The Orientation of Beavers (Castor canadensis) when Cutting Trees¹

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ABSTRACT. We studied patterns in the orientation of cutting when beavers (Castor canadensis) cut trees around Alum Creek Lake in central Ohio. For 462 trees, we measured the slope at the base of the tree, the orientation of the cut relative to this slope, the distance of the tree from the water, the radius of the tree, and the symmetry of the cut. The land around Alum Creek Lake generally slopes toward the water, so to direct the fall of a tree towards the water a beaver should cut a symmetrical tree from the downhill side. Cutting from the downhill side occurred for trees ≥ 9.0 m from the water. Near the shore, trees tended to lean toward the water and would fall toward the water regardless of the side from which the beaver cut. At distances < 9.0 m from shore, beavers cut predominantly from the uphill side where it should be easy to sit and there is little danger of the tree falling on them. At all distances, beavers showed random orientation when cutting trees on shallow slopes $(< 20^{\circ})$, whereas on steep slopes (especially slopes $\geq 30^{\circ}$) they cut predominantly from the uphill side. Beavers cut small trees (< 5.0 cm diameter) mostly from the downhill side, but tended to cut trees ≥ 5.0 cm in diameter from the uphill side. Overall, enough factors interacted that no single pattern of cutting existed for all trees.

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INTRODUCTION

Beavers (Castor canadensis) are known to be important ecosystem engineers, having a large influence on community diversity and ecosystem structure through their behavior (Pollock and others 1995). Beaver behavior creates habitat for some organisms while destroying habitat for others, thereby impacting species diversity (Grover and Baldassarre 1995; Colleen and Gibson 2001). In areas where beavers are common, they have a large influence on the abundance and structure of wetland and forest habitat (Gurnell 1998; Harkonen 1999). Expanding beaver populations in North America and Europe (Naiman and others 1988; Harkonen 1999; Colleen and Gibson 2001) will surely have a huge impact on forest ecosystems. Understanding these changes will require a better knowledge of the engineering behaviors of beavers, including dam building and tree cutting.

Considering how well known beavers are for felling trees, surprisingly few details about this process appear in the literature. Bartlett (1974) observed that cutting can be quite rapid. He recorded that a beaver cut through a submerged aspen branch over 6.0 cm in diameter in less than 30 seconds. A beaver can remove a chip over 2.0 cm wide and up to 15 cm long in a matter of seconds (Hilfiker 1990). Postural behavior during cutting has also been recorded. When felling trees, a beaver sits upright on its hind legs, props itself on its tail, and uses its front paws to stabilize the work (Allred 1986; Hilfiker 1990). For very large trees, beavers circle the tree and cut out chips, until the tree falls (Allred 1986). Moderately sized trees are usually cut in a characteristic pattern, with cuts on two sides angling up to the highest point on the cut. Beavers can fell such trees up to 15 cm in diameter without changing position (Hilfiker 1990). Both Morgan

Morgan (1868) noted that beavers tended to focus their cutting on one side of the tree, and considered it reasonable to infer that "it was the intention of the beavers to fell it in that direction." The idea that beavers can control the direction of a tree's fall is now out of favor based on two types of observations: 1) many trees get caught in the foliage of other trees, and 2) falling trees sometimes kill beavers (Longley and Moyle 1963; Hilfiker 1990; Kile and Rosell 1996). Morgan (1868) also noted that beavers cut leaning trees from the side opposite the direction of the lean and that beavers cut trees on a steep slope from the upper side. But none of these observations were accompanied by data. Similarly, Tevis (1950) reported that beavers typically cut on whatever side was easiest to access, and Allred (1986) reported that beavers cut exclusively from the upper side of very large trees if the slope was steep. Again, data supporting these generalizations are lacking.

In order to quantitatively describe the patterns by which beavers fell trees, we used measurements of beaver-cut tree stumps to infer the direction from which the beaver had cut the tree. We then compared how cutting orientation related to the direction to water, the slope of the hill around the tree, the size of tree, and the distance of the tree from the water.

MATERIALS AND METHODS

We selected eight areas 200 to 400 m² in size along both shores of Alum Creek Lake in Delaware County, OH. We chose areas that contained numerous trees cut by beavers and measured all cut trees with a diameter ≥4 cm at a height 15 cm above ground level from the shoreline to as far back into the woods as cut trees occurred, resulting in 462 measured trees. For each cut tree, we measured five parameters: 1) the diameter of the stump at a height of 15 cm, 2) the radius at the level of the cut, 3) the symmetry of the cut (the horizontal

⁽¹⁸⁶⁸⁾ and Ryden (1989) reported that beavers rush for the water when the tree starts to fall.

