Food caching behavior of the Eurasian beaver in northern Europe

Authors: Busher, Peter E., Mayer, Martin, Ulevičius, Alius, Samus, Arunas, Hartman, Göran, et al.

Source: Wildlife Biology, 2020(3)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00734

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

Wildlife Biology 2020: wlb.00734
doi: 10.2981/wlb.00734
© 2020 The Authors. This is an Open Access article
Subject Editor: Luc Wauters. Editor-in-Chief: Ilse Storch. Accepted 9 August 2020

Food caching behavior of the Eurasian beaver in northern Europe

Peter E. Busher, Martin Mayer, Alius Ulevičius, Arunas Samus, Göran Hartman and Frank Rosell

P. E. Busher (https://orcid.org/0000-0001-7612-1931) ✉ (pbusher@bu.edu), College of General Studies and Center for Ecology and Conservation Biology, Boston Univ., Boston, MA, USA. – M. Mayer (https://orcid.org/0000-0002-9905-3625), Dept of Bioscience, Aarhus Univ., Denmark. – A. Ulevičius and A. Samus, Inst. of Biosciences, Center of Ecology and Environment, Vilnius Univ., Vilnius, Lithuania. – G. Hartman, Dept of Wildlife, Fish and Environmental Studies, Swedish Univ. of Agricultural Sciences, Ultuna, Sweden. – F. Rosell (https://orcid.org/0000-0003-1047-0156), Dept of Natural Sciences and Environmental Health, Faculty of Technology, Natural Sciences and Maritime Sciences, Univ. of Southeast Norway, Bo i Telemark, Norway.

Food storage (caching, hoarding), which is observed in many species of animals, increases food availability during times of food insecurity. Both species of beaver (Eurasian beaver, *Castor fiber*, and the North American beaver, *C. canadensis*) living at northern latitudes where food may be scarce during winter are larder-hoarders, constructing a food cache of branches of woody species during autumn. We studied the food caching behavior of the Eurasian beaver in three northern European countries (Sweden, Norway, Lithuania) to provide additional insight into this important behavior. Thirty-seven of forty-seven (79%) active family groups had food caches by mid-November and 41 of 47 (87%) had caches by December. Water depth of caches ranged from 1 to 2.3 m and depths at caches in Sweden were significantly deeper than in either Norway or Lithuania. Construction of caches began as early as late September (week 39/40) in Sweden and Lithuania and by mid-October (week 42) in Norway. We observed plasticity in timing of cache initiation but the majority of active sites in all areas had food caches by the beginning of November (week 45). Declining air temperature and mean minimum temperatures of 0°C or below were associated with cache initiation. Caches in Lithuania were larger than in Sweden and Norway, which may be associated with colder winter temperatures. We did not find any relationship between family size or length of territory occupancy and cache size at our Norway sites where population demographics were available. Our results are generally consistent with other studies of food caching behavior in both species and suggest general similarities as well as behavioral plasticity in this important evolutionary strategy.

Keywords: *Castor fiber*, environmental stimuli, Eurasian beaver, food cache

Storing food is an evolutionary strategy that allows many species of animals to overcome times of food scarcity (Andersson and Krebs 1978, Smith and Reichman 1984). Food is stored either short-term (days/weeks) or long-term (weeks/months) and species may store small amounts in many locations (scatter hoarding) or larger amounts in one or two locations (larder hoarding) (Vander Wall 1990). While food stores can allow individuals to minimize predation risks while foraging or invest in other behaviors, food storage is often related to variable environmental conditions that either reduce the amount of available food, limit access to food or both (Clarkson et al. 1986, Vander Wall 1990, Steele et al. 2006, Delgado et al. 2014, Jakopak et al. 2017, Pitera et al. 2018).

The ability to collect and store food at one time and use it at another time is an important evolutionary adaptation and allows species to successfully cope with changing food supply and energy demands. Animals living in temperate climates experience periods of low plant productivity and freezing temperatures during winter and may store food to help meet nutritional demands. For example, the honeybee *Apis mellifera* in the northern part of its range stores up to 40% of the hive honey production for use in winter (Seeley 1985), and red squirrels *Tamiasciurus hudsonicus* make caches of conifer cones that are necessary for successful winter survival (Rusch and Reeder 1978).

The two extant species of beavers, the Eurasian beaver, *Castor fiber*, and the North American beaver, *C. canadensis*, are found across a large latitudinal range in the Holarctic biogeographical region occurring in most types of wetland habitats including large and small lakes, ponds, large and small rivers, streams, and in human modified systems such as agricultural drainage and irrigation ditches and fish ponds (Busher and Hartman 2001, Rosell et al. 2005, Sjöberg and

---

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <http://creativecommons.org/licenses/by/4.0/>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

Ball 2011, Busher 2016). Beavers in alpine habitats and at higher latitudes face periods of food scarcity during winter when plant productivity is low and mobility can be restricted by snow and ice. Under these conditions beavers store branches of woody species in a food cache usually placed in water outside the lodge or burrow where the beaver family will overwinter (Jenkins and Busher 1979, Busher 1991, 1996, 2003, Hartman and Axelsson 2004). The food cache along with fat storage (Aleksiuk 1970, Smith and Jenkins 1997) reduced activity (Aleksiuk and Cowan 1969, Potvin and Bovet 1975, Lancia et al. 1982), construction behaviors and social behaviors (Semyonoff 1953, Stephenson 1969, Buech et al. 1989) allows the beaver family to meet metabolic demands and overcome reduced food availability during the winter.

Beaver food caching is facultative (Wilsson 1971, Lavsund 1989, Osmundson and Buskirk 1993, Hartman and Axelsson 2004) depending on altitude, latitude and climatic regime. For example, in North America, beavers in the southeastern United States (below approximately 35 degrees N latitude) do not generally build food caches (Swafford 2002, Baker and Hill 2003), while farther north (above approximately 38 degrees N latitude) and at higher elevations they usually build caches (Hodgdon 1978, Busher 1980, 2016). The pattern in Europe, including European Russia, may be less consistent with beavers reported to show more variation in cache construction behavior (Wilsson 1971, Djoshkin and Safonov 1972, Hartman and Axelsson 2004). As an illustration of the facultative nature of cache construction beavers on the Rhone river typically do not cache food, but when a pair from the Rhone was translocated to Switzerland, they did build a food cache (Blanchet 1959). The construction of the winter food cache is related to other construction behaviors such as dam and lodge building and has an innate component (Richard 1967, 1983).

