

## An extensive study of the foraging ecology of beavers (*Castor canadensis*) in relation to habitat quality

D. Gallant, C.H. Bérubé, E. Tremblay, and L. Vasseur

**Abstract:** The objective of this study was to examine the foraging behaviour of the beaver (*Castor canadensis* Kuhl, 1820) and to explain its selection of terrestrial woody plant species according to central place foraging theory. Limitations in variety of food items in most studies with regard to size and (or) distance from the central place and information on availability of forage choices give a partial view of the subject. In this study, the theory is tested in a natural environment with high variability in food items with regard to these factors. Foraging choices by beavers were inspected by measuring variables on cut and uncut trees of every species encountered within 1 m of trail systems made by 25 beaver colonies in Kouchibouguac National Park in New Brunswick, Canada, thereby quantifying the availability of the different food items. The effect of habitat quality (food availability) on the foraging behaviour of beavers was also tested. The results of this study suggest that with increasing distance from the pond, beavers in high-quality habitats selected fewer, but larger, trees and are more species selective. This selectivity was diminished in habitats of lower quality. The results of this study are consistent with the predictions of the central foraging theory.

**Résumé :** Le comportement alimentaire du castor (*Castor canadensis* Kuhl, 1820) et son choix de plantes ligneuses terrestres en fonction de la théorie de la quête alimentaire à partir d'un point central font l'objet de cette étude. Les études précédentes constituent des bilans partiels du sujet, en raison de carences dans la diversité des plantes ligneuses disponibles, quant à la taille et la distance du point central, et (ou) dans l'évaluation de leurs disponibilités respectives. Notre étude teste les prédictions de la théorie dans un environnement naturel qui incorpore une grande variété de plantes ligneuses d'après la taille, la distance à l'étang et la composition spécifique. Nous avons déterminé les choix alimentaires des castors en mesurant les caractéristiques des plantes ligneuses coupées et non coupées présentes jusqu'à une distance de 1 m de part et d'autre des sentiers formés par les castors de 25 colonies dans le parc national Kouchibouguac au Nouveau-Brunswick, Canada afin de déterminer la disponibilité des plantes alimentaires. L'effet de la qualité de l'habitat (disponibilité des plantes alimentaires) sur le comportement alimentaire est également testé. En s'éloignant de l'étang, les castors deviennent plus sélectifs au niveau des espèces choisies et sélectionnent de plus gros arbres, mais en plus petit nombre. Cette sélectivité diminue dans les habitats de moindre qualité. Les résultats obtenus sont en accord avec les prédictions de la théorie de la quête alimentaire à partir d'un point central.

### Introduction

Animal foraging models have been developed to better understand the type of behaviour that animals will have as a function of the energy and time ratio of potential prey. For central place foragers, several models have been proposed in relation to the central place foraging theory (Orians and Pearson 1979; Schoener 1979). These models dictate that prey selection by predators should maximize net rate of en-

ergy intake by unit of time. A variant for single-prey loaders further suggests that while the best prey close to the central place should still be those that have the highest energy per provisioning time ratio, the best prey far from the central place would be those that provide the most energy, considering that provisioning time is negligible compared with traveling time (Orians and Pearson 1979). Examples of these models exist, but for many species, it is unclear whether they can be adopted to explain their behaviour. This is the case for the beaver (*Castor canadensis* Kuhl, 1820), a single-prey loader that forages from a central point, the pond. When considering the woody vegetation stems brought back to the pond as prey, this species' foraging behaviour may be explained a priori by these models.

The first studies on beaver foraging to detect selectiveness with regard to prey sizes suggested that they select trees of smaller diameters with increasing distance from the pond (Jenkins 1980; Pinkowski 1983; Belovsky 1984). Subsequent studies observed an increase in prey diameter with increasing distance from the central place when beavers were exposed to relatively small prey of up to 30 mm (McGinley and Whitham 1985) and 50 mm (Fryxell and Doucet 1991, 1993)

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in diameter. Other studies have also reported fewer stems selected by beavers as a function of distance from the pond (Donkor and Fryxell 1999, 2000). Within the theoretical framework of the central place foraging theory, beavers constitute an interesting scenario because they exert choices upon a very wide range of prey sizes that span both under and over their own body size. Within a range of smaller tree sizes for which the beaver can drag the whole tree back to the pond, it is expected that beavers will prefer larger trees with increasing distance from the central place. For this size range, Basey and Jenkins (1995) effectively determined that it did not take more time to drag back a tree with a mean diameter of 3.0 m compared with 1.5 m. On the other hand, for trees too large that have to be sectioned before being brought back to the pond, beavers should tend to select smaller trees within that size range, since sectioning implies additional time and energy expenditures. The most profitable food items thus constitute the largest trees that can be brought to the pond in one piece without requiring additional sectioning. When considering the range of stem sizes available to beavers in existing studies, they documented greater selectivity for prey sizes with increasing distance in a manner consistent with the central place foraging theory (e.g., Fryxell and Doucet 1991).

Beaver foraging habits can influence plant succession around ponds (McGinley and Whitham 1985; Donkor and Fryxell 2000). In spite of its preference for certain food types, the beaver is a generalist herbivore. Roberts and Arner (1984), as an example, identified 41 plant species through stomach inspections over a 1-year period. Beavers are even known to thrive in habitats where their preferred food items, like trembling aspen (*Populus tremuloides* Michx.) and willows (species of *Salix* L.), are absent (Northcott 1971). Past studies also revealed that beavers mostly avoid conifers (Roberts and Arner 1984; Donkor and Fryxell 2000). Because of their immense impact on ecological systems, it is important to gain a greater understanding of this key species' foraging behaviour to obtain better insight into changes in plant succession when beaver colonies are constantly present. This is especially important in protected areas where no trapping or other anthropogenic activities exist to help maintain a low-density population.

The two objectives of this study are to (1) examine the predictions of the central place foraging theory in a complex and variable natural setting and (2) determine how beaver foraging behaviour varies in relation to habitat quality around established beaver colonies. The study was conducted in Kouchibouguac National Park in New Brunswick, Canada, where beaver populations have increased since its establishment and several colonies are found in habitats considered less suitable. This study focuses on species, size, and distance from the pond of woody vegetation stems as important elements affecting beaver forage choices in the context of the central place foraging theory. It also considers how overall habitat quality around beaver ponds influences these choices. To verify the general hypothesis that beavers select forage items that maximize energy return relative to time invested, the following three predictions of the theory are tested: (1) beavers select fewer stems with increasing distance from the pond, (2) beavers are increasingly size selective in the stems that they cut with increasing distance from

the pond, and (3) beavers become increasingly selective relative to the woody species that they cut with increasing distance from the pond.

