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A SIZE-DISTANCE RELATION IN FOOD SELECTION BY BEAVERS[1]

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Abstract. The relationship between sizes of trees cut by beavers and distances from the borders of their ponds was examined at three sites in central Massachusetts. For most tree genera, the beavers cut a smaller range of sizes far from shore than close to shore, and relatively more small trees and fewer large trees at greater distances. The second of these results differs from the pattern of preference found in other studies in which predators were much larger than their prey, unlike this case of beavers feeding on trees. Both kinds of results are consistent with an optimal foraging model of size-distance relations in which pursuit or provisioning time depends on size of prey as well as distance (Schoener 1979).

Key words: beaver; Castor canadensis; *eastern deciduous forest; optimal foraging; prey selection; tree diameter.*

INTRODUCTION

Sophisticated theoretical treatments of optimal foraging abound in recent ecological literature (Schoener 1971, Pulliam 1974, Charnov 1976, Pyke et al. 1977). Empirical studies of these ideas are increasing in frequency (Emlen and Emlen 1975, Goss-Custard 1977, Krebs et al. 1977, Belovsky 1978, Pyke 1978), but many predictions of optimal foraging models remain untested, especially in field situations.

Two recent models (Orians and Pearson 1979, Schoener 1979) consider the relationship between distance to foraging site and characteristics of prey for central place feeders—animals which pursue prey at various distances from a fixed perch or collect food and store it at a fixed location in the home range. These models, like many other optimal foraging models, assume that predators maximize net rates of energy intake per unit feeding time, and ask what types of prey should be selected under various conditions. A central feature of the Orians and Pearson model is a comparison of central place feeders which carry one item at a time back to the central place with those which carry several items. The Schoener model considers the effects of variation in pursuit or provisioning time on optimal diets. Both models make a series of predictions about how optimal diets should change with distance from the central place. The models differ structurally and in some assumptions, and make at least one different prediction: in all versions of Schoener's model, selectivity increases with distance from the central place; in one version of Orians and Pearson's model, selectivity may be least at intermediate distances. Schoener (1979) compares the two models in detail.

Few data exist on the influence of distance on size-selection of prey for central-place foragers. Davidson (1978) reports that harvester ants show a stronger preference for moderately large seed particles over small ones far from their nest than close to the nest. Werner and Hall (1974) and O'Brien et al. (1976) provide indirect evidence that an increasing size-distance relationship may also exist for planktivorous sunfish. Likewise, insectivorous Great Tits and gnatcatchers appear to exhibit an increasing size-distance relationship (Royama 1966, Root 1967, Schoener 1979). A common feature of these examples is that individual prey items are small in relation to the size of the predators. As part of a recent study of food selection by beavers (*Castor canadensis*) in central Massachusetts (Jenkins 1975, 1978, 1979), I collected data on size-selection of trees for cutting as a function of distance from shore. Unlike the examples listed above, beavers use individual food items which are much larger than themselves. The size-distance relationship for beavers also differs, as predicted by Schoener's (1979) model.

Beavers are best known for their tree-cutting activity, although they eat much herbaceous and aquatic vegetation as well as the bark, twigs, and leaves of trees and shrubs. Most tree-cutting occurs during fall, when other food may be unavailable. At this time of year, beavers not only fell trees for current use but also haul branches and logs to the pond for storage. The bark of this stored material is used for food in winter, when beavers are limited in movements from their lodge (a wood and mud structure with underwater entrances) by ice covering the pond.

There is an extensive literature on beaver food habits, but most previously reported studies cannot be considered in the context of optimal foraging theory because they lack important details. For example, Hall (1960), Nixon and Ely (1969), and Simonsen (1973) all presented data on size-selection of trees, but none of them subdivided their data by distance. On the other hand, Hiner (1938) reported distances from shore at which aspen trees (*Populus* sp.) were cut but not the sizes of those trees. MacDonald (1956) considered distance and size simultaneously, also for aspens, but

