Food caching behaviour of the American beaver in Massachusetts

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Abstract: At northern latitudes in North America beavers (*Castor canadensis*) store branches of woody plants in caches during the autumn. The food cache provides food for the beaver family during the winter when plant productivity is low and snow and ice restrict beaver movements. I examined the initiation and development of food caches and physical aspects of food cache locations at eight sites during autumn 2001 and autumn 2002 in western Massachusetts. Construction of caches began on September 28 (week 39) in 2001 and September 18 (week 38) in 2002. Median start date for caches was during week 41 (October 9-10) both years. Mean cache volume was 60.4 m^3 in 2001 and 72.1 m^3 in 2002. Change per week in cache volume was 8.9 m^3 in 2001 and 9.2 m^3 in 2002. Water depths where caches were constructed ranged from 1.00-2.05 m (mean = 1.31 m) during 2001 and 0.75-1.85 m (mean = 1.26 m) during 2002. These observations of caching behaviour in the American beaver offer a means of comparison with the caching behaviour of the European beaver (*Castor fiber*).

Keywords: American beaver, *Castor canadensis*, food caching, initiation date, temporal change, environmental cues.

Introduction

Both species of beaver, the American beaver (*Castor canadensis*) and the European beaver (*Castor fiber*), are choosy generalist herbivores and at northern latitudes and high elevations (regardless of latitude) they are long term food cachers who engage in communal food caching (Jenkins 1975, Vander Wall 1990). Food caches are initiated in the autumn and branches of woody species are placed in the water usually near the winter lodge (Novakowski 1967, Aleksiuk 1970, Slough 1978, Busher 1991). Evidence exists that the two species are different in the construction of caches and that the cause may be related to environmental factors (Hartman & Axelsson, in press). North American beavers living in areas that are not subject to long periods of cold when the ponds freeze may not built food caches (Hill 1982, Echternach & Rose 1987). However, in areas where freezing of the ponds is common 100 percent of beaver families do construct a cache (Yeager & Rutherford 1957, Busher 1991, Busher 1996).

While species composition and location in a cache have been examined (Slough 1978, Busher 1991) no present study has fully documented the temporal development of the food cache. In this paper I report the development of food caches during the autumn comparing both intrafamily and interfamily behaviours. I designed the study to test the hypothesis that food caching behaviour will intensify as the autumn progresses. Specifically, once food caching is initiated (late September to early October) the beaver families should store food at a lower rate early in the autumn and increase their hoarding activity in late autumn (November). This hypothesis is reasonable since the food cache represents the primary food source during the energetically stressful period of cold and restricted movement in winter. Food caching behaviour may be tied to environmental cues such as air temperature, which in turn would influence water temperature. Increasing hoarding behaviour in response to increasing cold may represent an evolutionary strategy ensuring an adequate, high quality food supply for the winter. An inadequate food supply could cause reduced reproduction and increased mortality, which would reduce fitness.

Methods

Study Area

Research was conducted on the Prescott Peninsula, Quabbin Reservation, located in west-central Massachusetts (42° 25’ N, 72° 20’ W) (figure 1). The Quabbin Reservation, which contains the watershed and major reservoir for the drinking water supply for the metropolitan Boston area, was created in 1939 by damming the Swift River and Beaver Brook. The reservation’s area is 335 km^2 and the reservoir is 100 km^2. The climate consists of warm, usually moist summers and cold winters with major periods of snow. The construction of the reservoir and creation of the watershed area caused the relocation of 2500 people and the complete destruction of three towns (Hodgdon 1978, Lyons 1996). The reservoir was filled to maximum capacity by 1946. The Prescott Peninsula has an area of 50 km^2, is 16 km long and narrows from north to south (4.8 km to 0.6 km). The peninsula is heavily forested (approximately 92%) with dominant deciduous trees being red maple (*Acer rubrum*), oak (*Quercus* spp.), ash (*Fraxinus* spp.), and birch (*Betula* spp.). Eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and hemlock (*Tsuga canadensis*) are the most common conifers on the peninsula (Hodgdon 1978).

