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The Beaver *Castor fiber* (L.) and *Castor canadensis* (Kuhl) in Finland

The oldest subfossil evidence indicates that the beaver invaded Finland 6500—7000 years ago, at the latest. Beaver declined in numbers owing to heavy exploitation and the very last individual was killed in northern Finland in 1868. Nineteen European beavers were imported from Norway in 1935—36 and 7 North-American beavers from New York State in 1937. The numbers of the latter ones increased rapidly and since 1945 transport to new areas has been possible. The Finnish beaver population was estimated in 1945 at 130—140 individuals, in 1955 at 450—500, in 1960 at 500—600, in 1965 at 1800—3000, and in 1970 at 1800—3200 individuals. Most Finnish beavers are of the North-American type, which seems to reproduce more rapidly owing to its larger litter size (mean 4.7 per litter). The population is densest in southeastern and eastern Finland. Beavers cause damage to forests, mainly by building dams. As a result, in 1970 about 900 hectares of forest was reported as being killed by flooding and in about 1600 hectares tree growth was impaired by the high water level. About 1600 beavers have been harvested during the two last decades, mainly in southeastern and eastern Finland.

I. EARLY HISTORY OF THE BEAVER IN FINLAND

The postglacial history of the Finnish mammal fauna is closely connected with the development of the Baltic Sea and land uplift. When the glacier was melting, most of Finland was at first covered by water, but the land area gradually increased as a result of the uplift. The eastern part of the country was the first to emerge, and since this whole area was separated from Scandinavia and the Baltic countries by a sea far larger than the present one, many terrestrial mammals invaded Finland from the east or southeast.

This was presumably the route used by the beaver, *Castor fiber* fiber
Subfossil evidence of early beaver occurrences in the vicinity of Lake Ladoga and Lake Onega support this view (Andreev, 1963). Probably the oldest subfossil find of the beaver in Finland is an incomplete skull which was estimated by pollen analysis to be 6500—7000 years old (Metsävainio, 1950; Anonymous, 1951). There is also later subfossil evidence of beavers in Finland. Well preserved pieces of wood evidently cut by beavers, have been found in peat. The ages of two samples of this woody material, determined by the C\textsuperscript{14} method, were $4340 \pm 80$ (Lappalainen & Lahti, 1972) and $2250 \pm 70$ years old (Lappalainen & Lahti, 1973).

In Finland, all subfossil finds so far dated fall into the period when the Baltic Sea was in the Littorina phase. In Sweden, on the other hand, the beaver started to invade from the south some 8000 years ago and expanded its range during the Littorina phase of the Baltic Sea (Curry-Lindahl, 1967).

The beaver early became an important fur animal in Finland. It also provided castoreum, valued for medicinal purposes. Regulations relating to beaver hunting included in the first peace treaty between Sweden and Novgorod in 1323 indicate the great importance of this species (Mellander, 1952). Heavy exploitation caused a population decline, which began in southern Finland. During the sixteenth century beaver hunting still seemed to have some importance even in western Finland but by the seventeenth century the decline was obvious even in Lapland. Finally, during the nineteenth century, the original Finnish beaver population was exterminated. The hunters found their way even to the most remote beaver colonies and the very last individual was killed in 1868 on the river Enionjoki in Salla, northeastern Lapland (Granit, 1900). In the very year of its extermination an act was passed giving the species complete legal protection in Finland — perhaps a century too late.

There are many place-names all over the country which refer to the beaver and thus commemorate the original Finnish beaver population. These names also tell of the keen interest of our ancestors in this «wise» and valuable animal. Evidently the beaver had at one time occurred throughout almost the whole country. Owing to the very large number of lakes and numerous rivers and brooks connecting them the country offered suitable habitat for the species.

