# Habitat Factors Influencing Beaver Dam Establishment in a Northern Ontario Watershed

**Article** *in* Journal of Wildlife Management · October 1997

DOI: 10.2307/3802140



Azim U. Mallik
Lakehead University Thunder Bay Campus

Agricultura y Ganaderia of Costa Rica for permission to work at the Enrique Jimenez Nunez Research Station. We also thank G. Pomerleau, E. Williams, and I. Woolgar for field assistance. This is Publication No. 101 of the Groupe de recherche en écologie, nutrition et énergétique, Université de Sherbrooke.

## References

Barclay, R.M.R., Kalcounis, M., Crampton, L.H., Stefan, C., Vonnhof, M.J., Wilkinson, L., and Brigham, R.M. 1996. Can external radio-transmitters be used to assess body temperature and use of torpor in bats? J. Mammal. In press.

Brigham, R.M. 1992. Daily torpor in a free-ranging Goatsucker, the Common Poorwill (*Phalaenoptilus nuttallii*). Physiol. Zool. **65**: 457–472.

Brown, C.R., and Bernard, R.T.F. 1991. Validation of subcutaneous temperature as a measure of deep body temperature in small bats. J. Zool. (London), **224**: 315–318.

Herreid, C.F., and Kessel, B. 1967. Thermal conductance in birds and mammals. Comp. Biochem. Physiol. **21**: 405–414.

Incropera, F.P., and De Witt, D.P. 1990. Fundamentals of heat and mass transfer. John Wiley and Sons, New York.

Kenward, R. 1987. Wildlife radio tracking. Academic Press, London.

Kurta, A., and Fujita, M.S. 1988. Design and interpretation of laboratory thermoregulatory studies. *In* Ecological and behavioral methods for the study of bats. *Edited by* T.H. Kunz. Smithsonian Institution, Washington, D.C. pp. 333–352.

McNab, B.K. 1969. The economics of temperature regulation in neotropical bats. Comp. Biochem. Physiol. **31**: 227–268.

Reinertsen, R.E. 1983. Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions: a review. Polar Res. New Ser. **1**: 269–284.

Smith, E.N. 1980. Physiological radio telemetry. *In* A handbook of biotelemetry and radio tracking. *Edited by* C.J. Amlaner and D.W. Macdonald. Pergamon Press, Oxford. pp. 45–55.

Thomas, D.W., Bosque, C., and Arends, A. 1993. Development of thermoregulation and the energetics of nestling Oilbirds (*Steatornis caripensis*). Physiol. Zool. **66**: 322–348.

Wang, L.C.H., and Wolowyk, M.V. 1988. Torpor in mammals and birds. Can. J. Zool. **66**: 133–137.



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

**D.M. Barnes and A.U. Mallik**

**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.
[Traduit par la Rédaction]

Received August 31, 1995. Accepted March 8, 1996.

**D.M. Barnes.** Faculty of Forestry, Lakehead University, Thunder Bay, ON P7B 5E1, Canada
(e-mail: dmbarnes@cs_acad_lan.lakeheadu.ca).
**A.U. Mallik.** Department of Biology, Lakehead University, Thunder Bay, ON P7B 5E1, Canada.



## 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 km$^2$. 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 $100(1 - \alpha)\%$ confident that the intervals contain their respective true proportions, $p_{\text{actual}}$:

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

where $\hat{p}_{\text{actual}}$ is the predicted value of $p_{\text{actual}}$, $\alpha$ 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, $p_{\text{actual}}$, we constructed a Bonferroni confidence interval. When the expected proportion of usage, $p_{\text{exp.}}$, 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 $m^2$) in downstream and upstream plots of the three beaver dams.

| Woody plant categories | Downstream plots | Upstream plots | $p$ ($t$ 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.
[a]Considered 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.

