DIRECTIONAL TREE FELLING BY BEAVERS (*CASTOR CANADENSIS*)

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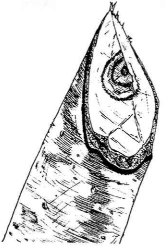
ABSTRACT—By measuring the falling angle of 888 trees of a variety of sizes cut near 8 different dams in southwestern Saskatchewan, we tested the hypothesis that beavers (*Castor canadensis*) fell trees in a non-random direction. We predicted that trees would be preferentially felled towards the dam to minimize the costs of transporting materials to the dam and to minimize the amount of time beavers spend on land. We established a 150 m wide × 250 m long transect at each dam and determined the felling angle of at least 100 aspen trees cut in each transect. We found that trees were felled by beavers with a mean felling angle of 357.9°, a direction not significantly different from that of the dam. In all, 62% of trees were felled within 45° of the direction of the dam. While our data are consistent with the hypothesis, an experimental test is required to establish the reason(s) for the pattern we found.

Key words: *Castor canadensis*, beaver, behavior, tree felling

Beavers (*Castor canadensis*) have been studied extensively in the context of optimal foraging theory, in particular their tendency for Central Place Foraging (for example, Jenkins 1980; McGinley and Whitman 1985; Basey and others 1988; Fryxell and Doucett 1991; Basey and Jenkins 1995). There are considerable data on the size of trees cut and the distance from water and/or the dam at which beavers fell trees. Previous studies have shown that beavers selectively choose smaller trees as the distance from the water and/or dam increases (Jenkins 1980; Pinkowski 1983; Basey and others 1988; Fryxell and Doucett 1991; Basey and Jenkins 1995; Barnes and Mallik 1996). However, little research has been done on the actual mechanics of cutting by beavers and in particular about the direction in which trees are felled. Wilsson (1971) suggested that European beavers (*Castor fiber*) fell trees in random directions, but trees fall more often towards water (the direction of the dam) because the trees often lean that way or have a well-developed crown on that side, but the author did not record actual measurements for these parameters. Cleland (1962) measured the direction of felling for 97 eastern cottonwoods (*Populus deltoides*), but conducted no statistical analysis. She qualitatively concluded that trees were not cut to fall in any particular direction. We hypothesize that to save time and energy transporting parts of the tree to the dam, beavers should selectively fell trees in the direction of the dam. Selective felling in terms of direction could also reduce the amount of time spent on land, potentially lowering the risk of predation.

STUDY AREA AND METHODS

The study was conducted in the West Block of Cypress Hills Interprovincial Park, Saskatchewan (109°53′W, 49°34′N), during August 2000, 2001, and 2002. Tree felling behavior by beavers tends to peak during August in our study area. We chose 8 active dams on separate tributaries of Battle Creek to measure felled trembling aspen (*Populus tremuloides*). A preliminary survey indicated aspen was the main species (>95%) harvested in the study area. At each dam, we established a 150 m wide × 250 m long transect centered on a dam (thus approximately 75 m upstream and 75 m downstream) running approximately perpendicular to the watercourse, and we measured 100 to 120 felled aspen in each transect. Due to historical beaver activity, most of the trees we measured were >50 m from the watercourse. For most trees (see below) we assessed the falling direction (hence forth "felling angle") based on the distinct cutting pattern observed on stumps (Fig. 1). The cutting pattern resulted in a central line running vertically from the tip of the stump to the bottom of the cutting area. We assigned a a)



b)

FIGURE 1. The distinct cutting pattern used to assess the angle at which the trees fell. Note the central line, which we used as an indicator of the felling direction. This central line is present in both a completely felled tree (a) and in a tree that was felled but still attached to the stump (b).

felling angle (to the nearest 10°) to 762 downed trees assuming that the central line on a beaver cut stump indicated the felling angle of the tree. For an additional 116 felled trees, distributed on all 8 transects, the main stem of the tree was still attached to the stump. In these cases, we measured felling angle directly and for these trees ascertained that the central line pointed in the same direction (± 5°) as the felling angle of the downed tree, based on a qualitative visual comparison.

A tree felled directly towards the dam was assigned a felling angle of 0° and a tree falling directly away from the dam was assigned a felling angle of 180° with all values between 0° and 360° used. We used a V-test to compare the circular uniformity of felling angles with a specified mean angle, which in this case was 0°, the direction of the dam (Zar 1999). In all, we performed 10 V-tests, 1 for each tree measured on each transect, 1 for the 116 trees felled but still attached to the stump where we could directly measure felling angle, and 1 for all 888 trees together. We conducted separate analyses to validate whether a pattern existed regardless of our assumption about the central line being indicative of the direction of felling and to assess the robustness of any pattern detected. If there was real pattern in felling angles, we expected most if not all 10 tests to confirm it.

To assess the impact of slope on felling angle, we measured slope (using a clinometer) at the location of each of the 116 trees felled but still attached to the stump and calculated the slope of each transect from the average of 10 measurements taken equidistantly along the transect. We compared the relationship between slope and felling direction using linear regression analysis. We set alpha = 0.05 as significant for all statistical tests.