In North America aspects of woody species selection (Busher 1991, 1996), general caching behavior (Hodgdon 1978, Slough 1978, Busher 2003) and the relationship between family group size and food cache size (Kafcus 1987, Easter-Pilcher 1990, Osmundson and Buskirk 1993) have been investigated. Additionally, there is evidence that the North American species increases caching behavior as environmental temperature declines during autumn and become less selective in species stored in the cache as autumn progresses (Hodgdon 1978, Busher 1996, 2003).

In Eurasia, Dzięciołowski and Misiukiewicz (2002) documented the woody species found in food caches in Poland, Hartman and Axelsson (2004) examined the prevalence of caches and physical parameters of the location of the caches in Sweden, and Vasin (2001) in Siberia, documented the volume stored per family member. Wilsson (1971) studied food caching by captive beavers in enclosures and beavers living free along a river in northern Sweden. He considered food storage to be associated with increased tree felling and suggested that both are potentially stimulated by a decline in temperature.

However, for the Eurasian species, less is known about the temporal and spatial development of the food cache, response to potential environmental stimuli, and any relationship between food cache size and family size.

We investigated the physical characteristics, spatial and temporal development of food caches at sites in northern Europe to better understand this evolutionarily important behavior. Our primary goal was to compare food caching behavior between populations in three European countries living in a variety of wetland habitats, something that had not been done before. We examined water depth at food caches, initial cache size and date, temporal growth of caches and the potential relationship between cache initiation and cache size and ambient temperature.

Moreover, knowledge of group size, age of the adult pair, duration of territory occupancy and relative water flow along three rivers in Norway allowed us to examine the relationship between food cache size and these variables. At the Norway sites, because accurate family sizes were known, we were able to test the hypothesis that families with more individuals build larger food caches since a larger food cache should be able to support more individuals during the energetically stressful winter period of confinement. Additionally, if a positive relationship between food cache size and family size exists then food cache size could be used to estimate population size. Tests of this hypothesis have been equivocal in North America with Kafcus (1987) and Easter-Pilcher (1990) reporting significant relationships between food cache size and family size while Osmundson and Buskirk (1993) reported no significant relationship. Our study is the first to test this hypothesis in the Eurasian beaver.

Methods

Data were collected at study areas in Sweden, Norway and Lithuania during autumn 2015 (Fig. 1) and again in Norway during autumn 2016. The Swedish sites were located near Uppsala and at the Grimsö Wildlife Area (latitude of both = 59 degrees) along small streams, a mid-sized river and a small lake. The Swedish sites were first visited 17–23 October (late week 42/week 43) and weekly visits were made through 17 November (week 47).

In Norway (latitude = 59 degrees) active sites were along three midsized river systems; Lunde on the Straumen river, Gvarv on the Gvarv River and Patmos on the Sauar river. This beaver population is part of a multi-dimensional, longitudinal research program (Rosell et al. 1998, Rosell and Hovde 2001, Mayer et. al. 2017a). At this study area family group size, individual age and length of territory occupancy were known due to annual intensive live capture and marking activities (Mayer et al. 2017b). In 2015, initial observations were made between 31 October and 3 November (week 44/45). These sites were revisited 11–18 December (week 50/51). In 2016 data were collected on 22 October (week 42; initial visit) and 13–25 November (week 46/47; revisit).

In Lithuania (latitude = 54 degrees) the active sites were usually associated with soviet era drainage ditches abutting agricultural land, or natural depressions in the morainic landscape. Many sites had well developed ponds, although others were essentially small water impoundments in marshy areas. These sites have been included in a number of long-term studies on beaver ecology (Ulevičius 1999, Ulevičius et al. 2009). Data were collected 9–13 November (week 46).

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

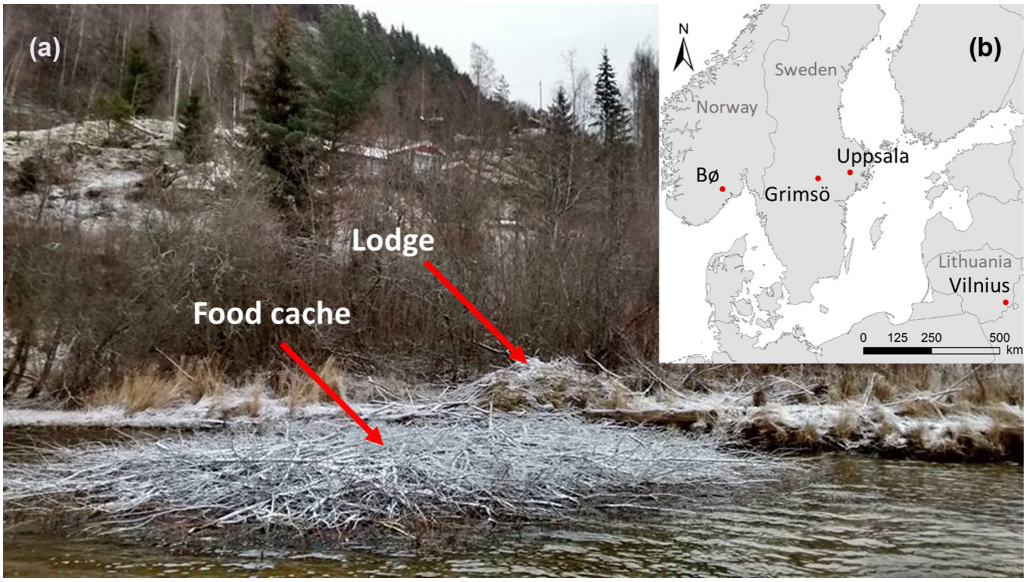

Figure 1. Beaver lodge with a large food cache from Bø, Norway (a), and a map illustrating the locations of the research sites (b).

Vegetation at all areas was mixed, with regions of *Salix* spp., *Alnus* spp. and *Populus* spp. Other species such as bird cherry *Prunus padus*, common ash *Fraxinus excelsior*, rowan *Sorbus aucuparia*, birch *Betula* spp., Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* were present in smaller amounts. Woody species composition in caches was determined by visual examination of branches. Dominant species in the cache was estimated by either visual means or taking subsamples of branches. All branches removed for sampling were returned to the cache.