II. REINTRODUCTION DURING THE 1930s.

Ever since the extermination of the beaver vague plans had been made for its reintroduction, but nothing was done until the 1930s. Suc-
cessful reintroduction of the beaver into Sweden from 1922 onwards (Curry-Lindahl, 1967) may have encouraged the Finns to import live beavers from Norway. There it had survived, thanks to protection already established in 1845 (Myrberg, 1967), and beavers were also despatched to Sweden from Norway.

Records on the first attempt to reintroduce beavers into Finland are not quite complete but from the information we have been able to gather (Lahti & Helminen, 1969) the events may be summarized as follows.

In 1935 altogether 17 beavers, *Castor fiber* Linnaeus were brought from Norway and released in five localities in different parts of the country (Fig. 1). In 1936 two more beavers were obtained from Norway and at first kept in an enclosure. They soon escaped, however, but probably became separated and one of them lived alone until the winter of 1966. Thus this individual, reached the age of at least 30 years, which is perhaps exceptionally high among wild beavers (Helminen & Lahti, 1970).

In 1937 seven North-American beavers, *Castor canadensis* Kuhl were introduced from New York State. These beavers do not represent the original beaver population of northern New York. There, too, species had once been exterminated and later reintroduced by bringing in stock from Canada and Yellowstone, Wyoming. Hence the true geographical origin of the North-American beaver in Finland seems difficult to ascertain (Anonymous, 1937; Bump, 1940). The first North-American beavers in Finland were released in three areas (Fig. 1), two of which were localities where Norwegian beavers had been introduced earlier (within area 2 in Fig. 1).

It was soon obvious that the beavers had acclimatized well and their reproductive performance was good. The beaver stock grew rapidly, especially in Sääminki in southeastern Finland, where two pairs of North-American beavers had been introduced. In 1945 the beavers in that particular area already numbered 130—140 (Linnamiées, 1956). In the same year trapping of beavers was started in that area, and some specimens were transported to other areas, especially in eastern and northern Finland (see Fig. 1). Thus the bulk of the present Finnish beaver population are offspring of two pairs of North-American beavers (Lahti & Helminen, 1969; 1972).

The population of the reintroduced beavers continued to grow during the 1950s and their range expanded around the sites where they had been released, particularly in southeastern Finland. In 1955 Linnamiées (1956) estimated that the number of beavers in Finland was
Fig. 1. The sites of reintroduction and the present range of the beaver in Finland. Black circles, release of European beaver; open circle, release of North-American beaver; semiopen circles, release of both types. Vertical hatching, range of European beaver; horizontal hatching, range of North-American beaver; cross hatching, both types introduced. Long arrows indicate transports of North-American beavers from southeastern Finland. Short arrows indicate natural expansion of the range to the U.S.S.R.

Explanations of the numbers are given in the text.
The beaver in Finland

In Finland in 1814—500 and in 1960 his estimate was 500—600 individuals (Linna- mies, 1961).

III. POPULATION GROWTH IN THE 1960s.

The first national beaver census based on an inquiry was organized in 1965 by the Game Research Institute. The inquiry was sent out to forestry personnel all over the country and each observer was asked to indicate the minimum and maximum number between which the true number of beavers was estimated to be. On the basis of these reports the Finnish beaver population in appeared to be between 1800 and 3000 individuals (Lahti & Helminen, 1969). Most of these beavers were assumed to be of North-American origin. Another inquiry was made 1970, and the population was estimated at 1800—3200 beavers (Lahti & Helminen, 1972). Thus the population growth has evidently slowed down since the first half of the 1960, except perhaps in eastern Finland. The range in 1970 is shown in Fig. 1.

More than half the Finnish beavers live in eastern Finland (area 7 in Fig. 1), which in fact is the only area where the population has noticeably increased since 1965. Another important beaver area is in southeastern Finland in the vicinity of Lake Saimaa (area 6 in Fig. 1). Both these populations consist of pure North-American beavers.