RESULTS

The 888 trees measured ranged considerably in circumference (measured just below the cut), from 21.0 to 122.3 cm ($\bar{x}$ = 31.7, s = 14.6 cm). Our analysis indicates that the mean felling angle of all trees felled was not significantly different from 0° for any of the 8 transects. Mean felling angles for transects ranged from 319.9° to 52.1°, r^2-values from 0.18 to 0.77, U-values from 2.17 to 10.9, and P-values from <0.025 to <0.0005. For the 116 trees that were felled but still attached to stumps where we could mea-

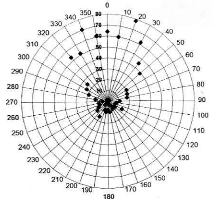


FIGURE 2. Circular plot for all trees sampled showing the number of trees that were felled in each direction. The 0° mark is the direction of the dam.

sure felling angle directly, the mean angle was 2.3°, again not significantly different than 0° ($r^2 = 0.68$, $U = 10.4$, $P < 0.0005$). Finally, the mean felling angle for all the trees sampled was 357.9°, also not different than 0° ($r^2 = 0.53$, $U = 22.5$, $P < 0.0005$; Fig. 2).

In total, 62% of all the trees felled were within 45° of either side of the dam (between 315° and 45°) and 83% were felled between 270° and 90°. The mean slope of all transects was <7.1° and there was no slope >18° for any transect or tree. There was no correlation ($r^2 < 0.01$, $n = 58$, $P = 0.97$) between the slope of the ground and the felling angle for the 116 trees felled but still attached to the stump (Fig. 3).

Discussion

We found that the mean angle at which beavers felled trees was not significantly different from the direction of the dam. These results support our hypothesis that beavers preferentially cut trees to fall towards the dam. Wilsson (1971) suggested that trees were not felled in random directions, but tend to be cut to fall towards the dam. He argued that this was simply because trees often lean in that direction and was not related to directional felling by beavers. This is a reasonable conclusion for many riparian systems given the shape of valleys. However, in our study area, the small creeks were moving slowly through a wide plain and not through a steep-sided valley. Thus, slope cannot be entirely responsible for the direction trees fell in our area. The shallow nature of the valleys is also consistent with our impression of limited evening down-slope winds. This combined with the variable valley orientation

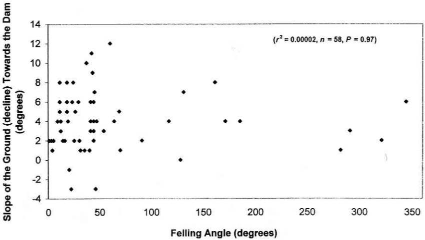


FIGURE 3. Felling angles of trees cut but still attached to the stump vs. the slope of the ground.

suggests that wind (typically from the west and declining through the evening) was also not a major factor.

Neither do our results support the qualitative conclusion of Cleland (1962), who suggested that trees were felled in random directions. Cleland also argued that the direction trees leaned at the time the trees are felled could be a factor. However, the mean slopes of the 8 transects in our study were small ($\leq 18°$). Further, the slope of the ground at the site of trees felled but still attached to the stump (where we made direct measurements of felling angle) was not correlated with the direction the tree fell (Fig. 3).

Other factors can influence felling direction. Wind (Cleland 1962), impediments at the base of the tree (for example, rocks or logs), the pattern of branching (Wilsson 1971), and the direction from which a beaver approaches a tree could all be important. While we acknowledge that any or all of these factors could affect the direction trees are felled, our results are consistent with the hypothesis that the direction of the dam is an important factor.

The direction a tree falls when being cut by a beaver or other direct means is a matter of torque and center of mass. When a tree is felled there is a well-defined point on the tree where the last bit of the cut is made. In order to fell a tree in the direction of the dam, a beaver would likely start cutting the tree from the dam side (0°) so the center of mass would be nearer to the dam. To create the diagonal central line (from a lateral view), beavers must alternatively turn their head and cut from each side, working their way from side to side until they get to the back of the tree. If the center of the mass of the tree is located directly above the last point cut, the tree will not fall at all until given a gentle push. If the center of the mass of the tree is not centered directly above the last cut, then the tree will fall toward the center of mass. Our description of the pattern of tree felling does not allow us to positively discriminate between approach and dam direction and thus we cannot claim that beaver intentionally chose the direction in which to fell a tree. However, our results document a pattern, and will hopefully stimulate an experimental test to evaluate it.

Central place foragers are animals that travel from a central location to select food to be eaten at the harvest site or to be transported back to a central location for later use (as food storage and/or building materials). Optimal foraging theory predicts that animals can increase their fitness by maximizing the net rate of energy intake per unit time (Stephens and Krebs 1986). One means of maximizing intake is to minimize costs. Because provisioning costs increase with distance, foragers should become increasingly more selective the farther away food is found from their central place (Jenkins 1980; Pinkowski 1983; McGinley and Whitham 1985; Barnes and Mallik 1996). Several studies on size-distance relationships of tree selection by beavers have found a positive correlation between selectivity for size and distance from the water (Jenkins 1980; Basey and Jenkins 1985); thus, beavers appear to increase selectivity with distance to minimize costs. Our results suggest that beaver minimize the cost of procuring material for dams by felling trees in the direction of dams.

To our knowledge, this study is the 1st quantitative demonstration of a pattern in the direction of tree felling by beavers. An experimental assessment for a larger sample of dams is needed to rigorously assess the potential confounding effects of slope, wind, branching pattern, direction of approach, and surrounding cover on felling direction.

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