## Materials and methods

### Field methods

Kouchibouguac National Park, founded in 1969, covers an area of 238.8 km<sup>2</sup> and is part of New Brunswick's lowlands, a particular section of the Maritime Plain with wide valleys and slightly entrenched rivers (Graillon et al. 2000). The topography is rather flat and supports bogs and swamps (Dubois et al. 1997). The two main rivers, Kouchibouguac and Saint-Louis, are both tidal and the park encompasses eight important watersheds: Portage River, Polly's Brook, Fontaine River, Black River, Rankin Brook, Kouchibouguac River, Major Brook, and Saint-Louis River (Desloges 1980). The climate is humid continental with important maritime influences close to shore (Graillon et al. 2000). Average annual temperature is 4.8 °C, the average freeze-free period is 177 days, and annual precipitation averages 979 mm (Desloges 1980). The dominant tree species are trembling aspen, red maple (*Acer rubrum* L.), speckled alder (*Alnus rugosa* (Du Roi) Spreng.), balsam fir (*Abies balsamea* (L.) P. Mill.), black spruce (*Picea mariana* (P. Mill.) D.S.P.), white pine (*Pinus strobus* L.), jack pine (*Pinus banksiana* Lamb.), gray birch (*Betula populifolia* Marsh.), and paper birch (*Betula papyrifera* Marsh.). Among species summed up as potential predators of adult beavers in Jenkins and Busher's (1979) review, coyotes (*Canis latrans* Say, 1823) and black bear (*Ursus americanus* Pallas, 1780) are present in the study area as well as mink (*Mustela vison* Schreber, 1777) and river otter (*Lontra canadensis* Schreber, 1777), both of which may prey on kits.

For this study, 25 sites with active beaver ponds were surveyed during the summers of 1999, 2000, and 2001 (Table 1). Only well-established colonies were selected, which had completed and maintained dams, about which ongoing terrestrial foraging would be the result of nutritional needs on the part of beavers. For each study site (i.e., beaver pond), habitat quality was determined by surveying 90-m transects perpendicular to the shore, each separated by 50 m. Transect length was based on the fact that few beavers seem to wander beyond 100 m from the pond (Jenkins 1980). The first transect was established at the end of the main dam and the subsequent transects were established to cover the full circumference of the pond. When pond circumference was irregular, some transects were deliberately not perpendicular to the pond's edge to prevent crossings with adjacent transects. Each transect contained five quadrats of 2 m × 2 m disposed at 10, 30, 50, 70, and 90 m from the pond's edge. Within each quadrat, every woody stem (cut or uncut) was identified and measured (circumference at 30 cm height). Numerous small stems were encountered at our study sites, and to facilitate their census, three classes of small stem circumferences were predetermined. They were classified as having an estimated circumference of  $x \leq 2.5$  cm,  $2.5 < x \leq 5.0$  cm, and  $5.0 < x \leq 7.5$  cm. When cut stumps were less than 30 cm high, they were measured at the highest possible point. For data analysis, stem circumferences were converted

**Table 1.** Proportions of deciduous species recorded by transect surveys around beaver (*Castor canadensis*) ponds studied in Kouchibouguac National Park between 1999 and 2001.

Pond	Systematic name	Frequency of deciduous stems	Total number of stems	Proportion of deciduous stems
Portage	B1	1394	1404	0.993
Polly's amount	D5	1652	1669	0.990
Eric's Pond	B8	561	603	0.930
Polly's aval	D3	1003	1091	0.919
Cimetière	E23	1149	1268	0.906
Vieux Pont	F9	136	158	0.861
South Polly's	D15	121	145	0.834
Patterson	F12	581	701	0.829
Kolloch	G19	202	247	0.818
Kelly's	G1	142	176	0.807
Tweedie	F13	80	102	0.784
La Source	F16	110	143	0.769
Comeau	E1	1228	1602	0.767
Vieux Pont amount	F19	103	137	0.752
Olivier	H29	105	148	0.709
134	F10	149	219	0.680
Carrigan	D16	230	340	0.676
Middle Kouchibouguac	F7	117	229	0.511
Loggicroft	F11	274	564	0.486
Loggicroft 2	F20	51	111	0.459
Polly's intermédiaire	D17	137	339	0.404
Barrages	F5	372	965	0.385
Middle La Source	F15	21	66	0.318
Cimetière 2	E42	34	128	0.266

**Note:** Systematic names according to Dubois et al. (1997) using a letter representing the watershed to which a pond belonged followed by a number differentiating each pond. B, Portage River watershed; D, Polly's Brook watershed; E, Black River, Fontaine River, and Rankin Brook watershed; F, Kouchibouguac River watershed; G, Major Brook watershed; H, Saint-Louis River watershed. The broken demarcation line represents the greatest difference in proportion of deciduous stems between adjacent ponds in the ordered list. See the text for information.

into diameter values to facilitate comparison with existing literature.

Habitat use by beavers was evaluated by documenting woody vegetation along their terrestrial trails. We consider here felled woody vegetation as food items, since beavers consume the bark, foliage, and small branches of most building material found on dams and lodges of studied colonies. Beavers primarily rely on close-range olfactory cues for identification of suitable food items (Fryxell and Doucet 1993; Doucet et al. 1994a). In this study, for each woody stem within 1 m either side of a beaver trail, species, state (cut or uncut), circumference, and distance from the pond were recorded. The length of each trail was recorded, and when different segments led to a common meeting point, the total distance traveled from the pond was computed by using the shortest trajectory. At the end of each trail, all woody vegetation in a radius of 3 m was documented. When plant density was too high, we limited the survey at a 1- or 2-m radius. Because of the abundance of trails that surrounded ponds harbouring active colonies, we documented half of all beaver trails found at any given pond by sampling every other trail encountered.

#### Data analysis of habitat quality

To discriminate between high- and low-quality habitats in relation to beaver forage, the proportion of deciduous spe-

cies was calculated for each pond based on transect data, with the intent of categorizing each of them as having a high or low proportion of deciduous woody species available to beavers. Ponds were then ordered in a gradient of decreasing proportion of deciduous stems (Table 1). A Fisher's exact test for proportions (Zar 1999) was used to test deciduous stem proportion for the two ponds either side of the cutoff point. Small stems with circumferences of 2.5 cm or less were not considered in the analysis because they tended to overrepresent certain species such as red maple and balsam fir. The analysis showed that 17 study sites ( $0.826 \pm 0.097$ ,  $n = 17$ ) had a greater proportion of deciduous trees (considered high-quality habitat) and seven ( $0.404 \pm 0.089$ ,  $n = 7$ ) had a lesser proportion (considered low-quality habitat) ( $Z = 3.883$ ,  $n = 2$ ,  $p < 0.001$ ) (Table 1). To obtain sufficient data for the analysis within these two established categories, trail data from several ponds were pooled based on heterogeneity  $\chi^2$  tests to form data sets of differing habitat quality against which to test our hypotheses. Beaver ponds were pooled on the basis that there was no significant difference in the proportion of preferred species (based on transect data). The proportion of cut stems (cut/(cut + uncut)) per species for all ponds (based on trail data) was used as a general index of selectivity to determine preferred species. Conifers in a forest can be regarded as a matrix of unpalatable species within which beavers travel to select deciduous species, predomi-

nantly the preferred ones. Our aim by this two-step process is to attain a classification of terrestrial habitats that is sensible to the beavers' foraging ecology, which are generalists but exert forage preferences.

