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Summer Diet Optimization by Beaver

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ABSTRACT: Foraging data collected for beaver (*Castor canadensis*) at Isle Royale National Park, Michigan, during the summer of 1973 provided basic natural history information pertaining to diet, food preferences, rates of consumption and activity cycle. Beaver foraging was consistent with a linear programming model of herbivore optimal foraging. The model was used to predict beaver diet, the maximum distance a beaver foraged from its pond, and the manner in which the minimum and maximum diameters of beaver-cut woody vegetation changed with distance from the pond.

INTRODUCTION

Although many investigators have studied beaver (*Castor canadensis*), few quantitative data have been collected on food preferences and the basis for observed preference (*see* Jenkins and Busher, 1979, for review). Beaver appear to change preferences of both the species and diameters of plants they cut with increasing distance from their pond (Jenkins, 1975, 1978, 1979, 1980) and Jenkins (1980) points out that this behavior might be explained by contingency models of optimal foraging (Schoener, 1971; Pyke *et al.*, 1977) and "central place foraging" [extension of contingency foraging models to species that return, like the beaver, to a nest or "home" (Schoener, 1979; Orians and Pearson, 1979)].

In this paper, preference for certain plant species exhibited by beaver and the diverse mixture of plant foods in their summer diet will be examined to determine whether they can be predicted using a quantitative optimal foraging model, a linear programming model of optimal foraging developed specifically for herbivores (Belovsky, 1978). Finally, this herbivore foraging model is modified to include "central place foraging" to account for beaver plant choice with increasing distance from the pond. The model is applied, with limited data, to the foraging of beaver at one site; however, the results indicate that the model might be of value to the study of beaver at other sites and in other seasons.

STUDY AREA

Data were collected at three sites (two ponds and Lake Superior) in a forest at Isle Royale National Park, Michigan. Isle Royale is a 520 km^2 archipelago in Lake Superior, 28 km from the nearest mainland. The upland forest surrounding all the sites is dominated by *Betula allegheniensis,* but the forest canopy in the lowlands immediately surrounding the two pond sites is primarily composed of *Thuja occidentalis* and *Picea* sp. These forests are more fully described by Belovsky and Jordan (1978).

The two pond sites are located on Grace and Washington creeks. The third site is Washington Harbor on Lake Superior. The Grace Creek pond is 3.5 ha and the Washington Creek pond 1.5 ha; each of these sites maintained a single beaver family and lodge. The Washington Harbor site is larger (20 ha) and contains several lodges. All three sites contain aquatic macrophytes and are surrounded by abundant terrestrial vegetation. The pond sites have soft bottoms but the lake site bottom is primarily sand and gravel. These substrate differences lead to different aquatic macrophyte production, species and species diversity.

METHODS

Data collected on beaver include: (1) use of woody vegetation in relation to availability by species and by distance from the water's edge, and (2) diet and behavioral observations. All measurements were made between 20 May and 31 August 1973.

The use of woody vegetation by beaver was determined by randomly locating a point on the water's edge of each site. Then, beginning with this point, transects extending perpendicular from the shore were placed at 100-m intervals around the shore. Each transect was 30 m long because beaver-cut plants were not common at distances greater than 30 m. Each transect had three plots, 4 m in diam, placed along it at 10, 20 and 30 m from the water's edge. A total of 21 transects (63 plots) were examined for the three sites. On each plot, the number of beaver-cut and uncut woody plants, taller than 20 cm, were counted, identified to species, and their diameters measured. The cut plants were measured at the point of cutting, while diameters of uncut plants were measured at 20 cm above the ground, the mean height at which cutting occurred. The cut plants were classified as freshly cut (current summer) or older, by the color of the wood.

Diameters of 64 plants (16 each of *Sorbus americana, Betula papyrifera, Acer spicatum* and *B. alleghaniensis*) were measured at 20 cm; all leaves, new growth of twigs and bark were collected, dried and weighed. These data were collected for plants between 0.5 and 10 cm diam, the sizes most common around the shoreline, and plants were sampled uniformly across the size range. Regressions were then constructed for stem diameter vs. leaf, twig and bark biomass for an average of all woody plants and for each of the four species. The regressions were used to estimate food and building material acquired by beaver.

Detailed diet and behavioral observations were made at the Grace Creek pond over five 24-hr periods during June-August 1973. This beaver family (two adults, two yearlings, four kits) was accustomed to the presence of humans, because this was a main research site for moose (*Alces alces*) (Belovsky and Jordan, 1978). An observer located on their lodge was permitted a clear view of most of the pond, the shoreline and entrance to the lodge. From this location, the observer was able to record the beaver family's feeding movements during 15-min periods, even at night by sound or flashlight. This information was used to compute daily feeding time as the sum of all adults and yearlings observed feeding in each 15-min period divided by the number of 15-min periods in a day and the number of adult-yearling beaver (4) in the lodge. The number of times and the duration of the periods that beaver engaged in either aquatic or terrestrial foraging were recorded. The ambient air temperature, water temperature (10 cm below surface) and the internal air temperature of the lodge were recorded at each half-hour for correlation with beaver feeding activity.

RESULTS

Beaver were selective in feeding on woody plants, cutting species of plants in proportions significantly greater or less than their relative availability (Table 1, $\chi^2 = 76.9$,

TABLE 1.—Species composition of woody plants cut by beaver at Isle Royale National Park, Michigan, and the percent availability of deciduous plants. Species composition of cut plants is based upon the number of stems cut. Availability is the percentage of plants of each species within 30 m of the pond, based upon cut and uncut stems. A X^2 goodness of fit test is used to compare the cut and available stems

Sample size (# plants)	% Cut 215	% Available 796	Significance ($p < 0.05$)
Acer rubrum	0.5		n.s.
A. saccharum	31.6	15.0	sig.
A. spicatum	2.8	3.5	n.s.
Alnus rugosa	41.9	37.4	n.s.
Betula alleghaniensis	4.2	1.4	sig.
B. papyrifera	1.9	6.3	sig.
Cornus stolonifera	0.5	2.6	n.s.
Corylus cornuta	0.9	5.3	sig.
Sorbus americana	14.9	20.1	n.s.
Others	0.9	8.3	

$p \leq 0.05$, df = 9). Beaver preferred (diet proportion significantly greater than available) *Acer saccharum* and *Betula alleghaniensis,* were indiffernt to (diet proportion not significantly different from available) *Alnus rugosa, Acer spicatum, A. rubrum, Cornus stolonifera* and *Sorbus americana,* and avoided (diet proportion significantly less than available) *Betula papyrifera, Corylus cornuta, Lonicera canadensis, Abies balsamifera, Thuja occidentalis, Picea* sp. and *Sambucus pubescens.* Furthermore, beaver did not change their preference for plant species with increasing distance from the water.