Active sites were identified by the presence of fresh mud on the lodge, fresh cutting in the area or the presence of a food cache. In 2015, cache volume (m^3) was calculated by measuring the length, width and depth of each cache using a calibrated avalanche probe. Depth was measured in multiple areas of the cache and averaged. In Norway, only cache area (length × width) was measured in 2016 so any comparisons between 2015 and 2016 uses area not volume for cache size.

Temperature data were obtained from the Norwegian Meteorological Institute (<www.eklima.met.no>), the Swedish Meteorological Hydrological Institute (<www.smhi.se>) and other international weather databases.

In addition to descriptive statistics we used ANOVA, Tukey's HSD test, Pearson's correlation coefficient and the Mann–Whitney U test to examine relationships between variables.

In Norway, to estimate variation in final food cache area (length × width at last measurement) within and between active sites, we calculated the standard deviation (SD) of food cache area between 2015 and 2016 separately for each individual active site (same family group) and combined for all active sites. Finally, we investigated the effect of water flow, family group size and duration of territory occupancy on final food cache area (dependent variable; log-transformed to meet the assumption of residual normality) using a linear mixed-effects models of the R package 'lme4' (Bates et al. 2015). We ran three separate analyses to avoid overfitting models. The first model included the water flow (categorized as 'none', 'slow', 'medium' and 'fast') and year (2015 versus 2016), because we measured food cache area at slightly different times between years). We did not include water depth in this model because it was only measured in autumn 2015. The second model included family group size and the third model included the duration of territory occupancy (in years; averaged for the male and female pair member). Duration of territory occupancy and the average age of the beaver pair were highly correlated ($r=0.91$, $p < 0.001$), so we did not include pair age in the analyses. Site ID was included as random intercept to account for multiple observations. An alpha of 0.05 was used as the cutoff for significance, and 0.1 as cutoff for a trend.

Results

Water depth at food cache

Water depths at caches in Sweden ($n=7$) ranged from 1.20 to 2.30 m (mean = 1.93 m, SD = 0.37), in Norway ($n=13$) from 1.00 to 2.30 m (mean = 1.47 m, SD = 0.36) and in Lithuania ($n=17$) from 1.10 to 1.90 m (mean = 1.47 m, SD = 0.26). The mean for all 37 caches was 1.55 m (SD = 0.34). There was a significant difference in water depths of caches between the research sites (ANOVA: $F=7.06$, $p=0.003$, $df=36$). Water depths at Swedish caches were significantly deeper than in Norway or Lithuania while there was no significant difference in depths between Norway and Lithuania (Tukey's HSD: Sweden–Norway $Q=4.74$, $p=0.005$; Sweden–Lithuania $Q=4.98$, $p=0.003$; Norway–Lithuania $Q=0.03$, $p=0.90$).

Number of caches and mean volumes

In Sweden, eight active sites were investigated beginning 17–20 October. Beavers at four sites (50%) had caches at this time (two near Uppsala and two at Grimsö), while two sites had caches by 2–8 November and a final site had

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

a cache by 17 November (week 47). Mean initial cache volume in Sweden (n = 7) was 10.75 m^3 (range 0.5–23.6 m^3, SD = 7.71). By week 47 seven of eight active sites (87.5%) had food caches and the mean volume was 41.47 m^3 (SD = 20.13). Sample sizes are small (3 at Uppsala and 4 at Grimsö) making statistical comparison difficult. However, both initial (Uppsala = 12.93 m^3, Grimsö = 9.11 m^3) and final (Uppsala = 46.03 m^3, Grimsö = 38.05 m$^{3)}$) mean cache volumes were larger at Uppsala sites than at Grimsö sites. The number of woody species in the caches ranged from one to three (Table 1).

In Norway 19 sites were visited between 31 October and 3 November (week 44) and 13 (68%) had food caches. When sampled again in December, 17 of 19 sites (89%) had caches. However, two sites could not be visited due to ice so this is a minimum estimate. Initial cache sizes ranged from 1.35 m^3 to 49.45 m^3 with a mean of 17.06 m^3 (SD = 15.58) (Table 1). Food caches at Lunde (n = 5) were the smallest (mean = 8.48 m^3, SD = 5.26), while caches at Patmos (n = 4, mean = 19.95 m^3, SD = 20.01) and Gvarv (n = 4, mean = 24.90 m^3, SD = 17.82) were larger. Twelve of the sites with caches in November were sampled again in

Table 1. Descriptive information on active sites including volume at time of initial visit, number of and dominant woody species in the food cache and mean water depth of the food cache. nc indicates no cache was present on the date of first visit.

