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## 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*)

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**Summary.** Several predictions of central place foraging theory were tested. As predicted, beavers foraged more selectively at increasing distance from the central place. With increasing distance from the river's edge, beavers cut fewer branches and deleted small branches from their diet. Large branches were favored at all distances, which differs from patterns observed in previous studies of beaver foraging. This difference, however, is expected and supports Schoener's (1979) predictions which are based on differences between provisioning costs and item size.

The selective harvesting of branches predicted by foraging theory affects plant growth form and may influence plant reproductive patterns. High rates of branch removal caused cottonwoods to develop a shrubby architecture. The importance of selective branch choice by beavers on patterns of cottonwood reproduction (i.e., delayed sexual maturity and induced cloning) is discussed.

Beavers (*Castor canadensis*) act as central place foragers: they come onto land to cut branches, which are subsequently hauled back to the water to be debarked (Jenkins and Busher 1979). Several authors (Andersson 1978; Orians and Pearson 1979; Schoener 1979) have modelled the behavior of such foragers using the assumption that animals feed in a way that maximizes net rate of energy or nutrient intake per unit time. Along the San Juan River in southern Utah beavers feed on cottonwoods (*Populus fremontii*). Because cottonwoods vary greatly in size and distance from the river's edge, this variation can be used to test predictions about the selective foraging behavior of beavers and the resultant impact on the growth form of cottonwoods.

Because provisioning costs increase with distance, Schoener (1979) predicted that animals should forage more selectively farther from the central place. In addition, Andersson (1978) predicted that the number of items chosen should decrease with distance from the central place. These predictions have been supported in studies of diverse taxa. Harvester ants (*Pogonomyrmex rugosa*) chose a narrower range of seed types as the distance from the nest increased (Davidson 1978). Eastern woodrats (*Neotoma floridana*) collecting house building materials under laboratory conditions were also more selective (decreased variance in stick

size) and collected fewer sticks farther from the central place (McGinley 1984). Similarly, field experiments showed that whinchats (*Saxicola rubetra*) chose more of the available food near to than far from the nest (Andersson 1981).

Which food items are dropped from the diet depends on the relationship between provisioning time and the size of food items (Schoener 1979). Two alternative foraging strategies are predicted. First, when provisioning time is independent of size, large food items are more profitable than small items at all distances from the central place, and should be preferred over small items. Second, when provisioning time increases with item size, the profitability of large food items may decrease, causing large items to be deleted from the diet as distance increases. Clearly, these predicted foraging strategies are very different.

The relationship between travel distance and the size of food items selected has been best studied in beavers feeding on trees. When beavers are feeding on large trees, where provisioning time is assumed to increase with tree size, Schoener's second prediction appears to be supported. In his studies of beaver cut trees around ponds in Massachusetts, Jenkins (1980) found that proportionally fewer large trees were felled as distance from the pond increased. Similarly, the average diameter of trees cut by beavers decreased with distance from the pond in North Dakota (Pinkowski 1983), and the size of the largest branches cut by beavers decreased with distance on Isle Royale (Belovsky 1984).

The above field studies examined large trees and support Schoener's second alternative, whereas our studies of small trees should allow us to test Schoener's first alternative. The feeding behavior and branch selectivity of beavers should be greatly influenced by a branch's food value, which increases with branch size, and by the cost of hauling a branch to the river's edge, which is influenced by the distance from the central place. Although hauling or provisioning costs also generally increase with food size, here we assume that due to the small sizes of branches cut by beavers in this study (diameters ranged from 1.5 to 30.0 mm) and the large size of these animals (13.5 to 27 kg, Burt and Grossenheider 1976), these costs should be essentially independent of branch size. With these small branches the influence of branch size on provisioning costs is trivial, so it should cost just as much to haul the smallest one as the largest. Because provisioning costs should increase linearly with distance from the river and are independent of branch size, the profitability of all branch sizes should

decrease with distance from the river and large branches should be preferred at all distances. Therefore, foraging patterns observed in this study should differ from those studies examining beavers feeding on large trees.

