A COMPARISON OF BEAVER FORAGING BEHAVIOUR IN TWO NATIONAL PARKS

By

Douglas Vincent

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Signature of Supervisor

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ABSTRACT

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Key Words: beaver, *Castor canadensis*, central place foraging, resource availability, vegetation communities,

Strategies adopted by foraging herbivores are influenced by the availability of resources. Beavers (*Castor canadensis*) are important ecosystem engineers, having the ability to modify the landscape through the consumption of selected resources. Predictions of central place foraging theory are that fewer food items are taken and that increased selection takes place by species and by size of food items at greater distances from the central place. These predictions were tested in Voyageurs National Park, Minnesota and Terra Nova National Park, Newfoundland. Cut and uncut trees were monitored during May-December, 2008 along transects surrounding 15 inland beaver ponds. Beavers selected fewer stems, larger diameter stems, and fewer different forage categories with increasing distance from ponds at both parks. The history and present state of vegetation communities are important to understanding beaver foraging and the overall role that beavers continue to have in boreal mixed-wood forest communities.

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INTRODUCTION

In animals, there must be a process or mechanism that determines which activity is to take priority at any particular time (McFarland 1977). Each possible activity has different consequences and activities have both costs and benefits associated with them. Schoener (1971) described foraging strategies as among the most important decisions made by an animal. All organisms must acquire energy to maintain their daily functions in order to grow, survive, and reproduce. An animal may endure a decrease in fitness from foraging, due to a lack of time to participate in defending a territory, reproducing, thermoregulating, or avoiding predators. There may also be a loss of fitness if an animal forages in a poor quality patch. Therefore, prey selection by predators should maximize net energy intake per unit of time, and this assumption is the basis for much of central place foraging (CPF) theory.

Central place foragers do not consume their prey items at the point of capture, but rather return with them to a central place where they are eaten, stored, or fed to offspring (Orians and Pearson 1979). Numerous studies have attempted to construct predictive mathematical models of food choice in CPF (Orians and Pearson 1979; Schoener 1979). These models pose two questions: (1) why does an organism use certain patches, food items, and prey load sizes; and (2) where does an organism optimally locate its central place (Orians and Pearson 1979)? The decisions associated with these questions are influenced by patch qualities, effects of predators and competitors on prey availability, and the risk of predation.

Terrestrial forays from the central place are energetically costly and increase predation risk, so energy gained should be maximized, and, as distance from the central place increases, prey with greater energy returns must be selected (Fryxell and Doucet 1991). Therefore, a relationship is assumed for size of selected prey between the highest profit, or energy return per unit time (e/t), and travel distance (Schoener 1979). For shorter travelling distances, prey selected will be those with the highest energy per provisioning time, while for longer travelling distances, prey selected will be those of highest energetic reward regardless of provisioning time, because a lower net energy is delivered with increased distance from the central place (Orians and Pearson 1979). Larger prey are also more profitable at longer distances, because of the greater amount of biomass offered.

The North American beaver (*Castor canadensis* Kuhl) has been used extensively as a model species to test predictions of CPF theory, because beavers return to a lodge after foraging (Jenkins 1980), and select resources in a manner in which the net rate of energy is maximized per unit of time (Orians and Pearson 1979; Schoener 1979). Both the availability and the spatial distribution of food items should influence the likelihood that a given item will be acceptable (Fryxell and Doucet 1993). After some time spent at a central place, beavers may deplete their food resources (Johnston and Naiman 1990a) and change their central place along a stream system (Warren 1932; Johnston and Naiman 1990b), with a cause-and-effect relationship generally supposed for this longer-term foraging pattern on the landscape (Martell et al. 2006; Johnston and Naiman 1990a). What remains to be investigated in more detail are the limits to CPF for beavers that may be a means to predict colony abandonment.

Beavers differ from most other central place foragers in both their type of food and that they are often smaller than their prey (Jenkins 1980; Basey et al. 1988). Beavers feed on a wide variety of woody and herbaceous plants, despite preference for certain foods (Northcott 1971; Roberts and Arner 1984; Fryxell and Doucet 1991; Doucet and Fryxell 1993; Baker and Hill 2003; Müller-Schwarze and Sun 2003; Gallant et al. 2004). Deciduous woody plants are usually the most important component of the beaver diet and their availability is the primary limiting factor where ice restricts subsistence on a winter food cache (Baker and Hill 2003). Willow (*Salix* spp.) is often the most available and most used woody plant in much of beavers' range. However, where aspen (*Populus* spp.) is available, it is usually more preferred than willow (Jenkins 1981). Cafeteria-style feeding experiments in Ontario showed the following preferences in descending order for the North American beaver: *Populus tremuloides* (trembling aspen), *Nymphaea odorata* (white water-lily), *Rubus idaeus* (red raspberry), *Alnus rugosa* (speckled alder), and *Acer rubrum* (red maple) (Doucet and Fryxell 1993). In a natural setting in New Brunswick, beavers cut the highest proportion of stems of *Populus tremuloides*, *Betula populifolia* (gray birch), *Alnus rugosa,* and *Acer rubrum* (Gallant et al. 2004). Alder, usually speckled alder (*Alnus rugosa*), is not primarily selected for nutritional purposes, but rather used for dam and lodge construction material (Doucet et al. 1994; Barnes and Mallik 1996).

For central place foragers, the total number of food items used is predicted to decrease with increasing distance from the central place (Andersson 1978) and this trend has been shown for beavers (Jenkins 1980; Pinkowski 1983; Belovsky 1984; McGinley and Whitham 1985; Haarberg and Rosell 2006). Greater selectivity for stem sizes also occurs with increasing foraging distance (Orians and Pearson 1979). In studies where beavers were experimentally offered small diameter stems (≤ 5 cm; McGinley and Whitham 1985; Fryxell and Doucet 1991, 1993) and in natural settings (Gallant et al. 2004; Haarberg and Rosell 2006; Raffel et al. 2009), a positive correlation between distance from the central place and diameter of stems used by beavers has been demonstrated. Beavers exposed to relatively larger diameter trees, on the other hand, cut smaller stems with increasing distance from the central place (Jenkins 1980; Pinowski 1983; Donkor and Fryxell 1999) or showed no difference in diameter cut with increased distance

(Belovsky 1984). Both scenarios follow CPF theory, because beavers exert selective choices on a wide range of stem sizes with masses both greater and less than their body mass (Gallant et al. 2004).

Beavers have great potential to alter plant communities, as they are able to fell mature trees, are spatially constrained to areas near the lodge, and cut far more biomass than is ingested (Johnston and Naiman 1990). Beaver effects are further intensified in the boreal forest, where limited light, temperature, and nutrients restrict the succession of woody plants browsed by beavers. Selective resource use by beavers can shift vegetative community structure to increase the importance of unbrowsed stems or species (Barnes and Dibble 1988; Pastor et al. 1988; Johnston and Naiman 1990b; Pastor and Naiman 1992; Donkor and Fryxell 1999; Donkor and Fryxell 2000). The cutting by North American beavers of large diameter trees of preferred, early successional species, particularly aspen (*Populus tremuloides* and *P. grandidentata*), causes canopy openings that often provide sufficient light penetration to allow regeneration of these shade intolerant species (Johnston and Naiman 1990b; Donkor and Fryxell 1999). Thus, beavers often convert mid successional forests to early successional forests (Gill 1972). Beaver foraging can also increase net primary productivity of subcanopy forest species, including balsam fir (*Abies balsamea*) and spruce (*Picea mariana* and *P. glauca*), hastening forest succession (Johnston and Naiman 1990b; Davidson 1993). This effect causes depletion of food resources close to a pond, forcing beavers to build more dams to extend their foraging area and predator refuge areas.