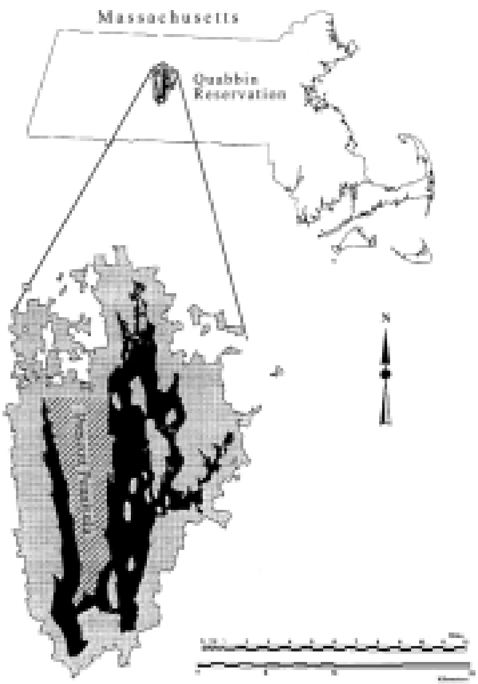

Figure 1. Location of the Quabbin Reservation, Massachusetts, USA. The research site is approximately 130 km (80 miles) west of Boston, Massachusetts.

The Quabbin Reservation is managed as a watershed by the Metropolitan District Commission (MDC); an agency of the Commonwealth of Massachusetts. In addition to serving as the water supply for approximately 3 million people in eastern Massachusetts, the reservation provides forest products, recreational opportunities, wildlife observation and research, and cultural resource protection. One of the unique features of the watershed and reservoir is that human use has been strictly controlled since its inception. Until recently, there has been a complete prohibition of trapping and hunting of all wildlife species on the reservation and, especially on the Prescott Peninsula, wildlife populations have been allowed to exist with little human interference. Beavers on the Prescott Peninsula are found on small streams, larger streams, ponds and along the shore of the reservoir.

Food cache analysis

In the autumn of 2001 a random sample of known active beaver family areas was selected for study. Eight beaver family areas were surveyed each year and six of the eight areas were occupied both years. Two areas active in 2001 were not active in 2002 and two additional sites were selected that year. The number of family areas surveyed each year represented 38% (8/21) of the known active interior (non-shoreline) areas in 2001 and 40% (8/20) of the known active areas in 2002. One family did not initiate cache building until very late in the season (week 47) in 2001 and is not included in the analysis. The number of known active areas was determined by an annual census, which used presence of a food cache as one of the primary criteria in determining beaver occupation. Beavers in every active family area on the Prescott Peninsula build a food cache each year.

Beginning in early September (week 36) and continuing through November (week 48) of 2001 and 2002 each family area was surveyed. Once the initiation of a food cache was observed the length, width and height (both above and below the water line) were measured weekly. The depth of the water where the cache was located was measured at the center of the cache (approximately 2 m from the shore). As the cache grew in size a number of depth measurements were taken at each cache and the mean depth was used to calculate the volume. Woody species composition in the cache was also documented. Woody species composition in the cache is not reported in this paper because the species composition did not influence the study design or general hypothesis being tested and simply reflected the abundance of woody species found in each family area. I report mean minimum daily and weekly air temperatures that were collected at the Harvard Forest, Petersham, MA, USA (Lat. 42.533 N, Lon. 72.190 W, Elev. 340 m). This site is approximately 12 km from the research area with a similar habitat and elevation.

Results

Cache initiation date

The first food cache was observed in week 39 (September 28) in 2001 and week 38 (September 18) in 2002. Five of the eight families initiated their cache by week 41 (October 10) and all caches were initiated by week 44 (the end of October) during both years. A different family initiated the earliest cache each year and each of the six families surveyed both years initiated their cache during a different week (figure 2).

Cache development

In 2001 the mean change in cache volume per week was 10.5 m^3 (range = 5.3-14.6 m^3) for 7 families. In 2002 the mean change in cache volume per week was 11.2 m^3 (range = 4.6-21.3 m^3) for 8 families. Beginning in late October or early November (week 43-44) a general pattern of increased cache building behaviour was observed although this was more pronounced in 2001 than 2002 (figure 3 and figure 4). The change in food cache volume stored by each family was then compared for two temporal periods, October and November, of each year. In 2001 a greater average change in cache volume during November was observed in all seven families, but the difference was only significant in two families, FF and R21 (*Chi-square* with Yates correction = 4.61, df=1, P<0.05 at area FF; *Chi-square* with Yates correction = 6.45, df=1, P<0.025 at area R21). A different pattern was observed in 2002 when only five of the eight families had greater cache volume changes in November than in October. However, only one of these families had a significantly greater mean change in cache volume (*Chi-square* with Yates correction = 7.49, df=1, P<0.01). Three of the families had a greater mean change in volume during October than November and two of these were significantly different. Beavers at area R21 had a significantly larger mean change in volume in October than November (*Chi-square* with Yates correction = 8.58, df=1, P<0.01). This was also true for beavers at area K where the mean volume change was greater in October than November (*Chi-square* with Yates correction = 7.13, df=1, P<0.01). Cache construction began during week 44 in both of these families and the initial volume of each cache was larger than caches began in September or early October. One additional family had a larger mean volume change in October than November but the difference was not significant.

