BALTIC FORESTRY

http://www.balticforestry.mi.lt
ISSN 1392-1355
eISSN 2029-9230

Baltic Forestry 2020 26(2): 492
Category: research article
https://doi.org/10.46490/BF492

Assessment of the effect of beaver foraging activities on the alteration of waterside forests in northern and middle taiga of Russian Karelia

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Fyodorov, F.V. 2020. Assessment of the effect of beaver foraging activities on the alteration of waterside forests in northern and middle taiga of Russian Karelia. *Baltic Forestry* 26(2): article id 492. https://doi.org/10.46490/BF492.

Received 5 May 2020 **Revised** 19 June 2020 **Accepted** 25 July 2020

Abstract

The territory of the Republic of Karelia is latitudinally elongated and traversing two boreal subzones such as the northern and middle taiga. Pine and spruce stands predominate in the northern taiga, while forests in middle taiga are more diverse, represented by secondary stands, and often dominated by deciduous species. These factors define the foraging behaviour of beavers and their role in alteration of riparian forests. Dispersing in the northern taiga, beavers tend to choose waterside areas with a higher proportion of deciduous species. However, such habitats occupy less than 1% of the forested area in this subzone, so the overall effect of beaver foraging on forest stands would be minor. On the other hand, inside beaver colonies, stand alteration is far more pronounced than changes in colonies in the middle taiga, and the effects are the following: 1) waterside forests in the northern taiga lose 2.5 times more deciduous trees than those in the middle taiga (61.4 and 26.3 %, respectively); 2) in waterside stands, aspen is totally removed, the share of conifers is doubled, and the share of birch is reduced (in the middle taiga, the share of birch around beaver colonies slightly increases, and the share of aspen is reduced by a factor of 1.5); 3) beavers in the north of Karelia consume thick birch trees more often than in the south of the region; 4) the regeneration capacity of damaged trees in the north is lower than in the south of Karelia.

Keywords: beavers, foraging activities, waterside forests, northern and middle taiga, tree stands

Introduction

The beaver is a strictly herbivorous animal, which stands out among other plant eaters owing to a very peculiar trait – the ability to log mature trees. The browsing activity of beavers can markedly alter the "appearance" of a waterside forest: when these animals arrive, the species and age compositions of the tree stand undergo changes; it becomes sparser, young growth and the understorey become more abundant, etc. Such changes are far more noticeable in Karelia compared to southern regions. First, the species composition and biomass of wetland vegetation in the region being poor, a substantial share in the summer diet of beavers in the study area belongs to trees and shrubs (Danilov et al. 2007). Second, because of the paucity of food supply available to beavers, their home range size in Karelia is larger than in other regions. Third, the recovery of disturbed forest communities is slower in northern ecosystems.

Since the region being latitudinally elongated and traversing two taiga subzones, beaver foraging grounds vary significantly from the north to the south relating to their tree species composition and foodstuff abundance for beavers. Therefore, the aim of this paper is to comparatively assess changes in waterside forests induced by the foraging activity of beavers in the north and the south of the Republic of Karelia.

Materials and methods

Surveys were carried out in the south of Republic of Karelia, in the Lamatozerskoye hunting ground (**LHR**) (2000–2003), and in the north, in the Kostomuksha Nature Reserve (**KNR**) and the Kalevala National Park (**KNP**) (2001 and 2018) (Figure 1). Beaver censuses were carried out in the study areas, and the effects of foraging activity in beavers on the structure and composition of the waterside tree stands were assessed.