The goal of my study was to compare the predictions of CPF theory in a natural environment at two study sites. The sites were chosen to represent an area where beavers have more recently been exploiting new stream habitats for impoundment (Voyageurs National Park, Minnesota; Johnston and Naiman 1990a), and an area where beavers have for several decades been observed to abandon impounded habitats (Terra Nova National Park, Newfoundland; Northcott 1964; Payne 1970; Bergerud and Miller 1977). My primary objective was to estimate how beaver foraging behaviour varied in terms of stem distance, diameter, and species in relation to vegetation community composition. The availability of different food items was quantified over one season by comparing available and cut woody stems. With a focus on species, diameter, and distance of these food items the following three predictions were tested in the context of CPF theory: (1) beavers use fewer stems with increasing distance from a pond's edge; (2) beavers are increasingly selective of stems by size with increasing distance from a pond's edge; and (3) beavers are increasingly selective of stems by species with increasing distance from a pond's edge. Variation in how beavers use stems may reflect differences in forage availability or may be the result of other factors influencing foraging behaviour. Foraging decisions made by beavers may play a role in the composition of boreal forest communities. In turn, the composition of forest around a pond may influence persistence of an inhabiting beaver colony. The results of this one-year study are discussed in the context of colony persistence and use of the landscapes presented to beavers in the boreal forest.

METHODS

STUDY SITES

Terra Nova National Park (TNNP) (48°56′N, 56°96′W; 404 km^2) was established in 1957. Forests cover approximately 70% of this site, with the remainder occupied by wetlands, heathlands, and barrens (Charest et al. 2000). The park overlaps the Central Newfoundland and North Shore ecoregions (Damman 1983). The former is distinctly boreal forest, with a gently rolling topography. Forest fires play an important role and post-fire stands of black spruce, white birch, and trembling aspen are present with mixtures of balsam fir. Wet areas are occupied by alder (*Alnus* spp.) and mountain maple (*Acer spicatum*), and drier areas by white pine (*Pinus strobus*). The North Shore ecoregion is coastal and is characterized by the presence of many bays and inlets extending far inland. It is similar to the Central Newfoundland ecoregion, except that white spruce is more abundant and trembling aspen is less abundant and does not form pure stands. Alder occurs on both dry and wet areas.

Voyageurs National Park (VNP) (48°30′N, 92°53′W; 882 km^2) was established in 1975. This site extends for over 50 km along the Canada-United States border, from 29 km east of International Falls, Minnesota, to the western edge of the Boundary Waters Canoe Area (Faber-Langendoen et al. 2007). Upland forests are dominated by trembling aspen, white birch and jack pine (*Pinus banksiana*) in both pure stands and mixtures (Kurmis et al. 1986). Balsam fir, white spruce, and other hardwoods are also found along with small, scattered stands of white pine and red pine (*Pinus resinosa*).

Prior to establishment, both parks experienced extensive disturbances, including logging (Cole 1982; MacEachern 2001), beaver trapping (Bergerud and Miller 1977; Naiman et al.

1988), fire (Cole 1982; Power 1996), and other factors. These disturbances promoted the regeneration of early successional species, such as aspen and birch, likely in similar proportions in both parks.

FIELD METHODS

Forage availability and use for 15 beaver colonies were surveyed in both parks, during summer (VNP, May 15-June 9; TNNP, August 13-25) and fall (VNP, October 19-24; TNNP, November 19-December 9) of 2008. Beaver colonies were selected from those located in lodges at impounded ponds, rather than on larger lake shorelines, to study localized foraging activity. Only ponds with established colonies, determined by a maintained dam or lodge or fresh cuttings were selected. The other consideration for colony selection was the vegetation composition surrounding the pond. Candidate ponds were primarily limited to those that supported <50% conifer in the surrounding vegetation.

Tree availability at each pond was estimated by surveying ten 100-m transects perpendicular to the pond's edge, each with a randomly selected start point. Transect length was based on the suggestion that beavers rarely travel >100 m from a pond (Jenkins 1980). Starting distance from the pond's edge for the first plot of each transect was controlled, such that only one transect started at 1 m, the next at 2 m, etc., to ensure complete coverage of the foraging area. Each transect was subsequently divided into 10-m sections, at each of which a 6-m diameter plot (28.27 m^2) was surveyed and the following were recorded: species, number and diameter (30 cm above ground) for each woody stem $\geq$ 2 cm diameter present, and species, number and stump diameter (at height of cut) of each recently cut stem. All cut stems encountered in the summer survey were marked with spray paint or saw marks on the stump, to ensure they were not recounted in the fall survey and to ensure that fresh cutting was included in both the availability and the use counts.

DATA ANALYSIS

Total foraging area was estimated using the UTM coordinates (Arc GIS 9.2) for the start of each transect to create a polygon approximating the pond's edge. A 100-m buffer was created around the pond representing a hypothetical maximum foraging area available to beavers.

To compare forage availability across ponds and at the two parks, records of tree stem diameters were grouped by forage category into ten distance categories from the edge of each of the ponds (0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90 and 90-100 m) and into 2 cm diameter classes (2-66 cm). Total number of stems for each forage category for each pond was divided by the number of plots (100) and the area of a plot (28.27 m^2) to estimate number of stems per m^2. The number of stems was multiplied by the potential survey area (100-m radius) and a grand mean was calculated for each pond. In comparing forage availability according to stem distance a similar method was used. Total number of stems for each forage category for each distance category was divided by the number of plots in that distance category (10) and the area of a plot (28.27 m^2) to determine number of stems per m^2. The number of stems was then multiplied by the potential survey area of each distance category and totals were used to calculate a grand mean for each pond.

Main forage species were categorized by genus into alder (*Alnus*), aspen (*Populus*), birch (*Betula*) and maple (*Acer*), based on highest abundance and use at VNP (Table 1) and TNNP (Table 2). Based on stem availability and the proportion of stems used, species with high use that were rare, only abundant in one or two of the 15 ponds, or not abundant at both parks included: balsam poplar (*Populus basamifera*), bush honeysuckle (*Lonicera* spp.), ash (*Fraxinus* spp.), red oak (*Quercus rubra*), viburnum (*Viburnum* spp.), willow (*Salix* spp.), pin cherry (*Prunus pensylvanica*), and dogwood (*Cornus* spp.). These species, along with all other less preferred deciduous items, were pooled into a fifth category named "other forage." All conifer items were pooled into a sixth category named "conifer." Relative availability of each forage category was compared by stem diameter and distance across all ponds and at the two parks using a general linear model.

Table 1: Selectivity index of woody plant species recorded along transects around 9 beaver colonies studied in Voyageurs National Park, Minnesota, 2008. The dashed line represents the position of the mean proportion of stems used from all species combined (0.036).