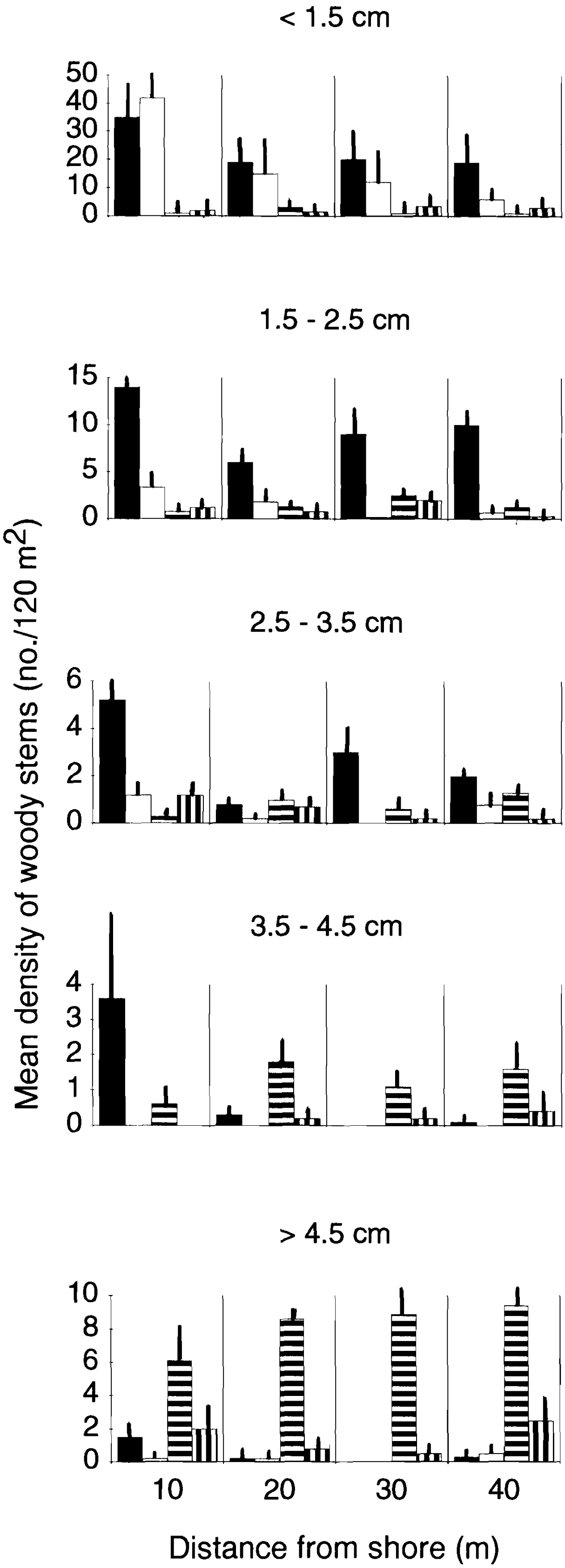


**Table 2.** Utilization–availability analysis of woody stems used in the construction of newly formed dams in the Chapleau Crown Game Preserve, Chapleau, Ontario.

| 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 ($p_{\text{actual}}$) | Bonferroni confidence interval of $p_{\text{actual}}$[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 | | | |

[a]Mean density of woody stems (number/120 m$^2$) available at three dams. Values in parentheses represent the standard errors.
[b]Mean number of woody stems used in three dams. Values in parentheses represent the standard error.
[c]If 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.
[d]Avoided plant stems (i.e., $p_{\text{actual}} < p_{\text{exp.}}$).
[e]Preferred plant stems (i.e., $p_{\text{actual}} > p_{\text{exp.}}$).
[f]Plant stems were selected by chance (i.e., $p_{\text{exp.}}$ within the Bonferroni confidence interval).
[g]The $p_{\text{actual}}$ value was not used, as we recorded no stems available.
[h]Considered 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.



## Acknowledgements

Financial assistance for this research was obtained from Ducks Unlimited, the Ministry of Universities and Colleges, and the Environmental Youth Corps. We thank Charlie Todesco of the Ontario Ministry of Natural Resources for providing logistic support at the study sites, V. Piercey, M. Sinclair, and M. Osika for technical assistance, and B. Barnes, H. Cumming, A. Rodgers, and R. Rempel for reading the draft manuscript. H.G. Murchison helped with statistical analyses.