### Data analysis of foraging behaviour

Predictions 1 and 2, relating to beaver forage choices, were tested by conducting forward stepwise logistic regressions. Logistic models (using SPSS version 10.0 for Windows) tested the effect of stem diameter and distance from the pond as well as the interaction between these two factors on the binary dependent variable (cut or uncut). For each data set of differing habitat quality, regressions were conducted for species that were the most ubiquitously abundant in all data sets with regard to the studied factors. For each species presenting a model where the three factors were significant, the logistic model's curve (constructed from the coefficients obtained in each regression) was graphed over a scatterplot where each dot represents a stem of given diameter ( $x_1$ ) and distance from the pond ( $x_2$ ) and is either represented as cut or uncut ( $y$ ). The resulting figures can illustrate the effects of the two factors as well as that of the interaction between those two factors. Each model's curve was obtained from the logistic model's equation in logit form (i.e., in terms of the log of the odds that a given event took place). In our study, for any particular stem, the event was "cut by a beaver". The model's logit equation is as follows:

$$[1] \quad \log[P_{\text{cut}}/(1 - P_{\text{cut}})] = b_0 + b_1x_1 + b_2x_2 + b_{12}x_1x_2$$

where  $b_0$  is a constant and the coefficients  $b_1$ ,  $b_2$ , and  $b_{12}$  were obtained from the results of conducted logistic regressions. Each coefficient indicates the degree of change in the dependent variable if the associated factor varies by one unit. By fixing a constant probability for the odds and solving the equation for  $x_2$  with a range of predetermined values for  $x_1$ , it is possible to plot the equation representing the data's tendencies in relation to the considered factors and their interaction for that fixed probability.

To test the third prediction, data were separated into four distance classes, 0–20, 20–40, 40–60, and 60–80 m, to ensure sufficient sample size within each class. To test beavers' selectivity towards food type categories within the different distance classes, the method of Neu et al. (1974) for analysing utilization–availability data was employed. The procedure uses a  $\chi^2$  goodness-of-fit test to determine any overall significant difference between expected and observed utilization of the different food type categories and employs Bonferroni confidence intervals to determine preference or avoidance for each category. Computational aspects of this method are further explained in Byers et al. (1984). Analysis was conducted for each distance category separately. Every species available up to the end of studied beaver trails and available in all distance categories was considered as a distinct food type category. To correctly assess the overall availability of the different food type categories for the test, data of less common species were included by dividing them into deciduous and coniferous food type categories. Two assumptions are of importance for this test: (1) the animals are able to select from each of the food type categories and

(2) observations are unbiased, random, and therefore independent from each other (Neu et al. 1974).

For the given food type categories, trends in the selectivity of beavers in relation to distance from the central place were illustrated by plotting usage–availability residuals, which we define as the proportion of observed cut stems ( $p_i$ ) minus the proportion of total stems that the given food type represents within the concerned distance category ( $p_{io}$ ). The values of  $p_i$  and  $p_{io}$  are computed as

$$[2] \quad \text{Usage–availability residual} = p_i - p_{io} \\ = (O_i/O_N) - (T_i/T_N)$$

where  $O_i$  is the number of cut stems observed for the concerned species,  $O_N$  is the number of cut stems observed over all species within the given distance category,  $T_i$  is the total number of stems for the given species, and  $T_N$  is the total number of stems over all species within the given distance category. After calculating this value in each distance category, a plot representing departure from what is usage in proportion to availability ( $p_i - p_{io} = 0$ ) as a function of distance from the central place was obtained for each food type category. Positive values means that beavers cut proportionally more of the given food type category in comparison with its availability, whereas negative values indicate the exact opposite. To graphically illustrate whether the difference between usage and availability was statistically significant, we plotted the corresponding confidence intervals' residuals (computed by subtracting  $p_i$  from the minimum and maximum values of Bonferroni confidence intervals of the given food type category) on the same graph as the usage–availability residuals. The difference between usage and availability proportions was statistically significant whenever the values of the usage–availability residuals were beyond the values of associated maximum and minimum residuals of the Bonferroni confidence intervals.

## Results

### Habitat quality around beaver ponds

Preferred species as indicated by their selection in higher proportions by beavers (value = 0.267) (Table 2) and supported by existing literature are beaked hazelnut (*Corylus cornuta* Marsh.) (Donkor and Fryxell 1999, 2000), pin cherry (*Prunus pensylvanica* L.f.) (Jenkins 1980), willows (Hall 1960; Northcott 1971), and aspen species such as largetooth aspen (*Populus grandidentata* Michx.) and trembling aspen (Hall 1960; Northcott 1971; Doucet and Fryxell 1993). Some species were not considered as preferred in spite of their high selectivity indexes because they were rare, with considerable numbers in only one or two of the 25 ponds and virtually absent in all others (zero to three stems per pond). These species were spreading dogbane (*Apocynum androsaemifolium* L.), northern red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britt.), dewberries and blackberries (species of *Rubus* L.), and eastern white-cedar (*Thuja occidentalis* L.). Red maple and speckled alder, two species with a high proportion of cut stems, were not considered as preferred by beavers, the reasons being discussed further in the discussion section of this paper. Sweet fern (*Comptonia peregrina* (L.) Coult.) bush

**Table 2.** Selectivity index of woody plant species recorded along beaver trails in Kouchibouguac National Park between 1999 and 2001.

	Total frequency	Frequency of selected stems	Selectivity index (proportion of stems selected)
Spreading dogbane, <i>Apocynum androsaemifolium</i>	7	7	1.000
Northern red oak, <i>Quercus rubra</i>	84	53	0.631
Yellow birch, <i>Betula alleghaniensis</i>	24	14	0.583
Dewberries and blackberries, <i>Rubus</i> spp.	61	32	0.525
Beaked hazelnut, <i>Corylus cornuta</i> *	1134	574	0.506
Large-tooth aspen, <i>Populus grandidentata</i> *	353	158	0.448
Pin cherry, <i>Prunus pensylvanica</i> *	395	176	0.446
Trembling aspen, <i>Populus tremuloides</i> *	2746	1215	0.443
Speckled alder, <i>Alnus rugosa</i>	8593	3483	0.405
Willows, <i>Salix</i> spp.*	2590	1041	0.402
Eastern white-cedar, <i>Thuja occidentalis</i>	455	159	0.350
Red maple, <i>Acer rubrum</i>	12 470	3778	0.303
<hr/>			
Common chokecherry, <i>Prunus virginiana</i> L.	1575	405	0.257
Gray birch, <i>Betula populifolia</i>	3828	974	0.254
Paper birch, <i>Betula papyrifera</i>	604	150	0.248
Alder-leaved buckthorn, <i>Rhamnus alnifolia</i> L'Hér.	246	37	0.150
Shadbushes and serviceberries, species of <i>Amelanchier</i> Medik.	888	127	0.143
White meadowsweet, <i>Spiraea alba</i> Du Roi	2425	345	0.142
Wild roses, species of <i>Rosa</i> spp.	134	16	0.119
Plants of the genus <i>Viburnum</i> L.	5247	485	0.092
White spruce, <i>Picea glauca</i> (Moench) Voss	223	19	0.085
Hawthorn, species of <i>Crataegus</i> L.	636	54	0.085
Wild holly, <i>Nemopanthus mucronatus</i> (L.) Trel.	141	11	0.078
Balsam poplar, <i>Populus balsamifera</i> L.	66	5	0.076
Jack pine, <i>Pinus banksiana</i>	24	1	0.042
Balsam fir, <i>Abies balsamea</i>	3390	138	0.041
Paradise apple, <i>Malus pumila</i> P. Mill.	27	1	0.037
Black spruce, <i>Picea mariana</i>	530	16	0.030
Silver maple, <i>Acer saccharinum</i> L.	273	8	0.029
Canada yew, <i>Taxus canadensis</i> Marsh.	50	1	0.020
White pine, <i>Pinus strobus</i>	61	1	0.016
Red spruce, <i>Picea rubens</i> Sarg.	65	1	0.015
Tamarack, <i>Larix laricina</i> (Du Roi) K. Koch	82	1	0.012
Sweet fern, <i>Comptonia peregrina</i>	2313	13	0.006
Alternate-leaf dogwood, <i>Cornus alternifolia</i> L.f.	4	0	0.000
Norway pine, <i>Pinus resinosa</i> Soland.	1	0	0.000
Sheep laurel, <i>Kalmia angustifolia</i> L.	7	0	0.000
Sweetgale, <i>Myrica gale</i> L.	2	0	0.000
Red-berried elder, <i>Sambucus pubens</i> Michx.	16	0	0.000
American beech, <i>Fagus grandifolia</i> Ehrh.	1	0	0.000
American mountain ash, <i>Sorbus americana</i> Marsh.	9	0	0.000
Rhodora, <i>Rhododendron canadense</i> (L.) Torr.	12	0	0.000
American fly honeysuckle, <i>Lonicera canadensis</i> Bartr. ex. Marsh.	22	0	0.000
Common winterberry, <i>Ilex verticillata</i> (L.) Gray	11	0	0.000