Species	Total frequency	Frequency of used stems	Proportion of stems selected
Balsam poplar, *Populus basamifera*	149	45	0.302
Bush honeysuckle, *Lonicera* spp.	11	3	0.273
Ash, *Fraxinus* spp.	482	70	0.145
Speckled alder, *Alnus rugosa*	1959	241	0.123
Red oak, *Quercus rubra*	186	15	0.081
Aspen, *Populus tremuloides* and *P. gradidentata*	1372	93	0.068
Birch, *Betula papyrifera* and *B. alleghaniensis*	988	61	0.062
Willow, *Salix* spp.	357	18	0.050
Dogwood, *Cornus sericea* and *C. alternifolia*	689	32	0.046
Maple, *Acer* spp.	1970	85	0.043
Pin cherry, *Prunus pensylvanica*	131	4	0.031
Black spruce, *Picea mariana*	223	5	0.022
White pine, *Pinus strobus*	182	4	0.022
Beaked hazel, *Corylus cornuta*	12919	210	0.016
Serviceberry, *Amelanchier* spp.	121	1	0.008
White spruce, *Picea glauca*	219	1	0.005
Balsam fir, *Abies balsamea*	2574	7	0.003
Basswood, *Tilia americana*	3	0	0.000
Eastern white cedar, *Thuja occidentalis*	1	0	0.000
Jack pine, *Pinus banksiana*	61	0	0.000
Red pine, *Pinus resinosa*	29	0	0.000

Table 2: Selectivity index of woody plant species recorded along transects around 6 beaver colonies studied in Terra Nova National Park, Newfoundland, 2008. The dashed line represents the position of the mean proportion of stems used from all species combined (0.017).

Species	Total frequency	Frequency of used stems	Proportion of stems selected
Aspen, *Populus tremuloides*	467	75	0.161
Maple, *Acer* spp.	64	5	0.078
Viburnum, *Viburnum* spp.	81	5	0.062
Birch, *Betula papyrifera* and *B. alleghaniensis*	925	50	0.054
Pin cherry, *Prunus pensylvanica*	281	12	0.043
Speckled alder, *Alnus rugosa*	3725	46	0.012
Balsam fir, *Abies balsamea*	171	1	0.006
Mountain ash, *Sorbus Americana* and *S. decora*	272	1	0.004
Black spruce, *Picea mariana*	5093	5	0.001
Willow, *Salix* spp.	26	0	0.000
White pine, *Pinus strobus*	1	0	0.000
Serviceberry, *Amelanchier* spp.	33	0	0.000
White spruce, *Picea glauca*	8	0	0.000
Mountain holly, *Nemopanthus mucronatus*	205	0	0.000
Canada yew, *Taxus canadensis*	2	0	0.000
Tamarack, *Larix laricina*	200	0	0.000

The prediction that fewer stems will be used with increasing distance was tested with a mixed effects model with park as the fixed variable and pond as a nested effect within parks (Gillies et al. 2006). The dependent variable was the probability that a stem of each of the forage categories might be used, based on its diameter and distance from a pond's edge, two random effects. The interaction between distance and diameter was also tested in predicting the probability of a stem being cut. Probability of use, P_{cut}, was modelled as an odds ratio, obtained from the logit model:

$$\text{Log}\ [P_{\text{cut}} / (1-P_{\text{cut}})] = b_0 + b_1 x_{\text{park}} + b_2 x_{\text{park(pond(transect))}} + b_3 x_{\text{stem distance}} + b_4 x_{\text{stem diameter}} + b_5 x_{\text{stem distance}} x_{\text{stem diameter}} + b_6 x_{\text{park}} x_{\text{stem distance}} + b7 x_{\text{park}} x_{\text{stem diameter}} + b_8 x_{\text{park}} x_{\text{stem distance}} x_{\text{stemdiameter}},$$

for which b_0 is a constant, and b_3, b_4, and b_5 are the coefficients associated with distance from the pond ($x_{\text{stem distance}}$), stem diameter ($x_{\text{stem diameter}}$), and their interactions. Odds of using a stem of a given forage category was expected to decrease with increasing distance from the central place (b_3 negative). A second set of logistic regressions was used as an illustration of the forage categories for which the prediction of selection of fewer stems with increasing distance held. For these cases, the regression curves for distance from the pond ($x_{\text{stem distance}}$) were plotted against the relative frequency of stems cut at 10-m distance intervals, separately for each park. Odds of larger diameters increasingly being used with increasing distance from the central place was also expected (b_5 positive and $b_5 > |b_4|$).

Selection of stems by forage category at increasing distances from the pond's edge was illustrated using Neu's method for analysing use-availability data (Neu et al. 1974; Byers et al. 1984). Bonferroni confidence intervals were constructed to estimate preference or avoidance of forage categories at each park. Analysis was conducted for each distance class separately. Using this technique, and meeting the assumptions associated with sampling theory, there is at least a 100(1-α) % chance that the intervals contain their respective true proportion, p_{obser} of stems consumed:

$$\hat{p}_{obser} - Z_{\alpha/2k}\sqrt{\hat{p}_{obser}(1-\hat{p}_{obser})/n} \leq p_{obser} \leq \hat{p}_{obser} + Z_{\alpha/2k}\sqrt{\hat{p}_{obser}(1-\hat{p}_{obser})/n},$$

where $\hat{p}_{obser}$ is the predicted value of p_{obser}, α is the level of significance, k is the number of categories tested, $Z_{\alpha/2k}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$, and n is the total number of stems. All statistical analyses were run in SPSS (SPSS for Windows version 16, 2007, Chicago, Illinois, USA).

RESULTS

Mean number of stems per pond of all woody forage categories (≥ 2 cm diameter) was greater at VNP than at TNNP for aspen, maple and "other" forage, and lower for alder, birch and conifer (Figure 1). Stems in all forage categories were on average closer to the pond's edge at TNNP than at VNP, with the exception of alder (Table 3). In all forage categories, diameter of available stems differed both across ponds within a park and between the two parks (Table 4). Within a pond, stem availability occurred at significantly different diameters only for alder, aspen and conifer. Differences in available diameters within a pond also varied between parks for all forage categories, with the exception of maple (Figure 2). The number of stems available by distance was more consistent across ponds within a park, differing only for alder and the "other" forage category. However, differences between parks in availability of stems by distance, as for diameter, were apparent in all forage categories (Figure 3), with the exception of alder. These differences in forage availability also varied between parks for all categories, with the exception of birch (Table 4).

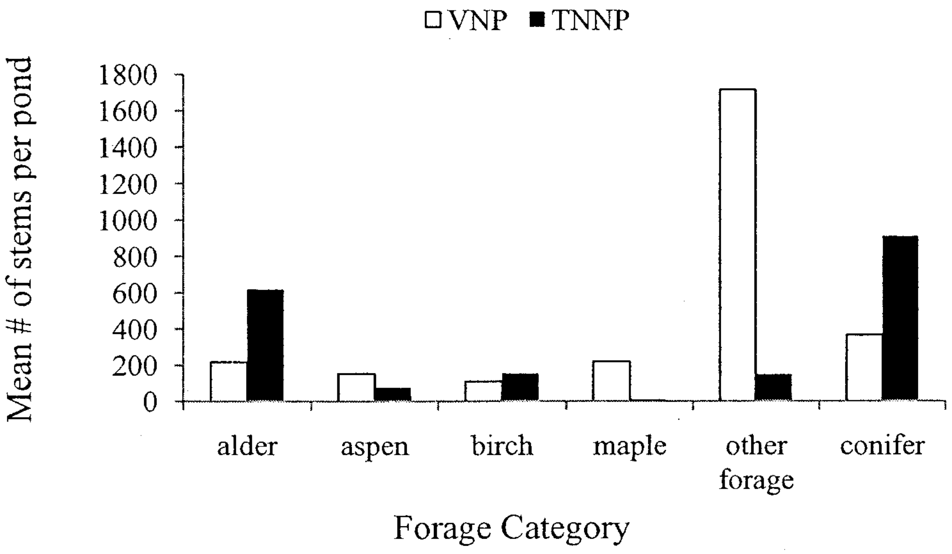

Figure 1. Mean number of stems of all forage categories surrounding beaver ponds in Voyageurs National Park, Minnesota (VNP) and Terra Nova National Park, Newfoundland (TNNP), 2008.

