Kansas. The species in the row heading should be read as to the left of the equality/inequality and the species in the column heading should be read as to the right of the equality/inequality (e.g., the cell in the first row of the first column indicates that “a significantly higher proportion of *Celtis* individuals were girdled than *Catalpa* individuals.”). Fisher’s exact test was used to test significance. Because multiple comparisons were made, we controlled the false discovery rate using Benjamini and Hochberg (1995)’s adjustment of the significance level.

Usage patterns based on girdling by beavers

	Catalpa	Celtis	Cornus	Fraxinus	Maclura	Morus	Populus	Salix
Celtis	>							
Cornus	=	=						
Fraxinus	=	=	=					
Maclura	=	<	<	<				
Morus	>	=	=	=	>			
Populus	=	<	=	<	=	<		
Salix	>	=	=	>	>	=	>	
Ulmus	=	<	=	<	=	<	=	<

Figure Legends.

Figure 1. Locations of study sites and south-central Kansas county boundaries. Study site abbreviations are: BW = Byron Walker Wildlife Management Area, CC = Chisholm Creek Park, CH = Chaplin Nature Center, HE = Harvey County East Park, HW = Harvey County West Park, KW = Kaw Wildlife Management Area, ML = Miller Family Farm, NI = Wichita State University Ninnescah Reserve, PP = Pawnee Prairie Park.

Figure 2. Tree species composition and size distributions at the nine riparian woodlands that were sampled for beaver damage. For all nine sites, tree species composition and size distributions are based on 48 trees.

Figure 3. Proportion of trees girdled as a function of distance from the stream. “*” indicates a significant difference in the proportion of trees girdled as compared to the proportion of trees girdled at 5 m from the stream at $p \leq 0.05$. “***” indicates a significant difference in the proportion of trees girdled as compared to the proportion of trees girdled at 5 m at $p \leq 0.001$.

Figure 4. Variation in the proportion of trees girdled among riparian woodland tree species. The number in parentheses above each bar is the sample size for the species when data from all nine sites were pooled.

Figure 1

Figure 2

Figure 2 cont.

Figure 2 cont.

Figure 2 cont.

Figure 2 cont.