**Note:** The broken demarcation line represents the proportion of selected stems from all species combined (0.267).

\*Species determined to be preferred by beavers.

was classified with the conifers in this study because of its low general selectivity index (Table 2); it was avoided by beavers and was found in very contagious distributions around two beaver ponds (D16 and D17) (Table 1) located in a postfire regrowth area.

Considering the frequency of preferred species, the data set was then divided into three categories. Out of a total of 25 beaver ponds (Table 2), 15 were pooled to form three data sets representing three particular habitat settings within

which we are able to test our hypotheses. Ponds F15, F5, F20, F11, and F7 ( $\chi^2_4 = 6.87$ ,  $0.25 > p > 0.10$ ) had a low proportion of both deciduous and preferred species and were considered low habitat quality (Fig. 1). Ponds with a high proportion of deciduous species (high quality) were fractioned into two data sets each containing five ponds. Ponds F12, B1, F13, H29, and F19 ( $\chi^2_4 = 1.57$ ,  $0.90 > p > 0.75$ ) were considered intermediate habitat quality, with a high proportion of deciduous species but a low proportion of pre-

ferred species (Fig. 1). Ponds B8, D5, F16, F9, and D16 ( $\chi^2_4 = 9.41$ ,  $0.10 > p > 0.05$ ) were considered superior habitat quality, having high proportions of both deciduous species and preferred species (Fig. 1). It is important to note here that this denomination pertains to the terrestrial habitat only and does not account for aquatic species that might be present in the ponds.

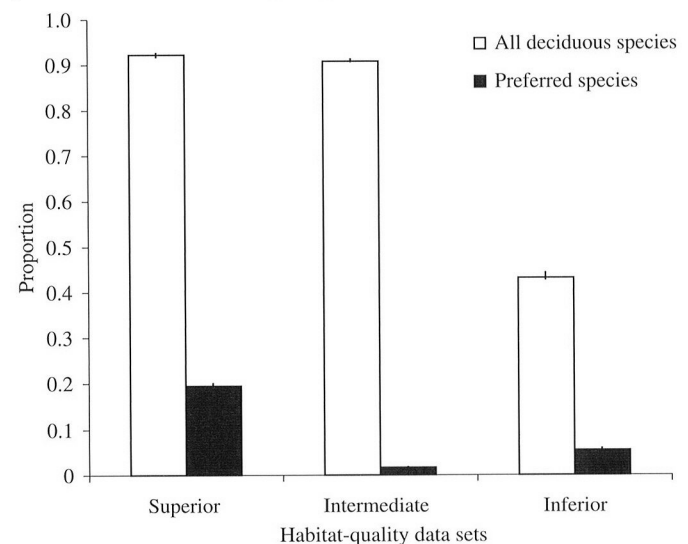
### Foraging behaviour in habitats of differing quality

The four species chosen for testing hypotheses 1 and 2 were trembling aspen, gray birch, speckled alder, and red maple, since they had the highest overall abundance, variety of stem sizes, and stem distances from the central place in all three habitat-quality data sets. Results of regressions testing the effect of stem diameter and distance from the pond on odds of being selected (cut) by beavers are shown in Table 3 for all three habitat-quality data sets. In the superior habitat category, the distribution of stems selected by beavers could be explained with a logistic model that included diameter, distance, and their interaction for three of the four species studied, namely trembling aspen, gray birch, and red maple. For these species, each of the three elements in the model had a significant effect on the dependent variable. Odds of stems being selected are diminished when farther from the central place (negative  $b$  coefficient). For speckled alder, distance from the pond did not have a significant effect on chances of being selected. The overall dominant factor was stem diameter (Wald's statistic; Table 3). For all four species in the superior habitat data set, the interaction between diameter and distance was significant with negative  $b$  coefficients indicating that beavers selected larger stems with increasing distance from the pond. The three-element model explained 85.4% of the foraging pattern of beavers regarding trembling aspen, 80.5% for gray birch, and 76.0% for red maple. Speckled alder, a species usually associated with wetlands and waterways, was only available closer to ponds, which could explain why the distance factor did not have a significant effect for that species. The mean distance of available stems (cut and uncut) from the pond is very low for speckled alder ( $8.1 \pm 7.4$  m,  $n = 1513$ ), with only 25 stems available beyond 20 m from the pond and none available beyond 48 m. The interaction of distance and diameter was nonetheless significant (Table 3), indicating a steep decline in probability of being cut with distance that is steeper for bigger trees in comparison with smaller ones.

Figure 2 illustrates foraging patterns in relation to stem diameter and stem distance from the pond for trembling aspen, gray birch, and red maple in the superior habitat data set. The resulting 50% probability curve shows how diameter of selected stems evolves with increasing distance from the pond. The area above the curve represents combinations of stem diameters and distances from the pond where the chance of being selected for a given stem is  $>50\%$  and the area under the curve  $<50\%$ . In general, beavers select larger trees with increasing distance from the pond (Fig. 2; Table 3, interaction coefficients). For gray birch and red maple, the 50% curve is abruptly exponential because beavers did not cut a lot of stems of those two species when farther than 25 m (Fig. 2).