Table 3. Mean and maximum diameter and distance of available and used forage categories at active ponds in Voyageurs National Park, Minnesota and Terra Nova National Park, Newfoundland, 2008.

		Diameter (cm)				Distance (m)			
		Available		Used		Available		Used	
Park	Forage Category	Mean	Max	Mean	Max	Mean	Max	Mean	Max
VNP	Alder (*Alnus* spp.)	3.5	10.0	3.8	8.0	45.5	98.0	20.1	48.0
	Aspen (*Populus* spp.)	13.2	60.0	16.9	52.0	63.8	100.0	38.3	88.0
	Birch (*Betula* spp.)	8.1	42.0	8.6	26.0	54.4	100.0	20.7	50.0
	Maple (*Acer* spp.)	5.8	38.0	5.7	28.0	56.8	100.0	30.4	78.0
	Other Forage	3.5	56.0	4.3	38.0	51.6	100.0	28.8	88.0
TNNP	Alder (*Alnus* spp.)	3.2	10.0	3.4	6.0	47.9	100.0	15.5	61.0
	Aspen (*Populus* spp.)	7.0	46.0	8.6	46.0	49.6	100.0	26.8	91.0
	Birch (*Betula* spp.)	7.3	30.0	7.0	14.0	50.1	100.0	13.2	48.0
	Maple (*Acer* spp.)	2.9	24.0	3.0	4.0	49.1	100.0	47.5	91.0
	Other Forage	3.5	18.0	4.3	8.0	46.7	99.0	30.4	92.0

Table 4. Results of the general linear model testing the availability of stems according to distance and diameter for six forage categories in Voyageurs National Park and Terra Nova National Park, 2008. Boldface type indicates significant factors in explaining differences in availability by diameter and distance and *n* equals the number of distance and diameter categories represented by available stems across all ponds.

	Diameter				Distance			
Forage Category	Factor	Wald Chi-Square	P-value	*n*	Factor	Wald Chi-Square	P-value	*n*
Alder	**Park (Pond)**	91.348	0.000	49	**Park (Pond)**	5.378	0.020	105
	Park	183.401	0.000		**Park**	134.441	0.000	
	Diameter	8.587	0.003		Distance	0.025	0.875	
	Park*Diameter	10.334	0.001		**Park*Distance**	6.945	0.008	
Aspen	**Park (Pond)**	59.654	0.000	178	Park (Pond)	1.978	0.160	96
	Park	148.177	0.000		**Park**	96.902	0.000	
	Diameter	6.065	0.014		**Distance**	11.709	0.001	
	Park*Diameter	2.206	0.138		**Park*Distance**	8.684	0.003	
Birch	**Park (Pond)**	190.679	0.000	150	Park (Pond)	0.040	0.841	123
	Park	362.454	0.000		**Park**	202.232	0.000	
	Diameter	1.291	0.256		**Distance**	5.457	0.019	
	Park*Diameter	7.896	0.005		Park*Distance	0.943	0.332	
Maple	**Park (Pond)**	132.777	0.000	86	Park (Pond)	0.004	0.952	101
	Park	21.921	0.000		**Park**	89.913	0.000	
	Diameter	0.238	0.625		**Distance**	5.884	0.015	
	Park*Diameter	1.650	0.199		**Park*Distance**	5.162	0.023	
Other Forage	**Park (Pond)**	52.529	0.000	105	**Park (Pond)**	24.730	0.000	139
	Park	195.228	0.000		**Park**	181.378	0.000	
	Diameter	0.511	0.475		**Distance**	5.182	0.023	
	Park*Diameter	6.917	0.009		**Park*Distance**	5.776	0.016	
Conifer	**Park (Pond)**	143.107	0.000	258	Park (Pond)	0.836	0.361	149
	Park	1106.809	0.000		**Park**	186.307	0.000	
	Diameter	7.499	0.006		**Distance**	89.737	0.000	
	Park*Diameter	14.243	0.000		**Park*Distance**	6.254	0.012	

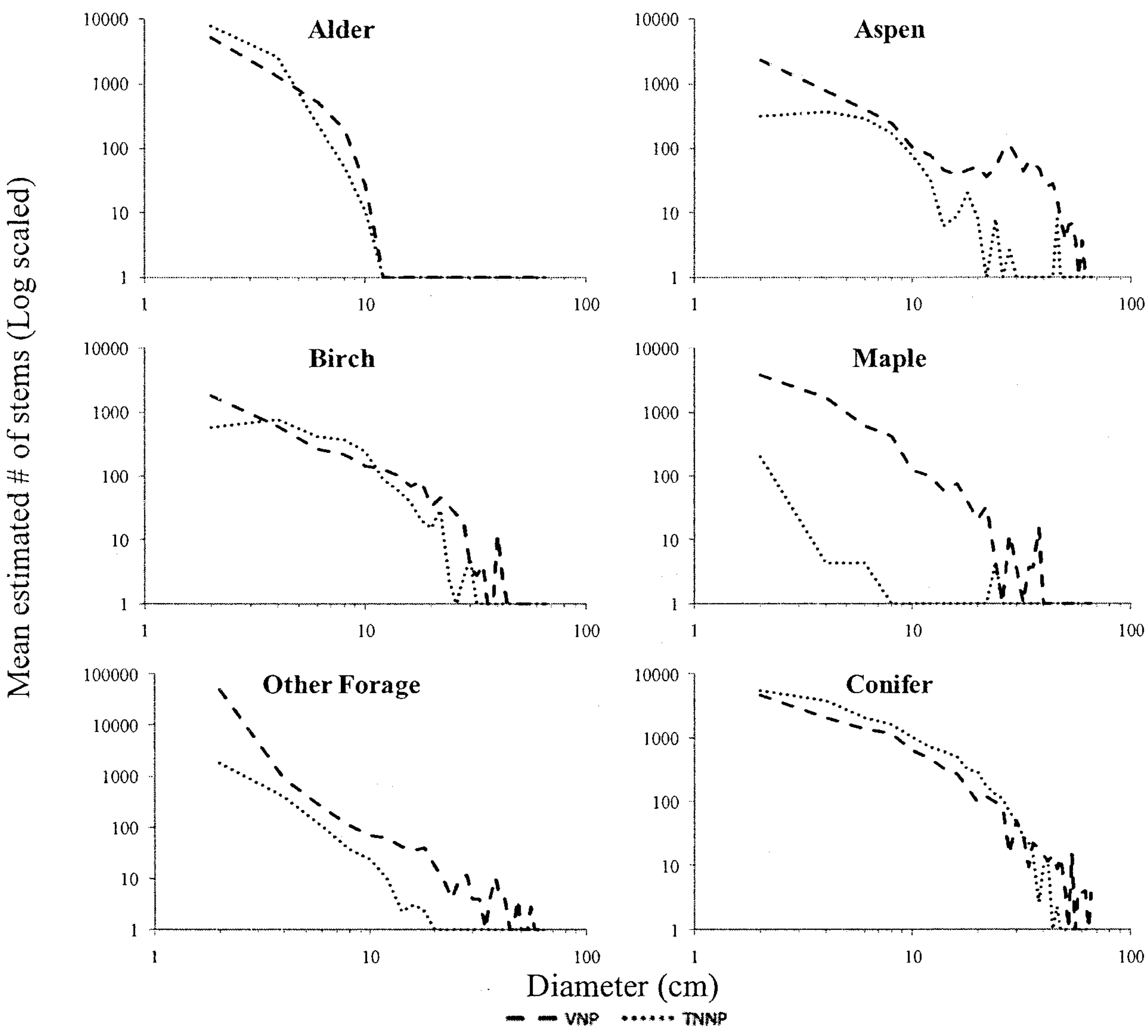

Figure 2. Estimated available number of stems of all forage categories in relation to diameter for beaver ponds in Voyageurs National Park, Minnesota (VNP) and Terra Nova National Park, Newfoundland (TNNP), 2008.