Location	Date of initial visit	Initial volume (m^3)	No. woody species.	Dominant species	Cache depth (m)
Sweden					
Uppsala: Brants.	10/17/15	7.40	2	*Prunus* spp.	2.0
Uppsala: Fortuna	10/17/15	23.6	3	*Salix* spp.	2.25
Uppsala: Lanna	11/6/15	7.80	2	*Salix* spp.	1.95
Grimsö: Sjoudden	10/20/15	12.60	3	*Sorbus* spp.	1.2
Grimsö: Sparudden	10/20/15	6.12	1	*Populus* spp.	1.8
Grimsö: Sjupenbacke	11/17/15	17.22	1	*Betula* spp.	2.05
Grimsö: övre forsen	11/7/15	0.50	1	*Betula* spp.	2.25
Grimsö: nedre forsen	11/7/15	nc			
Norway					
Lunde 1	10/31/15	nc			
Lunde 2a	10/31/15	14.40	2	*Salix* spp.	1.5
Lunde 3a	10/31/15	12.375	2	*Betula* spp.	1.65
Lunde 4a	10/31/15	1.35	1	*Betula* spp.	1.35
Lunde 4b	10/31/15	5.27	1	*Birch* spp.	1.2
Lunde 5b	10/31/15	9.00	2	*Salix/Betula*	1.5
Nordsjö	11/1/15	38.64	2	*Salix/Alnus*	1
Gvarv lower	11/1/15	38.78	2	*Salix/Betula*	2.05
Gvarv middle	11/1/15	20.79	1	*Salix* spp.	1.4
Gvarv upper	11/1/15	1.35	1	*Salix* spp.	1.35
Patmos 0	11/2/15	nc			
Patmos 1	11/2/15	nc			
Patmos 2a	11/2/15	5.04	1	*Betula* spp.	1.2
Patmos 3a	11/2/15	11.70	1	*Betula* spp.	1.3
Patmos 3b	11/2/15	nc			
Brafjorden a	11/2/15	nc			
Brafjorden b	11/2/15	13.61	2	*Salix/Betula*	1.3
Little Patmos	11/2/15	nc			
Patmos 4/5	11/2/15	49.45	4	*Salix* spp.	2.3
Lithuania					
#706	11/10/15	77.52	2	*Salix/Betula*	1.9
#707	11/10/15	77.82	3	*Salix* spp.	1.68
#708	11/10/15	nc			
#709	11/10/15	66.24	2	*Salix* spp.	1.2
#710	11/10/15	87.02	2	*Betula* spp.	1.85
#711	11/10/15	73.44	3	*Betula* spp.	1.8
#712	11/10/15	62.99	2	*Salix* spp.	1.2
#713	11/10/15	6.60	1	*Betula* spp.	1.3
#715	11/10/15	27.00	1	*Salix* spp.	1.5
#716	11/10/15	58.50	1	*Salix* spp.	1.5
#717	11/10/15	62.55	2	*Salix/Betula*	1.5
#719	11/10/15	7.92	2	*Salix* spp.	1.1
#720	11/10/15	20.16	1	*Salix* spp.	1.6
#721	11/13/15	nc			
#722	11/13/15	1.62	1	*Salix* spp.	1.2
#725	11/13/15	nc			
#726	11/13/15	7.92	1	*Salix* spp.	1.2
#727	11/13/15	149.00	7	*Salix/Betula*	1.5
#728	11/13/15	18.00	3	*Alnus* spp.	1.2
#729	11/13/15	81.60	1	*Salix* spp.	1.7

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

December and the pattern was similar with Lunde the smallest (mean = 23.8 m^3 SD = 17.8) and Patmos (mean = 42.2 m^3, SD = 47.6) and Gvarv (mean = 47.6 m^3, SD = 30.7) larger. The number of woody species in caches ranged from 1 to 4 (Table 1). When comparing food cache area between 2015 and 2016, the variation within the same individual active sites was 3.7-fold lower (SD = 7.7) compared to the variation across all active sites (SD = 28.2).

Seventeen of twenty (85%) active sites in Lithuania had food caches by week 46. The mean cache volume was 52.11 m^3 (range = 1.62–149.00 m^3, SD = 39.57). Five caches were less than 10 m^3 suggesting an initial stage of development, while 10 sites had caches larger than 50 m^3 indicating an earlier initiation date. The number of woody species in the cache ranged from 1 to 7 (Table 1).

By week 47 (mid-November) 37 of 47 (79%) active beaver sites in Sweden, Norway and Lithuania had food caches and by December, 41 of 47 (87%) active sites had food caches. This is a minimum estimate since sites in Sweden and Lithuania were not sampled in December and additional food caches may have been initiated by then.

Mean cache volume and mean monthly temperature

To compare cache development at the different research areas we examined the mean cache volumes observed 31 October–3 November (Norway), 10–13 November (Lithuania) and 17 November (Sweden). Mean volume in Lithuania (n = 17, mean = 52.11 m^3, SD = 39.57) was larger than in Sweden (n = 7, mean = 41.47 m^3, SD = 20.13) or Norway (n = 13, mean = 17.06 m^3, SD = 15.58). There was a significant difference in mean volume between the areas (ANOVA: F = 5.13, p = 0.01, df = 36). The mean volume in Lithuania was significantly different from the mean volume in Norway (Tukey's HSD: Q = 4.50, p = 0.01) but there was no significant difference between the mean volume in Sweden compared with either Norway or Lithuania (Tukey's HSD: Sweden–Norway Q = 2.46, p = 0.20, Sweden–Lithuania Q = 1.12, p = 0.69). Additionally, although not significant (ANOVA: F = 1.35, p = 0.27, df = 39) the December mean volume in Norway (n = 16, mean = 34.29 m^3, SD = 23.92), collected approximately 30 days later than in Lithuania or Sweden, was also smaller.

Mean monthly temperatures at the areas were relatively similar early in the autumn (September–November) with all areas recording mean monthly temperatures above freezing. However, Norway was the only area to record a monthly mean above freezing during December. All sites had monthly mean temperatures below freezing in January and February, although Norway was warmer (−0.8°C) compared to Sweden (−3.85°C) and Lithuania (−4.8°C) in February. Norway was the only site to record a mean monthly temperature above freezing (3°C) in March. Lithuania had the lowest mean monthly temperatures from November through March, while Sweden recorded lower temperatures than Norway during those months except in January.

Ambient temperature as a potential initiation stimulus

The first record of a minimum temperature below freezing in Sweden was recorded 29 September (week 40). Temperatures rebounded above freezing until 5 October, followed by daily minimum temperatures below zero through 18 October (week 42). In Norway minimum freezing temperatures were not recorded until 14 October (Week 42). In Lithuania the first period of minimum freezing temperatures began 6 October (week 41) and continued into the next week.

In Sweden sites were sampled weekly to bi-weekly and the daily change in cache volume ranged from 0.49 to 2.56 m^3 with a mean change of 1.56 m^3 (SD = 0.61) per day. The daily change was approximately 1.0 m^3 earlier in the autumn (up to week 45) and slightly higher (1.5 m^3) from week 45 to week 47. In Norway 11 caches sampled in both November and December had daily changes in volume ranging from 0.05 to 1.0 m^3 with a mean of .52 m^3 (SD = 0.33) per day. Using these data, we assumed that between 0.5 and 1.5 m^3 per day or 4 and 11 m^3 per week of branches are added to caches. We also assumed that growth of caches would be similar for sites in Lithuania.

This estimate of daily cache growth combined with the volume of each cache at first observation allowed us to estimate the week of initiation for each cache. These data suggest that food cache construction began between 28 September and 11 October (week 40–week 41) in Sweden and Lithuania, but not until 12–18 October (week 42) in Norway. The relationship between declining temperature and cache initiation is presented in Fig. 2.