For the intermediate and inferior habitat-quality data sets, diameter had a significant effect on the dependent variable

**Fig. 1.** Proportion of all deciduous plant species and preferred woody plant species for beaver (*Castor canadensis*) ponds pooled into three habitat-quality data sets.



and dominated the multifactor logistic models (Table 3). For red maple in intermediate habitat quality, the resulting regression coefficient was negative for stem diameter and positive for the interaction. This interaction coefficient indicates that the probability of being cut increases with distance in a steeper fashion for larger trees. For this species, most stems were small ( $<2.4$  cm) and close to the ponds ( $<20$  m). Neither the factors nor the interaction between them had a significant effect for gray birch, and distance from the pond had no significant effect for all four species in either of these two data sets. In inferior habitat, only the data for speckled alder could integrate two elements of the model, those of diameter and the interaction between diameter and distance from the pond. Distance had an effect on the diameter of cut stems in these two data sets as shown by statistically significant interactions, but beavers in these data sets did not travel as far from the ponds. A one-factor analysis of variance tested stem distance from the pond according to habitat quality. Since data on woody vegetation were collected along beaver trails, the mean distance from the pond of all stems (cut and uncut) can serve as a relative indicator of how far beavers generally traveled within each habitat data set. A significant difference was determined in the mean distance of stems from the pond (all species included) for all three habitat-quality data sets ( $F_{[2,279]} = 1937.3$ ,  $p < 0.001$ ). Tukey's multiple comparison tests revealed that mean distance from the pond of all stems was higher in the superior habitat-quality data set ( $22.0 \pm 20.5$  m) followed by the inferior habitat-quality data set ( $11.3 \pm 6.8$  m) and the intermediate habitat-quality data set ( $8.9 \pm 7.9$  m). Beavers therefore traveled farther on land in the superior quality habitats than in the intermediate and inferior ones.

The third hypothesis on the utilization versus availability of different food types in different distance categories from the central point was tested using only data from the superior habitat. The food type categories selected here, as ordered in Table 4, are aspens, willows, pin cherry, birches, red maple, species of the *Viburnum* L., as well as those



**Table 3.** Results of forward stepwise logistic regressions testing selectivity according to distance from the beaver pond, stem diameter, and their interaction for four woody plant species in all three habitat-quality data sets.

Habitat class	Species	Factor	<i>b</i>	SE	Wald's statistic	Significance	Factor added to model*	Percentage of data-model fit*	<i>n</i>
Superior	<i>Populus tremuloides</i>	Diameter	1.19	0.11	117.82	<0.0001	Diameter	83.7	1490
		Distance	-0.02	0.01	12.46	0.0004	Distance	85.1	
		Diameter × distance	-0.01	0.00	6.13	0.0133	Diameter × distance	85.4	
	<i>Betula populifolia</i>	Constant	-1.91	0.24	64.88	<0.0001			1908
		Diameter	1.39	0.12	130.24	<0.0001	Distance	76.5	
		Distance	0.02	0.01	4.01	0.0451	Diameter	79.8	
	<i>Alnus rugosa</i>	Diameter × distance	-0.05	0.01	78.31	<0.0001	Diameter × distance	80.5	1513
		Constant	-2.48	0.18	184.27	<0.0001			
		Diameter	1.16	0.08	218.37	<0.0001	Diameter	70.3	
	<i>Acer rubrum</i>	Diameter × distance	-0.02	0.04	23.55	<0.0001	Diameter × distance	71.3	4212
		Constant	-2.41	0.15	271.81	<0.0001			
		Diameter	0.86	0.06	178.09	<0.0001	Distance	73.8	
Intermediate	<i>Populus tremuloides</i>	Distance	-0.01	0.01	0.62	0.4323	Diameter	75.0	85
		Diameter × distance	-0.03	0.00	74.74	<0.0001	Diameter × distance	76.0	
		Constant	-1.68	0.13	163.66	<0.0001			
	<i>Alnus rugosa</i>	Diameter	7.07	1.98	12.77	0.0004	Diameter	90.6	3597
		Diameter × distance	-0.14	0.04	10.46	0.0012	Diameter × distance	97.7	
		Constant	-9.13	2.38	14.72	0.0001			
	<i>Acer rubrum</i>	Diameter	0.46	0.03	240.90	<0.0001	Diameter	61.7	342
		Diameter × distance	-0.01	0.00	82.96	<0.0001	Diameter × distance	65.6	
		Constant	-1.10	0.06	297.22	<0.0001			
	<i>Populus tremuloides</i>	Diameter	-0.23	0.11	4.88	0.0272	Diameter × distance	90.4	117
		Diameter × distance	0.03	0.01	10.75	0.0010	Diameter	91.5	
		Constant	-2.57	0.23	127.55	<0.0001			
Inferior	<i>Populus tremuloides</i>	Diameter	0.12	0.05	5.31	0.0212	Diameter	82.1	796
		Constant	0.76	0.33	5.28	0.0216			
	<i>Alnus rugosa</i>	Diameter	1.33	0.16	71.93	<0.0001	Diameter	71.9	1283
		Diameter × distance	-0.04	0.01	23.29	<0.0001	Diameter × distance	74.4	
	<i>Acer rubrum</i>	Constant	-2.03	0.17	149.30	<0.0001			
		Diameter	0.02	0.01	4.23	0.0398	Diameter	69.1	
		Constant	-0.88	0.07	161.80	<0.0001			

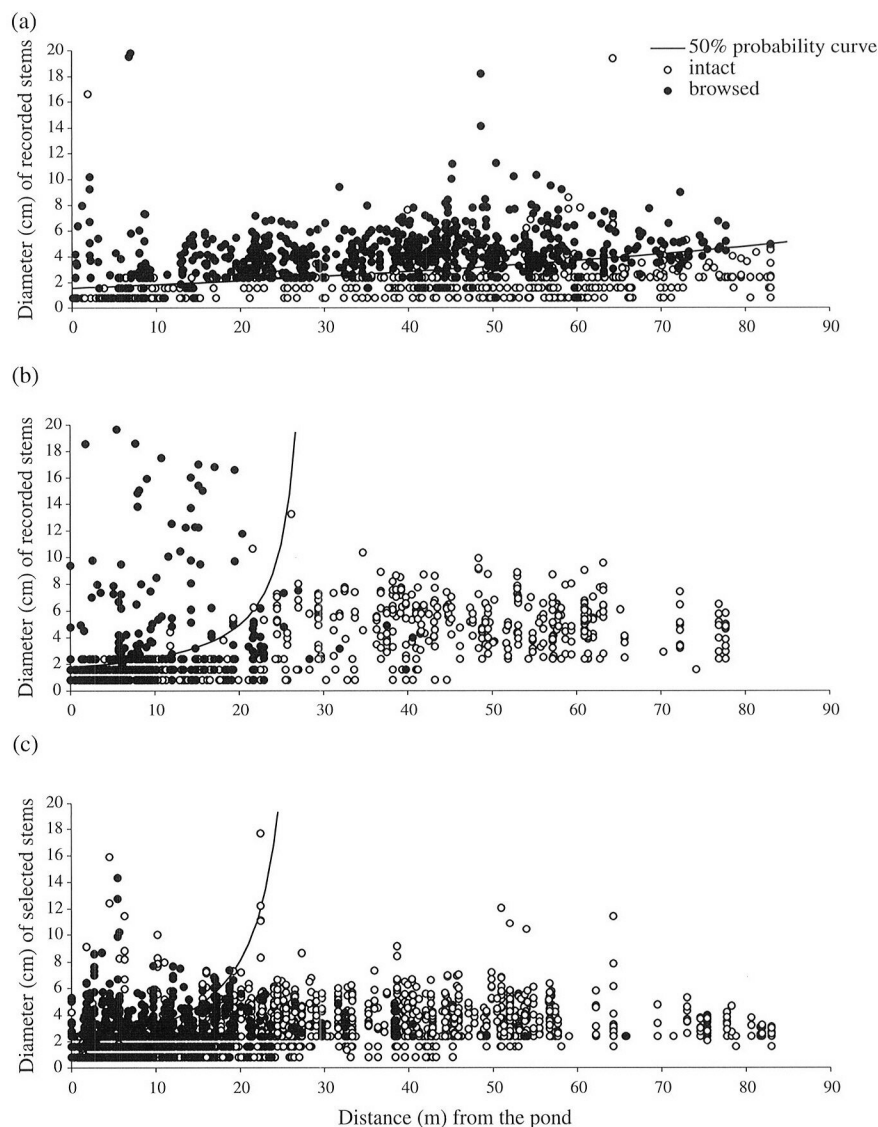
Note: All models are statistically significant and were tested using  $\chi^2$  analysis (df = 1).