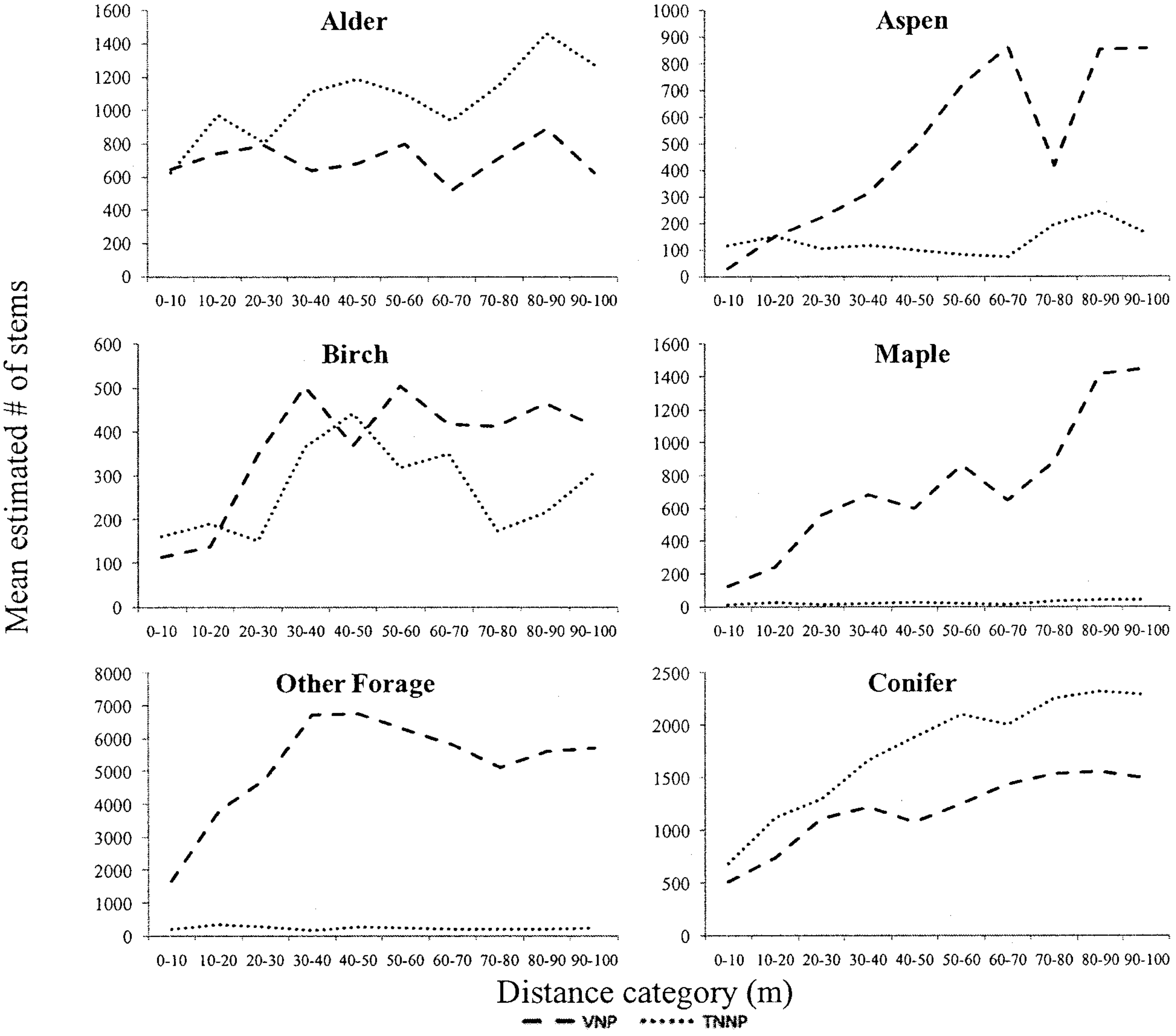

Figure 3. Estimated available number of stems of all forage categories in relation to distance from the pond's edge for beaver ponds in Voyageurs National Park, Minnesota (VNP) and Terra Nova National Park, Newfoundland (TNNP), 2008. Note that graphs are drawn to different scales.

Four of the 15 ponds studied (all at TNNP) were abandoned before winter or had an extremely low number of cut stems during the fall survey and were not included in the total number of available stems used in the mixed-effects model (Table 5). Beavers, on average, travelled longer distances to cut stems of alder, aspen and birch at VNP than at TNNP (Table 3). They used fewer stems of alder and "other" forage with increasing distance from the pond's edge at both parks (Table 6). However, the use of alder was highly variable across transects and across ponds within a park. Comparing parks, there was variable use of stems by distance for aspen and "other" forage. Beavers, on average, also used stems of larger diameters at VNP than at TNNP in all four main forage categories (Table 3). For both parks, there was selection of stems by diameter for alder, aspen, and birch; selection differed between parks for alder and aspen (Table 6). Generally, for the main forage categories, diameter selection did not differ at increasing distances from the pond's edge. However, in a comparison between parks, different selection of stems by diameter at different distance categories did occur for "other" forage (Table 6). Maple was removed from the analysis, because there were no significant factors explaining its use.

Table 5. Proportion of deciduous stems relative to total stems recorded along transects and by fall activity around 15 beaver colonies studied in Voyageurs National Park, Minnesota and Terra Nova National Park, Newfoundland, 2008.

Colony	Park	Total number of deciduous stems	Total number of stems	Proportion of deciduous stems	Fall Activity
South Hoist Bay	VNP	5294	5366	0.987	Y
West of Oleary Lake	VNP	3069	3229	0.950	Y
South of Mud Bay	VNP	1890	2103	0.899	Y
Deep Slu East	VNP	1926	2201	0.875	Y
Blind Ash - Nebraska	VNP	2717	3231	0.841	Y
East Mud Bay	VNP	1752	2183	0.801	Y
East Hoist Bay	VNP	1776	2277	0.780	Y
Deep Slu West	VNP	1503	1989	0.756	Y
East Junction Bay	VNP	1788	2425	0.736	Y
Papa Jacks	TNNP	2105	3044	0.692	Y
Northwest Brook	TNNP	1695	3030	0.559	Y
Southwest Arm	TNNP	750	1367	0.549	N
No Name	TNNP	950	2061	0.461	N
Pine Hill Pond	TNNP	385	1106	0.348	N
Ochre Hill	TNNP	186	938	0.198	N

Table 6. Results of mixed-effects binary logistic regressions testing the use of stems according to distance from the pond's edge, stem diameter, park, and their interactions for four forage categories in Voyageurs National Park, Minnesota and Terra Nova National Park, Newfoundland, 2008. Boldface type indicates significant factors in explaining differences in use by diameter and distance.

