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FOOD SELECTION BY BEAVERS: SAMPLING BEHAVIOR

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Abstract. Beavers in central Massachusetts frequently remove small pieces of bark (less than 25 cm^2) from standing trees. After removing a sample, the beavers may abandon these trees. At two ponds studied by the author in fall 1973, there were significant differences in species composition of trees sampled, felled, and available near the ponds. If beavers are physiologically capable of measuring the nutritional value of small pieces of bark, then sampling may be an economical way for them to assess spatial and temporal variation in relative nutritional value of different tree species.

INTRODUCTION

During a recent study of food selection by beavers (*Castor canadensis*) at two ponds in central Massachusetts (Jenkins, 1974), I observed numerous trees from which the beavers had removed small patches of bark (often less than 25 cm^2). Without using them further, the beavers then abandoned these trees. During September and October 1973, beavers at Blue Heron Cove cut into or partially stripped the bark from the lower trunks of 46 trees without completely felling them. At Tamplin Road Pond, there were 36 such trees. The beavers removed less than 25 cm^2 of bark from 25 of the 46 trees at Blue Heron Cove and the same amount from 17 of the 36 trees at Tamplin Road Pond.

Chabreck (1958) reported that beavers in Louisiana stripped the bark from the lower trunks of many trees without felling them. Aldous (1938) and many others have noted that beavers may not use all the bark of the trees they fell. The present study is the first to describe and to consider the possible adaptive significance in the beavers' pattern of removing small pieces of bark (less than 25 cm^2)

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from standing trees. Secondly, the study compares the beavers' patterns of selection of species for sampling with their patterns of selection of species for more complete utilization.

For economy of expression, I will call the beavers' incomplete use of trees (described above) *sampling*. I define light sampling as use of less than 25 cm^2 of bark near the base of a tree without felling it and heavy sampling as cutting into the wood of a tree and/or stripping more than 25 cm^2 of bark near its base without felling it. Several authors (Rozin, 1969; Freeland and Janzen, 1974; Westoby, 1974) have attached functional connotations to the word *sampling* in their discussions of optimal foraging. I wish to avoid a specific functional connotation in using the word. Instead, I present six alternative hypotheses which could account for beavers' incomplete use of trees. The first of these hypotheses argues that beavers' sampling might not be of direct adaptive value but is rather an incidental byproduct of the foraging process. The remaining five suggest five different ways in which sampling might function as an adaptive component of a beaver's foraging strategy. My data are insufficient to discriminate completely among these hypotheses; I present them to establish that sampling by beavers is a phenomenon worth further study, especially in the context of recent developments in optimal foraging theory (Krebs et al., 1977; Pyke et al., 1977).

RESULTS AND DISCUSSION

Table 1 shows the generic distributions of trees sampled, felled, and available at the major tree cutting sites of Blue Heron Cove and Tamplin Road Pond between 1 September 1973 and 6 November 1973 (Blue Heron Cove) or 2 November 1973 (Tamplin Road Pond). The following hypotheses might explain beavers' tree sampling behavior.

(1) A beaver may be interrupted while starting to fell a tree. Sampled trees simply represent those abandoned because of such interruption. If the probability of interruption is independent of tree genus, and if the time to remove less than 25 cm^2 of bark from a tree is less than the time to fell even a small tree (but one more than 2.5 cm diameter, the lower size limit considered in this study), then this hypothesis predicts that the generic distributions of lightly sampled and felled trees should be the same. (Heavily sampled

TABLE 1

Generic Distributions of Trees Sampled, Felled, and Available at Blue Heron Cove and Tamplin Road Pond, Fall 1973

	Lightly Sampled*	Heavily Sampled**	Felled	Available†
	Blue Heron Cove			
Oak (*Quercus* spp.)	11 (44%)	16 (76%)	31 (51%)	63 (25%)
Maple (*Acer* spp.)	4 (16%)	1 (5%)	14 (23%)	97 (38%)
Birch (*Betula* spp.)	9 (36%)	3 (14%)	1 (2%)	41 (16%)
Others	1 (4%)	1 (5%)	15 (25%)	53 (21%)
Totals	25	21	61	254
	Tamplin Road Pond			
Oak (*Quercus* spp.)	6 (35%)	7 (37%)	2 (6%)	15 (12%)
Maple (*Acer* spp.)	4 (24%)	9 (47%)	12 (34%)	59 (45%)
Cherry (*Prunus* spp.)	5 (29%)	3 (16%)	15 (43%)	18 (14%)
Others	2 (12%)	0 (0%)	6 (17%)	38 (29%)
Totals	17	19	35	130

*Less than 25 cm^2 of bark removed.
**Wood cut and/or more than 25 cm^2 of bark removed.
†Based on randomly placed, 78.5 m^2, circular quadrats. See Jenkins (1975) for details.