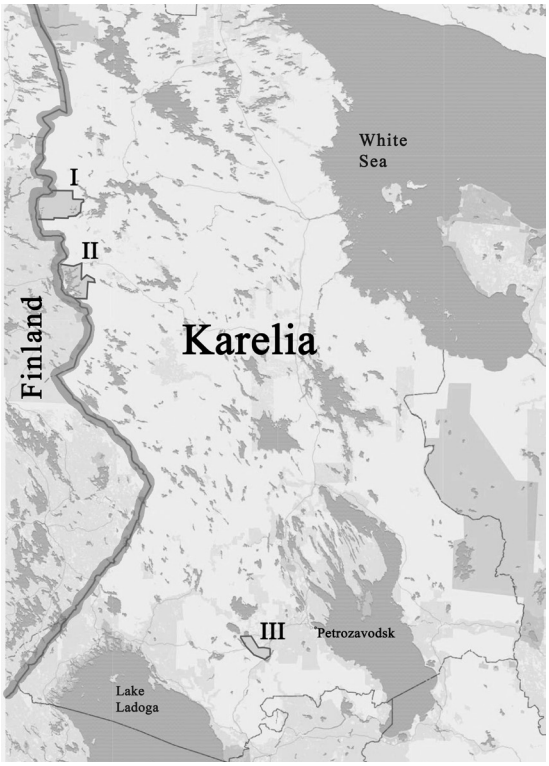

Figure 1. Studied areas: I – Kalevalsky National Park, II – Kostomukshsky Strict Nature Reserve (the northern taiga), III – Lamatozerskoye Game Management (the middle taiga)

The Lamatozerskoye hunting ground (215 km^2; 61°35' N, 33°19' E) is situated in the middle taiga subzone. According to the game management register, spruce stands occupy 7.8% of its wooded area, pine stands cover 28.7%, mixed forests cover 37.8%, deciduous stands cover 26.0%. Some 15% of the forest area is young mixed stands and low deciduous forests. Usually pine and spruce form primary communities, while birch, aspen and alder communities are secondary forests.

Inventory surveys and interviews revealed the presence of 65 beaver colonies in the ground; 19, i.e. 65.5% of the 29 colonies surveyed by the staff of the Zoology Laboratory, were active. The effect of foraging activity of the animals was studied at 7 model waterbodies.

The Kostomuksha NR (492.59 km^2; 64°28' N, 30°16' E) and Kalevala NP (744 km^2; 64°59' N, 30°12' E) are situated in the north of Karelia, in the northern taiga subzone. Forests in these protected areas are represented by two formations: pine stands (85% of wooded area) and spruce stands (up to 15%). Secondary birch and aspen stands are fragmentary and cover less than 1% of the forest area. Spruce forests tend to grow along the hydrographic network (Gromtsev et al. 1998, Khokhlova et al. 2000, Kovalevsky 2017a,b). Surveys conducted in 2018 revealed 31 beaver colonies: 11 active and 20 abandoned ones. Waterside vegetation was described in detail for 7 colonies, and the browsing activity was assessed for 5 colonies (Fyodorov and Krasovsky 2019).

Two to four sample plots were established in each model colony. Their size varied depending on the waterside topography and averaged 625 m^2 (25 × 25 m). There were 10 sample plots totalling 5525 m^2 in the north of Karelia, and 20 plots (12,500 m^2) in the south. All woody plants, including beaver-logged trees, were documented in each sample plot; trunk diameters were measured at the browsing point. Therefore, we managed to reconstruct the tree stand composition prior to the arrival of beavers and estimate the browsing level.

Although southern and northern Karelia is inhabited by different beaver species, Eurasian (*Castor fiber* L.) and North American (*C. canadensis* Kuhl) ones, respectively, the effect of their foraging activity on forest communities is quite comparable. This statement is corroborated by the studies on ecology of this beaver species living within the same area: the distance between their colonies was sometimes less than 10 km (Danilov et al. 2007, Danilov and Fyodorov 2015). We were convinced that geographical distinctions in the diet of beavers are not species-specific and determined by the availability of certain foods in the habitats. In other words, when in our region, the North American beaver would consume the same trees and shrubs as the Eurasian one.

Results

Beavers in Russia mostly feed on 40 species of trees and shrubs (Fedyushin 1935, Dyakov 1975, Dezhkin et al. 1986). The diversity of foods is however much lower in the European North and declines even more northwards. The southern taiga was found to harbour 23 species, middle taiga 14, and northern taiga only 8 species of trees and shrubs browsed by beavers (Danilov et al. 2007).