Forage Category	Factor	*b*	Wald Chi-Square	P-value	*n*
Alder	**Distance**	-0.169	152.125	0.000	3789
	Diameter	1.223	25.734	0.000	
	Park		1.492	0.222	
	Diameter * Distance		0.000	0.999	
	Park * Distance		0.144	0.704	
	Park * Diameter	-1.828	13.072	0.000	
	Park * Diameter * Distance		2.810	0.094	
	Park(Location(Transect))		11.297	0.001	
Aspen	Distance		108.568	0.360	1767
	Diameter	0.407	31.919	0.000	
	Park		11.398	0.001	
	Diameter * Distance		0.000	1.000	
	Park * Distance	0.300	7.985	0.005	
	Park * Diameter	-0.391	9.729	0.002	
	Park * Diameter * Distance		1.066	0.302	
	Park(Location(Transect))		1.597	0.206	
Birch	Distance		48.040	1.000	1797
	Diameter	0.126	38.596	0.000	
	Park		0.009	0.925	
	Diameter * Distance		0.000	0.999	
	Park * Distance		0.117	0.733	
	Park * Diameter		2.676	0.102	
	Park * Diameter * Distance		0.005	0.944	
	Park(Location(Transect))		2.107	0.147	
Other Forage	**Distance**	-0.050	340.209	0.000	16176
	Diameter		1.050	0.306	
	Park		30.057	0.000	
	Diameter * Distance		0.000	0.999	
	Park * Distance	0.070	12.197	0.000	
	Park * Diameter		0.518	0.472	
	Park * Diameter * Distance	0.002	5.947	0.015	
	Park(Location(Transect))		0.050	0.824	

When park data were analyzed separately, beavers used fewer stems with increasing distance from the pond's edge, following prediction 1. In VNP, beavers used fewer stems at greater distances for all main forage categories (alder: -0.018, $P=0.022$; aspen: -0.025, $P<0.001$; birch: -0.098, $P<0.001$; maple: -0.049, $P<0.001$; Figure 4). In TNNP, beavers used fewer stems for three of the four main forage categories at greater distances (alder: -0.066 $P<0.001$; aspen: -0.034, $P<0.001$; birch: -0.142, $P<0.001$). Except for stems in the "other" forage category, beavers did not use larger stems with increasing distance from the pond's edge, as suggested by prediction 2. The relative use of different forage categories at increasing distance from the pond's edge varied between the two parks. Alder was used in greater proportion than its availability in three distance categories ($\leq$50 m) at VNP, while it was not used in greater proportion than its availability at TNNP (Figures 5-6). Aspen was used in greater proportion than its availability in three distance categories ($\leq$90 m) at VNP and five distance categories at TNNP ($\leq$100 m). Birch was only used in greater proportion than its availability in one distance category at VNP ($\leq$20 m) and only one distance category at TNNP ($\leq$10 m). Beavers were thus increasingly selective of stems by forage category with increasing distance from a pond's edge, following prediction 3.

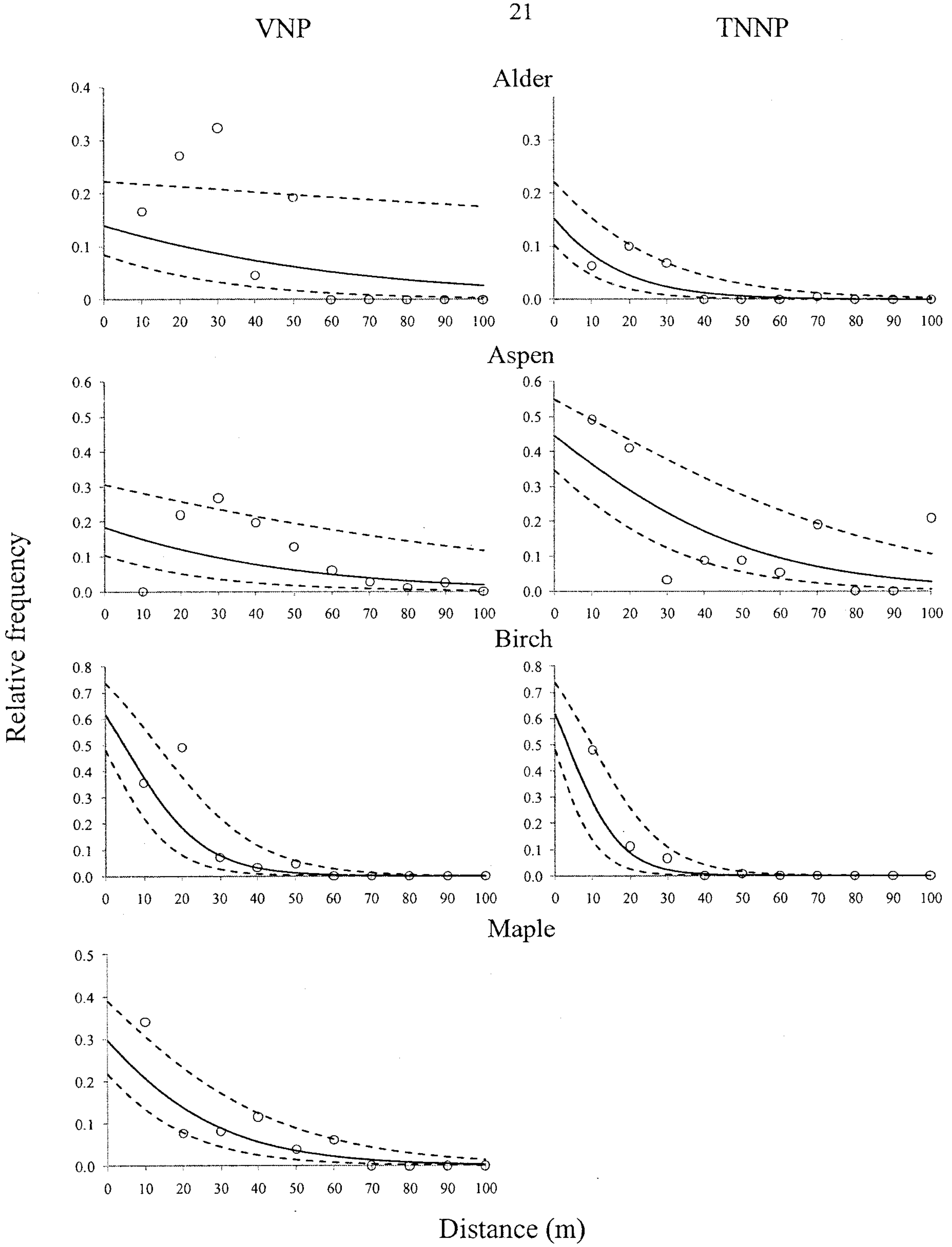

Figure 4. The probability of stem use as a function of distance for main forage categories in Voyageurs National Park, Minnesota (VNP) and Terra Nova National Park, Newfoundland (TNNP) with the logistic regression (solid line) and its 95% confidence intervals (dashed lines) predicting the likelihood of selection at increasing distance.