Whether a branch is chosen also depends on the abundance of more profitable branches (Pyke 1984). At our study site along the San Juan River, the average branch size increased with distance from the river. Consequently, small branches should drop out of the diet as the distance from the river increases due to both decreasing profitability and the increasing abundance of more profitable branches.

With this conceptual background, five specific predictions can be made about the foraging behavior of beavers at our study site. First, the number of branches cut per plant should decrease with increasing distance from the river. Second, within a plant the average size of cut branches should be larger than the average size of branches avoided. Third, the size of the smallest branches cut should increase with distance from the river. Fourth, the proportion of the available small branches cut by beavers should decrease with distance from the river. Fifth, there should be a positive relationship between distance from the river and the mean branch size harvested.

The foraging patterns of beavers predicted above should also have important implications for the host plant. Relative to trees that escape attack, trees that suffer herbivory should show changes in the patterns of tree architecture, delayed sexual maturity, and increased vegetative reproduction.

## Methods

The sandy shores along the San Juan River near Chinle Wash in southern Utah are sparsely vegetated by riparian trees and shrubs. We chose to study one well developed stand that appeared to be even-aged. In quantifying the impacts of herbivores on plant growth, even-aged stands are useful because one can compare the growth forms of trees suffering various levels of beaver damage with those that completely escape. Furthermore, by holding age constant, we could examine distance effects separately from age-related plant defenses (see Whitham et al. 1984), which could complicate animal foraging decisions. This stand had developed on an older beach formed when the river had a different channel. Due to flooding within the past few years, this stand measuring approximately 140 m in length by 17 m in width now runs at an angle away from the river. Consequently, trees of apparently the same age varied greatly in distance to the river's edge.

To establish whether or not the stand was even-aged as assumed, we chose 10 trees near the river and 10 trees far from the river, cored them with an increment borer, and counted the number of rings. We also measured the basal stem diameters of these same 20 trees.

To examine beaver foraging behavior and their impacts on *P. fremontii*, we sampled trees at selected distances ranging from 3.5 m to 73 m from the river. The numbers of cut and uncut branches were recorded for 10 plants at each distance. Because it was occasionally difficult to tell where one plant ended and the next began, we chose the center of each plant and sampled all branches within a 15 cm radius of that point. Because intense beaver cutting had reduced many plants to a shrub growth form, the height of each

plant was determined by measuring the four tallest branches. To examine the relationship between the distance of trees from the river and the size of branches chosen by beavers, we examined plants at nine different distances from the river. We measured the diameter of all cut and uncut branches, with all measurements taken at approximately 45 cms above the ground, the average height of cuts by beavers.

Because changes in the level of the river could have changed the distance of trees from the river between the time branches were cut and the time we sampled, only very recent cuts were measured in another sampling regime. These newly cut branches could be distinguished from older ones by their light color and generally fresh condition. At eight sites we arbitrarily chose the center of each plant and measured the diameter of the five nearest branches, excluding old cuts. Because there were no significant differences in the average size of branches cut (Wilcoxon Signed-rank test;  $V_s = 12$ ,  $n = 7$ ,  $P > 0.05$ ) or avoided (Wilcoxon Signed-rank test;  $V_s = 7$ ,  $n = 7$ ,  $P > 0.05$ ) between the sample including all cuts and the sample containing only new cuts, we concluded that changing water levels had not influenced our results, and data from both samples were combined in Table 3.

## Results and discussion

### Beaver foraging

The foraging models predict that as the distance from the river's edge increased beavers should forage more selectively by cutting fewer branches per plant. Beavers cut significantly fewer branches per plant as they foraged farther from the river, (Table 1; Spearman Rank Correlation,  $r_s = 0.62$ ,  $P < 0.05$ ). For example, at a distance of only 3.5 m from the river's edge 71% of the branches were cut by beavers, whereas at a distance of 73 m only 20% of the branches were cut. This result supports the prediction of the foraging models, but similar patterns could result from other foraging strategies. For example, beavers cutting branches randomly with regard to size might still cut a higher proportion