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distance from the edge of the stump to the highpoint of the cut as a proportion of the radius), 4) the shortest distance to the shore from the stump, and 5) the slope of the land from 25 cm downhill of the midpoint of the stump to 25 cm uphill (using a carpenter's level and a meter stick).

We accepted Hilfiker's (1990) observation that beavers generally remained in one position while cutting trees of the size range measured in this study, because the vast majority of trees were less than 10 cm in diameter. We assumed that this one position was the side of the stump opposite that which contained the last bit of cut tree based on the orientation of tooth marks on the cut stumps. For the few trees greater than 10 cm, we assumed the beaver spent a majority of its cutting time on this side of the tree. We identified the last bit of cut tree as being either the highest point on the cut or the center of the break if the tree fell before the beaver cut completely through the trunk. We divided the cross-section of the cut stump into quarters with relation to the slope around the tree, and recorded which quarter contained the last bit of cut tree using a numerical code: 1 = the downhill quarter, 4 = the uphill quarter, 2 or 3 = the two lateral quarters. We also recorded the orientation of the last bit of cut tree with respect to the lake. However, since the ground generally sloped toward the water, 83% of the time the orientation of the cut was the same for both the local slope and relative to the lake. As a consequence, analyses for both sets of data showed the same patterns and we report here only the results pertaining to the orientation of the cuts relative to the slope around the tree.

We investigated whether trees leaned downhill by choosing five points near our study sites with a range of slopes. We found the ten nearest uncut, live trees with trunks between 4.0 and 8.0 cm in diameter and measured the slope at the base of each tree as before. We then used a plumb line to measure the lean, attaching the plumb line at a height of 2.0 m to the downward side of the tree and measuring from the plumb bob to the base of the tree. We categorized the direction the tree leaned using the same four directions as before.

To identify patterns in the orientation of cutting, we used chi-square analysis of contingency tables. The orientation of the cut was always categorical data, and we established categories for the slope at the base of the tree (<20°, 20°-29.9°, and ≥30°), the distance to the water (<3.0 m, 3.0-8.9 m, 9.0-15.9 m, and ≥16.0 m), and the radius at the cut (<2.5 cm, 2.5-3.9 cm, and ≥4.0 cm). Categories were chosen to include enough trees to run statistical tests. We were not interested in differences between quarters 2 and 3 (to either side), so we pooled these data. To identify other patterns, we used Pearson correlation analysis. Before analyzing proportional data, we performed the arcsine of the square root transformation of the proportion to correct for platykurtosis (Sokal and Rohlf 1981).

RESULTS

Beavers showed patterns in how they cut trees in a variety of circumstances. Near the shore (<9.0 m), bea-

vers cut most trees from the uphill side, but at greater distances, especially at ≥16.0 m, they cut mostly from the downhill side of the trees (Fig. 1, $\chi^2 = 23.017$, d.f. = 6, P = 0.001). On steep slopes, especially slopes $\geq 30^{\circ}$, beavers cut most trees from the uphill side, whereas if the slope at the base of the tree was relatively flat (<20°), beavers cut trees equally from all four directions (Fig. 2, χ^2 = 9.511, d.f. = 4, P = 0.050). This pattern of cutting from the uphill side on steep slopes complements the first result in that the slope at the base of the tree was negatively correlated with distance from shore (r = -0.527, d.f. = 460, P = 0.000), so steep slopes tended to be near shore. Beavers also showed patterns of cutting with respect to the size of the tree. Beavers tended to cut small trees (radius <2.5 cm) from the downhill side, but usually cut larger trees (radius ≥2.5 cm) from the uphill side (Fig. 3, χ^2 = 38.432, d.f. = 4, P = 0.000). Again, this pattern is related to the first pattern because beavers tended to cut large trees only near shore whereas they cut small trees at all distances. Thus, overall there was a negative correlation of diameter of cut tree with distance from shore (r = -0.153, d.f. = 460, P = 0.001) and the large trees were near shore where the slope was steep.

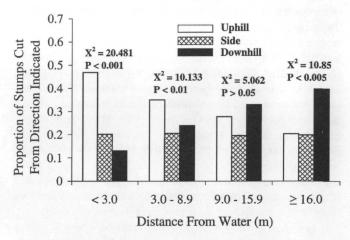


FIGURE 1. Direction from which beavers cut trees in relation to distance from water. χ^2 test statistics for each distance category are shown.

The symmetry of the cut was independent of the slope at the base of the tree (r = 0.034, d.f. = 460, P = 0.467). This same result obtained for large trees \geq 5.0 cm in radius (r = 0.182, N = 21, P = 0.430), even though symmetry of the cut increased with the radius at the cut (r = 0.272, d.f. = 460, P < 0.001).