Counts of browsed plants in the south of Karelia show that aspen is the main food species for beavers (Danilov et al. 2007, Fyodorov and Yakimova 2012). This finding is confirmed by other zoologists who have studied the diets of the animals in other parts of Russia. Aspen is, however, exceptionally rare in primary northern taiga forest, and beavers must switch over to other foods, such as birch and alder. In the north of Karelia, the combined share of birch and alder in the diet of beavers is three times higher than in the south, where aspen is the main food item accounting for 66.4% (Table 1). Aspen contributes as little as 5% to the diet of beavers in the north but is almost 100% consumed. Thus, geographical distinctions in the diet of

Table 1. Shares of some tree species in the diet of beavers in the northern and middle taiga, %

Species	Northern taiga	Middle taiga
Aspen	5.0	66.4
Birch	64.3	26.7
Alder	30.7	6.9
Σ	100 (*n* = 443)	100 (*n* = 768)

beavers are primarily due to the availability of certain food items in the habitats. Yet, aspen is preferred to other foods in the north, too. In both the KNP and KNR it is not uncommon to see trees of this species logged by beavers 100 or more metres away from the edge of water, although the core foraging area does not reach farther than 30 m from the shoreline into the woods. As a rule, all solitary aspen trees growing along northern waterbodies in areas inhabited by beavers get logged by the animals in their first or second year in the area.

On Lake Sudno (Kalevala NP), 500 m away from a beaver colony, there is a small aspen-covered shore area. Beavers used this 220 m^2 area as an additional foraging ground. Among the 10 aspen trees with an average diameter of 31.2 cm (65 cm at maximum) nine were logged and one was partially browsed by beavers. Remarkably, all the 8 birch trees (average diameter is 23.6 cm) growing in the site remained intact.

Waterside forests change in different ways under the effect of beaver foraging activities. The changes depend on the species composition of the tree stand around beaver colonies.

In the northern taiga, beavers remove four times more birch (a major stand-forming species) than in the middle taiga. Overall, the primary northern forests lose 61.4% of deciduous trees (n = 722, conifers excluded), while the secondary forests lose 26.3% (n = 2,923) (Table 2).

Thus, the tree stand structure around beaver colonies is altered substantially. The occasional aspen trees in the Kalevala NP and Kostomuksha NR were all gone, the share of birch in the stands decreased, while the shares of pine and spruce doubled: from 8.4 and 18.8% (n = 991) to 15.1 and 33.9% (n = 547), respectively. On the contrary, in the LHG, the proportion of birch increased from 52.6% to 61.0% that of aspen dropped 1.5-fold, and the share of conifers around beaver colonies remained almost unchanged (Figure 2).

Studies of the woody foods consumed by beavers show that the animals have preferences not only for certain tree species, but also for their size. Firstly, when procuring foods, they choose a larger diameter in aspen than in birch (Table 3). Secondly, beavers in the south of Karelia more often pick birch of a smaller diameter than in the north. Our observations in the LHG showed that 88.9% of beaver-logged trees were up to 12 cm in diameter, whereas in the KNP and KNR trees of this diameter were logged less frequently, 68.3%. Although the average diameter of birch in the northern tree stands is smaller than in the southern (10 and 17 cm, respectively), beavers tended to use thicker trees oftener (Figure 3). The fact that beavers tend to prefer thinner birch, but thicker aspen trees can probably be explained by the different wood densities of

Table 2. The effect of beaver foraging activity on waterside forest in the northern taiga (the Kostomuksha NR and Kalevala NP) and the middle taiga (South Karelia) subzones

Taiga subzone	Aspen		Birch		Alder		Total	
	I	II	I	II	I	II	I	II
Northern	23	22 (95.7)	530	285 (53.8)	169	136 (80.5)	722	443 (61.4)
Middle	1085	510 (47.0)	1647	205 (12.4)	191	53 (27.7)	2923	768 (26.3)

Notes: I – the number of trees that had grown in the foraging site; II – the number of trees logged or browsed through more than a half of their diameter by beavers (percentage share of beaver-logged trees among all trees of the same species is shown in parenthesis). Data on the northern taiga reflect results of surveys conducted in 2018, on the middle taiga are given after Danilov et al. 2007.