When woody vegetation occurred in all three plots along a transect, a highly significant inverse relationship existed between distance (d) from the water and percentage of plants cut ($r = 0.48$, $\% = 88.0e^{-0.08d}$, N = 33, $p \leq 0.01$). This relationship indicated that beaver limited their cutting away from water. Mean diameters of woody plants that were cut by beaver were significantly larger than the diameters of woody plants that were not cut (cut: 2.5 cm ± 1.5, N = 215; cut + uncut: 1.3 cm ± 0.9, N = 796, t = 10.0, $p < 0.05$). No difference existed between the mean diameters of woody plants cut at the different distances from water, but the smallest and largest 10% of cut-diameters were different. The largest diameters of woody plants cut (10 m: 5.7 cm ± 2.1, N = 10; 20 m: 5.4 cm ± 0.4, N = 6; 30 m: 3.8 cm, N = 2) decreased with increasing distance ($r^2 = 1.0$, Spearman rank correlation, $p < 0.05$). The smallest diameters of woody plants cut (10 m: 0.6 cm ± 0.2, N = 10; 20 m: 1.0 cm ± 0.2, N = 6; 30 m: 1.4 cm, N = 2) appeared to increase with increasing distance $r^2 = 1.0$, Spearman rank correlation, $p < 0.05$).

Beaver fed 269 min/day with distinct feeding periods (Fig. 1a). Beaver activity can be correlated with the thermal environment (Fig. 1b). The main activity period (1900-0700) occurred during the coolest ambient air temperatures. The activity peak from 1300-1500 occurred when the water was cooler than the air, and no major temperature difference existed between the lodge and the water; thus, it is thermally as equitable to forage as it is to rest.

When the beaver were close to the observer (< 50 m), and their selection of food could be observed, beaver at Grace Creek pond 82 min ate aquatic macrophytes 4.9% of the time (4 min). While feeding on aquatics, beaver averaged two dives/min with two plants per dive. If the average aquatic plant weighed 1.3 g dry wt (Belovsky and Jordan, 1978), beaver were averaging an intake of 69.0 g dry wt/day (0.049 X 269 min/day X 1.3 g/plant X 4 plants/min). The remainder of the feeding observations involved the cutting, transporting and consuming of leaves of woody plants (95.1%, 82 min).

At Grace Creek pond, 0.48 woody plants/m² were cut by beaver between 20 May and 15 August (88 days) on 18 plots monitored regularly and on which plants cut by beaver (108 cut) were marked. From mapping the pond and the 30 m of land surrounding the shore used by beaver (Belovsky and Jordan, 1978), beaver were found to use approximately 21,313 m² of terrestrial area surrounding the pond. From this and the fact that four beaver (two adults, two yearlings) were cutting these plants, foraging beaver averaged 29 plants cut/day. Deciduous plants have an average leaf biomass equal to:

$$l = 3.4D^{1.7} \qquad (1),$$

N = 64, $r^2 = 0.83$, $p < 0.05$) where l is measured in g dry wt and D is the diameter of the main stem, 20 cm above the ground. Computing the average leaf biomass for a woody plant using all diameters of beaver-cut woody plants, a beaver had an average leaf intake of 551 g dry wt/day (19.2 g times 29 plants/beaver/day). Both terrestrial and aquatic consumption will be slight overestimates since a portion of the food will be supplied to kits.

The time required by beaver to cut woody vegetation was not measured because no beaver was observed cutting from start to finish. Limited information from other studies on the cutting time vs. diameter of the plant exists (Fig. 2), indicating a relationship:

$$t_c = 0.63e^{0.24D} \qquad (2)$$

($r^2 = 0.94$, $N = 9$, $p < 0.05$), where t_c is the cutting time in minutes. A beaver requires an average of 1.24 min to cut a plant, based upon observations of all diameters of woody plants cut by beaver.

DISCUSSION

Belovsky (1978; in press a & b) constructed a linear program model of optimal foraging by herbivores using constraints for digestive capacity, foraging time, energy requirements and nutrient requirements. The model can be solved for either energy-maximizing or feeding time-minimizing strategies given species and site-specific values for each constraint. An energy maximizer presumably acquires more energy than can presently be used, so that fat can be stored for use in future periods of food scarcity or reproduction. A time minimizer reduces its energy intake through feeding to enable it to devote more time to other activities (grooming, lodge construction, etc.) or to reduce