**Table 1.** Selective beaver cutting and plant growth form data are shown as a function of distance from the river's edge

Distance from river (m)	Mean available branches per tree <sup>a</sup>	Mean no branches cut per tree <sup>a</sup>	% Cut	Mean tree height <sup>a</sup> (m)	Number trees examined
3.5	11.1 ± 4.35	7.9 ± 2.92	71	0.96 ± 0.30	10
3.8	12.0 ± 6.39	9.1 ± 6.21	76	0.63 ± 0.16	20
8.2	8.3 ± 2.35	5.5 ± 1.85	66	0.96 ± 0.37	10
9.9	13.7 ± 5.27	10.3 ± 5.47	75	1.14 ± 0.30	20
13.0	12.7 ± 5.62	10.7 ± 5.34	84	1.07 ± 1.52	10
16.0	10.7 ± 4.28	6.4 ± 3.50	60	1.03 ± 0.28	20
18.1	11.9 ± 5.83	8.0 ± 4.57	67	0.85 ± 0.32	10
19.0	10.3 ± 4.03	6.2 ± 2.97	60	1.50 ± 0.23	10
20.7	10.1 ± 2.23	4.7 ± 2.10	46	1.16 ± 0.42	10
73.2	3.7 ± 2.43	0.8 ± 0.85	20	3.62 ± 1.02	20

<sup>a</sup> Mean ± 1 standard deviation

**Table 2.** Branch size selectivity of beavers as a function of distance from the river's edge

Distance from river (m)	Mean diameter cut branches (mm) <sup>a</sup>	Mean diameter uncut branches (mm) <sup>a</sup>	Preference <sup>b</sup>
3.5	4.36 ± 1.74 (45)	3.28 ± 1.46 (65)	1.32
3.8	4.24 ± 2.03 (45)	3.00 ± 1.34 (46)	1.16
8.2	5.33 ± 3.47 (24)	3.03 ± 0.99 (31)	1.32
9.9	6.98 ± 4.34 (48)	3.05 ± 1.26 (62)	1.47
13.0	7.15 ± 3.52 (20)	3.68 ± 1.75 (35)	1.44
14.3	9.56 ± 5.28 (24)	4.16 ± 4.43 (41)	1.55
16.0	11.25 ± 3.32 (7)	4.46 ± 2.05 (15)	1.64
18.1	7.11 ± 3.12 (22)	3.70 ± 1.73 (40)	1.43
20.7	12.33 ± 0.57 (3)	5.28 ± 1.15 (18)	1.96

<sup>a</sup> Mean ± 1 standard deviation (sample size)

<sup>b</sup> Preference = mean size cut / mean size available

of branches near the river if they selectively foraged near the river because it provided safety from predators.

When food value of a branch increases with branch size and provisioning time is independent of branch size, as we assumed in this study, foraging theory predicts large branches should be preferred at all distances from the river. Beavers chose significantly larger branches than they avoided at all distances from the river (Table 2; Wilcoxon Signed-rank test,  $V_s = 0$ ,  $P = 0.002$ ), which is in agreement with the prediction. The mean diameter of cut branches averaged 97.9% greater than uncut branches.

Because the profitability of small branches decreases with distance from the river's edge, small branches should be excluded from the diet away from the river. Table 3 shows the percentage of the available branches of each size that were harvested by beavers at various distances from the river. With increasing distance the smallest branches (< 5 mm) were almost completely excluded from the diet. The largest branches (> 10 mm), however, were equally preferred at all distances with nearly 100% of these branches harvested at all sites. The average size of the five smallest branches cut by beavers increased with distance from the river (Spearman Rank Correlation;  $r_s = 0.87$ ,  $n = 9$ ,  $P = 0.0023$ ), ranging from 1.6 mm at 3.5 m from the river to

12.3 mm at a distance of 20.7 m from the river. Similarly, Belovsky (1984) found that the size of the smallest branches collected by beavers on Isle Royale increased with distance. Although support of the first prediction (fewer branches cut with increasing distance) could be consistent with a pattern of choosing branches randomly with regard to size, support of the other predictions indicates that beavers are selectively choosing branches based on size.