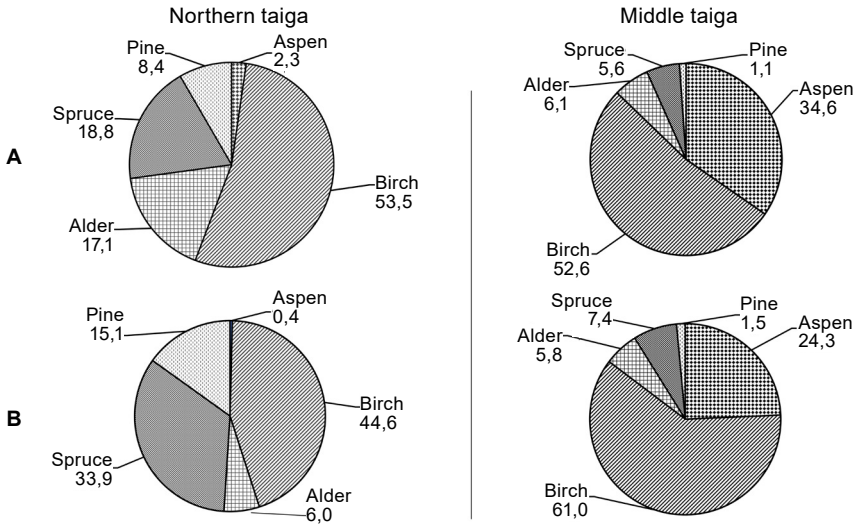

Figure 2. Shares of tree species (%) that had grown in the beaver sites: A – before the beaver colonization (a reconstructed situation) (n = 991 for the northern taiga, n = 3133 for the middle taiga), B – after beaver move out (n = 549 for northern taiga, n = 2365 for the middle taiga)

Table 3. Average diameter of trees of major species that had grown in the site before the arrival of beavers (a reconstructed situation) (I), and of those logged by beavers for foraging purposes (II), cm $\left(\frac{M \pm \sigma}{\lim}\right)$

Middle taiga			
Aspen (n = 1145)		Birch (n = 1680)	
I	II	I	II
22.7 ± 11.28 6 – 80	23.1 ± 9.05 6 – 48	17.0 ± 6.22 1 – 40	11.9 ± 4.04 1 – 28
Northern taiga			
Aspen (n = 23)		Birch (n = 530)	
I	II	I	II
25.3 ± 13.6 4 – 65	24.6 ± 13.9 4 – 65	10.0 ± 5.1 1 – 26	8.2 ± 5.2 1 – 25

these species. The energy costs of browsing on larger birch trees are much greater than for gnawing aspen, and so beavers prefer felling thinner birch trunks (Zavyalov 2015). Living in the north, beavers must switch over to thick birch in the absence of their preferred food like aspen, which is more calorie- and nutrient-rich than birch (Sokolov 1949, Tomme 1964, Solovjev 1973). A possible explanation for the higher share of thick birch trees in the beaver diet in the north is re-colonisation of the areas where thin trees had already been removed from the foraging grounds.

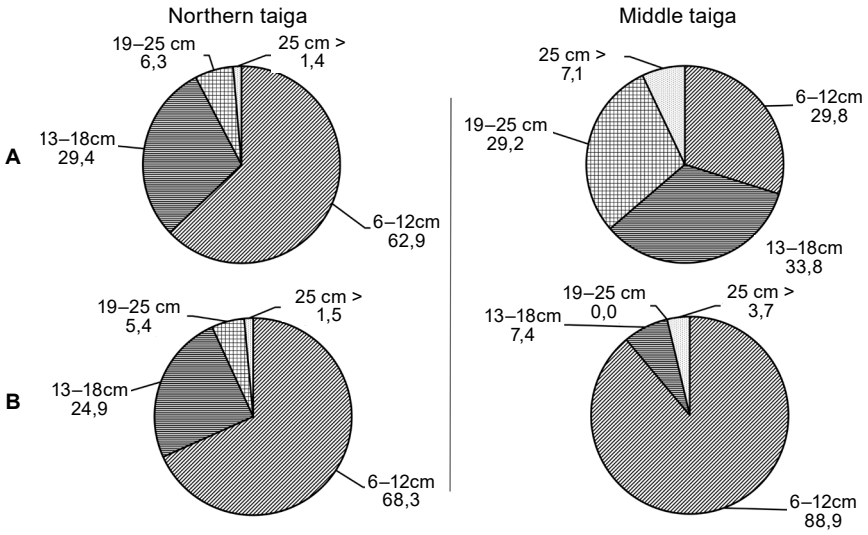

Figure 3. Percent shares of birches of the different diameters that had grown prior to the arrival of beavers (A) and logged by beavers (B) in the northern and middle taiga

Logging by beavers is followed by a regeneration of trees and shrubs. It depends, primarily, on the regeneration capacity of different species. In the KNP and KNR we observed that stump sprouts were formed by 18.1% of beaver-logged birch trees (n = 285) and by 28.4% of alder trees (n = 136). The regeneration capacity of these species in the south of Karelia is somewhat higher: 21.9% (n = 205) and 50.9% (n = 265), respectively (Danilov et al. 2007). The regeneration capacity is the lowest in aspen, both in the south and in the north of Karelia, below 10%.