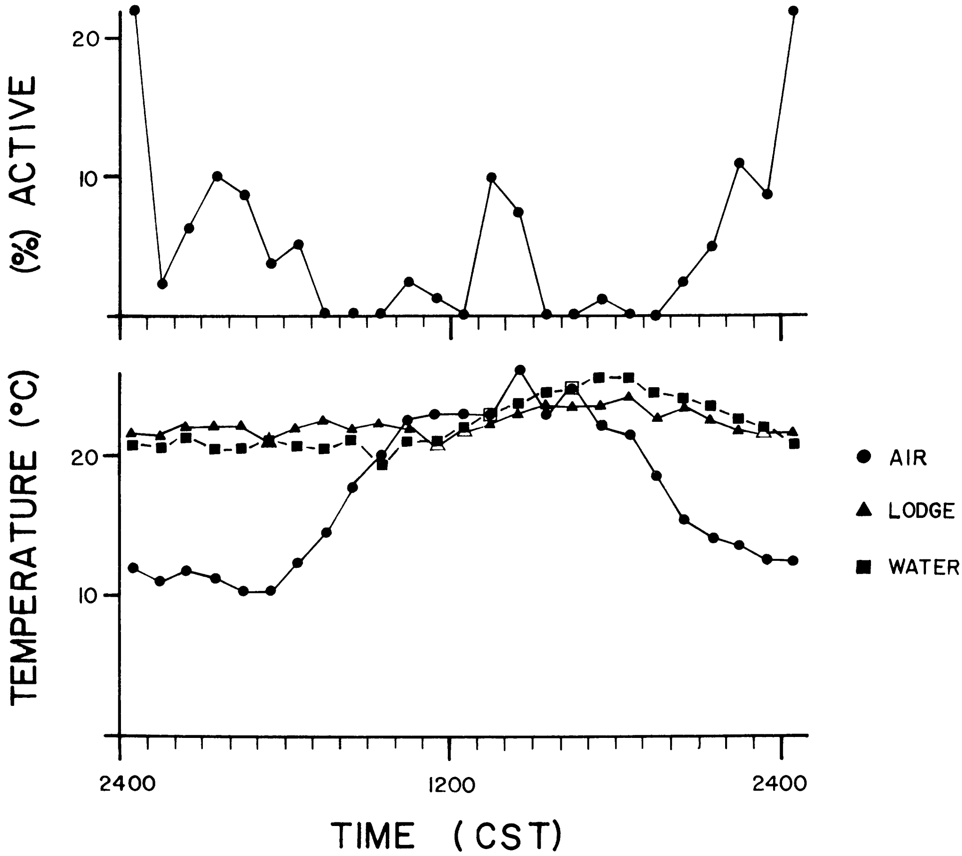

Fig. 1.—a. The percentage of daily beaver foraging activity observed at each hour over an average summer day, based upon 84 (adult-yearling) beaver exit-returns to the lodge over 5 days. b. Average hourly air, water and internal lodge temperatures at Grace pond over 5 summer days

its exposure to predators and other deleterious factors in the environment (Belovsky, 1978).

A linear program model is composed of a set of constraint equations:

$$C \geq \text{ or } \leq \sum_i a_i x_i$$

where C is a constraint value that either cannot be exceeded or must be exceeded, x_i is the quantity of food i eaten and a_i converts the quantity of food i eaten into the constraint units. With the constraint equations, an objective function is solved either for energy-maximization or time-minimization:

$$P = \sum_i b_i x_i$$

where P is energy intake or feeding time, and b_i converts the intake of food i into either energy or time. Linear programming models can be solved graphically if two foods are considered, or by the Simplex algorithm for n foods (Belovsky, 1978).

To evaluate beaver foraging behavior and the results presented above, a quantitative foraging model can be applied. To solve the linear programming model for a

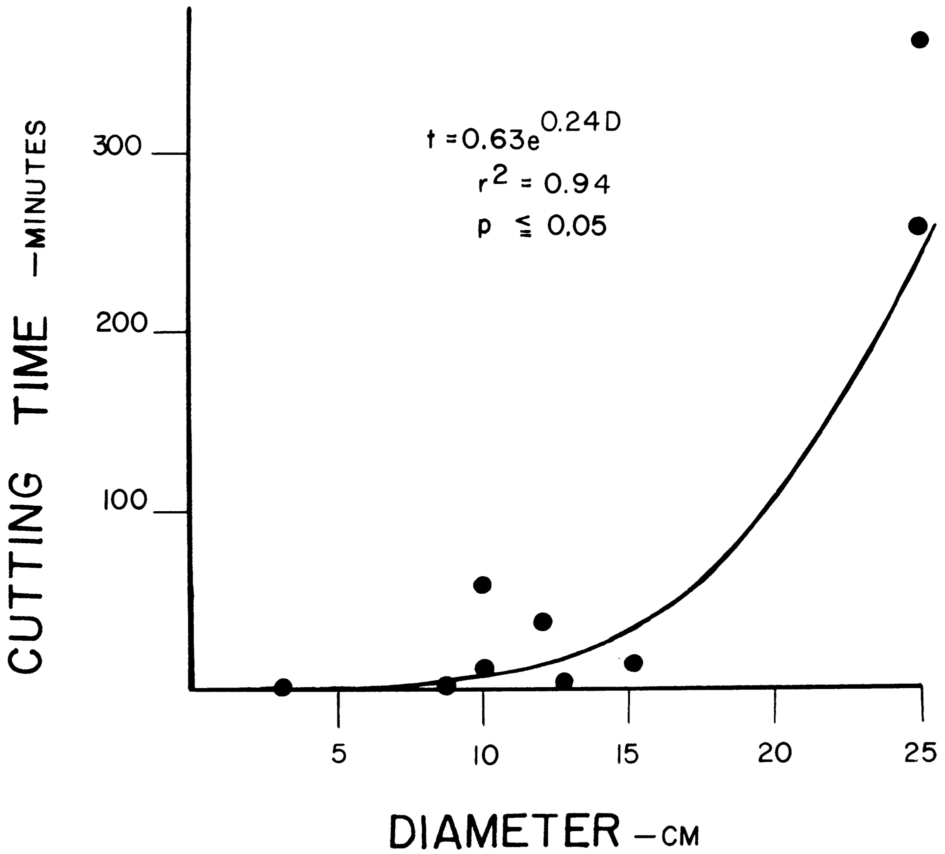

Fig. 2.—The time a beaver took to cut a woody plant as a function of the plant's diameter. The time-diameter data were taken from Warren (1927), Rue (1964) and Wilsson (1971)

beaver foraging during summer (June-August), four constraints are required (digestive capacity, foraging time, energy requirements and nutrient requirements). All parameter values are based upon an adult beaver weighing 15 kg. The model is set up for two food plant types: aquatic macrophytes and deciduous leaves.