trees are excluded because it may take less time to fell a small tree than to sample heavily a large tree, and a difference in the generic distributions of sampled and felled trees might arise from differences in the available diameter distributions of various genera.) At Blue Heron Cove, generic distributions of lightly sampled and felled trees are significantly different ($\chi^2 = 15.0$, 2 df, $p < 0.001$, only oak, maple, and birch considered because few trees of other genera were sampled). At Tamplin Road Pond, these distributions are not quite significantly different ($\chi^2 = 5.2$, 2 df, $0.05 < p < 0.10$, only oak, maple, and cherry considered). This hypothesis may account for the existence of some sampled trees. However, it does not explain the marked difference in generic distributions of felled and sampled trees at Blue Heron Cove (Table 1).

(2) Beavers cannot identify trees taxonomically without tasting their bark, so sampling is necessary for selection of preferred tree genera. If this is true, the generic distribution of trees felled or sampled (the sum of columns 1, 2, and 3 in Table 1) should match that of trees available. The significant differences between these distributions at both ponds (Blue Heron Cove: $\chi^2 = 50.4$, 3 df, $p < 0.001$; Tamplin Road Pond: $\chi^2 = 31.3$, 3 df, $p < 0.001$) cast doubt on this hypothesis.

(3) Sampling is used to avoid ingestion of potential toxins and demonstrates cautiousness with novel food items (Freeland and Janzen, 1974). This hypothesis suggests that unfamiliar food types will be sampled more than familiar ones. Comparison of lightly sampled and felled trees at both Blue Heron Cove and Tamplin Road Pond refutes this hypothesis. In particular, oak is the genus most often sampled as well as felled at Blue Heron Cove, and cherry is most often felled and also frequently sampled at Tamplin Road Pond. Cautiousness in using new, potentially toxic foods may lead to sampling behavior in some species, but it does not explain these instances of sampling behavior by beavers.

(4) Sampling satisfies a requirement for certain vitamins or minerals, needed in small quantities and available only in some tree species. This hypothesis fails to explain the extensive sampling of maples and oaks at Blue Heron Cove and maples and cherries at Tamplin Road Pond. Many trees of these species are felled. The felled trees should supply any micronutrients which may be uniquely available in these species, unless the felled trees have concentrations of particular micronutrients several hundredfold less than sampled trees of the same species.

(5) Sampling represents practice at tree selection by young animals. I have no data on the amount of sampling done by individual members of the two colonies. However, young animals could practice tree selection on branches and logs brought to the edge of the pond by adults with less risk of predation than if the young animals sampled standing trees at distances as great as 50 m from shore. Therefore, it is unlikely that sampling would evolve solely to serve this function.

(6) Sampling is used by beavers to assess possible spatial and temporal variation in the nutritional quality of alternative foods. Unlike some of the others, this hypothesis cannot be tested by

comparing generic distributions of trees sampled, felled, and available. I present evidence elsewhere that beavers select different genera of trees for cutting at different sites around a pond (Jenkins, 1975), and different genera in different years at the same site (Jenkins, in preparation). There is evidence of spatial (Cowan et al., 1950) and temporal (Kramer and Koslowski, 1960) variation in nutritional value of some tree species. It seems reasonable to suggest that the spatial and temporal variation in beavers' tree selection is related to spatial and temporal variation in relative nutritional value of different tree species. Sampling may be a mechanism for achieving an optimal diet in the face of such variation.

CONCLUSIONS

Two kinds of data, both difficult to collect, are needed to prove more conclusively which of the above hypotheses are incorrect. First, direct observations of beavers in the act of sampling would help decide the validity of hypotheses 1 and 5. Unfortunately, beavers are primarily nocturnal, so special methods (e.g., radio telemetry, use of night vision instruments) would be needed to assist in making such observations. Data might be obtained on sampling during twilight hours without such assistance. However, such data probably would be inconclusive. For example, failure to observe sampling by young animals during twilight would certainly not prove that young animals don't sample; they might in fact be active samplers, but only at night. Second, data on toxin and nutrient content of bark of individual trees would help decide the validity of hypotheses 3, 4, and 6. To get adequate data of this sort would require analyzing a large number of samples for numerous nutrients and possible toxins (since both intraspecific and interspecific, as well as spatial and temporal variations in these attributes of tree bark are important components of these hypotheses). In addition, some of the toxins probably are unidentified or incompletely characterized at the present time.

In this note, I show that beavers are highly selective in sampling trees, but that they choose genera in different proportions than in felling trees. I suggest that sampling may be an economical way for beavers to assess spatial and temporal variation in relative nutritional value of different tree species, assuming they are capable of measuring the nutritional value of small pieces of bark. The physiological and behavioral mechanisms by which sampling functions are important subjects for future research.

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