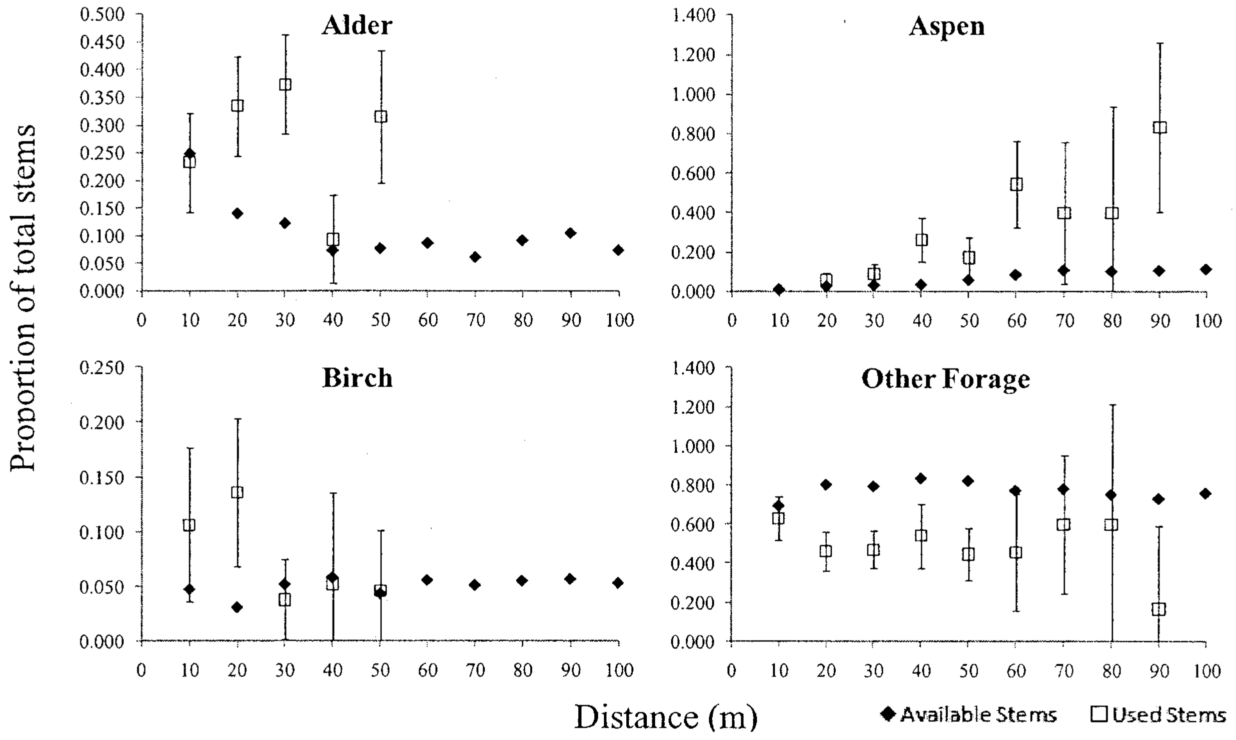

Figure 5. Use and availability of forage categories according to distance from the pond categories along survey transects in Voyageurs National Park, Minnesota. 2008. Note that graphs are drawn to different scales.

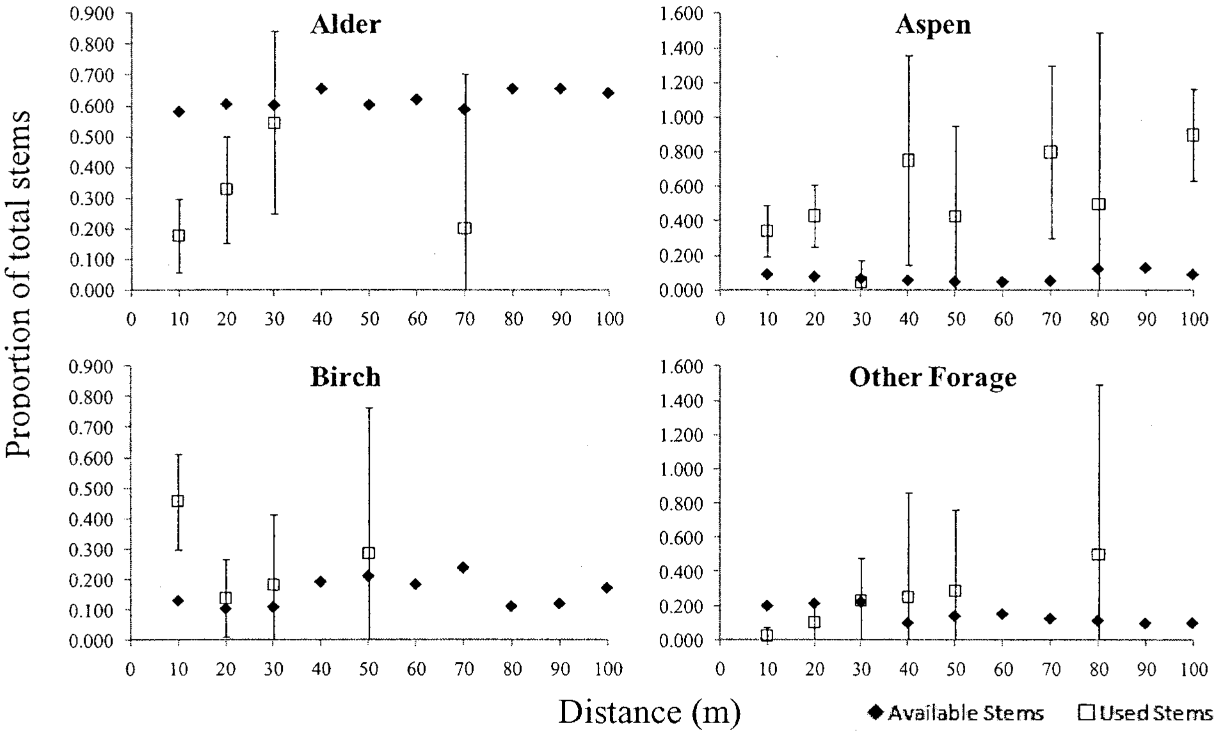

Figure 6. Use and availability of forage categories according to distance from the pond categories along survey transects in Terra Nova National Park, Newfoundland, 2008. Note that graphs are drawn to different scales.

DISCUSSION

Resource availability in a landscape varies considerably, as does the diet of individuals in different habitats (Boyce and McDonald 1999). Availability of certain resources influences diet and habitat-use patterns (Mysterud and Ims 1998). Thus, forage availability influences the behaviour of beavers, constantly changing as a function of foraging itself; thus a change in relative use of habitats by beavers is constantly occurring. Within active ponds in this study, beavers appear to have foraged in a way that is consistent with the predictions of CPF theory, suggesting that energy content of food items and the time and energy associated with acquiring and provisioning food items are important in influencing beaver foraging.

Due to the decrease in net energy gain, foraging for trees farther from the pond becomes much less profitable. Alder was only used at relatively short distances from the pond's edge at both VNP and TNNP. This observation may be a result of my selection of well established colonies in this study, for which the use of alder stems may have been restricted to the maintenance of existing dams and lodges. Most alder used at VNP was found with bark intact and on lodges, in dams, or as structural support in food caches (D. Vincent, personal observation). Mean diameters of used stems of alder were those preferred for construction purposes (Barnes and Mallik 1996). Barnes and Mallik (1997) showed the importance of accessibility to these building materials for colony establishment and continued occupancy, where active beaver dams had significantly greater densities of woody stems in the 1.5 to 4.4 cm diameter range near the pond’s shoreline occurred than at non-dam sites.