Temporal growth in cache volume in Sweden

In Sweden four food caches initiated by 17–20 October (week 42/43) were followed through 17 November (week 47) with the mean volume increasing from 17.12 to 56.18 m^3 (mean change = 39.05 m^3 SD = 16.2) and a significant difference in mean cache volume between weeks (ANOVA: F = 10.08, p = 0.005, df = 11). The mean volume in week 43 was significantly different from week 47 (Tukey's HSD: Q = 6.35, p = 0.004, df = 11) but no significant difference existed between weeks 43 and 45 or between 45 and 47.

Water flow, demographic factors and cache size in Norway

In Norway food cache area tended to be larger at sites with no water flow compared to sites with slow and medium water flow (water flow (none): estimate ± SE: 0.68 ± 0.38, p = 0.087; Fig. 3a). No food caches were constructed at sites with fast water flow. No correlation was found between water depth and water flow (r = 0.13, p = 0.67) and means were similar (none = 1.38 m, slow = 1.53 m, medium = 1.49 m).

The final food cache area at Norwegian sites (n = 37 in 2015 and 2016 combined) ranged from 3 to 158 m^2 (mean = 22.8 m^2, SD = 28.2) and the final food cache area was larger in 2015 compared to 2016 (estimate ± SE: −0.54 ± 0.11, $p < 0.001$). The mean family group size at sites with a food cache (n = 19 in 2015 and 18 in 2016) was 4.1 (range 2–9, SD = 2), with no difference between years (Mann–Whitney U test: U = 115, p = 0.221). The duration of territory occupancy ranged between 1 and 13 years (mean = 4.7, SD = 3.6).

Family group size and duration of territory occupancy had no significant effect on the food cache area ($p > 0.2$; Fig. 3b–c).

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

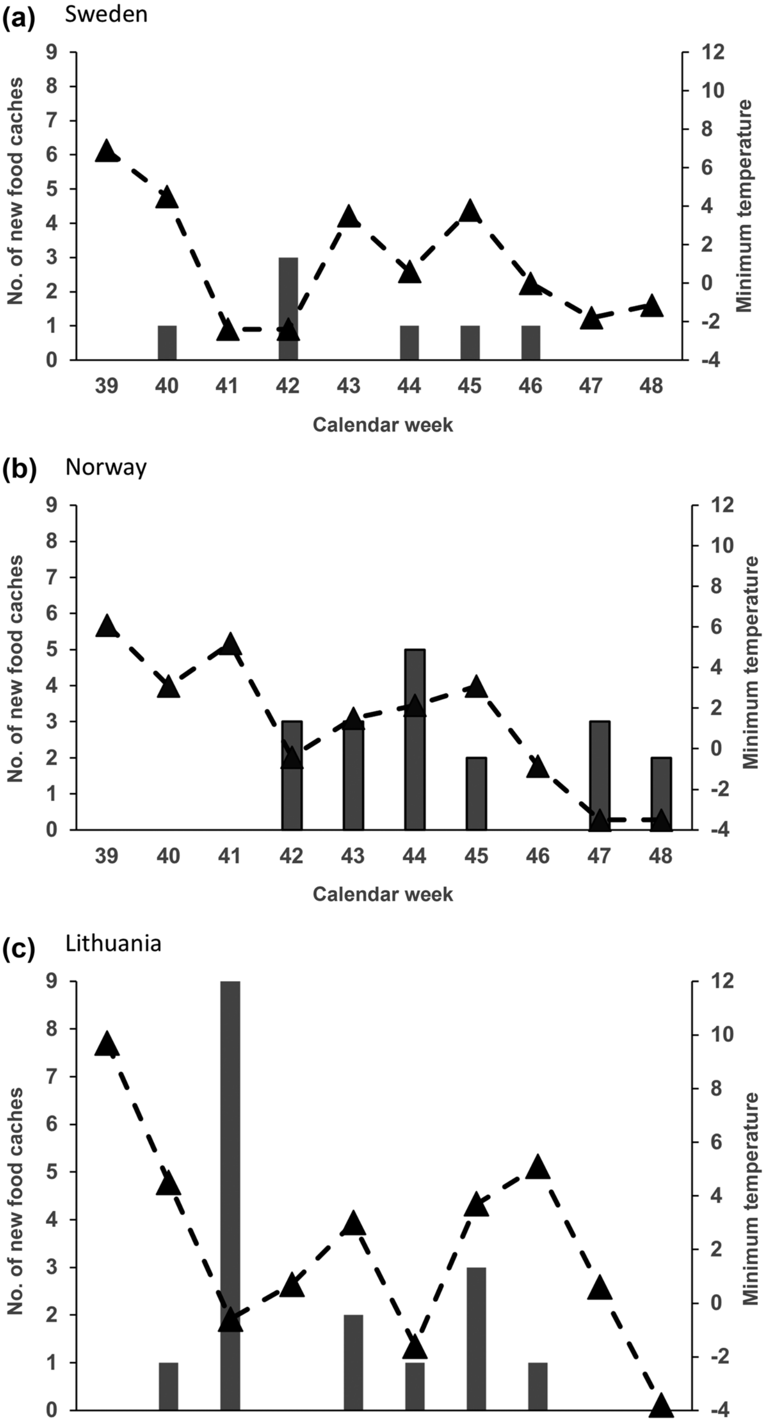

Figure 2. (a–c) Estimated and observed initiation dates of new food caches and mean weekly minimum temperatures at research sites. Dotted line is mean weekly temperature (degrees C) and solid bars are number of new food caches. The Norway data includes two caches sampled in December but not in November.