1. *The beaver's digestive capacity* depends upon the g wet wt capacity of the caecum/upper colon and stomach, and the rate at which food passes through the digestive tract. Both the stomach and caecum/upper colon are used as a continuous flow system by herbivorous rodents to break down plant tissues (McBee, 1971). A 15-kg adult beaver has a full stomach capacity of 530 g wet wt (Grinnell *et al.*, 1937), where partially filled stomachs were estimated to the full value based upon the investigators' estimates of the fraction filled, and the size of the beaver was proportionally scaled to a 15-kg individual. Herbivorous caecal digesters have a caecal/upper colon capacity approximately 1.8 times the stomach capacity (Belovsky, in press a, b for *Microtus pennsylvanicus* and *Lepus americanus*; McBee, 1971). Hoover and Clarke (1972) report a much lower caecal/upper colon capacity (3.7% of body wt) for beaver. However, by their admission, their techniques will underestimate capacity and their largest value of 6.1% provides a comparable value to my estimate of 1.8 times stomach capacity. Therefore, a beaver has a digestive organ capacity (stomach plus caecum/upper colon) of approximately 1484 g wet wt of food.

No information on the passage rate of green foods through a beaver's digestive tract is available. Currier *et al.* (1960) and Stephenson (*vide* Currier *et al.*, 1960) report that beaver require 60-72 hr to eliminate 95-100% of the chromic oxide added to a dry pelleted grain ration; however, they do not provide the mean retention time, average time for a food particle to traverse the gut. Furthermore, green vegetation should pass more rapidly through the digestive tract than a dry pelleted ration or a twig diet. Data are available on the passage of green foods through the nutria (*Myocaster coypus*), another large (>8 kg) aquatic herbivorous rodent. In nutria which are fed lettuce and a marker of dyed oat kernels, the average passage time is 10.3 hr (recalculated from Gill and Bieguszewski, 1960). Thus, the digestive tract empties 2.33 times/day. Accordingly, using the passage rate for nutria and assuming that passage time is similar for all green plant tissues, a beaver has a total digestive capacity of 3458 g wet wt/day.

Digestive capacity also depends upon the rate at which different plant types fill the organs (wet wt/dry wt). These parameters were measured by Belovsky and Jordan (1978). Using these values, the digestive capacity constraint is:

$$3458 \text{ g wet} \geq 4L + 20A \qquad (3),$$

where L is the beaver's g dry weight daily intake of leaves and A is the g dry wt daily intake of aquatic plants.

2. *The foraging time constraint* depends upon the amount of time available to a beaver each day for foraging and the rate at which beaver crop aquatic plants and deciduous leaves. I suggested that available foraging time might best be obtained by some means independent of observing the animal's behavior (Belovsky 1978). An optimization model of maximum allowable daily feeding time based upon thermal balance may be used (Belovsky, 1981a). This concept avoids any chance that observed foraging time is linked to the cropping time for different foods. This precaution is not available for the beaver model because insufficient thermal physiology data are available. Coles (1966), however, in a laboratory study of beaver thermoregulation, demonstrated that beaver summer activity is probably limited by excessive heat gain and loss in temperate areas. Therefore, given the correlation of observed beaver activity with thermal conditions, I assume that a beaver's observed feeding time (269 min/day) equals its maximum allowable time. Furthermore, the beaver lodge (Fig. 1b) may function as a constant thermal environment: cool when the air is hot and warm during the cool nights.

One might argue that beaver can forage all night (the period of most equitable thermal conditions), such that the maximum time would be approximately 720 min. The observed daily feeding activity, however, is far less than the 720 min suggested by Busher (1975); but peak activity did occur in the same period found by Busher (1900-0700) and a second activity peak from 1300-1500 was also found. Little nonfeeding related activity was observed, less than 10%, suggesting that inclusion of other activities (dam repair, unexplained swimming, etc.) would not increase activity time to approach Busher's (1975) estimates. Two explanations for this discrepancy may be proposed. First, Busher's (1975) estimate includes spring and autumn observation periods of less thermal stress, perhaps permitting more feeding. Second, beaver might only forage for 269 min as time minimizers to avoid predatory risk. However, the latter explanation might not result in a correlation between thermal conditions and when they forage.

The rate for cropping aquatic plants is 0.19 min/g dry wt. When cropping deciduous plants, beaver swim an average of 106 m to the edge of the pond and then walk 16 m on land. On average, beaver swim 69 m/min and walk 28 m/min (Green, 1936). At Grace Creek pond, it is estimated that beaver halve their walking and swimming speeds while hauling cut branches. No cut branch or stem larger than 2.5 cm diam is hauled intact, but more than one smaller branch is carried. Using this information and eqns. 1 and 2, the cropping rate for deciduous leaves (C_D: min/g dry wt) is:

$$C_D = \frac{0.63e^{0.24D} + \frac{3.4D^{1.7}}{16.1}\left[3\left(\frac{106\text{ m}}{69\text{ m/min}} + \frac{d}{28\text{ m/min}}\right) + \begin{cases} 0 & \text{for } D \leq 2.5\text{ cm} \\ 1.20 & \text{for } D > 2.5\text{ cm}\end{cases}\right]}{3.4D^{1.7}\text{ g dry wt}} \quad (4),$$

where $3.4D^{1.7}/16.1$ is the scaling factor for additional trips and cutting required for plants with diameters different from 2.5 cm, d is the distance (m) from the pond, 3 is the equivalent number of trips given the slower speed of transport, and 1.20 is the time (min) required to cut a 2.5-cm branch from a larger plant. Averaging eqn. 4 over all observed D and d values, the cropping rate for leaves is 0.49 min/g dry wt. Therefore, on average, the feeding time constraint equals:

$$269\text{ min} \geq 0.49L + 0.19A \quad (5).$$

3. *A beaver's energy requirement* is estimated from the standard body weight-metabolism relationship for mammals (Kleiber, 1961; Hemmingsen, 1960), increased by 12% because beaver are known to have a basal metabolism 12% greater than the average mammalian estimate (Coles, 1966). Furthermore, it is assumed that a beaver requires twice its basal needs to satisfy additional energy expenditures for minimum growth, winter fat storage and reproduction. Therefore, an adult beaver (15 kg) requires on average 1213 kcal/day.