Beaver skulls collected from eastern Finland are of the typical North-American type and so far show no indication of European beavers invading Finland from the adjacent area of the U.S.S.R. On the other hand, North-American beavers are known to have crossed the boundary to the Soviet side in the areas indicated with short arrows in Fig. 1 (Segalli & Orlova, 1961).

As mentioned above European and Canadian beavers have had a change to interbreed in Finland, since in some areas both species were introduced. However, Lavrov & Orlov (1973) have recently shown that European and Canadian beavers have different chromosome numbers and concluded that these two types are evidently different species. Despite copulations no hybrid offspring were born in captivity. The chromosomes of the Finnish beavers have not yet been investigated, but craniological data reveal that the bulk of the Finnish beavers are of Canadian type (Lahti unpublished).

In Sweden the possibility of invaders coming from the Finnish side has caused some concern (Curry-Lindahl, 1967). This intrusion would threaten the racial purity of the Swedish beaver population. In the beaver census carried out in Sweden in 1969 no such intruders were found (Anonymous, 1971). The fact that the bulk of the present Finnish
beaver population are not of the European type should always be kept in mind. We consider it improper to export Finnish beavers to other countries without adequate concern about this fact. For instance, some have recently been sent to Bavaria (FRG) (Anonymous, 1972).

The only population in Finland known to be of pure European type is in the west of the country (area 1 in Fig. 1) (Lahti, unpubl.). It seems totally isolated from the other beaver populations in Finland and is estimated to consist of 40—75 individuals. Protection of this particular population is important.

In general, the growth of the Finnish beaver population after reintroduction has been favourable, although it must be kept in mind that the number of beavers in Finland is only about one third of that in Sweden. The species was exterminated in Sweden in 1871 and reintroduced from 1922 onwards. By 1940 altogether 80 beavers brought from Norway had been released in various parts of Sweden (Curry-Lindahl, 1967). In 1969 the Swedish beaver population was estimated to be 7500 individuals (Anonymous, 1971). We assume that the difference in the present population size cannot be ascribed solely to the larger number of beavers released in Sweden than in Finland but that factors limiting population growth (for instance, hunting) have been more effective in Finland than in Sweden.

IV. HABITAT SELECTION

Most beavers inhabit relatively small lakes. In eastern Finland, with its extensive peatland areas, beavers frequently live in quiet rivers and brooks. Mostly beavers avoid human habitations, but in central and western Finland these animals, if they are not frequently disturbed, are often found close to farms or other buildings.

They prefer woods where hardwood species are dominant but may also occupy a lake with a limited hardwood supply on the shores. However, lack of food may force them to abandon such a lake after a short stay. Even in the best habitat types beavers tend to change their home ranges frequently and, in any case, before they have exhausted the available food supply. Since Finland is still relatively thinly populated with beavers, these local movements present no difficulty. In Norway, on the other hand, beavers frequently occupy areas where the food supply is much more limited (Lahti, unpubl.). This difference may be ascribed to the greater density of the Norwegian population (5000—10000 beavers according to Myrberg et, 1967).

In Finland each family of beavers usually occupies one whole lake or several small ones (Fig. 2). Members of the family may disperse
over a wider area, especially in summertime, but in autumn the parents with their young ones and yearlings reconvene at the main lodge.

V. FOOD HABITS

The food habits of the beaver in Finland have been worked out by Lahti (1966, 1972). Beavers will use almost any of the hardwood species found in Finland, although they show a clear preference for a few species. No particular species of tree seems essential to them and availability affects food selection. Aspen (Populus tremula) and the birches (Betula pubescens and B. verrucosa) are preferred, especially in autumn, when larger trees are felled for the winter food stores. Rowan (Sorbus aucuparia) is in many areas the tree species cut most numerous but owing to the small size of the trees felled the quantity of food obtained may be smaller than that provided by large aspens or birches. Alders (Alnus incana and A. glutinosa) are also frequently consumed (the latter does not occur in Lapland). Willow species, Salix caprea and S. phylicifolia, in particular, are included in the diet of the beaver but their importance as food items does not seem to correspond to their great availability in beaver habitats.
Beavers mainly fell small trees and bushes. The mean diameter of the stems cut in all seasons together is roughly 3 cm. Large trees are usually felled only in autumn for the winter storage. The peak of this food-collecting activity in southern Finland is in October and early November. Lahti (1972) has observed that in one year a carefully studied beaver family felled 1974 stems with an average diameter of only 2.2 cm. Not more than 112 of them had a diameter exceeding 5 cm.