## References

Alldredge, J.R., and Ratti, J.T. 1986. Comparison of some statistical techniques for the analysis of resource selection. J. Wildl. Manage. **50**: 157−165.

Alldredge, J.R., and Ratti, J.T. 1992. Further comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. **56**: 1−9.

Andersson, M. 1978. Optimal foraging area: size and allocation of search effort. Theor. Popul. Biol. **13**: 538−544.

Belvosky, G.E. 1984. Summer diet optimization by beaver. Am. Midl. Nat. **111**: 209−222.

Bergerud, A.T., Wyett, W., and Snider, B. 1983. The role of wolf predation in limiting a moose population. J. Wildl. Manage. **47**: 977−988.

Byers, C.R., Steinhorst, R.K., and Krausman, P.R. 1984. Clarification of a technique for analysis of utilization−availability data. J. Wildl. Manage. **48**: 1050−1053.

Frenzel, L.D. 1974. Occurrence of moose in food of wolves as revealed by scat analyses: a review of North American studies. Nat. Can. **101**: 467−479.

Fryxell, J.M. 1992. Space use by beavers in relation to resource abundance. Oikos, **64**: 474−478.

Fryxell, J.M., and Doucet, C.M. 1991. Provisioning time and central-place foraging in beavers. Can. J. Zool. **69**: 1308−1313.

Hodgdon, K.W., and Hunt, J.H. 1953. Beaver management in Maine. Maine Game Div. Bull. No. 3.

Jenkins, S.H. 1980. A size−distance relationship in food selection by beaver. Ecology, **61**: 740−746.

Johnson, C.E. 1932. Boughs, butts, and beaver dams. Science (Washington, D.C.), **75**: 132.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, **61**: 65−71.

Johnston, C.A., and Naiman, R.J. 1990. Browse selection by beaver: effect on riparian forest composition. Can. J. For. Res. **20**: 1036−1043.

Kolenosky, G.B. 1972. Wolf predation on wintering deer in east-central Ontario. J. Wildl. Manage. **36**: 357−368.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators. *In* Behavioural ecology. *Edited by* J.R. Krebs and N.B. Davis. Sinauer Associates, Sunderland, Mass. pp. 23−63.

MacDonald, D. 1956. Beaver carrying capacity of certain mountain streams in North Park, Colorado. M.S. thesis, Colorado State University, Fort Collins.

Macnamara, C. 1931. Position of wood in beaver dams. Science (Washington, D.C.), **74**: 630.

McGinley, M.A. 1984. Central place foraging for nonfood items: determination of the stick size−value relationship of house building materials collected by eastern woodrats. Am. Nat. **123**: 841−853.

McGinley, M.A., and Whitham, T.G. 1985. Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia, **66**: 558−562.

Nash, J.B. 1951. An investigation of some problems of ecology of the beaver in northern Manitoba. M.S. thesis, University of Manitoba, Winnipeg.

Neu, C.W., Byers, C.R., and Peek, J.A. 1974. A technique for analysis of utilization−availability data. J. Wildl. Manage. **38**: 541−545.

Nixon, C.M., and Ely, J. 1969. Foods eaten by a beaver colony in southeast Ohio. Ohio J. Sci. **69**: 313−319.

Novak, M. 1976. The beaver in Ontario. Ontario Ministry of Natural Resources, Toronto.

Novak, M. 1987. Beaver. *In* Wild furbearer management and conservation in North America. *Edited by* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch. The Ontario Trappers' Association, North Bay. pp. 283−312.

Orians, G.H., and Pearson, N.E. 1979. On the theory of central place foraging. *In* Analysis of ecological systems. *Edited by* D.J. Horn, R.D. Mitchell, and G.R. Stains. Ohio State University Press, Columbus. pp. 155−177.

Pimlott, D.H., Shannon, J.A., and Kolensky, G.B. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ont. Dep. Lands For. Res. Rep. Wildl. No. 87.