The relationship between the size of branches cut by beavers and the distance from the river's edge is exactly opposite the pattern found in other studies of beaver foraging behavior. We found a positive correlation between distance from the river and the average size of branches harvested (Table 2; Spearman Rank Correlation;  $r_s = 0.90$ ,  $n = 9$ ,  $P = 0.0023$ ). In contrast, previous studies (Jenkins 1980; Pinkowski 1983; Belovsky 1984) found that large trees were deleted from the diet as distance from the water increased.

Schoener predicted that the relationship between food size and distance depends on the relationship between food size and provisioning time. When provisioning time is independent of food size, large items should be favored at all distances. When provisioning time increases with item size, however, large items become less profitable and should be excluded from the diet as distance increases. The foraging of beavers offers an opportunity to test these predictions because the relationship between branch size and provisioning time differs between studies. In studies where provisioning time should increase with food size (i.e., beavers felled large trees; Jenkins 1980; Pinkowski 1983; Belovsky 1984), large branches were excluded from the diet with increasing distance. In our studies where provisioning time should be independent of food size (i.e., beavers harvested small branches from shrubs and small trees), large branches were preferred at all distances. Thus, these studies support both alternative predictions.

The differences in the foraging patterns between beavers harvesting small branches and those harvesting large trees can be further highlighted by examining the ratio of the mean branch size cut to the mean branch size available. This ratio increased significantly with distance from the river in this study (Table 2; Spearman Rank Correlation;  $r_s = 0.80$ ,  $n = 9$ ,  $P = 0.007$ ). Because large branches are preferred, the value of this ratio was always larger than one,

**Table 3.** Beaver selectivity for different sized branches at various distances from the river's edge. Selectivity is measured as the percent of available branches harvested

Distance from river (m)	Branch size (mm) <sup>a</sup>						
	2	3	4	5	6-7	8-10	> 10
3.5	23 (22)	33 (27)	41 (12)	53 (15)	86 (8)	100 (2)	-
3.8	29 (35)	39 (33)	39 (13)	75 (12)	70 (10)	100 (3)	-
8.2	17 (12)	31 (13)	25 (12)	60 (5)	100 (6)	100 (3)	100 (1)
9.9	0 (24)	13 (21)	44 (16)	70 (10)	84 (19)	100 (11)	100 (4)
13.0	11 (9)	17 (12)	30 (10)	33 (6)	43 (7)	80 (5)	89 (9)
14.3	0 (22)	20 (5)	20 (5)	17 (6)	53 (15)	71 (7)	100 (3)
16.0	0 (3)	0 (1)	0 (2)	0 (4)	0 (3)	83 (6)	100 (3)
18.1	9 (11)	0 (9)	11 (9)	44 (9)	67 (12)	83 (6)	100 (3)
20.7	-	0 (3)	0 (6)	0 (5)	0 (4)	-	-
	*	*	*	*	*	*	ns

\* Denotes Spearman Rank Correlation of percentage available cut as a function of distance,  $P < 0.05$

<sup>a</sup> Numbers in ( ) indicate sample size

ranging from 1.16 at 3.8 m from the river to 1.96 at 20.7 m from the river. Jenkins (1980) found that this ratio was larger near the river and that most of the values were less than one, showing that beavers were avoiding large trees (Wilcoxon Signed-rank test;  $V_s=1$ ,  $n=6$ ,  $P=0.016$ ). The only plant species with a ratio larger than one, witch-hazel (*Hamamelis*), had small diameters (approximately 3.2 cm) indicating its size is in the range where provisioning time is independent of branch size. This was the only species in Jenkins' study where the ratio was larger far from the pond. The foraging behavior of beavers observed in the present study and the above example of witch-hazel appear to represent examples of exceptions that prove the rule.