Information on the net energy content of plants eaten and the energetic expenditure for cropping by beaver is needed also. Belovsky and Jordan (1978) presented gross energy values of 4.2 kcal/g dry wt for deciduous leaves and 4.1 kcal/g dry wt for aquatic plants. Using data on the beaver's ability to digest different plant components (protein, fat, NFE, cellulose) and rations (Novakowski, 1967; Cowan *et al.,* 1957; Currier *et al.,* 1960), the dry matter digestibility for a beaver is estimated to be 68% for deciduous leaves and 80% for aquatic macrophytes.

Schmidt-Nielsen (1972) found that the cost of swimming to a mammal is the same as running; using Schmidt-Nielsens' data on energetic cost of running vs. body size, a beaver expends approximately 0.02 kcal/m or 0.04 kcal/m in a foraging round-trip. Brody (1945) found that farm draft animals are approximately 35% efficient in carrying a load, and a unit of work costs the animal 0.00234 kcal/kg-m or $6.7X10^{-6}$ kcal/kg-m for actual energetic cost. The weight hauled by a beaver depends upon the leaf and stem or twig weights. The stem-twig weight (T: g dry wt) equals:

$$T = 12.1D^{2.8} \qquad (6),$$

($r^2 = 0.81$, N = 64, $p \leq 0.05$). Using eqns. 6 and 1 and increasing dry weight by a multiple of two for stems-twigs and four for leaves to compute wet weight (Belovsky, 1981b), the average stem transported weighs 379 g wet weight. The energetic cost of transporting woody foods (E_t: kcal/g dry wt of leaves) is estimated as:

$$E_t = \frac{\frac{3.4D^{1.7}}{16.1}(106\ m + d)[0.04 + (6.7X10^{-6})\ (379\ g\ wet\ wt)]}{3.4D^{1.7}} \qquad (7).$$

Averaging eqn. 7 over all D and d values observed, E, equals 0.30 kcal/g dry wt and the energy requirement constraint equals:

$$1213\ kcal/day \leq [(4.2\ kcal/g\ dry\ wt)(0.68) - 0.30\ kcal/g\ dry\ wt]L + (4.1\ kcal/g\ dry\ wt)(0.80)A \qquad (8).$$

4. *Nutrient requirements of beaver* were not measured because captive beaver were not kept and feces and urine could not be collected in the water where beaver deposit them. Isle Royale is known to be a potentially sodium-poor habitat for beaver (Botkin *et al.*, 1973), and two other Isle Royale herbivores (*Alces alces* amd *Lepus americanus*) are limited in their foraging by sodium intake (Belovsky, 1978, in press b). However, Schmidt-Nielsen and O'Dell (1961) demonstrate that beaver urine is very low in solutes suggesting that beaver might have low sodium excretory losses.

The linear program model could be constructed without nutrient constraints and solved for time minimization and energy maximization. If one of the two alternative strategies predicts the observed beaver diet, nutrients can be discounted as an important foraging constraint for Grace pond beaver. However, if neither strategy could be demonstrated, then either other constraints might be operating, for which sodium is a likely alternative, or beaver might not be employing either of the two foraging strategies (Lewontin, 1979).

The model for beaver diet selection can be solved using eqns. 3, 5 and 8. The constraint equations are plotted in Figure 3 and the alternative strategies are examined. Beaver appear to be energy maximizers (Table 2) because the time-minimizing diet is significantly different from the observed diet on the basis of feeding observations converted into food items (leaves, aquatic plants) (N = 82, $X^2 = 15.85$, $p \leq 0.005$) and did not differ from the energy-maximizing diet ($X^2 = 0.001$, $p \leq 0.95$). Beaver do not appear to have any nutrient constraints, especially sodium, probably due to sufficient intake from aquatic plants during summer (Botkin *et al.*, 1973) and bark at other times of the year (Likens and Bormann, 1970). Also, beaver do not appear to consume certain plants for sodium, as Isle Royale moose do with aquatics (Belovsky, 1978).

As pointed out above, one might argue that the 269 min/day for feeding is less than the maximum because of risk considerations. If this is true, one cannot claim that beaver are energy maximizers in their overall foraging strategy, but one can still point out that given the foraging time, beaver maximize their energy intake. Given the close fit between the model and observed behavior, even with limited data for the model's parameters, the diet optimization approach appears potentially useful.

The model can be solved to determine how the diameters of woody plants selected by beaver change with distance from the pond. Belovsky (1981b) demonstrates that herbivores may be limited in their selection of plants by quality (digestibility) and quantity (cropping rate). Net energy content or digestibility of deciduous plants is not important for determining a beaver's movement away from the pond, because a beaver requires only 1.9 kcal/g dry wt to satisfy its energy requirements with the digestive capacity available after consuming aquatic vegetation [(1213 kcal required — 223 kcal from aquatics)/(3458 g wet wt of digestive organ — 1360 g wet wt intake of aquatics)/(4 g wet/g dry for leaves)] or a 52% digestibility for leaves. In addition, using eqn. 7 summed over all D, the beaver are able to forage 253 m from the pond, a distance far greater than observed.