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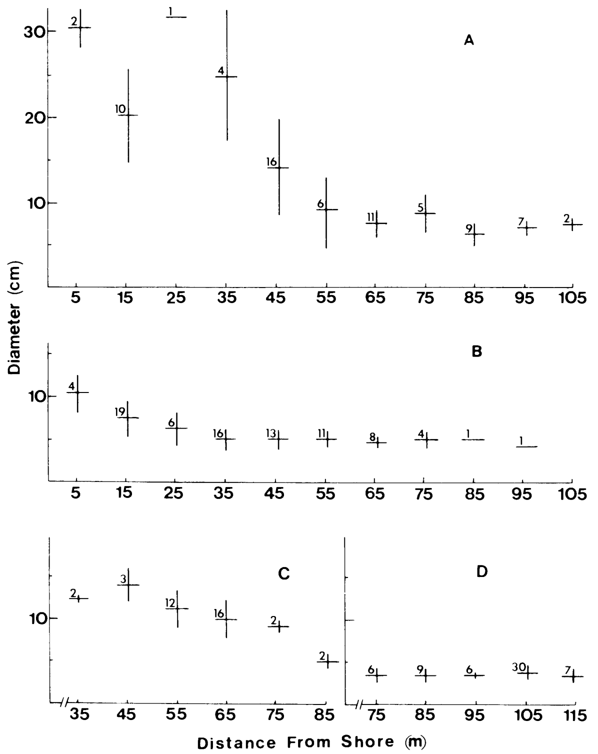

FIG. 1. Mean diameters of trees cut at BHC as a function of distance from shore. A: oak, B: maple, C: birch, D: witch-hazel. The total number of cut trees and the standard deviations of their diameters are also given at each distance.

found no correlation between the two variables. The present study is the first to report such a correlation, and to interpret data on beaver food selection in the framework of a specific optimal foraging model.

STUDY SITES AND METHODS

I collected the data for this study at three beaver ponds in the Quabbin Reservation in central Massachusetts: Blue Heron Cove (BHC), Tamplin Road Pond (TRP), and East Fever Brook (EFB). Each pond is bordered by a variety of forest types which differ in tree species composition because of differences in topography, soil, and land-use history. One tree-cutting site at each pond was selected for analysis of size-distance relationships. These sites met the following criteria: (1) shorelines were neither marshy nor excessively sinuous, so the variable "distance from shore" could be precisely defined and measured; (2) spatial variations in tree species composition within sites were small compared with variations between sites; and (3) numbers of trees cut and available at various distances from shore were large enough for statistical analysis for at least one genus per site.

Data were collected between 12 September 1972 and 8 March 1974 at the west shore of BHC, 30 August and 28 December 1973 at the west shore of TRP, and 11 October and 10 December 1973 at the southwest shore of EFB. I visited the ponds at approximately weekly intervals during fall, and less often during other seasons, and recorded species, stump diameter, location, and disposition of all trees >2.5 cm diameter which had been cut since my last visit. Beavers use trees for construction and repair of lodges and dams as well as for food. Many trees were completely re-

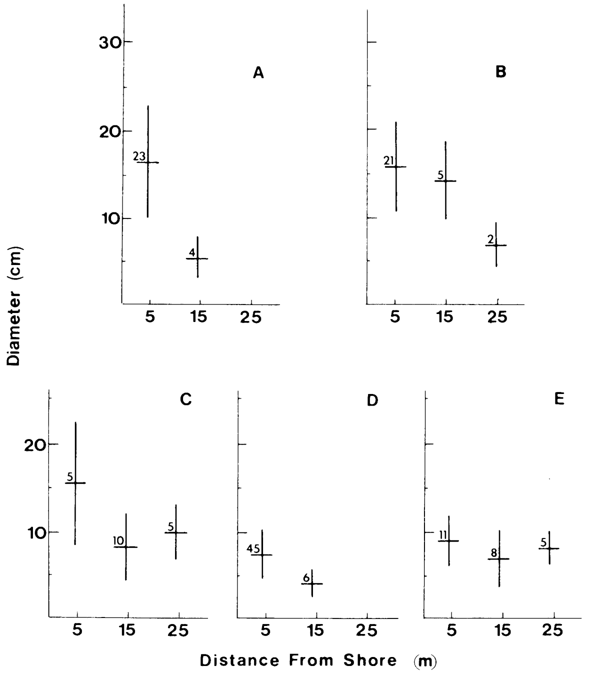

FIG. 2. Number of trees of various diameters cut at TRP and EFB as a function of distance from shore. A: maple at TRP; B: cherry at TRP; C: oak at EFB; D: maple at EFB; E: birch at EFB.