#### *Impacts of selective beaver foraging on trees*

Even though the trees at our study site varied greatly in size and growth form (shrub versus tree), the trees were nearly identical in age. Tree-ring counts showed no significant age differences in comparisons of trees growing near the river ( $X=8.8+1.05$  years,  $n=10$ ) versus those growing far from the river ( $X=8.1+1.59$  years,  $n=10$ ) (Wilcoxon Rank-sum Test,  $W_s=79.5$ ,  $P\geq 0.05$ ). Consequently, our study trees were even-aged so differences in growth form were most likely due to beaver harvesting and/or micro-habitat differences with distance. Plants near the river's edge exhibited a shrub-like growth form, whereas trees away from the river assumed an upright growth form. The number of branches per plant at the height of beaver foraging (approximately 45 cm above the ground) decreased significantly with distance from the river (Table 1; Spearman Rank Correlation;  $r_s=-0.56$ ,  $n=10$ ,  $P<0.05$ ) and plant height increased significantly with distance (Table 1;  $r_s=0.72$ ,  $n=10$ ,  $P<0.011$ ). For example, the average plant 3.5 m from the river's edge had 11.1 branches and was 0.96 m tall, whereas the average plant 73 m away from the river had only 3.7 basal branches and was 3.62 m tall. Thus, plants adjacent to the river had 3 times more basal branches and were only about 1/4th as tall as plants of the same age positioned away from the river.

The selective foraging of beavers is responsible for the observed differences in *P. fremontii* growth form. The more plants were fed upon by beavers the shrubbier their growth form became. Plants with the most branches also suffered the greatest removal of branches (Table 1; Spearman Rank Correlation;  $r_s=0.98$ ,  $n=10$ ,  $P<0.0001$ ). For example, the plants with the highest number of basal branches (13.5 branches per plant) suffered 75% branch removal, whereas plants with the fewest number of basal branches (3.7 branches per plant) suffered only 20% branch removal. The observed levels of herbivory induce the production of adventitious buds which develop below the cut and result in the production of a shrub. At our study site the foraging of beavers does not kill the plants, but their pruning results in the production of a dense hedge. Similar impacts of herbivores on plant architecture are probably common. Whitham and Mopper (1985) showed that the chronic shoot mortality suffered by pinyon pine (*Pinus edulis*) resulted in a dramatic change in tree architecture, as well as the complete loss of female reproductive function.

Differences in micro-habitat are not associated with tree growth form. Because a stunted shrub-like growth form is often associated with lack of water, trees farthest from

the river should be the most stressed and shrublike in growth. Because the upright or tree growth form occurred away from the river's edge in our study, this alternative can be eliminated. Additionally, there were no significant differences in the mean basal stem diameter of cut trees growing near the river ( $X=46.6+10.9$  mm,  $n=10$ ) in comparison with trees suffering much less herbivory growing far from the river ( $X=49.5+14.2$ ,  $n=10$ ) (Wilcoxon Rank-sum Test;  $W_s=108$ ,  $P\geq 0.05$ ). Thus, even though growth form is greatly altered, basal stem diameters (i.e., growth rates) remained relatively constant over the extremes of distance from the river's edge, indicating environmental factors did not affect basal growth rates.

Tree reproductive patterns may be strongly influenced by the selective foraging of beavers. Near the river continual pruning by beavers should maintain these cottonwoods in a perpetual juvenile condition, delaying reproductive maturity in comparison to plants away from the river. Although not studied in this system, with narrowleaf cottonwood, *Populus angustifolia*, beaver cutting stimulates the production of adventitious buds by the roots of cut plants which sprout around the base of the tree to form a clone. Such cloning can spread, and individual clones of *P. angustifolia* may contain 60 mature connected trees each with its own root system (Whitham unpublished data).

Trees growing adjacent to the river and suffering the selective harvesting of beavers should reproduce predominantly by vegetative mechanisms. In contrast, trees growing away from the river and not suffering herbivory, should reach reproductive maturity at a much earlier age and reproduce sexually rather than asexually or vegetatively. Thus, tree reproductive patterns may segregate out as a function of distance from the river due largely to the selective foraging of beavers.

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