On the other hand, the cropping rate constraint requires a beaver to acquire 3.87 kcal/min [(1213 kcal required — 223 kcal from aquatics)/(269 min/day — 13 min/day spent cropping aquatics)] after intake of the energy-maximizing quantity of aquatic vegetation. Combining the caloric value for leaves (2.86 kcal/g-dry wt) with eqns. 4

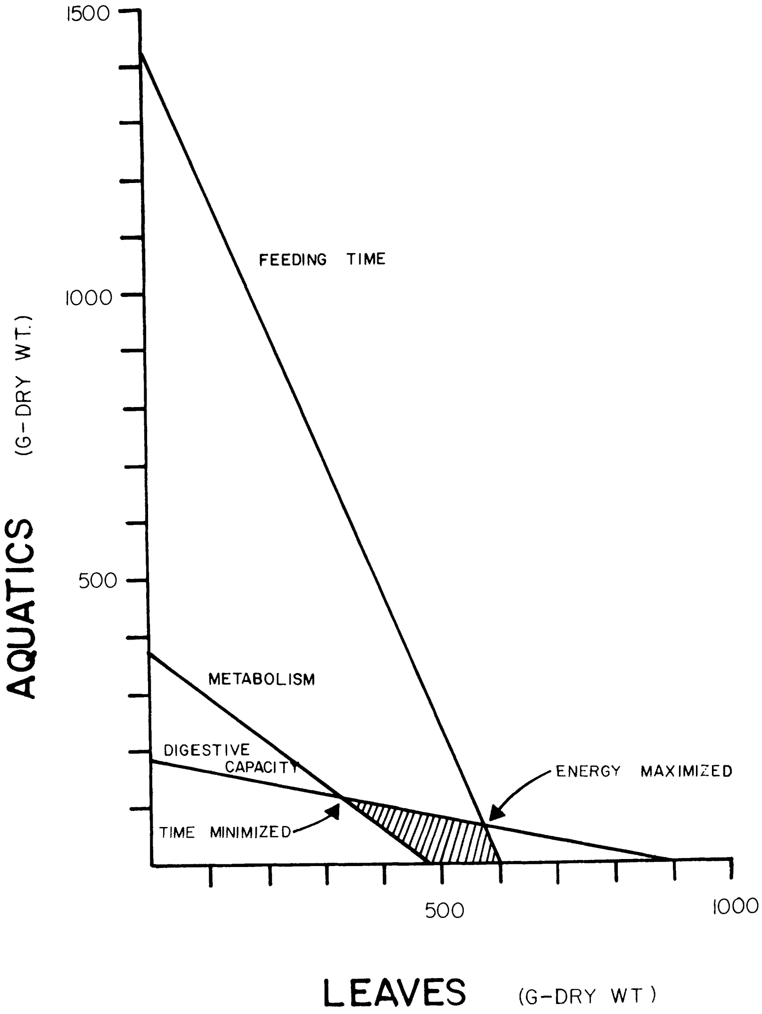

Fig. 3. — The linear program constraints for a beaver. The striped area represents diet combinations capable of satisfying a beaver's energy requirements. The predicted time-minimizing and energy-maximizing feeding strategies are labelled

and 7 summed over all D and simplifying, the following inequalities must be satisfied by a beaver:

$$3.87 \text{ kcal/min} \leq \frac{2.58\text{-}2.65\text{X}10^{-3}\text{d}}{\frac{0.19e^{0.24D}}{D^{1.7}} + 0.007\text{d} + \begin{cases} 0.29 \text{ for } D \leq 2.5 \text{ cm} \\ 0.37 \text{ for } D > 2.5 \text{ cm} \end{cases}}$$

Using the above inequality, the minimum and maximum diameters predicted to be cut by a beaver at Grace pond are presented in Figure 4, along with the kcal/min isoclines for values greater than 3.87 kcal/min. These solutions confirm the general size-distance relationship found by Jenkins (1980); *i.e.,* maximum size declines with distance while minimum size increases. The minimum observed diameters of woody plants cut at 10, 20 and 30 m are predicted (Fig. 4: $r^2 = 0.98$, $p \leq 0.06$). The maximum sizes cut are far less than those predicted at 10 and 20 m; however at 30 m the observed and predicted values were in closer agreement. This lack of agreement may be due to the absence of woody plants with diameters large enough to limit beaver cutting at 10 and 20 m, but at 30 m available stem diameters are large enough that beaver must be selective.

At Grace Creek, the maximum distance from the pond at which woody plants are cut is predicted to be 40 m and the observed maximum distance is 48 m. Both the minimum-maximum diameters selected and the maximum distance of cutting by beaver from water should change from site to site. These changes in diet selection by beaver with energy costs and transport time are as expected from "central place foraging" theory (Jenkins, 1980). This behavior might also arise from predatory risk. The fit to the quantitative foraging model and the changes in diameters selected by beaver, however, indicate that the energetic and time considerations for foraging may be more appropriate than the predation hypothesis.

The model can be solved to determine whether beaver preferences for woody plant species depend upon leaf biomass of each species obtained/minute spent cropping. The measured g dry weight of leaves available per plant vs. diameter is used to calculate regressions for several plant species. Using the above regressions, eqn. 4 solved for a mean distance travelled of 16 m, and the distributions of available diameters by species, the g dry weight of leaves removed/minute cropping for each of four species is computed (Table 3). These values are compared with the percentage of each species used by beaver (Table 3: # cut X 100/# available), indicating that plants may be selected for their weight of leaves per unit time in harvesting ($r^2 = 0.93$, $p \leq 0.05$).

It is interesting that *Sorbus americana* is not preferred by beaver since this species is highly preferred by moose in summer and winter (Belovsky and Jordan, 1978; Belovsky, 1981b). *Betula alleghaniensis* is preferred by beaver but not by moose in summer (Belovsky and Jordan, 1978), and preferred by both in winter (Belovsky, 1981b). Other than these two exceptions, beaver and moose preferences for deciduous species are the same. The differences may be explained in part by the foraging behavior of beaver and moose. Moose crop woody plants, like most herbivores, by items (leaves or

TABLE 2.—Diets of beaver predicted by the linear program model are compared with the observed diet of beaver at Grace Creek pond

	Time minimization		Energy maximization		Observed	
	g dry wt	%	g dry wt	%	g dry wt	%
Deciduous leaves	339	76	523	88	556	89
Aquatic plants	105	24	68	12	69	11
Total	444		591		625	
Energy (kcal)	1213		1562		1647	
Time (min)	186		2699		286	

twigs), incurring a small cropping time expenditure per item. On the other hand, beaver crop woody vegetation by the plant, subsequently cropping leaves, twigs and bark. This leads to an initially large cropping time expenditure by beaver. Therefore, beaver preference might be related to the quantity of items available per plant cut, a consideration not faced by most herbivores that would be concerned with items per unit area and item size (Belovsky, 1981b).