Discussion and conclusions

The dense hydrological network (approx. 64,000 lakes and 26,700 rivers) and uneven distribution of food resources in Karelia are the key factors for the dispersal of beavers, their numbers, distribution across the territory, family size, engineering activity, diet, foraging site size, and some other ecological features. All the above defines the response of the ecosystem to the arrival of beavers. A comparison of the conditions for the life of beavers in the primary northern taiga forests and the secondary middle taiga forests of Karelia has revealed some distinctive features.

1. The distribution of beaver colonies and animal numbers depends on the distribution of food resources. In the KNR and KNP, where coniferous forests predominate, beavers choose to settle where the share of deciduous species is higher. Tree counts have demonstrated that in areas with beaver colonies birch accounts for 53.5% of all trees, alder – 17.1, aspen – 2.3, spruce – 18.8, pine – 8.4% (n = 991) (Fyodorov and Krasovsky 2019). The share of such abundant sites, however, is less than 1% of the wooded area, wherefore the animals must abandon the colonies oftener and migrate in search for better habitats. As a result, the 2018 census in the national park and strict nature reserve produced a record of 35.5% active colonies (11 ones of the total 31 in the counts). In the Kostomuksha NR, where beavers appeared earlier than in the Kalevala NP, the proportion of active colonies was even smaller, 18% (n = 22) (Fyodorov and Krasovsky 2019). Beaver counts carried out in the KNR 20 years ago also yielded a high proportion of abandoned colonies, 60% (n = 49) (Fyodorov and Kanshiev 2003).

In the LHG, beaver food resources are distributed more evenly, and so the distribution of beaver colonies is also more even than in the north. The proportion of active colonies is higher, 65% (n = 29).

2. Proportion of single-beaver settlements. Analysis of traces of beaver activity has shown that abandoned colonies in the north are usually re-occupied by single animals. This is probably nothing more than a temporary winter stopover pattern for bachelor beavers who have failed to find a permanent habitat. Three of the seven active settlements, 43%, on Lake Sudno (Kalevala NP) were inhabited by a single beaver. In the Kostomuksha NR, 45% of settlements (n = 20) were represented by single animals or pairs (Fyodorov and Kanshiev 2003, with additions). In the southern parts of Karelia, only 9.2% (n = 76) of settlements had a single inhabitant (Danilov et al. 2007).

Studies by other zoologists also show that larger beaver families comprising three or even four generations are an indicator that the region is rich in food resources and the population is doing well. The smallest and simplest families live in the northern regions. As example, at the edge of beaver distribution range in the Kola Peninsula, an absolute majority of all settlements comprises single animals, while the share of family colonies was 10–12% (Kataev 2007, 2018). In the southern part of the Russian North-West, the Leningrad Region, the share of single-beaver settlements was 7.0%, while families of six accounted for 57.3% of colonies (Kanshiev 1981).

3. Engineering activity of beavers. Although this paper deals with tree stand alteration under the effect of beaver foraging activity, it is also important to provide some data on the animal engineering activity, since the

construction of lodges and dams makes the wood sparser and changes its species composition. Our previous studies have demonstrated that in Karelia a) the engineering activity of beavers is high; b) under the same orographic, edaphic and hydrological conditions in their habitats (southern Karelia), North American and Eurasian beavers build lodges and dams with equal frequency (Danilov and Fyodorov 2015). The engineering activity of beavers is their response to environmental changes rather than a species-specific display of the building instinct.

Surveys in the strict nature reserve and national park revealed a very high engineering activity of beavers in their territories. All colonies surveyed in 2018 (100%, $n = 31$) had lodges, and almost all colonies occupying creeks (96%, $n = 25$) had dams. Combining these figures with previous data (surveys conducted in 1999 and 2001), the share of colonies with beaver-built structures is nearly 90%, which is slightly higher than in Karelia on average [1]. The main reason for such high level of engineering activity is habitat conditions in the north of Karelia, namely low, water-logged or rocky shores/banks, inexplicit channels of watercourses, and small size of rivers and creeks.

