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Use of woody plants in construction of beaver dams in northern Ontario

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Abstract: Newly formed beaver dams were studied in the Chapleau Crown Game Preserve of northern Ontario to determine if beavers (*Castor canadensis* Kuhl) showed any preference in their choice of woody plants in building the dams. Application of Neu's utilization–availability technique showed that beavers exhibited a high preference for alder (*Alnus* spp., plant species not commonly used as food) stems with diameters of 1.5–3.5 cm and a lesser preference for food-tree stems with diameters of >4.5 cm. We maintain that beavers used large food-tree stems only because they became more accessible after dam construction. Since the alder stems available close to the water's edge accounted for most of the stems of the preferred size, 1.5–3.5 cm, we postulated that selection of woody stems by beavers for construction purposes was based on size rather than on species.

Résumé : L'examen de barrages de castors fraîchement construits dans la réserve faunistique de la couronne à Chapleau, dans le nord de l'Ontario, nous a permis d'étudier le choix des plantes ligneuses chez le Castor du Canada (*Castor canadensis* Kuhl) lors de la construction des barrages. L'application de la méthode Neu (basée sur la disponibilité et l'utilisation) a démontré que les animaux avaient une préférence marquée pour les troncs d'aulnes (*Alnus* spp., arbres qui ne servent pas souvent de nourriture) de 1,5 à 3,5 cm de diamètre, et une préférence moins grande pour les troncs d'arbres de diamètres supérieurs à 4,5 cm d'espèces qui leur servent de nourriture. Nous croyons que les castors utilisaient des gros troncs d'arbres-aliments aux sites des barrages seulement parce que ces arbres devenaient plus accessibles après la construction des barrages. Comme les troncs d'aulnes disponibles près des rivages étaient pour la plupart des troncs de taille idéale, 1,5–3,5 cm, nous concluons que le choix des troncs d'arbres pour construire les barrages est basé sur la taille plutôt que sur l'espèce.

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Introduction

Optimal foraging theory suggests that animals can increase their fitness by maximizing the net rate of intake of some essential resources per unit time (Pyke et al. 1977; Krebs 1978). Several authors have presented the special case of the central-place forager (Andersson 1978; Orians and Pearson

1979; Schoener 1979). They postulated that when prey are smaller than the predator, central-place foragers should select progressively larger food items with increasing distance from the central place. Beavers (*Castor canadensis* Kuhl) are an exception because they feed on such large trees in relation to their body size, so they have been the focus of many foraging studies (Jenkins 1980; Pinkowski 1983; Belvosky 1984; McGinley and Whitham 1985; Fryxell 1992; Fryxell and Doucet 1991). Although these studies have contributed greatly to our understanding of beaver foraging behaviour, they dealt primarily with foraging for food.

Beavers are known for their extensive construction activity. Impounded water is crucial for their survival (Retzer et al. 1956; Nixon and Ely 1969), as it provides protection from predators. Impounded water also provides an efficient means to access and transport food items (Novak 1987). To accomplish this engineering activity, beavers need a ready supply of shoreline shrubs and trees (Novak 1976). To date, little research has been done to understand the cutting behaviour of beavers in obtaining items for constructing dams.

A review of the literature on beaver dams showed that emphasis has largely been placed on effects monitoring and control of beaver dams. The studies that focused on beaver dams were based on evaluation of construction materials used in the dam, not on resource availability (Shaw 1948; Nash 1951; Hodgdon and Hunt 1953; MacDonald 1956; Pullen 1975; Pinkowski 1983). Thomas and Taylor (1990) stated that studies evaluating resource use but not availability have resulted in inferences about use but not preference. Over the years, wildlife researchers have presented many definitions of "preference." Despite these inconsistencies, it is generally agreed that the best way to study resource preference is to employ techniques for comparing use and availability (Johnson 1980; Alldredge and Ratti 1986, 1992; Thomas and Taylor 1990; Schooley 1994).