Two patterns in the way trees lean may also affect the way beavers cut trees. Trees leaned downhill rather than uphill or to the side ($\chi^2 = 44.217$, d.f. = 2, P < 0.001), and trees leaned more on steep slopes than on shallow slopes (r = 0.331, d.f. = 48, P = 0.019).

DISCUSSION

We interpret the various patterns as resulting from a combination of factors. The preference shown by beavers to cut trees near shore from the uphill side probably relates to the lean of the trees and the topography of the

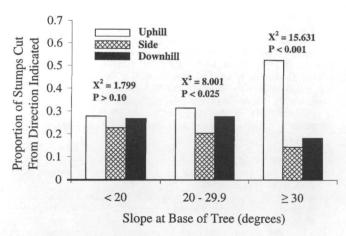


FIGURE 2. Direction from which beavers cut trees in relation to the slope at the base of the stump. χ^2 test statistics for each slope category are shown.

land. As Loehle (1986) reported, we found that trees growing near the shoreline tended to lean toward the water where there is more light available. Thus, trees growing near the water should tend to fall toward the water no matter how a beaver cuts them. At Alum Creek Lake, the slope is generally steep near shore. This means that beavers can cut from the uphill side (where they can sit safely and easily) when cutting near shore and still have the trees fall toward the water.

The simplest explanation for why beavers tended to cut trees far from the water from the downhill, shoreward side is that they merely cut the tree from the side reached first when they came from the water. However, we think a more complex explanation is more likely. Part of the explanation may involve an attempt by beavers to direct the fall of these trees toward the water as Morgan (1868) suggested. Far from the shore, the trees tend to be fairly symmetrical and vertical (Loehle 1986). Thus trees should fall in the direction from which they are cut. Since beavers usually lop off limbs and cut large trees into smaller pieces before dragging them to water (Morgan 1868), we assumed that the direction in which the tree fell would not affect the

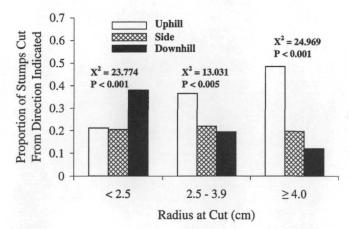


Figure 3. Direction from which beavers cut trees in relation to the radius of the cut stump. χ^2 test statistics for each size category are shown.

ease with which a tree is dragged through the forest. Therefore, beavers trying to control the direction trees fall should cut from the side nearest the water to minimize the distance the trunk or branches need to be dragged. At Alum Creek Lake, beavers can do this without needing to sit awkwardly on a steep slope leaning away from the tree because slopes tend to be minimal at >9.0 m from shore. Alternatively, beavers may orient themselves in this way to minimize vulnerability to predators. The primary local predators would be coyotes, feral dogs, and humans (Rosell and others 1996), all of which would most likely approach from the uphill, terrestrial side of the tree. Thus, another contributing factor to this pattern could easily be ease in escape from the threat of terrestrial predators (Basey and Jenkins 1995).

The differences between how beavers cut large and small trees may relate to some of these same factors. Beavers may have cut large trees primarily from the uphill side because most of the large, cut trees were near shore, where trees lean toward the water. Large trees near shore would fall toward the water irrespective of the direction of cut, so beavers could be expected to cut them from the uphill side where it is easier to stand and the tree is less likely to fall on them. as noted above. Beavers may have cut a disproportionate number of small trees (radius <2.5 cm) from below because they were attempting to direct the fall toward the water from the shallow, distant slopes where many small trees were cut. Furthermore, smaller trees are less likely to injure or kill beavers than large trees if they should fall unexpectedly (Longley and Moyle 1963; Hilfiker 1990; Kile and Rosell 1996).

The observation that beavers cut larger trees more symmetrically than smaller ones likely reflects the pattern that they cut large trees from multiple sides, whereas they cut smaller trees more nearly from a single direction as earlier reports suggest (Allred 1986; Hilfiker 1990). However, the lack of correlation between the symmetry of the cut and the slope at the base of the stump was counter to Allred's (1986) report that beavers cut large trees from all sides on shallow slopes but only from uphill on steep slopes. A possible reason for the difference between our results and those of Allred (1986) may be the overall range of sizes of cut trees that Allred refers to. The largest cut tree in this study had a diameter of only 22.4 cm, and there were only four trees of greater than 15 cm; Allred (1986), however, describes cut trees between 20 and 25 cm in diameter as relatively small.

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