The initial cache volume was dependent on the week of initiation. In general caches initiated early in the autumn were smaller than caches initiated later in autumn. This pattern was

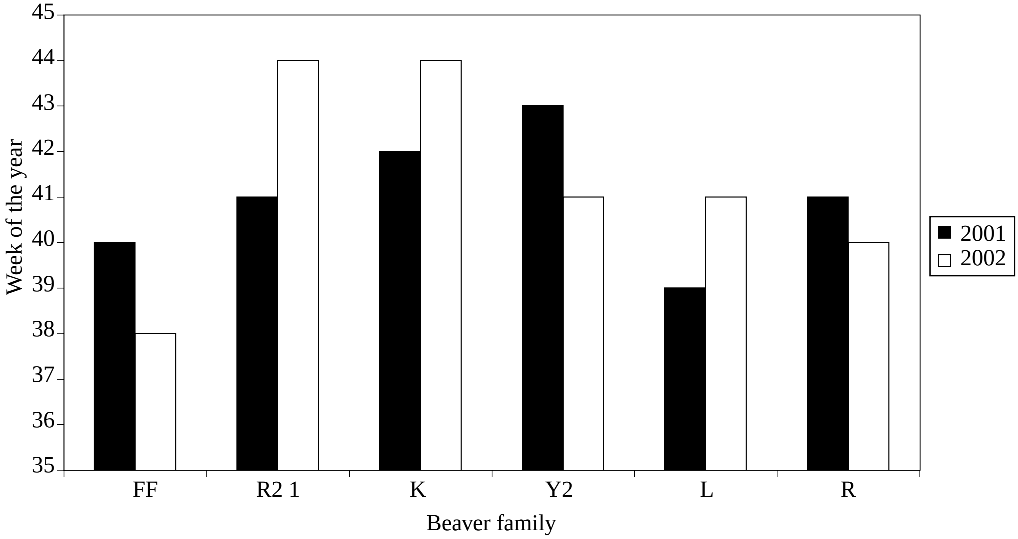

Figure 2. Yearly food cache initiation dates for the six beaver families observed both years. Weeks 38-39 are in September, weeks 40-43 in October and weeks 44-45 in November.

especially pronounced in 2002 when three of the eight families initiated caches during week 44 while the other five families had all initiated caches by week 41. The mean volume of caches initiated early in autumn 2002 was 4.9 m^3 (range 2.3-10.5 m^3) while the mean volume of caches initiated during week 44 was 25.3 m^3 (range 17.3-38.6 m^3) and this difference was significant (*Chi-square* with Yates correction = 12.5, df=1, P<0.01). This pattern is not as pronounced in 2001 since no caches were initiated late in October.

The total volume of all food caches was not significantly different in 2001 and 2002. The total volume in 2001 was 510.4 m^3 and in 2002 it was 576.5 m^3. A similar pattern in total volume change per week was observed each year. October volumes were larger during 2001 while November volumes were larger in 2002. The total change in volume of all caches in October was 202.3 m^3 in 2001 and 254.3 m^3 in 2002. The change in November was 289.9 m^3 in 2001 and 316.8 m^3 in 2002. These data are significantly different from each other in both years (*Chi-square* with Yates correction = 15.23, df=1, P<0.01 in 2001; *Chi-square* = 6.64, df=1, P=0.01 in 2002). The mean final volume of caches in 2001 was 72.9 m^3 (range = 41.6-105.4) and 72.1 m^3 (range = 34.0-153.8 m^3) in 2002.

Water depth at cache

The water depth at the center of each cache was measured multiple times during the autumn. No weekly variation in depth was observed. The mean depth of all caches in 2001 was 1.30 m (range = 1.00-2.05 m) and the mean depth in 2002 was 1.26 m (range = 0.75-1.85). There was no relationship between the water depth and final cache volume.