We applied Neu's utilization-availability comparison to test whether, in constructing dams, the beavers showed a preference for particular woody plant species or for specific sizes of materials.

Study area

The study was conducted in the Swanson River drainage basin of the Chapleau Crown Game Preserve (48°05'N, 83°20'W) in northern Ontario. This drainage area was free from trapping and hunting and thus provided a natural boreal forest setting where beaver dams could be studied with minimum disturbance. The Swanson River has a 200-km network of streams covering an area of 228 km². Riparian habitats were dominated by alder (*Alnus* spp). The forests were dominated by jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* Mill.) interspersed with mixed stands of white spruce (*Picea glauca* Moench), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.). Associated with these forest trees were numerous understory trees and shrubs such as willow (*Salix* spp.), pin cherry (*Prunus pensylvanica* L.), mountain maple (*Acer spicatum* Lam.), dogwood (*Cornus stolonifera* Michx.), mountain ash (*Sorbus americana* Marsh.), choke cherry (*Prunus virginiana* L.), black ash (*Fraxinus nigra* Marsh.), serviceberry (*Amelanchier* spp.), hazel (*Corylus cornuta* Marsh.), and river birch (*Betula glandulosa* Marsh.).

Methods

In June 1993, we conducted a ground reconnaissance to locate newly formed dams in the study area, i.e., the dams constructed during the previous fall. Newly formed dams were chosen because beavers would have had multiple options for obtaining woody plants, one of which would be to harvest woody plants from the sides of the stream. The use of streamside vegetation would not be an option at older dam sites because these materials would have been flooded and (or) browsed.

Of the 25 active colonies located during our survey, we selected three newly formed dams for this study. Dam 1 had a length of 24 m and was situated on a 2 m wide second-order stream. The stream-order classification was based on Strahler (1957). Dam 2 was established on a 30 m wide third-order stream and had a length of 59 m. Dam 3 had a length of 8 m and was situated on a 5 m wide third-order stream.

We established a 0.25 m wide transect on the face of each dam and identified and measured all woody materials visible along the dam face. Using calipers, we determined the diameter of each stem base, where the cut portion interfaced with the bark. We divided the plant diameters into five classes: < 1.5, 1.5–2.5, 2.5–3.5, 3.5–4.5, and > 4.5 cm.

Each alder stem was examined for evidence of feeding. We decided against a detailed examination of all stems because this would have meant dismantling the dams in high spring water conditions. There was no way of ensuring that stems would not be washed away or broken. As a compromise, we examined the alder stems visually without removing them from the dam. Any evidence of feeding was noted.

The pre-dam-construction vegetation composition was reconstructed by studying the vegetation above and below the main beaver dam, where the stream returned to its original width. We established 40 m wide and 170 m long plots upstream and downstream. The plot dimensions were derived from analysis of the woody plant harvesting pattern around 15 active dammed colonies (unpublished data). Within each plot, we randomly selected three 1 × 40 m transects that extended perpendicularly from the stream's edge inland, and measured the diameter of all shrubs and trees at a height of 30 cm above ground. The 30-cm height was established by measuring 20 beaver-cut stumps. This value was consistent with that reported by Johnston and Naiman (1990). Average values from the upstream and downstream plots were used to simulate the impoundment pre-dam-construction shoreline vegetation. We used *t* tests to determine if the upstream and downstream vegetation composition differed significantly.

We chose Neu's utilization-availability comparison (Neu et al. 1974; Byers et al. 1984) to test the hypothesis that beavers have a preference for particular woody species or a specific size class of stems irrespective of species in the construction of dams. The utilization-availability method involves the use of Bonferroni confidence intervals. Using this technique, one can be at least 100(1 - α)% confident that the intervals contain their respective true proportions, p_{actual} :

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

where \hat{p}_{actual} is the predicted value of p_{actual} , 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 number of stems used.