TABLE 1. Numbers of trees cut by beavers at three sites, classified by species.

	Blue Heron Cove	Tamplin Road Pond	East Fever Brook
Oak (*Quercus* spp.)*	73	3	20
Maple (*Acer* spp.)†	83	27	51
Birch (*Betula populifolia*)	37	3	23
Witch-hazel (*Hamamelis virginiana*)	58	0	0
Cherry (*Prunus* spp.)‡	4	28	9
Blueberry (*Vaccinium corymbosum*)	3	0	20§
Pine (*Pinus strobus*)	7	2	1
Others	11	5	5
Totals	276	68	129

* Includes 62 *Q. alba*, 10 *Q. rubra*, and 1 *Q. velutina* at BHC; 2 *Q. alba* and 1 *Q. rubra* at TRP; 17 *Q. alba* and 5 *Q. rubra* at EFB.

† All *A. rubrum* except 1 *A. saccharum* at BHC.

‡ All *P. serotina* except 1 *P. virginiana* at TRP.

§ All within 10 m of shore.

TABLE 2. Spearman rank-order correlation coefficients between tree diameter and distance from shore for trees of various genera cut by beavers at three sites.

Site	Genus	n	r_s	P
BHC	Oak	73	−0.80	<.001
BHC	Maple	83	−0.51	<.001
BHC	Birch	37	−0.61	<.001
BHC	Witch-hazel	58	+0.05	=.344
TRP	Maple	27	−0.56	=.002
TRP	Cherry	28	−0.33	=.043
EFB	Oak	20	−0.23	=.162
EFB	Maple	51	−0.41	=.002
EFB	Birch	23	−0.27	=.109

moved from the cutting sites so their ultimate disposition could not be determined. However, there was little new construction work at these three ponds during the course of the study, and most branches and logs added to dams or lodges were stripped of their bark, so I believe the assumption that trees were selected for cutting by beavers primarily because of their food value is valid.

All trees cut at TRP and EFB were within 30 m of shore, and most of those cut at BHC were within 100 m. Therefore, sites were sampled for available trees by recording all trees which had been alive at the beginning of the study period in 3-m wide transects perpendicular to the shoreline and extending away from shore 30 m (TRP and EFB) or 100 m (BHC). Transects were 30 m apart, and the position of the first transect at a site was randomly chosen. There were nine such transects at TRP, nine at EFB, and five at BHC. I divided each transect into segments 10 m long for determination of changes in the size distribution of available trees with distance from shore.

RESULTS

Table 1 shows generic distributions of trees cut at BHC, TRP, and EFB. Sizes and distances from shore of trees available differ markedly among genera, so it is not appropriate to combine genera for analysis of size-distance relationships. (Species belonging to the same genus are combined because such differences are much less between congeners, and because one species of each genus is always much more abundant than all the others [See Table 1]). Sufficient data exist to justify examination of size-distance relationships for oak (*Quercus*), maple (*Acer*), birch (*Betula*), and witch-hazel (*Hamamelis*) at BHC, maple and cherry (*Prunus*) at TRP, and oak, maple, and birch at EFB. Figs. 1 and 2 show diameters of trees cut as a function of distance from shore for these nine cases. There are significant negative correlations between size and distance for oak, maple, and birch at BHC, maple and cherry at TRP, and maple at EFB. Correlations are not significant for the other three cases (Table 2).

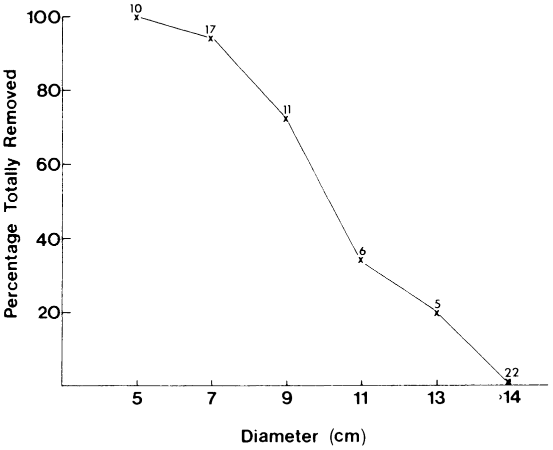

FIG. 3. Disposition of oaks cut at BHC as a function of diameter. The y-axis is the percentage of all trees of a particular diameter class which were totally removed from the site of cutting. Numbers above points are sample sizes for each diameter class.