The linear program model of beaver foraging can be examined for sensitivity to constraint changes. The feeding time and digestive capacity constraints are the only constraints operative in the energy-maximized solution. Each constraint can be varied (both increased and decreased) to determine how large a change is needed to vary leaf intake by 10%. If daily feeding time is increased by more than 26% or decreased by 10%, leaf intake will vary by 10%. Digestive capacity must be increased by 69% or decreased by

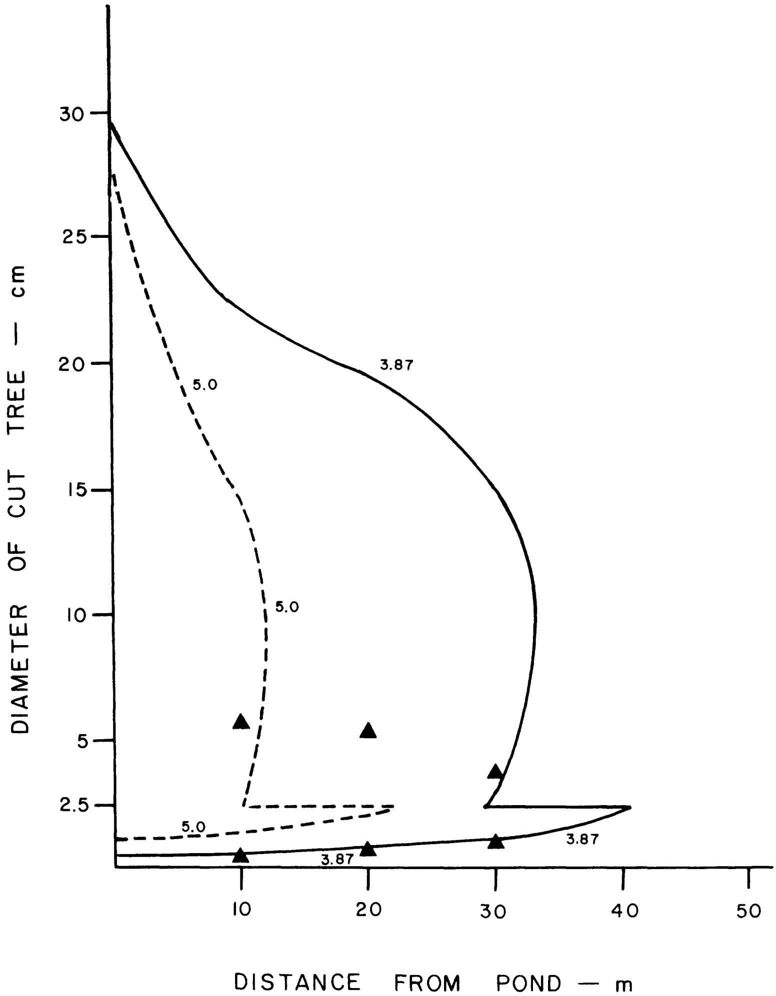

Fig. 4.—Predicted maximum and minimum diameters of woody plants that a Grace pond beaver can cut at varying distances from the water. The solid line refers to the estimated beaver requirement of 3.87 kcal/min, while the dashed line refers to minimum-maximum diameters if a beaver's energy/time food intake requirements are 5 kcal/min. Triangles represent the observed minimum-maximum diameters cut by beaver at varying distances from Grace pond

34% to cause leaf intake to vary by 10%. In terms of relative diet change, the above constraint variations lead to diets of 72-100% leaves. Finally, if a beaver's energy requirements are increased by 38%, the energy-maximizing diet can satisfy only basic requirements. These results indicate that the model is potentially insensitive to realistic errors in the constraint values, and beaver diets at other Isle Royale sites and temperate areas may not be influenced by changes in these constraints.

Parameter values converting food intakes into constraint values, however, may be important. Bulk (wet/dry weights) values for different foods are probably not sources of variation, because they are likely not to vary by more than 5-10%. Cropping times, however, can change dramatically with abundance of vegetation and distance travelled to the water's edge. Cropping times of aquatic and terrestrial herbaceous plants (the latter not important at Grace Creek pond) should be particularly susceptible to vegetation abundance; however, woody plant cropping rates should depend upon cutting time. Svendsen (1980) found that the proportion of woody vegetation in beaver diets did not change very much even though woody vegetation abundance changed by a large amount. From the model, the cropping rate of aquatic plants must increase by 158% to decrease woody vegetation consumption by 10%, while woody vegetation consumption is insensitive to declines in aquatic cropping rates. On the other hand, woody vegetation cropping rates must increase by 11% to decrease woody vegetation consumption by 10%, and decrease by 9% to increase consumption by 10%. Therefore, with the combination of abundant herbs in adjacent meadows with woody vegetation, a beaver might increase terrestrial foraging, but changes in aquatic plant abundance have little effect on terrestrial diet.

CONCLUSION

Beaver at an Isle Royale pond appear to select their diet in a manner consistent with an energy-maximizing solution to a linear programming model (Belovsky, 1978). This model was originally developed for an examination of moose diet optimization (Belovsky, 1978). With slight modifications for a beaver's "central place" foraging, the model predicts not only the beaver's diet but also its selection of woody plant diameters, species and distance foraged from the pond. Cropping rates of foods were potentially the most important factor that could lead to diet changes. The successful predictions of the model given limited data indicate that this approach may merit further consideration for beaver foraging.