For each of the actual utilization proportions, p_{actual} , we constructed a Bonferroni confidence interval. When the expected proportion of usage, p_{exp} , fell within the interval, we concluded that the expected and actual utilizations were not significantly different, i.e., selection was by chance. If the Bonferroni confidence interval was greater than the expected usage, then the vegetation type was being utilized more than its availability, i.e., it was preferred. If the

Table 1. Mean densities of woody stems (number/120 m²) in downstream and upstream plots of the three beaver dams.

Woody plant categories	Downstream plots	Upstream plots	<i>p</i> (<i>t</i> test)
Alder	134 (30)	165 (61)	0.7
Shrubs	79 (22)	89 (45)	0.9
Conifers	59 (21)	48 (21)	0.7
Food ^a	27 (14)	19 (10)	0.7

Note: Values in parentheses show the standard error of the mean.

^aConsidered to be trembling aspen, white birch, and willow.

Bonferroni confidence interval was less than the expected usage, then the vegetation type was being utilized less than its availability, i.e., it was avoided (Byers et al. 1984).

To ensure a convincing case for determining the beavers' selection process, we analyzed the joint effects of species and diameter on selection. In addition, we recorded the spatial distribution of the plant categories adjacent to the water's edge. These data were used to determine the forage–distance relationships as they applied to the collection of construction material.

Results

Our results showed that the downstream and upstream vegetation did not differ significantly in structure (Table 1). This provided the justification for averaging the data from the upstream and downstream plots.

Alder stems were used for construction only. Our analysis of the stems used in dam construction showed that all alder stems were placed in the dam intact, with no sign of feeding activity.

Beavers showed a preference for stems in the 1.5–2.5 cm diameter class when cutting alder, other shrubs, and conifers (Table 2). In addition, they showed a preference for alder stems of 2.5–3.5 cm diameter and food stems of >4.5 cm diameter. Beavers demonstrated a preference for alder over the other plant categories when cutting stems of <4.5 cm diameter. For stems of >4.5 cm diameter, beavers preferred to search out food trees (Table 2).

We found that the highest concentration of 1.5–3.5 cm diameter alder stems was within 10 m of the shore. No other plant group had as many stems of the preferred size class in close proximity to the shoreline. The densities of food plants were low within 40 m of shore, therefore beavers had to travel beyond their average foraging distance to obtain food items for use in dam construction.

Discussion

We found that beavers showed a preference for alder stems of diameter class 1.5–3.5 cm. Although previous studies have demonstrated that plant species not commonly used as food, such as alder, were utilized to a great extent in establishing dams (Hodgdon and Hunt 1953; Slough and Sadleir 1977; Slough 1978; Novak 1987), none have shown the nature of this preference by using utilization–availability comparisons.

In his work on eastern wood rats, McGinley (1984) noted that they collected large twigs to ensure that the house was strong enough, whereas small twigs were used to ensure that it was adequately waterproofed. We postulate that beavers

Fig. 1. Composition and stem-diameter classes of woody plants within 40 m of the shorelines of dams 1, 2, and 3: alder (■), shrubs (□), conifers (▨), and food trees (▩). Vertical lines represent the standard error of the mean.