4. Concentration of colonies along roads and power lines. Food supplies in the North being scarce, beavers are forced to settle along roads and power lines. The capacity of beaver habitats is enhanced by changing in the tree and shrub composition after logging and deciduous species regrowth in the right-of-way strips. Almost half of all colonies at watercourses in the Kostomuksha NR surveyed in 2001 and 2018 (25 out of 55, i.e. 45.5%) concentrate along highways, railway tracks, power lines, and other engineering facilities (Fyodorov and Krasovsky 2019).

5. Foraging activity. As many authors from Fedyushin (1935) to contemporary zoologists (Zavyalov 2015, etc.) have indicated, beaver most prefer aspen, willows, and poplar. Yet, the high contribution of these plants to the diet of beavers is not universal. Geographical distinctions in the dietary composition are associated with the local presence/abundance of certain plants. The dominant species in the autumn and winter diet of beavers in the south of the range (Voronezh Region, Belarus, etc.) being aspen, poplar and various willows (Khlebovich 1934, 1938, Fedyushin, 1935, Dyakov 1975, Dezhkin et al. 1986, Papchenkov 2011). Their share declines northwards, while the contribution of birch and grey alder increases. In the Kola Peninsula, birch becomes the primary food item for beavers comprising 97.5% of their diet (Danilov et al. 2007).

A comparison of the roles of two major forest species, aspen and birch, in beaver diet shows that beavers not only consume aspen first, but also clearly prefer thicker trees. The average diameter of beaver-logged aspen trees in our studies was often greater than that of aspen trees left intact. The same was observed by N.A. Zavyalov in the southern parts of Russia (Zavyalov et al. 2005, Zavyalov 2015). In Karelia, beavers consume birch as much as aspen, but, on the contrary, their preference is given to thinner trees, leaving thick trunks intact. In Karelia, 50 to 70% of beaver-logged birch trees were less than 12 cm in diameter. Other authors indicated that the diameter of over 90% of all logged trees did not exceed 12 cm (Hall 1956, Simonsen 1973, Balodis 1990, Szczepański and Janiszewski 1997, Brozdnyakov and Shestun 2005, etc.). A probable explanation is that beaver habitats in their study areas were richer in food supply, with more shrub-like plants to choose from.

It is noteworthy that beavers living in the north of Karelia, exposed to food shortage, must utilize thick birch trees oftener. Other researchers have obtained similar results for the northern taiga (Brozdnyakov 2016).

Therefore, the following features can be highlighted in the alteration of trees stands by the foraging activity of beavers in the northern taiga (primary forests) and the middle taiga (secondary forests).

1. Pristine forests of the northern taiga are very poor in food supply for beavers. Beavers choose to disperse to waterside areas with a higher share of deciduous species. In the KNR and KNP, such habitats occupy less than 1% of the total wooded area. The overall effect of beaver foraging on the forests would be minor; however, the stands inside beaver habitats would be altered much more noticeably than around colonies in the middle taiga:
– primary forests lose 61.4% of deciduous trees, secondary forests lose 26.3%;
– in the north, the scarce aspen gets totally removed from waterside stands, the proportion of conifers in stands is doubled, and the share of birch decreases; in the south of Karelia, on the contrary, the share of birch in the stand increases, while the proportion of aspen is reduced 1.5-fold;
– beavers consume thicker birch more often in the north than in the south that strongly influenced stand structure;
– damaged trees in the north of Karelia have a lower regeneration capacity than in the south.

2. Although the colony size is much smaller in the north of Karelia than in the south, beavers re-occupy abandoned colonies twice or thrice within a short time interval. This is an explanation of the higher share of thick birch trees in the diet of beavers, since they now primarily must consume more accessible rather than preferred foods.

3. The habitat conditions for beavers in the north are near pessimal, so some further decrease in the population size and its stabilisation at a very low level are to be expected in the nearest future.

Acknowledgements

The study was performed under State order #0218-2019-0080 and supported by the RFBR through grant #18-05-00-646-a and the RAS Presidium Programme through grant #0221-2018-0002.

[1] 74.2% of North American beaver colonies had lodges, 76.6% had dams, $n = 124$; the figures for the Eurasian beaver were similar, 70.4 and 74.4%, respectively ($n = 125$) (Danilov and Fyodorov 2015)

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