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The Beaver, Castor fiber Linnaeus, 1758 in Sweden -Extermination and Reappearance

Castoriana IV.

[With 3 Figs.]

The beaver invaded Sweden about 6000 B.C. During the following millenia it expanded to suitable habitats all over the country. At the climatic change in about 500 B.C. the beaver was favoured by a swamping up of vast forest areas. Until the 13th or 14th century the beaver still occurred throughout Sweden, but already at that time it seems to have become scarcer in the three southernmost provinces. In other parts of Sweden beavers were common in the 15th and 16th centuries, but in the 17th century the number of exported skins went down. In the following two centuries the beaver decreased rapidly, and in 1871 the last individual was killed. A series of reintroductions was initiated in 1922 and continued until 1940, when about 80 beavers, all originating from Norway, had been released in various parts of Sweden. These operations were successful. A census in 1961—1963 indicates that the population has increased to 2,206 individuals. The species enjoys total protection. Dispersal from the areas, where introductions were made, have generally followed the rivers downwards. Spectacular expansions have occurred in some areas. The ecology and biology of the Swedish beavers are summarized. The only actual menace to the population is by extensive water-regulations in lakes and rivers. Future immigration by Castor canadensis from Finland may become a threat to the pure Scandinavian population of C. fiber.

I. INTRODUCTION

Though the beaver is dependent on foliferous trees for food and constructions of barrages and lodges, it is in Scandinavia essentially an animal of the great conifer forests, the Scandinavian taiga. During about 8000 year the beaver has contributed a great deal to the present "landscape architecture" of the northern lands. Many of the bogs, muskegs, marshes and fens in Scandinavia's coniferous forests have in the past expanded due to beavers' dam constructions, which can hold back enormous quan-

tities of water. In this way vast areas of forests became inundated and evolved to the peculiar type of swampy woodland of spruce and willows, which today are so common in the taiga. Hence the hydrology and water conservation of many present bogs and marshes in coniferous Scandinavia are results of beavers' work in the past. Probably there is no other mammal in Sweden except man that in postglacial time has altered the landscape in such a large scale as the beaver.

II. HISTORY

About 6000 B.C. the climate in Sweden was dry and mild. Deciduous forests dominated. At this period several mammals invaded Sweden from Denmark using the then existing land bridge. We know from fossils that the beaver was among them. Others were wild cat, lynx, bear, fox, badger, red deer and roe deer. The beaver settled along the water courses, and was apparently much favoured by the landscape which at that time was incredibly rich in aquatic habitats.

During 5000 years the climate remained warm but became moister. The mean temperature was several degrees higher than in present time. The beaver expanded and apparently increased its range up to northern Sweden. About 500 B.C. the climate changed to coolness. The July mean temperature decreased with about two degrees, and humidity increased. During the following 1500 years the water level in lakes, marshes and bogs rose and swelled over vast forest areas. This swamping up of the country must have favoured the beaver, that spread into the interior of the northern forests and probably during this period, if not earlier, conquered the whole of Sweden below the tree limit. This optimal status of the beaver came to an end, when man began to exploit it.

At an early time man in Sweden discovered that the beaver was a precious animal: its flesh was estimated, its skin became famous and the castoreum from the anal glands had a high value for medical purposes.

A very great number of geographical names all over Sweden refer to beavers and indicates how common the animal was before and during the Middle Ages. These names are particularly numerous in northern Sweden, where the beaver population must have been very dense. Such names are scarce in southernmost Sweden (from where fossils of beavers are known), probably because the beaver became exterminated or very rare at an early stage in this part of the country. Already in the 10th century the export of beaver skins from Scandinavia had developed. During later centuries taxes in Sweden were paid with skins of beaver. Provincial laws from the 13th century stipulate the rights of the land owners to beavers and their huts. In 1574 3,384 beaver skins were

exported from the harbour of Stockholm alone, in 1641 they were 2,088. From many other Swedish harbours beaver skins were shipped out as well. The consumption of beaver skins within Sweden was certainly even greater, because the demand was very high.

Obviously it was the enormous hunting pressure on the beaver and not changements of habitats that wiped out the beaver in Sweden. The chronology of the beaver's extermination is as follows.

Still during the 17th century large quantities of beavers were killed, but in the following century it became clear that the population did not withstand such a toll. In the middle of the 18th century it was reported that the beaver had decreased and withdrawn to distant and remote areas (Gisler, 1756). Already before that time the beaver had apparently become exterminated in the three southernmost provinces, Scania, Blekinge and Halland. In the 18th century the species disappeared from most of the provinces in southern Sweden. Only some few, scattered groups remained in this part of the country. In Småland the last strongholds ended in the beginning of the 1800ies, in Värmland in 1834, and in Dalecarlia in 1842. This was the end of the beaver in Sweden south of 62°N.