Pinkowski, B. 1983. Foraging behaviour of beavers (*Castor canadensis*) in North Dakota. J. Mammal. **64**: 312−314.

Potvin, F., Breton, L., and MacQuart, M. 1992. Impact of an experimental wolf reduction on beaver in Papineau−LaBelle Reserve, Quebec. Can. J. Zool. **70**: 180−183.

Pullen, T.M., Jr. 1975. Observations on construction activities of beaver in east-central Alabama. J. Ala. Acad. Sci. **46**: 14−19.

Pyke, G.H., Pullaim, H.R., and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. **52**: 137−154.

Retzer, J.L., Swope, H.W., Remington, J.D., and Rutherford, W.H. 1956. Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. Col. Dep. Game Fish Tech. Bull. No. 2.
Schoener, T.W. 1979. Generality of the size–distance relation in models of optimal foraging. Am. Nat. **114**: 902–914.
Schooley, R. 1994. Annual variation in habitat selection: patterns concealed by pooled data. J. Wildl. Manage. **58**: 367–374.
Shaw, S.P. 1948. The beaver in Massachusetts: a research and management study. Mass. Dep. Conserv. Res. Bull. No. 11.
Slough, B.G. 1978. Beaver food cache structure and utilization. J. Wildl. Manage. **42**: 644–646.
Slough, B.G., and Sadleir, R.M.S.F. 1977. A land capacity classification system for beaver (*Castor canadensis* Kuhl). Can. J. Zool. **55**: 1324–1335.
Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union, **38**: 913–920.
Theberge, J.B., Oosenburg, S.M., and Pimlott, D.H. 1978. Site and seasonal variations in food of wolves, Algonquin Park, Ontario. Can. Field-Nat. **92**: 91–94.
Thomas, D.L., and Taylor, E.J. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manage. **54**: 322–330.
Voigt, D.R., Kolenosky, G.B., and Pimlott, D.H. 1976. Changes in summer foods of wolves in central Ontario. J. Wildl. Manage. **40**: 663–668.



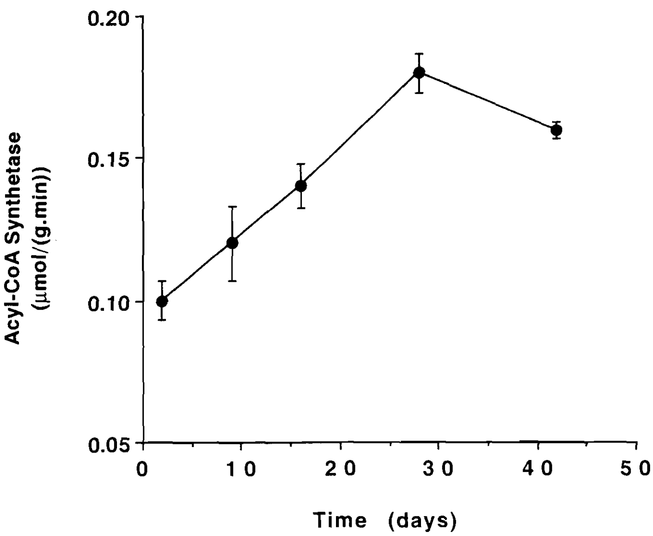
# Erratum: Acclimation to low temperature is associated with an increase in long-chain acyl-CoA synthetase in rainbow trout (*Oncorhynchus mykiss*) heart

**Jason M.T. Hicks, John R. Bailey, and William R. Driedzic**

**Ref.**: Can. J. Zool. **74**: 1–7 (1996).

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 ± SEM ($N$ = 5 in all cases). The increase in enzyme activity is highly significant ($P < 0.01$) from days 2 to 28.




Received at NRC June 25, 1996.

**J.M.T. Hicks,[1] J.R. Bailey, and W.R. Driedzic.[2]** Biology Department, Mount Allison University, Sackville, NB E0A 3C0, Canada.

[1] Present address: Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
[2] Author to whom all correspondence should be addressed.