Discussion

Our data are unique in that we compared food caching behavior in three populations in three countries in northern Europe. We observed both similarities as well as plasticity within and between these Eurasian beaver populations in food caching behavior. We found general similarities in water depths at caches, percentage of active sites with caches, and the pattern of cache initiation associated with declining autumn temperature between the research areas. Variability existed in observed cache sizes both within and between the populations. We also found no relationship between cache

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

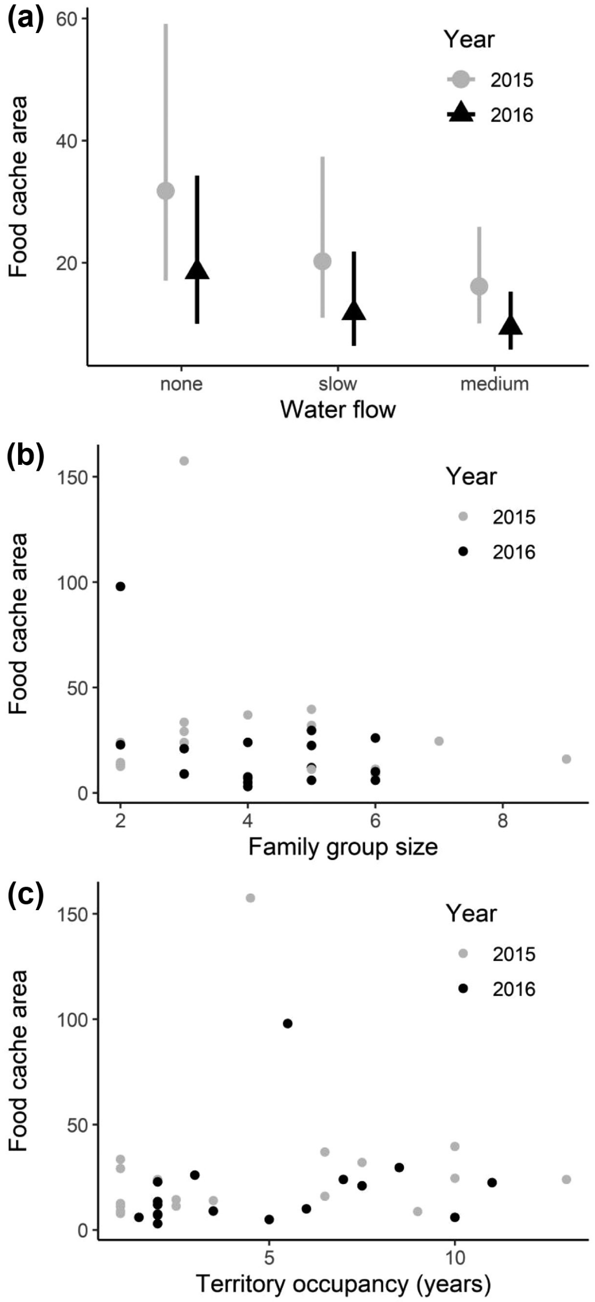

Figure 3. The effect of water flow (a) on the final food cache area (m^2) at Norwegian sites. The 95% confidence intervals are given as bars. (b) shows the relationship between food cache area and family group size and (c) between food cache area and duration of territory occupancy (both not significant).

size and group size or duration of territory occupancy in the Norwegian population.

The comparison of water depth of the food caches suggests reasonable similarity in choice of location for the winter lodge with the water depth near the entrance being critical to avoid freezing, allowing access to the food cache and allowing winter mobility. The results of our depth analysis found that no cache was located in water shallower than 1 m or in water deeper than 2.3 m. The only comparable data to ours is from Hartman and Axelsson (2004), who studied beaver food caching in Värmland, Sweden. They measured the water depth outside the lodge (not directly in the cache) and reported the mean depth at sites with a cache to be 1.1 m. This mean depth is less than either the total mean depth from all our study sites (1.6 m) or the mean depth for our Swedish sites (1.9 m). Hartman and Axelsson (2004) also reported finding caches in water less than 1.0 m, which differs from our observations in Sweden, Norway and Lithuania.

Hartman and Axelsson (2004) also found that caches in shallower water were significantly smaller than in deeper water and their overall mean cache volume was approximately half the mean volume we observed in our Swedish sites. However, since many of their caches were in shallow water this may partially account for volume differences between our studies. Wilsson (1971) also reported that caches on smaller watercourses (with an assumed shallower depth) were smaller than caches on larger rivers. Differences between Hartman and Axelsson (2004) and our study may be due to the specific habitat types they studied in Värmland, could indicate plasticity in selection of sites for the winter cache, or reflect differences in data collection.

Given the specific local habitat differences between our three major sites the similarity in choice of cache location is compelling. Water depths were significantly greater at the Swedish sites, but very similar between the sites in Norway and Lithuania, which are very different habitats (river versus small streams and ponds). However, the ranges were similar between all three areas. While certainly habitat dependent, it seems reasonable to assume that most beaver food caches will occur in water at least 1 m deep. Additional data to document this across the Eurasian range could provide an additional management tool to access beaver habitat quality.

Our three study areas were generally similar in percentage of active sites with food caches. Only one site in Sweden, two sites in Norway and three sites in Lithuania did not have food caches at the time of the last observation in 2015. Since we did not sample in Sweden and Lithuania in December and some sites in Norway were not visited due to ice cover, it is possible that our final percentage (approximately 90%) is low. In Sweden and Norway approximately 70% of sites had caches by the end of October (week 44/45). In 2016, in Norway, we also observed a lower percentage of sites with food caches in October, but by November (week 46/47) caches were observed at all sites.

Hartman and Axelsson (2004) reported a lower percentage of sites with food caches (67%) than we observed, but 50% of their lodges without caches had water depths of 0.5 m or less suggesting water depth as a limiting factor for cache construction. Wilsson (1971), studying farther north in Sweden (approximately 5° north of our sites) suggested that most, if not all, beavers constructed caches, even animals he kept in enclosures. Based on our results it appears that a high percentage of, if not all, beaver families living in Northern Europe should construct food caches. Specific site characteristics (type of wetland, water depth, water flow rate) may also influence this behavior.

We observed differences in final cache volume among the areas, with caches in Lithuania the largest and caches in Norway the smallest. The sites in Norway were on mid-sized

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

rivers while the sites in Lithuania were on smaller streams, drainage ditches or ponds, which may have influenced cache size. However, caches in Sweden were also larger than those in Norway and some were on mid-sized rivers. The monthly autumn–winter temperature pattern for 2015–2016 shows Lithuania recording consistently colder temperatures than Sweden and Norway, especially during the winter months. Lithuania is influenced by cold, dry continental air masses during winter while Norway is influenced more by warmer maritime air masses associated with the Norwegian current. Our Swedish sites, with caches smaller than Lithuania but larger than Norway, were between 50 and 150 km from the Baltic coast and winter temperatures were generally colder than Norway but warmer than Lithuania. Interestingly, both Lithuania and Sweden recorded mean March temperatures below freezing while Norway had a mean March temperature above freezing. Our data, which appear to be unique in the literature, suggest that ambient air temperature is associated with larger food cache volume.