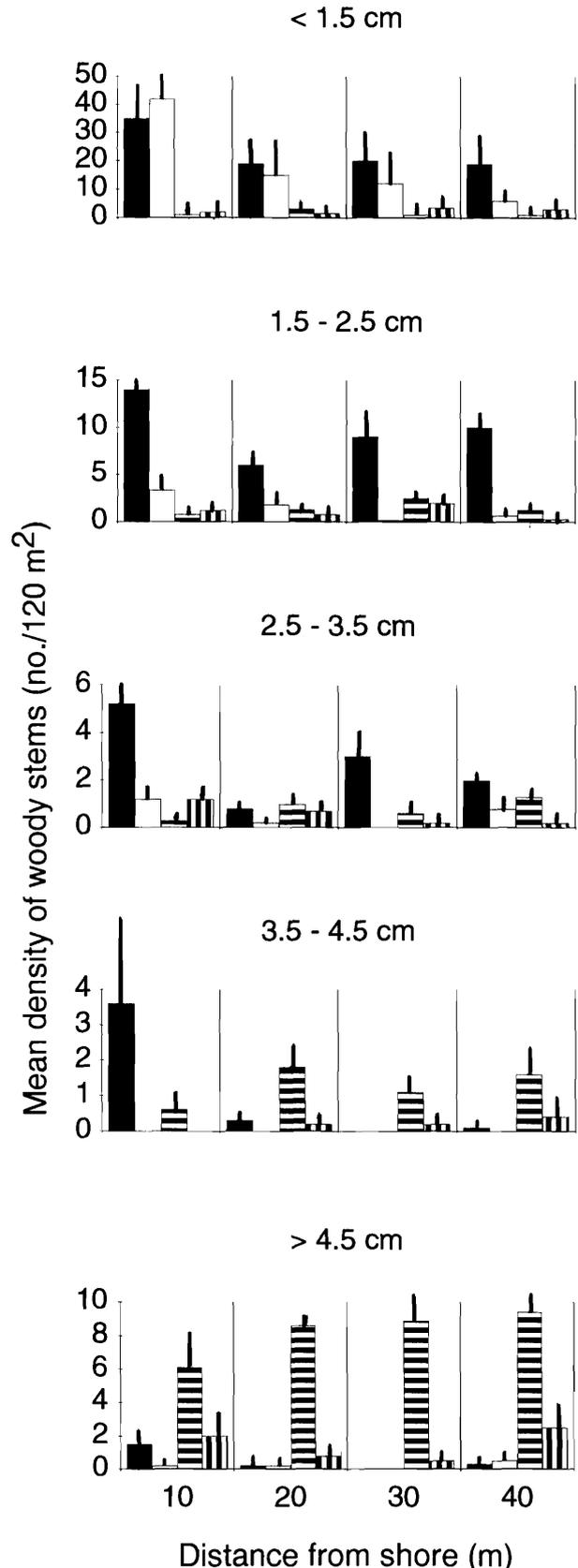


Table 2. Utilization–availability analysis of woody stems used in the construction of newly formed dams in the Chapleau Crown Game Preserve, Chapleau, Ontario.