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LITERATURE CITED

ALDOUS, S. E. 1938. Beaver food utilization studies. *J. Wildl. Manage.*, **2**:215-222.

BELOVSKY, G. E. 1978. Diet optimization in a generalist herbivore, the moose. *Theor. Pop. Biol.*, **14**:105-134.

TABLE 3.—Prediction of food intake rate by a beaver cutting an average plant of four species compared with the observed beaver use of the species

	% Observed use	Expected gain (g/min)
Betula papyrifera	8.0	0.6
Sorbus americana	20.0	1.3
Acer spicatum	21.0	0.8
Betula alleghaniensis	82.0	2.5

______. 1981a. Optimal activity times and habitat choice of moose. *Oecologia,* **48**:22-30.
______. 1981b. Food plant selection by a generalist herbivore: the moose. *Ecology,* **62**:1020-1030.
______ AND P. A. JORDAN. 1978. The time-energy budget of a moose. *Theor. Pop. Biol.,* **14**:76-104.
______. In press. Herbivore optimal foraging: a comparative test of three models. *Am. Nat.*
______. In press. Snowshoe hare optimal foraging and its implications for population dynamics. *Theor. Pop. Biol.*
BOTKIN, D. B., P. A. JORDAN, A. DOMINSKI, H. LOWENDORF AND G. E. HUTCHINSON. 1973. Sodium dynamics in a northern forest ecosystem. *Proc. Natl. Acad. Sci. U.S.A.,* **70**:2745-2748.
BRENNER, F. J. 1962. Foods consumed by beavers in Crawford County, Pennsylvania. *J. Wildl. Manage.,* **26**:104-107.
BRODY, S. 1945. Bioenergetics and growth. Reinhold, New York. 1023 p.
BUSHER, P. E. 1975. Movements and activities of beavers, *Castor canadensis,* on Sagehen Creek, California. M.A. Thesis, San Francisco State University, San Francisco, California. 86 p.
COLES, R. W. 1966. Thermoregulation of the beaver. Ph.D. Dissertation, Harvard University, Cambridge, Massachusetts. 82 p.
COWAN, I. MCT., A. J. WOOD AND W. D. KITTS. 1957. Feed requirements of deer, beaver, bear and mink for growth and maintenance. *Trans. N. Am. Wildl. Conf.,* **22**:179-188.
CURRIER, A., W. D. KITTS AND I. MCT. COWAN. 1960. Cellulose digestion in the beaver (*Castor canadensis*). *Can. J. Zool.,* **38**:1109-1116.
GILL, J. AND H. BIEGUSZEWSKI. 1960. Die Durchgangszeiten der Nahrung durch den Verdauungskanal der Nutria, *Myocaster coypus* Molina, 1782. *Acta Theriol.,* **4**:11-25.
GREEN, H. V. 1936. The beaver of the Riding Mountain, Manitoba: an ecological study and commentary. *Can. Field Nat.,* **50**:1-8, 21-23, 36-50, 1-67, 85-92.
GRINNELL, J., J. S. DIXON AND J. M. LINSDALE. 1937. Fur bearing mammals of California. Univ. Calif. Press, Berkeley. 777 p.
HEMMINGSEN, A. M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno Memorial Hospital,* **9**:1-110.
HOOVER, W. H. AND S. D. CLARKE. 1972. Fiber digestion in the beaver. *J. Nutr.,* **102**:9-16.
JENKINS, S. H. 1975. Food selection by beavers: a multidimensional contingency table analysis. *Oecologia (Berl.),* **21**:157-173.
______. 1978. Food selection by beavers: sampling behavior. *Breviora,* **447**:1-6.
______. 1979. Seasonal and year-to-year differences in food selection by beavers. *Oecologia (Berl.),* **44**:112-116.
______. 1980. A size-distance relation in food selection by beavers. *Ecology,* **61**:740-746.
______ AND P. E. BUSHER. 1979. *Castor canadensis. Mamm. Species,* **120**:1-8.
KLEIBER, M. 1961. The fire of life. Wiley, New York. 453 p.
LEWONTIN, R. 1979. Fitness, survival, and optimality, p. 3-21. *In*: D. J. Horn, R. D. Mitchell and G. R. Stairs (eds.). Analysis of ecological systems. Ohio State Univ. Press, Columbus.
LIKENS, G. E. AND F. H. BORMANN. 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. *Yale Univ. Sch. For. Bull.,* **79**:1-25.
MCBEE, R. H. 1971. Significance of intestinal microflora in herbivory. *Annu. Rev. Ecol. Syst.,* **2**:165-176.
NOVAKOWSKI, N. S. 1967. The winter bioenergetics of a beaver population in northern latitudes. *Can. J. Zool.,* **45**:1107-1118.
ORIANS, G. H. AND N. E. PEARSON. 1979. On the theory of central place foraging, p. 155-177. *In*: D. J. Horn, R. D. Mitchell and G. R. Stairs (eds.). Analysis of ecological systems. Ohio State Univ. Press, Columbus.
PYKE, G. H., H. R. PULLIAM AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.,* **52**:137-154.
RUE, L. L. 1964. The world of the beaver. Lippincott, Philadelphia. 155 p.
SCHMIDT-NIELSEN, K. 1972. Locomotion: energy cost of swimming, flying, and running. *Science,* **177**:222-228.
SCHMIDT-NIELSEN, B. AND R. O'DELL. 1961. Structure and concentrating mechanism in the mammalian kidney. *Am. J. Physiol.,* **200**:1119-1124.
SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.,* **2**:369-404.
______. 1979. Generality of the size-distance relation in models of optimal feeding. *Am. Nat.,* **114**:902-914.

SVENDSEN, G. E. 1980. Seasonal change in feeding patterns of beaver in southeastern Ohio. *J. Wildl. Manage.*, **44**:285-290.
WARREN, E. R. 1927. The Beaver, its work and its ways. Williams and Williams, Baltimore. 177 p.
WILSSON, L. 1971. Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). *Viltrevy (Stockh.)*, **8**:115-266.

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