Timing of food cache construction depends on specific environmental conditions at the research location. For example, for the North American beaver, Aleksiuk (1970), in northern Canada, reported caching to begin as early as late August, Osmundson and Buskirk (1993) in Wyoming (at elevations between 2300 and 3500 m) reported caches were begun as early as mid-September, while in Massachusetts, in the northeastern United States, cache construction may not occur until early October (Hodgdon 1978). In Varmland, Sweden, Hartman and Axelsson (2004) reported cache construction beginning as early as mid-September (week 38) and continuing through late November, while Vasin (2001), in northwestern Siberia, reported that beavers begin caching in mid-August with freeze up in mid-October.

Initiation of cache construction at our research locations was fairly consistent. The earliest estimates suggest cache construction began as early as late September/early October (week 39/40) in Sweden and Lithuania, but not until mid-October (week 42) in Norway. There is extensive variability in timing of cache initiation at individual sites and it may reflect behavioral plasticity in individual animals. Moreover, in Norway, food cache size within active sites varied much less between years compared to the variation between active sites. This suggests that individual family groups may show consistent food caching behavior. More research is required to determine why some families begin caching early while others wait until later and if there is a consistent annual pattern.

While many variables may influence cache construction (photoperiod, deciduous leaf fall, changing woody species nutritional value) the relationship to declining minimum temperatures and the first period of below freezing temperatures during the autumn is compelling. This relationship has been suggested by Wilsson (1971) in Sweden and Busher (2012) in Massachusetts, USA. Wilsson (1971) noted that beavers in outdoor enclosures began cache construction at similar times to beavers living free along the river, but that beavers held in indoor terraria started caching at different times. Wilsson (1971) goes on to suggest that temperature may be the environmental stimulus since beavers in terraria, under more controlled (warmer) temperature regimes, showed more variability in caching behavior. Our data connect decreasing minimum temperatures and the time of first period of below freezing temperatures with the onset of caching behavior and imply that declining temperature during the autumn may act as an environmental stimulus for initiation of food caching behavior in beavers.

No other study of the Eurasian beaver has documented the temporal development of beaver food caches and our results from Sweden over a five-week period provide insight into this aspect of cache development. Cache development was relatively slow early in the autumn but increased as the season progressed. Mean cache volume in mid-October was significantly smaller than in mid-November. These data are relatively consistent with data from the North American beaver where caches have an initial slow rate of development, followed by a more rapid phase and then a slower growth phase near the end of the caching period (Busher unpubl.).

Our Norway data allowed us to compare the relationship between water flow speed, family size, duration of territory occupancy and cache size. Although not significant, we found that beavers at sites with no water flow (lakes, oxbow lakes) tended to build larger caches compared to sites with moving water (main river). This seems reasonable, since these sites froze over first limiting access to food resources other than from the cache. Conversely, the one active site with fast flowing water did not have a food cache in either year of the study. This could indicate that beavers in calmer water bodies (lakes, ponds) require larger caches to sustain them throughout winter due to prolonged periods of ice cover. Alternatively, the slow water flow allows for the construction of larger caches compared to more fast flowing water bodies (streams and rivers), whereas the two hypotheses are not mutually exclusive.

Water flow and water depth at active cache sites may be related and together influence caching behavior. In Norway, the precise location of the lodge and cache were variable but tended to be on areas of the river systems with slower moving water. We found no significant correlation between water depth and water flow and cache depths were similar regardless of flow. However, additional data are required to better understand any relationship between water flow rate and water depth and how these variables influence food caching behavior.

We found no significant effect of either family group size or length of territory occupancy and food cache size, which was surprising since we assumed that a larger family group and a more experienced adult pair would construct larger caches. Our results are similar to what Osmundson and Buskirk (1993) reported for the North American beaver, but different from the significant relationship between food cache size and family group size reported by both Kafcus (1987) and Easter-Pilcher (1990) also for the North American beaver. These different findings on the relationship between group size and cache size may be due to methodological differences (cache area versus cache volume, population sampling techniques), specific habitat differences or behavioral differences between populations. However, the lack of agreement on the relationship between family group size and food cache size suggests that caution should be used when relating cache size to number of beavers present in a family.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

Acknowledgements – The stimulus for this study comes from numerous discussions among the authors and with other scientists at International Beaver Symposia. We thank Per Edenhamn for his guidance and assistance with the field work near Uppsala and Kent Sköld for his support at Grimsö.

Author contributions – All authors contributed to the field work and data collection in their respective countries and contributed equally to this work.

References

Aleksiuk, M. 1970. The function of the tail as a fat storage depot in the beaver (*Castor canadensis*). – J. Mammal. 51: 145–148.

Aleksiuk, M. and Cowan, I. M. 1969. The winter metabolic depression in Arctic beavers (*Castor canadensis*) with comparison to California beavers. – Can. J. Zool. 47: 965–979.

Andersson, M. and Krebs, J. R. 1978. On the evolution of hoarding behavior. – Anim. Behav. 26: 707–711.

Baker, B. W. and Hill, E. P. 2003. Beaver (*Castor canadensis*). – In: Feldhamer, G. A. et al. (eds), Wild mammals of North America: biology, management and conservation, 2nd edn. The Johns Hopkins Univ. Press, pp. 288–310.

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Blanchet, M. 1959. Was machen die 'Taler-Biber' an der Versoix? – Heimatschutz 53: 119–123.

Buech, R. R. et al. 1989. Temperature in beaver lodges and bank dens in a near-boreal environment. – Can. J. Zool. 67: 1061–1066.

Busher, P. E. 1980. The population dynamics and behavior of beavers in the Sierra Nevada. – PhD thesis, Univ. of Nevada.

Busher, P. E. 1991. Food caching behavior by the North American beaver, *Castor canadensis*, in western Massachusetts. – In: Bobek, B. et al. (eds), Global trends in wildlife management. Trans. XVIII IUGB Congress, pp. 111–114.

Busher, P. E. 1996. Food caching behavior of beavers (*Castor canadensis*): selection and use of woody species. – Am. Midl. Nat. 135: 343–348.

Busher, P. E. 2003. Food caching behaviour of the American beaver (*Castor canadensis*) in Massachusetts. – Lutra 46: 139–148.