Woody plant class	Diameter class (cm)	Total no. of stems available ^a	Actual no. of stems used ^b	Expected proportional usage ($p_{\text{exp.}}$)	Actual proportional usage (p_{actual})	Bonferroni confidence interval of p_{actual} ^c
Alder	<1.5	93 (29.1)	65 (30.5)	0.62	0.19	$0.09 \leq p_{\text{actual}} \leq 0.29^d$
	1.5–2.5	39 (8.6)	172 (93.7)	0.26	0.49	$0.36 \leq p_{\text{actual}} \leq 0.62^e$
	2.5–3.5	11 (3.8)	79 (47.9)	0.07	0.22	$0.11 \leq p_{\text{actual}} \leq 0.33^e$
	3.5–4.5	4 (2.1)	32 (10.4)	0.03	0.09	$0.02 \leq p_{\text{actual}} \leq 0.16^f$
	>4.5	2 (0.5)	2 (0.6)	0.02	0.01	$-0.02 \leq p_{\text{actual}} \leq 0.04^f$
Shrubs	<1.5	75 (17.8)	5 (0.9)	0.86	0.29	$0.22 \leq p_{\text{actual}} \leq 0.36^d$
	1.5–2.5	6 (4.5)	9 (3.2)	0.08	0.53	$0.45 \leq p_{\text{actual}} \leq 0.61^e$
	2.5–3.5	2 (0.5)	1 (0.3)	0.04	0.06	$0.02 \leq p_{\text{actual}} \leq 0.10^f$
	3.5–4.5	0 (0)	1 (0.3)	0.0	0.06	$0.02 \leq p_{\text{actual}} \leq 0.10^g$
	>4.5	1 (0.4)	1 (0.3)	0.02	0.06	$0.02 \leq p_{\text{actual}} \leq 0.10^f$
Conifers	<1.5	6 (2.7)	1 (0.3)	0.13	0.20	$0.06 \leq p_{\text{actual}} \leq 0.25^f$
	1.5–2.5	6 (2.1)	2 (0.6)	0.11	0.32	$0.21 \leq p_{\text{actual}} \leq 0.45^e$
	2.5–3.5	3 (1.2)	1 (0.3)	0.06	0.16	$0.06 \leq p_{\text{actual}} \leq 0.25^f$
	3.5–4.5	5 (1.8)	1 (0.3)	0.09	0.16	$0.06 \leq p_{\text{actual}} \leq 0.25^f$
	>4.5	33 (2.3)	1 (0.3)	0.60	0.16	$0.06 \leq p_{\text{actual}} \leq 0.25^d$
Food ^h	<1.5	10 (3.6)	7 (5.3)	0.44	0.08	$0.01 \leq p_{\text{actual}} \leq 0.15^d$
	1.5–2.5	4 (1.4)	16 (10.9)	0.20	0.17	$0.07 \leq p_{\text{actual}} \leq 0.27^f$
	2.5–3.5	2 (0.7)	16 (11.3)	0.08	0.17	$0.07 \leq p_{\text{actual}} \leq 0.27^f$
	3.5–4.5	1 (0.3)	11 (6.1)	0.04	0.11	$0.03 \leq p_{\text{actual}} \leq 0.19^f$
	>4.5	6 (4)	44 (24.3)	0.24	0.47	$0.34 \leq p_{\text{actual}} \leq 0.60^e$
Alder	All	149 (42.3)	350 (181.2)	0.49	0.75	$0.64 \leq p_{\text{actual}} \leq 0.86^e$
Shrubs	All	84 (21.8)	17 (3.0)	0.27	0.04	$-0.01 \leq p_{\text{actual}} \leq 0.10^d$
Conifers	All	53 (4.7)	6 (0.87)	0.17	0.01	$-0.01 \leq p_{\text{actual}} \leq 0.04^d$
Food	All	23 (7.7)	94 (56.7)	0.07	0.20	$0.10 \leq p_{\text{actual}} \leq 0.30^e$
Total		309	467			

^aMean density of woody stems (number/120 m²) available at three dams. Values in parentheses represent the standard errors.

^bMean number of woody stems used in three dams. Values in parentheses represent the standard error.

^cIf the $p_{\text{exp.}}$ value is within the Bonferroni confidence interval, the hypothesis of proportional use, $H_0: p_{\text{exp.}} = p_{\text{actual}}$, is accepted.

^dAvoided plant stems (i.e., $p_{\text{actual}} < p_{\text{exp.}}$).

^ePreferred plant stems (i.e., $p_{\text{actual}} > p_{\text{exp.}}$).

^fPlant stems were selected by chance (i.e., $p_{\text{exp.}}$ within the Bonferroni confidence interval).

^gThe p_{actual} value was not used, as we recorded no stems available.

^hConsidered to be trembling aspen, white birch, and willow.

show a similar collection bias. We concur with Macnamara (1931) and Johnson (1932), who showed that beavers construct dams by positioning whole, intact woody stems so that the leafy branches are oriented upstream. In our study, for the most part beavers used intact alder stems with diameters of >4.5 cm when constructing dams. J.M. Fryxell (personal communication) found that beavers were able to haul intact aspen stems up to a diameter of 4.2 cm. In his opinion, no appreciable energy was utilized by beavers hauling these large alder stems to the water. Based on this, we felt that the beavers were probably selecting smaller stems for the practical reason that energy and time were invested for in-water rather than out-of-water effort. We suspect that the larger alder stems would probably be more difficult to handle in the fast-flowing water associated with dam locations. Further, the smaller (<1.5 cm) stems probably made the dam less porous, as they could be easily woven amongst the larger stems.

Beavers showed a secondary preference for food stems of >4.5 cm diameter when constructing new dams (Table 2).