These negative correlations result partially from differences in the densities and sizes of trees available at the various distances. For example, the density of oaks within 30 m of shore at BHC was 1.11/100 m^2, and all oaks at this distance in transects were >11.2 cm in diameter. However, there were 3.78 oaks/100 m^2 at 30–60 m from shore, 41% of which were less than 11.2 cm in diameter. Few small oaks were cut at 0–30 m because few were available at this distance, at least during the time period of this study. However, such availability differences are not the sole explanation for the negative correlations observed. Table 3 provides evidence for this. For oak at BHC and maple at all three sites, there exist two distances at which densities and size distributions of available trees are the same, yet mean sizes of cut trees differ significantly. Sizes of cut and available trees are compared by t tests with separate variance estimates rather than 2-way analyses of variance because unequal variances for cut trees at various distances are expected from the optimal foraging model under consideration (see Discussion section).

Figs. 1 and 2 also show an apparent decrease with distance in the range of sizes of trees cut, for oak at BHC and maple at all three sites. These patterns are documented statistically in Table 3. For all four cases, mean deviations in diameter from mean sizes cut are significantly less at greater distances.

Birch at BHC shows a negative correlation between size and distance in Fig. 1, but no significant difference in mean sizes cut at two distances selected for equal availabilities (50–70 m vs. 70–90 m; Table 3). Unlike the above four cases, variances in sizes of cut trees are the same at the two distances selected for analysis (variance at closer distance/variance at farther distance = 0.9 for birch at BHC, but 15.3 for oak at

TABLE 3. Comparisons of size distributions of trees available and cut at selected distances from shore.†

			Available				Cut		
					Diameter (cm)			Diameter (cm)	
Site	Genus	Distance (m)	*n*‡	Density§ (inds/100 m^2)	Mean‖	Mean deviation¶	*n*‡	Mean‖	Mean deviation¶
BHC	Oak	close = 30–60	17	3.78	16.08	7.29	26	14.58	5.81
				NS	NS	NS		**	**
		far = 60–90	13	2.89	13.27	7.97	25	7.14	1.54
BHC	Maple	close = 0–30	21	4.67	12.22	4.12	29	7.50	1.87
				NS	NS	NS		**	*
		far = 30–60	20	4.44	9.40	4.57	40	4.93	1.01
BHC	Birch	close = 50–70	10	3.33	10.69	1.91	28	10.20	1.86
				NS	NS	NS		NS	NS
		far = 70–90	11	3.67	12.15	2.07	4	6.86	2.03
BHC	Witch-hazel	close = 70–80	7	4.67	3.23	0.42	6	3.26	0.47
				NS	NS	NS		NS	NS
		far = 80–90	8	5.33	3.21	0.48	9	3.41	0.38
TRP	Maple	close = 0–10	15	5.57	18.58	6.26	23	16.08	4.95
				NS	NS	NS		**	*
		far = 10–20	15	5.57	15.58	6.94	4	5.21	2.16
EFB	Maple	close = 0–10	28	10.37	13.41	6.62	45	7.53	2.33
				NS	NS	NS		**	*
		far = 10–20	12	4.43	11.96	5.27	6	4.36	1.07

† Statistical significance is indicated as follows (all tests are two-tailed): NS, $P > .05$; *, $.01 < P < .05$; **, $P < .01$.

‡ *n*'s for available trees are based on 10% samples; *n*'s for cut trees represent all those cut at the study sites.

§ Densities compared by *t* tests based on five transects at BHC, nine at TRP, and nine at EFB.

‖ Mean diameters compared by *t* tests for two means with unequal variances (see text for justification).

¶ Mean deviation = $(\Sigma|x_i - \bar{x}|)/n$. These are compared by Levene's test (Van Valen 1978; see also Levene 1960, Brown and Forsythe 1974).