\*These columns indicate model efficiency at explaining the dependent variable relative to each additional factor incorporated into the model.

named "other deciduous" and "coniferous" (i.e., remainder of species not included in the other categories). A significant difference was found between overall availability and utilization as shown by  $\chi^2$  goodness-of-fit tests for the 0–20 m category ( $\chi^2_7 = 325.9$ ,  $p < 0.001$ ), the 20–40 m category ( $\chi^2_7 = 547.9$ ,  $p < 0.001$ ), the 40–60 m category ( $\chi^2_7 = 690.0$ ,  $p < 0.001$ ), and the 60–80 m category ( $\chi^2_7 = 123.8$ ,  $p < 0.001$ ) (Table 4). For the 0–20 m category, Bonferroni confidence intervals show that aspen, red maple, and the "other deciduous" categories were selected in greater proportion compared with their respective availabilities (Table 4). Willows, pin cherry, and birch were selected in proportion to their availability, whereas *Viburnum* spp. and conifers were

consumed in proportions lower than their availability. For the 20–40 m category, aspen and willows were preferred, pin cherry, birch, and "other deciduous" categories were consumed in proportion to their availability, whereas red maple, *Viburnum* spp., and conifers were consumed in proportions lower than their availability (Table 4). For the 40–60 and 60–80 m categories, the results were the same. Aspen was the only species preferred by beavers and pin cherry was selected in proportion to availability. Willows, birch, red maple, *Viburnum* spp., "other deciduous", and conifers were selected in proportions lower than their availability. Figure 3 illustrates the trends of usage–availability residuals and Bonferroni confidence interval residuals according to

**Fig. 2.** Diameter of selected stems and intact stems of trembling aspen, *Populus tremuloides* (a); gray birch, *Betula populifolia* (b); and red maple, *Acer rubrum* (c), in relation to distance from the beaver pond in the superior habitat data set with the logistic model's 50% probability curve.



distance from the central place for aspens, pin cherry, and willows.

## Discussion

Our results indicate that beavers select fewer trees with increasing distance from the pond. These results are consistent with previous studies (Fryxell 1992; Donkor and Fryxell 1999, 2000). It is argued that in addition to the question of energy, the probability of being predated increases when beavers are far from the pond (Basey and Jenkins 1995) and this can render trees farther from the pond less profitable. In habitats of lesser quality, distance did not have a significant effect on species' chances of being selected by beavers. The fact that beaver trail systems themselves did not extend far from the pond in habitats of lesser quality could indicate that distance from the pond might have an even greater effect in those habitats in comparison with the superior habitat data

set. However, the type of data collected in this study does not permit rigorous testing of this aspect. Additional information would be necessary for better understanding of this relationship.

Beavers selected larger trees with increasing distance from the central place in superior quality habitat. In the present study, there was a wide range of available tree sizes, and for trembling aspen far from the pond, they manipulated very large trees compared with a typical adult beaver's body size. In such a situation, Jenkins (1980), Pinkowski (1983), and Belovsky (1984) found that beavers selected smaller tree sizes farther from the pond. For beavers, significant time and energy expenditures are associated with processing a prey. Four principal factors can influence prey processing: time required cutting down prey, time required dragging the prey to the central place, time spent consuming the prey, and time required for digestion (Fryxell 1999). Larger trees offer more edible biomass such as bark, branches, and foliage



**Table 4.** Utilization and availability of food-type categories according to distance from the beaver pond categories along beaver trails in the superior habitat data set in Kouchibouguac National Park.

Distance (m)	Species	Total number of stems ( $T_i$ )	Proportion of total stems ( $p_{io}$ )	Observed number of cut stems ( $O_i$ )	Expected number of cut stems ( $E_i = O_N p_{io}$ )	Proportion observed per species ( $p_i = O_i/O_N$ )	Bonferroni intervals for $p_i$
0–20	<i>Populus</i> spp.	347	0.031	149	103	0.045	$0.035 = p_1 = 0.055^*$
	<i>Salix</i> spp.	328	0.029	128	98	0.039	$0.029 = p_2 = 0.048$
	<i>Prunus pensylvanica</i>	25	0.002	5	7	0.002	$0.000 = p_3 = 0.003$
	<i>Betula</i> spp.	1418	0.127	429	422	0.129	$0.113 = p_4 = 0.145$
	<i>Acer rubrum</i>	4109	0.369	1438	1223	0.434	$0.410 = p_5 = 0.457^*$
	<i>Viburnum</i> spp.	1088	0.098	87	324	0.026	$0.019 = p_6 = 0.034^\dagger$
	Other deciduous	2811	0.252	928	837	0.280	$0.258 = p_7 = 0.301^*$
	Conifers	1014	0.091	152	302	0.046	$0.036 = p_8 = 0.056^\dagger$
	Total ( $n$ )	11140		3316			
20–40	<i>Populus</i> spp.	331	0.129	212	61	0.448	$0.386 = p_1 = 0.511^*$
	<i>Salix</i> spp.	268	0.105	88	50	0.186	$0.137 = p_2 = 0.235^*$
	<i>Prunus pensylvanica</i>	38	0.015	10	7	0.021	$0.003 = p_3 = 0.039$
	<i>Betula</i> spp.	277	0.108	44	51	0.093	$0.056 = p_4 = 0.130$
	<i>Acer rubrum</i>	635	0.248	89	118	0.188	$0.139 = p_5 = 0.237^\dagger$
	<i>Viburnum</i> spp.	520	0.203	16	96	0.034	$0.011 = p_6 = 0.057^\dagger$
	Other deciduous	102	0.040	13	19	0.027	$0.007 = p_7 = 0.048$
	Conifers	385	0.151	1	71	0.002	$0.000 = p_8 = 0.008^\dagger$
	Total ( $n$ )	2556		473			
40–60	<i>Populus</i> spp.	655	0.276	315	98	0.890	$0.844 = p_1 = 0.935^*$
	<i>Salix</i> spp.	95	0.040	5	14	0.014	$0.000 = p_2 = 0.031^\dagger$
	<i>Prunus pensylvanica</i>	95	0.040	19	14	0.054	$0.021 = p_3 = 0.086$
	<i>Betula</i> spp.	197	0.083	2	29	0.006	$0.000 = p_4 = 0.017^\dagger$
	<i>Acer rubrum</i>	460	0.194	5	69	0.014	$0.000 = p_5 = 0.031^\dagger$
	<i>Viburnum</i> spp.	459	0.193	5	68	0.014	$0.000 = p_6 = 0.031^\dagger$
	Other deciduous	136	0.057	3	20	0.008	$0.000 = p_7 = 0.022^\dagger$
	Conifers	276	0.116	0	41	0.000	$na^{\dagger,\ddagger}$
	Total ( $n$ )	2373		354			
60–80	<i>Populus</i> spp.	380	0.425	99	44	0.952	$0.894 = p_1 = 1.009^*$
	<i>Salix</i> spp.	31	0.035	0	4	0.000	$na^{\dagger,\ddagger}$
	<i>Prunus pensylvanica</i>	6	0.007	2	1	0.019	$0.000 = p_2 = 0.056$
	<i>Betula</i> spp.	85	0.095	0	10	0.000	$na^{\dagger,\ddagger}$
	<i>Acer rubrum</i>	99	0.111	1	12	0.010	$0.000 = p_5 = 0.036^\dagger$
	<i>Viburnum</i> spp.	156	0.174	0	18	0.000	$na^{\dagger,\ddagger}$
	Other deciduous	105	0.117	2	12	0.019	$0.000 = p_7 = 0.056^\dagger$
	Conifers	32	0.036	0	4	0.000	$na^{\dagger,\ddagger}$
	Total ( $n$ )	894		104			