Spatial analysis of woody plants showed that the larger food stems occurred outside the foraging range of the beavers (Fig. 1). In his beaver-foraging study, Pinkowski (1983) found that larger trees used for food as well as construction were likely to be cut at a greater distance than larger trees of the species used primarily for construction. He claimed that trees used for both food and construction would yield more benefits per unit cost than the species used for construction only. Based on the results of our study, we offer an alternative explanation. We believe that it is the smaller stems which are advantageous in dam building, and that larger food stems may be selected primarily on a net energy gain basis. Since the utilization and availability data were collected in the spring following dam establishment, we contend that these food trees were harvested largely in the previous fall and stored in food caches for over-winter consumption. The impounded water of the beaver dam then served to reduce the distance to the higher densities of food plants. We speculate that the flowing spring waters would push the utilized food

stems towards the dam. We feel that beavers, being very opportunistic (Pullen 1975), would make use of these stems to maintain dam integrity. All food items had been fully debarked before use in dam construction, indicating that their primary purpose was nutrition. This may explain why beavers in our study area would haul these large food stems over such long distances.

From our analysis, we found that beavers used alder for construction purposes only. From an evolutionary standpoint, the use of specific plants solely for construction would seem to be a good strategy, as it ensures that other food items are not depleted unnecessarily (Pinkowski 1983). However, based on our research, we feel that there is a more basic, utilitarian reason for the extensive use of alder. In boreal areas, the timber wolf (*Canis lupus* L.) is very effective at preying upon beavers on land (Pimlott et al. 1969; Kolenosky 1972; Frenzel 1974; Voigt et al. 1976; Theberge et al. 1978; Bergerud et al. 1983) and has been shown to reduce beaver populations (Potvin et al. 1992). As a result, beavers must establish a dam as quickly as possible to guarantee a safe home place. We feel that whole alder plants provide beavers with a source of ideally sized building material to harvest and use in close proximity to water. In our study, virtually no other plant groups contributed nearly as many stems of a suitable diameter class. For beavers, this situation is ideal, as it minimizes the time they need to be on land, thus minimizing predation.

Based on our utilization—availability study of new dams, we postulate that beavers require shoreline concentrations of woody plants with a diameter range of 1.5–3.5 cm to effectively dam boreal streams. Further fieldwork is planned to establish cause-and-effect relationships to further validate our findings.

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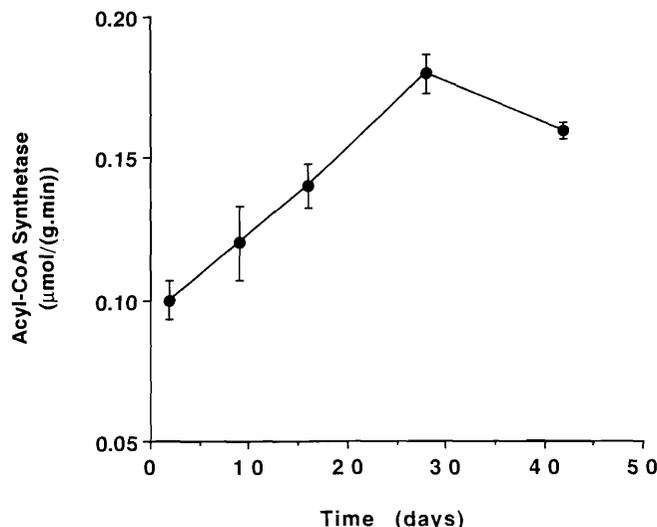
Erratum: Acclimation to low temperature is associated with an increase in long-chain acyl-CoA synthetase in rainbow trout (*Oncorhynchus mykiss*) heart

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The legend on the y axis of Fig. 3 on p. 5 was incorrect. The corrected figure is reprinted below.

Fig. 3. Acyl-CoA synthetase activity in hearts from acclimated trout as a function of time after transfer from 14 to 5°C. All values are given as means \pm SEM ($N = 5$ in all cases). The increase in enzyme activity is highly significant ($P < 0.01$) from days 2 to 28.



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