Air temperature and food caching behaviour

In both years there was a significant inverse correlation between the mean weekly minimum air temperature and the mean weekly change in volume of the food cache per family (r^2=0.47, F=6.2, df=1 and 7, P<0.05 in 2001; r^2=0.53, F=8.0, df=1 and 7, P<0.05 in 2002). The mean weekly minimum temperature was slightly lower in 2001 than in 2002 from weeks 38 to 41 (8.3 °C in 2001 vs. 10.4 °C in 2002) but higher from

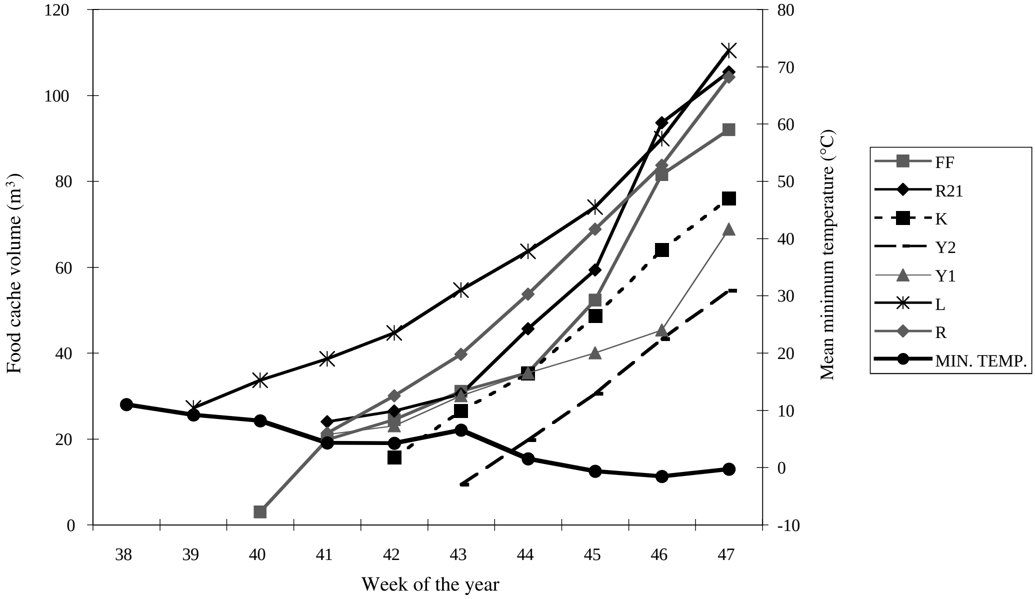

Figure 3. Weekly change in food cache volume for seven beaver families in 2001 and the mean weekly minimum temperature (°C). Weeks 38-39 are in September, weeks 40-43 in October and weeks 44-47 in November. The legend codes refer to the individual beaver families on the annual census routes (for example, FF is one family, R21 is a second family, etc.) and Min. Temp. is the mean weekly minimum temperature (°C).

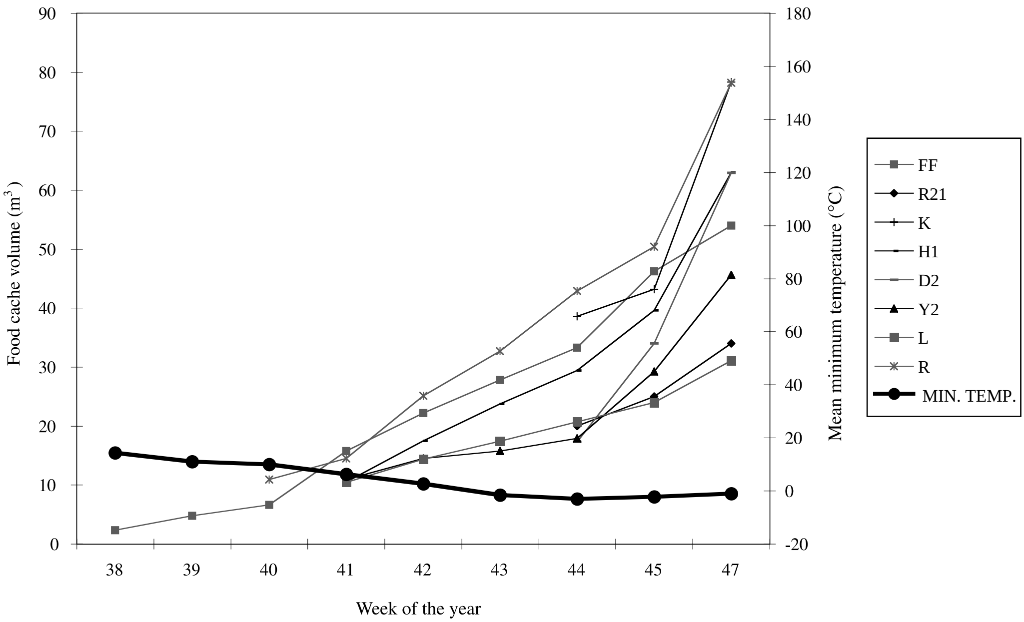

Figure 4. Weekly change in food cache volume for eight beaver families in 2002 and the mean weekly minimum temperature (°C). Weeks 38-39 are in September, weeks 40-43 in October and weeks 44-47 in November. The legend codes refer to the individual beaver families on the annual census routes (for example, FF is one family, R21 is a second family, etc.) and Min. Temp. is the mean weekly minimum temperature (°C).