Busher, P. E. 2012. What goes in a larder? Using woody species selection and food caching to better understand beaver behavioral ecology. – Abstracts, 6th International Beaver Symposium Faculty of Forestry, Univ. of Zabreb.

Busher, P. E. 2016. Family *Castoridae* (beavers). – In: Wilson, D. E. et al. (eds), Handbook of mammals of the world, Vol. 6. Lagomorphs and Rodents I. Lynx Edicions, Barcelona, pp. 150–168.

Busher, P. E. and Hartman, G. 2001. Beavers. – In: MacDonald, D. (ed.), New encyclopedia of mammals. Oxford Univ. Press, pp. 590–595.

Clarkson, K. et al. 1986. Density dependence and magpie food hoarding. – J. Anim. Ecol. 55: 111–121.

Delgado, M. et al. 2014. Fox squirrels match food assessment and cache effort to value and scarcity. – PLoS One 9: e92892.

Djoshkin, W. W. and Safonov, W. G. 1972. Die biber der alten und neuen welt. – A. Ziemsen Verlag, Wittenberg Lutherstadt.

Dzięciołowski, R. and Misiukiewicz, W. 2002. Winter food caches of beavers *Castor fiber* in NE Poland. – Acta Theriol. 47: 471–478.

Easter-Pilcher, A. 1990. Cache size as an index to beaver colony size in northwestern Montana. – Wildl. Soc. Bull. 18: 110–113.

Hartman, G. and Axelsson, A. 2004. Effect of watercourse characteristics on food-caching behaviour by European beaver, *Castor fiber*. – Anim. Behav. 67: 643–646.

Hodgdon, H. E. 1978. Social dynamics and behavior within an unexploited beaver (*Castor canadensis*) population. – PhD thesis, Univ. of Massachusetts.

Jakopak, R. P. et al. 2017. Organizing the pantry: cache management improves quality of overwinter food stores in a montane mammal. – J. Mammal. 98: 1674–1681.

Jenkins, S. H. and Busher, P. E. 1979. *Castor canadensis*. – Mammal. Species 120: 1–8.

Kafcus, E. N. 1987. Census and exploitation of a discrete beaver population in Michigan. – MSc thesis, Central Michigan Univ.

Lancia, R. A. et al. 1982. Winter activity patterns of two radiomarked beaver colonies. – J. Mammal. 63: 598–606.

Lavsund, S. 1989. Winter activity of beaver (*Castor fiber*) in Sweden. – Fifth ITC Abstracts 1: 303.

Mayer, M. et al. 2017a. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. – Anim. Behav. 123: 375–382.

Mayer, M. et al. 2017b. Couch potatoes do better: delayed dispersal and territory size affect the duration of territory occupancy in a monogamous mammal. – Ecol. Evol. 7: 4347–4356.

Osmundson, C. L. and Buskirk, S. W. 1993. Size of food caches as a predictor of beaver colony size. – Wildl. Soc. Bull. 21: 64–69.

Pitera, A. M. et al. 2018. Daily foraging routines in food-caching mountain chickadees are associated with variation in environmental harshness. – Anim. Behav. 143: 93–104.

Potvin, C. L. and Bovet, J. 1975. Annual cycle of patterns of activity rhythms in beaver colonies (*Castor canadensis*). – J. Comp. Physiol. A Sensory Neural Behav. Physiol. 98: 243–256.

Richard, P. B. 1967. Le determinisme de la construction des barrages chez le Castor du Rhone. – Terre Vie 21: 339–470.

Richard, P. B. 1983. Mechanisms and adaption in the construction behaviour of the beaver (*C. fiber* L.). – Acta Zool. Fenn. 174: 105–108.

Rosell, F. and Hovde, B. 2001. Methods of aquatic and terrestrial netting to capture Eurasian beavers. – Wildl. Soc. Bull. 29: 269–274.

Rosell, F. et al. 1998. Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. – J. Chem. Ecol. 24: 207–219.

Rosell, F. et al. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. – Mammal Rev. 35: 248–276.

Rusch, D. A. and Reeder, W. G. 1978. Population ecology of Alberta red squirrels. – Ecology 59: 400–420.

Seeley, T. D. 1985. Honeybee ecology: a study of adaptation in social life. – Princeton Univ. Press.

Semyonoff, B. T. 1953. Beaver biology in winter in Archangel province. – In: Translations of Russian game reports. Can. Wildl. Service, Ottawa 1, pp. 71–92.

Sjöberg, G. and Ball, J. P. 2011. Restoring the European beaver: 50 years of experience. – Pensoft Publishers.

Slough, B. G. 1978. Beaver food cache structure and utilization. – J. Wildl. Manage. 42: 644–646.

Smith, C. C. and Reichman, O. J. 1984. The evolution of food caching by birds and mammals. – Annu. Rev. Ecol. Syst. 15: 329–351.

Smith, D. W. and Jenkins, S. H. 1997. Seasonal change in body mass and size of tail of northern beavers. – J. Mammal. 78: 869–876.

Steele, M. A. et al. 2006. The innate basis of food-hoarding decisions in grey squirrels: evidence for behavioural adaptations to the oaks. – Anim. Behav. 71: 155–160.

Stephenson, A. B. 1969. Temperatures within a beaver lodge in winter. – J. Mammal. 50: 134–136.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use

Swafford, S. R. 2002. Population survey methods, immobilization approaches and morphological characteristics for beaver in Lowndes County, Mississippi. – MSc thesis, Mississippi State University.

Ulevičius, A. 1999. Density and habitats of the beaver (*Castor fiber*) in Lithuania. – Proc. Latvian Acad. Sci. Sect. B 53: 101–106.

Ulevičius, A. et al. 2009. Morphological alteration of land reclamation canals by beaver (*Castor fiber*) in Lithuania. – Estonian J. Ecol. 58: 126–140.

Vander Wall, S. B. 1990. Food hoarding in animals. – Univ. of Chicago Press.

Vasin, A. 2001. Beavers of the north of West Siberia. – In: Busher, P. E. and Gorshkov, Y. (eds), Proc. 1st Euro-American beaver Congr. Transactions of Volga-Kama National Nature Zapovednik, pp. 51–60.

Wilsson, L. 1971. Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). – Viltrevy 8: 115–266.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 22 Sep 2024
Terms of Use: https://bioone.org/terms-of-use