Some signs of feeding on conifers are usually found in each beaver colony but fortunately only a few beavers have developed the habit of debarking the bases of tall pine trees. This debarking injures the trees and causes damage which, from the point of view of forestry, is less acceptable than the felling of hardwood trees close to the shorelines. The beaver prefers to work close to the water. In one area in northern Finland half of the trees felled were taken right from the shoreline (Lahti, 1966). Only exceptionally are trees felled more than 100 metres from the water. The average distance from the shoreline is greatest in autumn when larger trees are felled, and of all the hardwood species aspen seems to be taken from sites farthest from the water.

The bulk of the diet in spring and early summer consists of aquatic plants and their rhizomes as well as of small trees and bushes. Preferred plant species include Nuphar luteum, Menyanthes trifoliata, Calla palustris, Equisetum fluviatile and Carex spp.

VI. DWELLINGS AND BREEDING BIOLOGY

Usually beavers in Finland build mound-shaped lodges on the lake shores or in the middle of ponds above the dams they construct. These lodges are used regularly during the cold seasons, i.e. in southern Finland from September to the end of April. In summertime beavers often live in underground burrows in the shore banks. Only on some rapid rivers are the bank dens regularly used in winter also.

The largest lodges are 3 metres high and cover more than 10 sq. m. One family may have several lodges, which are used alternately. We assume that, for instance, the amount of woody refuse accumulating in front of the lodge may limit access to the lodge and finally lead the occupants to the move to another den. The usual type of lodge built by the North-American beaver in Finland seems to correspond to the »brook lodge« described by Wilson (1971). In this type there is no extensive tunnel system under the lodge.

We have observed that in southern Finland lone beavers may survive
over the winter in small underground dens without any food stores. Reproductively active families tend to build a lodge where the female gives birth to the litter.

We have only scanty data on the breeding biology of the Finnish beavers in nature, mainly collected in connection with spring trapping programmes in the years 1969—71 in eastern Finland (North-American beaver). The young are born in May and early June, which, if pregnancy is assumed to last 105—107 days (Wilsson, 1971), means that copulation takes place in January or February. Breeding in midwinter is successful only if the pair overwinters as a family unit, since wandering in search of a mate would be hazardous to beavers in the northern winter conditions.

The material trapped in spring (see above) included nine pregnant females with an average of 4.7 embryos. One of the females had as many as 8 embryos. The mean weight of the pregnant females, including the embryos, was 23.2 kg (n=9, range 17.0—31.0 kg), that of nonpregnant females 13.0 kg (n=34, range 2.9—21.5 kg) and of males 14.9 kg (n=33, range 5.7—26.0 kg). According to Hinze (1950), the mean weight of adult males of North-American beaver is 15.1 kg and that of adult females 15.3 kg. The mean weight of yearling males was reported to be 8.1 kg and that of yearling females 7.4 kg. Our data are in good accord with the values given by Hinze, since among nonpregnant females there were evidently some yearlings in our material.

In Finland the population of the North-American beaver has evidently grown faster than that of the European beaver. This difference may partly, at least, be ascribed to the higher reproductive rate of the North-American beaver due to its larger litter size. Deshkin (1957, cited by Wilsson, 1971) pointed out that the European beaver has smaller litters than the North-American subspecies. Hinze (1950) reported that the European beaver usually has 2—3 young in a litter, 4 young per female being exceptionally high. Wilsson (1971) indicates that in a study area in Sweden beavers have usually had only 2 young per litter and never more than four.