weeks 42 to 45 (2.9 °C in 2001 vs. -0.9 °C in 2002). In week 46 it was cooler during 2001 (-1.6 °C) than in 2002 (4.1 °C), but then warmer the following week (-0.3 °C in 2001 vs. -1.1 °C in 2002). Although it was slightly warmer during early autumn in 2002, the first food cache was initiated a week earlier than in 2001 (figure 5). However, two caches were initiated during each year from weeks 38-40. The weekly mean minimum temperature during week 41, the week the median number of food caches were initiated (5 of 8 caches were initiated by week 41 each year), was 4.3 °C in 2001 and 6.2 °C in 2002. The first hard frost (minimum air temperature below freezing) occurred during week 41 (3 days with a minimum temperature below freezing) in 2001, but not until week 42 in 2002. In 2001 the weekly mean minimum temperature remained above freezing through week 44 (time when all food caches were initiated) while in 2002 the weekly mean temperature dropped to -1.6 °C during week 43 and -3.0 °C in week 44. Three families initiated their food caches during week 44 in 2002 (figure 5).

There is an inverse relationship between increasing food cache volume and mean minimum air temperature (figures 3 and 4) during both years. Only October of 2002 had a significant correlation between the mean weekly minimum temperature and the mean weekly change in food cache volume per family (r^2=0.68, F=8.62, df=1 and 4, P<0.05). There was no significant correlation for October 2001, November 2001 and November 2002.

Discussion

The cache initiation patterns observed were consistent with data collected on the Prescott Peninsula during 1972-1973. The earliest initiation date in 1972-1973 was week 38, the median date was week 41 and the latest initiation date was week 43 (Hodgdon 1978). These initiation dates are similar with my observations of week 37, week 41 and week 44 for the earliest, median and latest initiation dates. Hodgdon (1978) suggested that peak cache initiation activity was stimulated by the first hard frost. This is also true for 2001 in my study where the median initiation date (week 41) occurred after the first frost. However, in 2002 the first hard frost occurred during week 42 yet 5 of 8 caches were initiated by week 41. In Sweden, caches were first initiated in week 38, week 43 was the median date and week 48 the last date of initiation (Hartman & Axelsson, in press). The climate in the study area in Sweden is similar to that in central Massachusetts with both areas recording mean minimum temperatures below freezing in mid-October (G. Hartman, personal communication) and there is reasonable agreement between initiation dates. However, the variation in initiation dates within the same family group between years and the overall variation in initiation dates within a population suggest a plasticity of cache initiation behaviour. Additionally, I have only examined the mean minimum air temperatures and these are from a weather station approximately 12 km from the research site. In future years I plan to collect air and water temperatures at the family areas being studied and hope to be able to examine the relationship between food caching behaviour and temperature with more precision. Further investigation of the actual environmental cues that may trigger cache construction in both beaver species is necessary.

The only other study to report cache development patterns similar to this study is from a relatively high elevation (2300-2500 m) population in Wyoming (Osmundson & Buskirk 1993). They reported that cache growth rates and final cache sizes did not deviate between years, comparable to my observations in Massachusetts. Cache growth rates in Wyoming were 0.45 m^3 per day or 3.15 m^3 per week (0.45 m^3 x 7 days). No temporal change in cache growth rates was reported. In Massachusetts, the mean weekly growth rates were larger each year (10.5 m^3 and 11.2 m^3) and even the lowest mean changes for a specific family were larger (5.3 m^3 in 2001; 4.6 m^3 in 2002). Cache construction effectively stopped earlier in