\*Usage in greater proportion than availability is statistically significant.

†Usage in lower proportion than availability is statistically significant.

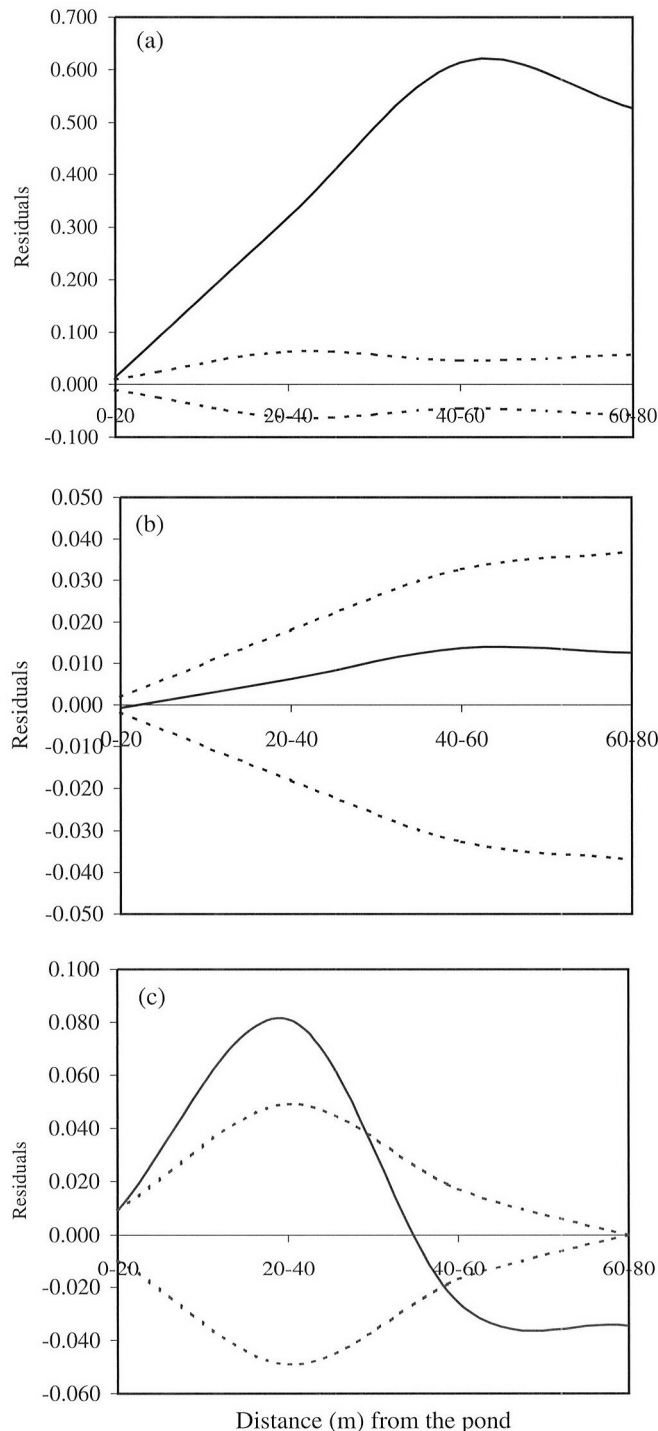
‡Confidence interval nonexistent because  $O_i = 0$ .

(Fryxell and Doucet 1993) but take much more time to cut down and provision (to fraction into manageable pieces and bring back to the pond). Both of these activities were shown to increase allometrically with stem diameter (Fryxell and Doucet 1991, 1993). Our results are similar to more recent results (McGinley and Whitham 1985; Fryxell and Doucet 1991, 1993), but unlike these studies, ours also included

trees of large sizes (>5.0 cm in diameter), a situation leading most likely to greater provisioning time.

In well-established beaver colonies such as those in our study, aspen saplings, notably juvenile-form sprouts, are to be found in considerable quantities in superior quality habitats. As an example, Basey et al. (1988) observed that as much as 14% of the living aspen around a pond had juve-

**Fig. 3.** Plots of minimum and maximum residuals of the Bonferroni confidence intervals (broken lines) and usage–availability residuals (solid line) as a function of distance from beaver ponds for aspens, *Populus* spp. (a); pin cherry, *Prunus pensylvanica* (b); and willows, *Salix* spp. (c), along beaver trails in the superior habitat data set in Kouchibouguac National Park.



nile-form sprouts after only a year of occupation by beavers. Studies show that beavers avoid the juvenile-form sprouts growing from aspens cut by beavers compared with adult-form sprouts from uncut aspen clones (Basey et al. 1988,

1990). A secondary metabolite, 1,3 disubstituted glycerol (Basey and Jenkins 1993), has been found in increased quantity in juvenile-form sprouts from aspens that were cut by beavers (Basey et al. 1990). This is the result of a shift in resource allocation of chemical compounds on the part of aspens as a defensive response to browsing by beavers (Basey et al. 1990; Basey and Jenkins 1993). This could partly explain why beavers would select larger aspen stems in general over smaller ones. However, since beavers start on-land browsing near the ponds before ever having to travel farther inland, the older and thus largest sprouts would be close to the ponds, whereas those farther from the ponds would be more recent and consequently smaller sprouts linked to cut aspens. If beavers behaved strictly in avoidance of aspen stems containing defensive chemicals, the pattern of cut stems would be contrary to the pattern of foraging that we actually observed. The trend in this study is that beavers leave standing stems that are of increasing size as they opt for larger and larger trees as distance from the pond increases. Considering this, avoidance of secondary metabolites does not appear to be directly responsible for the overall pattern observed for this woody species here.