BHC, 3.6 for maple at BHC, 5.6 for maple at TRP, and 3.8 for maple at EFB). Therefore, a 2-way ANOVA was performed on the BHC birch data. Cut and available trees differ significantly in size ($F = 5.713$, $P = .021$), near and far trees do not ($F = 0.304$, $P = .584$), and there is significant interaction effect ($F = 7.709$, $P = .008$). For birch at BHC, the mean size of cut trees was less at 70–90 m than at 50–70 m, despite the fact that the mean size of available trees was greater at the farther distance.

Cherry at TRP shows a negative correlation between size and distance in Fig. 2, but is not included in Table 3 because the sample size of trees available is too small for testing the assumption that densities and size distributions are the same at various distances from shore (there were only two cherries at 0–10 m, two at 10–20 m, and five at 20–30 m in the nine availability transects at TRP).

For two of the three cases which do not exhibit a size-distance relationship in Fig. 1 or 2: oak and birch at EFB, densities of trees available were very low at some distances (oak: 0.37/100 m^2 at 0–10 m, birch: 0.74/100 m^2 at 0–10 m). For the third case, witch-hazel at BHC, a very limited range of sizes was available for cutting. In particular, all witch-hazels were less than 6.1 cm in diameter, well below the threshold size for a major change in the disposition of cut trees (see Fig. 3). Thus the absence of a significant correlation between size and distance for these three cases may reflect a lack of opportunity for choice by the beavers rather than a lack of generality in the relationship.

The BHC data can be used to examine temporal patterns in the size-selection of trees for cutting. I define three time periods for this analysis: fall 1972 (12 September–18 November 1972), spring 1973 (19 November 1972–31 August 1973), and fall 1973 (1 September–15 December 1973). Partial correlation coefficients of diameter with distance controlling for time and location (in a N–S direction parallel to the shoreline) are negative and significant for oak ($r = -0.72$ on 67 df for $P < .001$), maple ($r = -.54$ on 75 df for $P < .001$), and birch ($r = -.43$ on 33 df for $P = .009$). Partial correlation coefficients of diameter with time, controlling for distance and location, are positive and significant for oak ($r = .27$ on 67 df for $P = .023$) and maple ($r = .42$ on 75 df for $P < .001$) but not birch ($r = -.27$ on 33 df for $P = .114$). At a given distance and location, beavers cut small oaks and maples first and larger ones later. This suggests that a general preference for small-diameter trees may be superimposed on the size-distance relationships described above, at least for some genera.

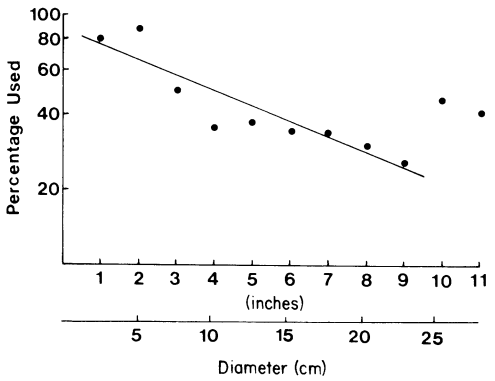

FIG. 4. Percentage utilization of aspen trees as a function of tree diameter, plotted from columns 1 and 5 in Table 2 of Aldous (1938). The total sample is 456 trees in all diameter classes, with more than 20 in each of the classes 5–20 cm. There is a significant regression of log(fraction utilized) on tree diameter ($r = .913$, $P < .001$; points for 25 and 28 cm excluded because Aldous calculated mass of food available from trees of these sizes by an incorrect extrapolation of his Fig. 1). The slope is −0.056/cm.

DISCUSSION

The most salient features of these results in relation to central place foraging theory are the greater selectivity by size at greater distances from the ponds and the decrease in mean size of trees cut with increasing distance. For four of the six cases for which the equal availability assumption is satisfied, selectivity is greater at greater distances from shore. For the other two cases, the range of sizes cut does not change with distance (Table 3). For five of the six cases which satisfy the equal availability assumption, mean size cut decreases with increasing distance from shore (Figs. 1 and 2, Table 3). For the sixth case, witch-hazel at BHC, mean size cut is independent of distance, but only very small trees are available for choice.