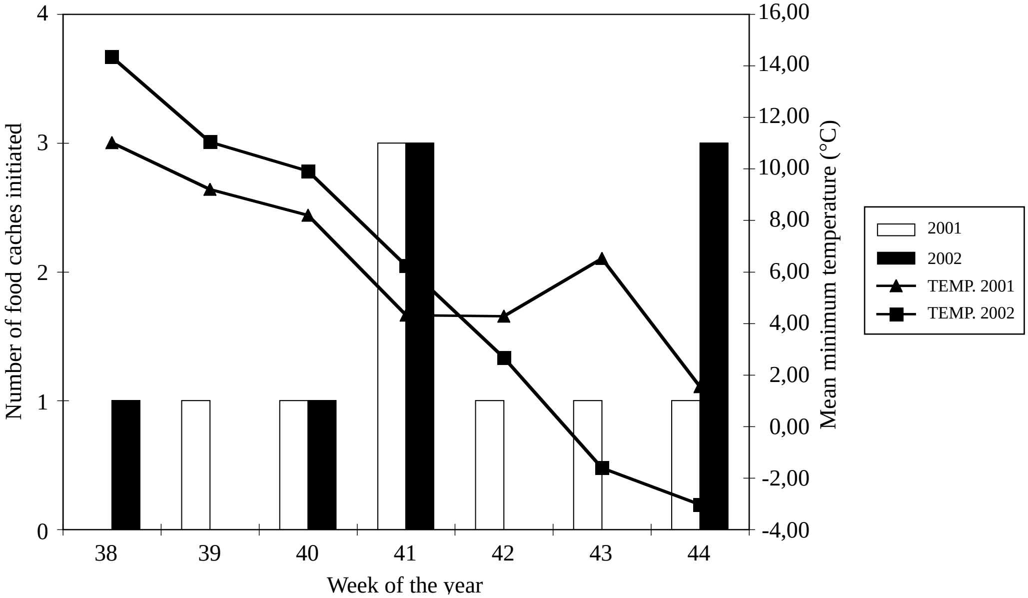

Figure 5. The number of food caches initiated each week and the mean weekly minimum temperature (°C) for 2001 and 2002. Weeks 38-39 are in September, weeks 40-43 in October and week 44 in November. Min. Temp. in the legend is the mean weekly minimum temperature (°C).

Wyoming when freeze up was reported between November 1-11. This is at least 2-3 weeks if not 4-5 weeks earlier than normal freeze up in Massachusetts.

No correlation between family size and cache size was found in Wyoming (Osmundson & Buskirk 1993) although a correlation between cache size and family size had been reported in Montana (Easter-Pilcher 1990). Family size in Massachusetts was estimated to range from 2-6 and no clear pattern was evident between final cache size and family size. However, additional data are required to adequately resolve the relationship between family size and finite cache size. Additionally, age of family members and actual time beaver are dependent on the cache for food may play a role in the cache construction behaviour.

Further investigations into food cache construction behaviour, including field experiments on species selection and nutrient evaluation of the stored food will provide better understanding of this critical aspect of beaver life history. Additionally, since beavers exhibit individual and family variability in many behaviours the observed variability in cache construction behaviour, both within and between populations, may reflect the overall behavioural plasticity that has evolved in both beaver species.

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Samenvatting

Aanleg van voedselvoorraden door de Amerikaanse bever (*Castor canadensis*) in Massachusetts

In de noordelijke delen van Noord-Amerika leggen bevers (*Castor canadensis*) in de herfst voorraden aan. Deze bestaan uit takken van houtachtige gewassen, en dienen als voedselvoorziening voor groepen bevers tijdens de winter. In die tijd is er moeilijk aan voedsel te komen vanwege de afwezigheid van plantengroei en omdat de actieradius van bevers wordt beperkt door sneeuw en ijs. In het westen van Massachusetts werd in de herfst van 2001 en 2002 onderzoek gedaan naar de fysieke omstandigheden van acht verschillende locaties waar voorraden werden aangelegd. De bouw van opslagplaatsen voor voedselvoorraden begon op 28 september in 2001 en op 18 september in 2002, de aanleg van voorraden zelf op 9-10 oktober in beide jaren. Het gemiddelde volume van de voorraden bedroeg 60,4 m^3 in 2001 en 72,1 m^3 in 2002. De verschillen in volume per week bedroegen 8,9 m^3 in 2001 en 9,2 m^3 in 2002. De diepte van het water waar voorraden werden aangelegd lag tussen 1,00 en de 2,05 m (gemiddeld 1,31 m) in 2001 en 0,75-1,85 m (gemiddeld 1,26 m) in 2002. De in dit artikel beschreven observaties kunnen worden gebruikt voor een vergelijking met het gedrag van de Europese bever (*Castor fiber*).

Received: 30 October 2003
Accepted: 6 February 2004