The average number of embryos (4.7) in our material supports the view that the reproductive rate of the North-American beaver in Finland in higher than that observed elsewhere in the European beaver. Our data are still scanty, however, and we have no data on the pure European type in Finland.

The difference observed in the population growth between the two species of beavers cannot be ascribed to differences in habitat or food, since both habitat selection and food habits are much alike.
Some exceptionally late litters have been observed in the North-American beaver in Finland. Females not becoming pregnant during the first oestrus may repeat the cycle and become pregnant later, as was found with captive female beavers more than 5 years old by Krüger (1963). In these cases the young may be born in late summer or even in autumn.

VII. DAMAGE PROBLEMS, HUNTING AND THE FUTURE OUTLOOK FOR THE BEAVER IN FINLAND

The main damage caused by beavers in forests is due to their building dams. The value of the trees they fell is relatively small compared with that of the trees killed by flooding in beaver ponds. According to the inquiry of 1965 some 800 hectares of forest was actually flooded and in some 1900 hectares the growth of the trees was impaired by the raised water level (Lahti & Helminen, 1969).

In 1970 the figures were 900 and 1600 hectares, respectively (Lahti & Helminen, 1972). Spruce (Picea excelsa) is particularly sensitive to flooding and dies within two years even in shallow ponds. In some forest drainage areas in the peatlands of eastern Finland beavers have been especially troublesome building dams in the ditches and thus counteracting man's attempts to lower the water table. It is obvious that forest drainage has created some new habitat for the beaver, at the same time introducing a new conflict situation between wildlife conservationists and forestry experts.

Flooding damage can be controlled to some extent by penetrating the dams with long water pipes, spraying repellents on the trunks of trees that are to be protected (Raja et al., 1972) and controlling the population by live trapping and hunting. The beaver (including its lodges and dams) is protected by law in Finland but in areas with a high population density where substantial damage is caused levying of the beaver population has been allowed during short open seasons (in eastern and southeastern Finland) on a special licence basis. Approximately 1600 beavers have been shot or trapped since their reintro-

duction.

The outlook for the future of the beaver in Finland is good. The reintroduced populations are well established and already sustain some limited harvesting. In the absence of predators regulating their density man will have to control their numbers. We have good reason to believe that this control will aim at maintaining a beaver density appropriate to the needs of both forestry and wildlife conservation.
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Streszczenie

БОБРЫ В ФИНЛЯНДИИ

Резюме

Ископаемые остатки указывают на то, что речные бобры поселились в Финляндии самое позднее 6500—7000 лет тому назад. Из-за высокого промысла численность бобров снизилась, и последний зверек был убит на севере Финляндии в 1868 году. В 1935—1930 годах из Норвегии было доставлено 19 речных бобров, а в 1937 году из штата Нью-Йорк 7 американских бобров. Численность последних резко увеличилась и с 1945 года стал возможен их перевод в новые районы (Рис. 1). Учет численности финской популяции бобра указывает, что в 1945 году было 130—140 особей, в 1955 — 450—500, в 1960 их было 500—600, в 1965 году — 1800—3000 и в 1970 — 1800—3000 зверьков. Большинство финских бобров является североамериканского типа, причиной этого можно считать большую величину их помета (M = 4,7 особей в помете). Популяция наиболее многочисленна в юго-восточной и восточной части Финляндии. Бобры приносят вред лесам, главным образом, благодаря постройкам плотин. В результате этого, согласно сообщениям, в 1970 году около 900 га леса было уничтожено наводнением и около 1600 га растущих деревьев было повреждено высоким уровнем воды. За последние два десятилетия добыто около 1600 штук бобров, в основном, на юго-востоке Финляндии.