These results for trembling aspens in our study is more readily explained by the observations that for large trees, beavers often only took back canopy branches and leaves as well as secondary branches back to the pond and that bark on the main trunk appears to be ingested on site (D. Gallant, personal observation). It is common to observe large trunks lying where beavers felled them, whereas research shows that smaller trees are more readily found at the pond in dams and huts (Barnes and Mallik 1996). In addition, large trees can serve for more than one visit to the foraging area without additional search effort. Such behaviour by beavers would cause the cost/benefit ratio not to significantly increase with tree size by rendering large trees as more profitable in terms of energy maximization theories. This is also encompassed by the central place foraging theory, which predicts that single-prey loaders foraging optimally should consume on site the food items that cannot economically be brought back to the central place (Orians and Pearson 1979; Schoener 1979).

Similar results were obtained for gray birch and red maple in the superior habitat data set. However, in scrutinizing the respective scatterplots for these two species, it appears that beavers seem to prefer small- to medium-sized trees beyond 25 m from the pond. This is consistent with the central place foraging theory when considering the wide range of tree sizes included in this study. Within a range of small tree sizes, the larger stems are more profitable, whereas for the range of larger trees, it is preferable to tend towards a selection of smaller trees because of rising provisioning costs. Unfortunately, beavers cut a very small number of stems for that distance range, since they are not as preferred as trembling aspen and this precludes the application of meaningful statistics about the matter.

Beavers appear to become less selective with regard to stem diameter and distance from the central place in habitats of lesser quality. The interaction between the two factors had a significant effect for three of four prey species in the intermediate habitat group. This suggests that distance from the central place still affects beavers' choices with regard to

stem size. However, the fact that no clear pattern was found in the intermediate and inferior habitat-quality data sets can be attributed to the fact that beavers did not travel very far on land in habitats of lesser quality. Beavers in some of these ponds access other food sources by foraging farther upstream or downstream when adjacent watersheds permit easy and secure travel (D. Gallant, personal observation). We also suspect that more effort may be allocated towards foraging aquatic plants in those habitats. Aquatic plants are recognized as an important seasonal food item (Northcott 1971; Svendsen 1980). Furthermore, it is highly plausible that colonies in bad quality habitats simply have less beavers in them, since they would have lower reproductive success compared with colonies established in prime habitat, or that they are sporadically occupied by nonreproducing dispersing adults. In either case, this would equate to a smaller number of beavers compared with colonies in better habitats and explain the less extensive terrestrial trail network, which in turn would limit our ability to detect trends.

Species selectivity increases with distance from the central place, leaving aspens as the only species actively selected beyond 40 m. Profitability of given woody species is defined not only by their crude nutrient contents but by their digestibility and retention time as well. As an example, trembling aspen was shown to have higher protein contents and digestibility than speckled alder and red maple (Fryxell and Doucet 1993), and speckled alder has a mean retention time 2.6 times longer than that of trembling aspen (Fryxell et al. 1994). Chemical plant defences such as secondary metabolites also influence the palatability of different plant species to beavers. To this effect, Müller-Schwarze et al. (1994) showed that these chemical compounds in red maple bark diminished the palatability of aspen stems to beavers when they were painted with red maple extracts.

The inclusion of red maple and speckled alder as preferred species would have greatly influenced our results by affecting which ponds eventually got pooled into our different habitat-quality data sets. Despite their relatively high selectivity indexes (Table 2), we did not consider them as preferred by beavers. Red maple is generally considered as a secondary food source because of its relatively low digestibility to beavers (Doucet and Fryxell 1993; Fryxell and Doucet 1993). Red maple's high selectivity index appears to be the result of beavers directing their foraging efforts toward this species after the preferred ones became scarce, as was observed during Fryxell and Doucet's (1993) diet choice experiments with captive beavers. Furthermore, Jenkins (1980) observed that beavers consumed the bark on 88% of felled pin cherry tree trunks in comparison with only 14% for red maple at a given beaver pond. Speckled alder was also excluded because this species is not primarily selected for nutritional purposes, as shown by the majority of alder stems found with intact bark on lodges and dams in our study (D. Gallant, personal observation). Beavers select it mainly as structural material for dams and lodges (Doucet et al. 1994b; Barnes and Mallik 1996) or for structural support in food caches (Slaugh 1978) rather than for immediate consumption. Availability of accessible building material for initial construction of dams and lodges affects the beavers' choice of habitat in terms of establishment location, as shown by Barnes and Mallik's (1997) study where beavers

relied on shoreline concentrations of woody plants 1.5–4.4 cm in diameter. Our data were collected around established colonies where building material needs are restricted to the maintenance of existing structures. In our study, data collected along beaver trails would concern resource exploitation for feeding purposes, in which case speckled alder documented close to shore would have minimal influence on the current foraging behaviour being documented along trails reaching farther inland.

The present study aimed to determine whether beavers select forage items that maximize energy return relative to time invested. Compared with other studies (Fryxell and Doucet 1991, 1993; Donkor and Fryxell 2000), beavers in our study area traveled very far from the ponds where preferred species are to be found (up to 83 m). They cut large aspens, about which they sectioned and ate the trunk bark on site where they were felled (D. Gallant, personal observation). Low predation risks could have explained this trend observed in Kouchibouguac National Park. To this effect, Basey and Jenkins (1995) determined that beavers did not exert forage choices consistent with minimization of predation risks or energy maximization but that they used trade-off strategies between these two hypotheses when foraging on trembling aspen. Basey and Jenkins' (1995) model, based on observational data on beaver and coyote performances, determined that beavers had to be no farther than 5–7 m from the pond if they were to outrun a coyote approaching from the shore or perpendicular to the pond. The most potent predator of beavers in our study area would indeed be the coyote. However, coyotes in the park seem to prey very little on beavers. Dumond et al. (2001) observed that beavers constituted only 5.4% of the annual diet and only 1.1% in May–June and 0.8% in September–October. Coupled with our results on trembling aspen foraging, this indicates that predation risks on beavers in the park are probably low and did not affect our testing of the basic predictions of the central place foraging theory.

In conclusion, the results of this study are consistent with predictions of the central place foraging theory. Although not completely assessed, literature cited to this effect shows that energy contents (benefits) and the time and energy associated with acquiring and processing various food items (costs) are important in influencing beaver foraging pattern. Beaver selectiveness in relation to studied variables was primarily observed in superior quality habitat where a large availability of different types of food items creates better opportunity for exerting optimal foraging choices. Selectivity may thus be associated with habitat quality and distance from the pond. Better knowledge of beaver foraging behaviour can help understand their role in forest community composition and succession. In a protected area such as Kouchibouguac National Park, such consequences are important to consider in the light of ecological integrity and the conservation of natural processes. It is expected that in some areas of the park where succession is moving from abandoned farmlands to forested ecosystems, beavers may find new suitable habitats, thus increasing the pressure on these newly established ecosystems. Because managed forests and agricultural lands currently surround the park, the monitoring of beaver populations will have to be maintained to reduce the threat on the regenerating forests.

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