The first result is unequivocally predicted by Schoener's (1979) model of size-distance relationships in optimal foraging. According to this model, a food item of a given size located far from the central place will yield less net energy per unit feeding time than one close to the central place because the cost of pursuit or provisioning increases with distance. Therefore, if the densities and size distributions of prey available are independent of distance, the range of sizes worth feeding on will be less at greater distances, and the predator should be more selective by size at greater distances.

Orians and Pearson (1979) present several versions of a model of food selection by central place feeders, in one of which selectivity first decreases and then increases with distance from the central place (their Fig. 4). Several assumptions of this version of their model do not apply to beavers harvesting trees. In particular, they assume that pursuit and provisioning costs are independent of food size. For beavers, several trips are required to transport the branches of a large tree to the pond, while a single trip may suffice for a small tree. Although this version of the Orians and Pearson model is not appropriate for beavers harvesting trees, their prediction of minimum selectivity at intermediate distances from the central place may be true for other predator-prey combinations, and even for beavers feeding on other types of food such as grasses and forbs.

Schoener's model also addresses the question of whether greater selectivity with distance should favor large prey or small prey. The model predicts that if pursuit or provisioning time is independent of prey size, larger prey should be preferred at greater distances, but if pursuit or provisioning time increases with prey size, smaller prey may be preferred at greater distances. This reversal is especially likely if pursuit or provisioning time is a sigmoid function of prey size (Schoener 1979, especially Fig. 4c).

Provisioning time (T_p) for beavers is an increasing function of tree diameter, because carrying the pieces of a large tree to the pond for storage requires more trips than carrying the pieces of a small tree. Furthermore, provisioning time may be a sigmoid function of diameter, because a smaller fraction of large trees than of small trees is utilized. Aldous (1938) determined the mass and percentage utilization by beavers of the bark, twigs, and leaves of aspen trees of various sizes. His results suggest that the proportion of a tree hauled to the pond for storage may be described by a function of the form $p = e^{-b\ell}$, where ℓ is tree diameter (Fig. 4). Similar patterns exist for the tree genera cut by beavers in this study (exemplified by oak at BHC in Fig. 3), although explicit data on masses of material utilized from trees of various diameters are lacking.

If branches or logs of approximately equal mass are carried to the pond in each trip, the T_p is proportional to the mass of a tree which is stored. Total aboveground masses for trees of various species are well described by power functions of the form $W = c\ell^a$ (Whittaker and Woodwell 1968). Therefore,

$$T_p = \frac{k_1}{k_2}[(\text{distance})(\text{total mass of tree})(\text{fraction stored})] = \frac{k_1}{k_2}(rc\ell^a e^{-b\ell}),$$

where k_1 is the amount of time required to carry one load a unit distance, k_2 is the average mass of each load, and r is distance from shore. For a given r, this function is 0 at $\ell = 0$, has a maximum at $\ell = a/b$, and an inflection point at $\ell = (a - \sqrt{a})/b$. If $a = 2.34$ (the median for 11 tree and shrub species studied by Whittaker and Woodwell 1968, and Whittaker et al. 1974) and $b = 0.056$ (Fig. 4), then T_p as a function of ℓ has a maximum at 41.9 cm, larger than 97% of all trees available to beavers at the sites of this study, and an inflection point at 14.5 cm, larger than the largest trees cut far from shore but considerably less than the largest trees cut close to shore (Figs. 1 and 2). This implies that the provisioning time-size relationship may be sigmoid over a range of tree diameters which is relevant to a foraging beaver, and thus strengthens the argument that Schoener's (1979) model may explain these data.

Mortality risks associated with foraging have not yet been considered here, but may influence strategies of food selection. For beavers, there is probably a greater risk of predation at greater distances from the pond, not only because more time must be spent travelling back and forth, but also because there is a greater chance that a predator can come between beaver and pond, and thus block the beaver's return to safety. The extent of this risk for beavers at my study sites is difficult to predict; there are very few potential predators in central Massachusetts, yet predation by wolves (*Canus lupus*) on beavers may be substantial under more pristine conditions (Voigt et al. 1976), and beavers evolved in association with these and other carnivores. If predation is important beavers may be "time-minimizers" rather than "energy-maximizers" (Schoener 1974). Schoener's model of size-distance relationships applies to both cases (Schoener 1979), and makes the same predictions whether an animal's energy requirement or feeding-time limit is a more important constraint on its foraging behavior, because in both cases the animal is assumed to maximize its net rate of energy intake per unit time.