Aspen was the only species used in greater proportion to its availability at distances >50 m from the pond’s edge. The importance of aspen is most likely due to its nutritional content, digestibility, and low retention time in comparison to the other forage categories. Aspen has been shown to have a retention time of 37% relative to that of alder (Fryxell et al. 1994), and as retention time decreases, consumption of available biomass increases (Doucet and Fryxell 1993). Aspen also has higher gross energy content and energy digestibility than red maple and speckled alder (Doucet and Fryxell 1993). The use of larger diameters of aspen may be a result of induced chemical defences in regenerating aspen suckers as a response to browsing by beavers, which may shift use by beavers to larger stems, which likely have lower concentrations of these chemicals (Basey et al. 1998; Basey et al. 1990; Basey and Jenkins 1993). At TNNP, aspen may have been used in greater proportion regardless of distance, because it is one of the least abundant foraging items available and its lower availability may have left beavers to use it regardless of its size and location (Northcott 1971). In an earlier study of beaver colonies in central Newfoundland, at two abandoned ponds in Newfoundland, 100% of the available aspen was used, as opposed to six ponds with active colonies, where only 65% of available aspen was used (Northcott 1964).

Birch was similar in abundance by distance surrounding beaver ponds at TNNP and VNP, but birch stem diameter was highly variable between ponds. Regardless of diameter, beavers were only willing to travel a maximum of ~50 m to use birch. The high variability in diameter of birch stems did not entice beavers, while they were willing to travel greater distances for all other forage categories (except alder at VNP). This finding suggests that birch may be a secondary forage species for beavers (Aldous 1938; Novak 1987; Barnes and Mallik 2001; Gallant et al. 2004).

Maple was removed from the analysis, because its use could not be explained by the mixed-effects model. Despite the high selectivity of maple, red maple (*Acer rubrum*) could be considered a secondary food source, based on its relatively low digestibility and energy content and high retention time (Doucet and Fryxell 1993). Maple may be most used when more preferred species, such as aspen, are depleted from a foraging area. At TNNP, the low abundance of aspen may be a contributing factor to the low abundance of maple, also depleted, as beavers already made a shift to foraging less preferred species.

Many of the species in the "other" forage category are considered both preferred and secondary food items for beavers, including ash (Pinkowski 1983; Raffel et al. 2009), balsam poplar (Gallant et al. 2004), pin cherry (Barnes and Mallik 2001; Raffel et al. 2009), and willow (Jenkins 1981). These forage items are greater in abundance at VNP than at TNNP, as part of a more heterogeneous mixed-wood forest (Broschart et al. 1989). They are also highly variable in availability among ponds, and may be important food items in the absence of preferred aspen.

Availability of forage items with increasing distance from the pond's edge varies little, but significant variation in diameter occurs for all forage categories, especially alder, aspen and conifer at all levels, including within ponds, across ponds and between parks. The selection of larger-diameter stems by beavers creates gaps in the overstorey canopy surrounding their ponds and subsequently allows for a higher abundance of smaller stems, due to increased light penetration (Pastor and Naiman 1992; Donkor and Fryxell 1999). As suggested by Jones et al. (2009) for the Eurasian beaver, I interpret from the results of my study that coppicing and suckering from stumps is the ultimate result of beaver selection and explains the high variation in diameter that occurs around ponds both at TNNP and at VNP. Thus, beavers create an atypical succession in mixed-wood boreal forests, in which canopy closure should be nearly complete in an early to mature stage (Davidson 1993; Donkor and Fryxell 1999). This idea further suggests that beaver foraging can itself allow for the continued presence of some forage stems (Jones et al. 2009), especially at smaller diameters (Barnes and Mallik 1997). However, the regeneration of small-diameter stems and a switch by beavers to use these stems may create increasingly smaller gaps in the understorey which also allow the release of shade-tolerant species, contributing to the eventual dominance of conifers around ponds (Fryxell 2001). This effect would over time accelerate succession, shaping a forest to be dominated by shade-tolerant, less nutritious species.

Beavers at TNNP have exhausted the available resources to an extent that frequent colony abandonment has occurred over the last several decades (Northcott 1964; Payne 1970; Bergerud and Miller 1977; D. Vincent, personal observation). On the other hand, beavers at VNP appear to have less influence on their foraging landscape. At VNP, new ponds are still being created on the landscape, although at a decreasing rate, suggesting carrying capacity may be soon achieved (Johnston and Naiman 1990a; VNP unpublished data). These trends related to carrying capacity and the limits of ponds to create opportunities for beaver foraging may be related to the number of available forage species, their abundance, and different food preferences by beavers within forest communities in the two parks. The available forage at TNNP is dominated by alder and smaller diameter stems of forage than at VNP. A theoretical model was developed to suggest when food is the limiting factor, successful foragers will increase their home range size to include a certain minimum amount of food (Mysterud and Ims 1998), a suggestion made specifically for beavers by Donkor and Fryxell (1999) and Campbell et al. (2005) and elaborated by Fryxell (2001). In TNNP most dispersal is a result of limited food supply, and beavers are reluctant to occupy the same pond for more than two consecutive winters (Northcott 1964). Campbell et al. (2005) suggest that beavers may have territories with multiple lodges in order to reduce the rate of resource depletion within a site, thus increasing the long term viability of the larger territory, which is proportionally richer in terms of resource abundance. The pattern by beavers of colonization, abandonment, and recolonization tends to perpetuate a dynamic vegetation community structure and composition, promoting habitat diversity (Broschart et al. 1989). Fryxell (2001) suggests that beavers move between source colonies, those that are permanently occupied, and sink colonies, those that are transient in nature. The accelerated succession to shade-tolerant species caused by beaver foraging would deny source colonies to sustain themselves indefinitely on terrestrial vegetation, and eventually degraded territories can only be supported on sink colonies.

Comparing the two sites used in this study, I have found that foraging opportunity for beavers has become more limited at TNNP. Beavers at TNNP may once have travelled longer distances for larger stems and for preferred stems, sooner after the forest disturbances that made such forage more broadly available. However, in 2008 they travel short distances for smaller stems and continue to switch ponds they occupy over presumably broader ranges than those maintained at VNP. A long-term result of limited foraging opportunity may be that beavers adopt a strategy of pond switching, maintaining larger home ranges around several ponds that each provide short-term foraging opportunities, themselves maintained by beaver cutting.

CONCLUSIONS

This study illustrates the influence of beaver foraging decisions relative to plant community composition at the colony scale. It indicates that the availability of resources influences the foraging decisions made by beavers according to CPF theory at two different sites. Beavers at TNNP likely have accelerated forest succession, forcing their frequent movement among many resource-depleted sites, while beavers at VNP likely have influenced vegetation to a lesser extent and appear more often to occupy the same pond year round. Among the several studies on forest effects created by beaver occupation of a pond site (Barnes and Dibble 1988; Johnston and Naiman 1990b, 1992; Donkor and Fryxell 1999, 2000; Barnes and Mallik 2001; Fryxell 2001), only the studies by Barnes and Dibble (1988), Barnes and Mallik (2001), and Fryxell (2001) were undertaken where beaver occupied a site for >10 years. A long-term study investigating beaver foraging strategies in boreal-forest communities at the landscape scale may shed new light on the importance of beavers in shaping vegetation communities.

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