An alternative explanation for the results of this study is that size "selection" of trees by beavers is not a result of optimal foraging decisions at all but simply an artifact of foraging behavior. Perhaps a beaver chooses to begin cutting a tree without regard to its size. It is able to fell a small tree in one cutting session, but returns to the pond for rest before a large tree is completely felled (Wilsson 1971). When it resumes foraging, the beaver may or may not continue working on the partially felled large tree—it is more likely to do so if the tree is close to the pond, since the beaver begins each foraging session at the edge of the pond and would encounter partly cut trees near the pond sooner and more often than those farther away. Hence, trees of all sizes are felled close to the pond but only small trees are felled farther away.

This hypothesis predicts the presence of partially cut trees, especially far from shore. I have observed such trees at all three ponds (see Jenkins 1978 for data for BHC and TRP). However, these trees are few in number, compared both with felled trees and with trees having some bark stripped from their bases but no wood cut from them. Also, they are as abundant close to shore as far from shore, in contrast to the prediction. Therefore I believe size-selection of trees by beavers is not artifactual, at least as outlined above.

The data reported here are consistent with the hypothesis that beavers maximize their net rate of energy intake by size-selection of trees for cutting. Furthermore, selectivity increases with distance, as predicted by Schoener's (1979) optimality model of central-place foraging. Data on energy benefits and time and energy costs of harvesting trees of various sizes are essential for more refined tests of the model. These data will be difficult to collect because beavers are active primarily at night, in habitats where visibility is poor even during daytime. Wilsson's approach of confining beavers in relatively large outdoor enclosures (Wilsson 1971) seems most likely to yield this type of information. With this information, it will be especially interesting to compare various tree species in terms of nutritional value, handling time and energy, and provisioning time and energy as functions of tree diameter. My results suggest that there may be different size-distance relationships for different tree genera. For example, larger oaks than maples were cut close to shore at BHC (Fig. 1A and 1B), and larger cherries than maples at 10–20 m from shore, but not 0–10 m from shore, at TRP (Figs. 2A and 2B). An intriguing correlate of these differences is that the trunks of large oaks and cherries left lying where they had been cut were more often stripped of their bark than were the trunks of large maples (40% of such oaks at BHC and 88% of such cherries at TRP were substantially stripped, but only 14% of such maples at BHC and 31% of such maples at TRP were so utilized). Trees of genera such as oak and cherry for which less size-selectivity exists appear to be used more completely than those of genera such as maple for which greater size-selectivity is exhibited. However, the apparent differences among these genera in size-selectivity may result from differences in availability—few small oaks were available close to shore at BHC, and few small cherries at any distance at TRP. Field tests of optimal foraging models such as Schoener's (1979) or Orians and Pearson's (1979) may often be confounded by differences in food availability at various sites being compared.

Another hint that there may be different size-distance relations for different types of trees comes from MacDonald's (1956) report of no correlation between distance from shore and size of aspens cut at several beaver ponds in Colorado. In MacDonald's study, very few trees were cut at extreme distances, but these were generally smaller than those cut close to shore. Perhaps size-selection is only manifested at relatively large distances from shore for highly preferred genera such as aspen but at small distances for less preferred genera such as maple (Jenkins 1979).

An implication of my results for other studies of beavers harvesting trees, and of other predator-prey combinations also, is that taxonomic selectivity is not independent of size-selectivity. This is most clearly seen in the use of witch-hazel by beavers at BHC. This species was highly preferred to others beyond 70 m from shore (37% of trees cut between 70 and 100 m but only 16% of trees available at this distance). Witch-hazel may have been preferred not because its bark is nutritionally better than that of other species but because it is characteristically small in size and there are strong time and energy constraints against taking large trees at such distances.

Orians and Pearson's (1979) and Schoener's (1979) size-distance models are welcome additions to optimal foraging theory because they make more specific, and more subtle, predictions than some earlier models. For example, Schoener's (1979) model predicts the occurrence of both increasing and decreasing size-distance relationships. Which of these is expected for a particular situation depends on the form of the provisioning time-size function, which in turn depends on the relative sizes of prey and predator in a manner consistent with the few data which exist so far for various predator-prey combinations.

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