In northern Sweden the remains of the formerly so rich beaver population was locally given a few more decades of existence. However, it did not last long before these northern beavers too were gone, and in most areas it was even exterminated before 1850. The last beavers in Medelpad, Härjedalen and Norrbotten were killed in the 1840ies, in Ångermanland in 1854, in Swedish Lapland in 1864, and in Västerbotten in 1869 or 1870. The very last Swedish beaver was killed in the province of Jämtland in 1871. Two years later the species became protected in Sweden, about 100 years too late!

The Swedish beaver population was exterminated incredibly fast, in less than 300 years, due to a merciless persecution for profit. A valuable natural resource was wiped out without any thought of the future.

III. THE PERIOD OF REINTRODUCTIONS

Fortunately, the Norwegians were more careful with their beavers. A private landowner, Nicolai Aall, gave protection to the beaver already in the beginning of the 1840ies. In 1845 the beaver became protected by law in Norway for 10 years. By this protection the Scandinavian population of the beaver was saved. It was also the background to the recovery of the species in southern Norway (Olstad, 1937) as well as the basis for the following reintroductions in Sweden as well as in Finland and Latvia.

By cooperation between the Nordiska Museum and Skansen in Stockholm and conservationists in Jämtland, the province where the last Swedish beaver was killed, the species was reintroduced in 1922 in the river Bjur ("bjur" is the old-Swedish name for beaver) in northwestern Jämtland. Two beavers were successfully released there (Festin, 1923). In 1925 and 1934 other beavers from Norway were released in the same river (Faxén, 1935). During the following decade the beavers spread along the river Bjur and some of them invaded another river system situated more northward and also called "Bjur" since ancient time. They settled there and in 1947 a thriving colony had been established (Curry-Lindahl, 1948 a). Since the first reintroduction of beavers in 1922 many more have followed. In the period 1924—1939 beavers were released in 19 different areas in the following provinces: Småland, Västergötland, Västmanland, Närke, Värmland, Dalarna, Härjedalen, Jämtland and Swedish Lapland (Faxén, 1935, Fries, 1940). Most of these reintroductions and all of those made in northern Sweden have been successful and have led to reproduction and establishment of sedentary populations as well as dispersal to other neighbouring areas.

In the 1940ies the expansion of the beaver continued. The last introduction was made in 1940. During 18 years (1922—1940) about 80 beavers, all from Norway, had been released.

In 1931 the number of beavers in Sweden was estimated to 180 (Geete, 1932) and in 1935 to more than 400 (Faxén, 1935).

IV. DISPERSAL AND PRESENT DISTRIBUTION

In 1930 beavers were detected in the Fax river system in Angermanland, where they must have come from one of the introductions in Jämtland. During the following years the Fax and Ångerman river systems became the scene of a rapid colonization of beavers and a spectacular population increase resulting in a wide dispersal also southwards to the province of Medelpad. Apparently the species had found an optimal habitat in this area. This happy situation ended in tragedy when at the end of the 1950ies the rivers were regulated for a hydro-electric scheme. In winter the water level was drastically changed from one day to another which caused a catastrophe for the beavers. Rescue operations tried to save the starving animals and to release them elsewhere in the same province (von Post, 1958; Wilsson, 1959; 1960; 1961; 1964). The legal protection of the beaver is meaningless if the habitats, lodges and store food supplies are destroyed or washed away during the winter. Thanks to the conservation work in Angermanland the bulk of the beaver population has been saved.



Fig. 1. Map of Sweden showing the various provinces to which data in the text refer.

Also in other areas the expansion of the beaver during the 1940ies continued. Thanks to the beaver's tree cutting and building activities it was rather easy to detect where new colonies had been established. Apparently beavers can travel widely from areas where population pressure releases emigration, because at the end of the 1940ies beavers appeared in provinces situated far from the areas where introductions had taken place. In 1947 the beaver arrived in Södermanland and settled there (Curry-Lindahl, 1948b; 1949), in the beginning of the 1950ies it occurred in Östergötland and in Västerbotten (Curry-Lindahl, 1955) and in 1965 in Norrbotten.

Population estimates of the beaver in Sweden during the last 25 years have been based on reports regularly received by the Swedish Society for Protection of Nature (Svenska Naturskyddsföreningen). In the beginning of the 1950ies the population was estimated to about "several hundred animals" (Fries, 1953) and in 1955 to about 500 animals (Curry-Lindahl, 1955). These figures do not seem to correspond with the estimate in 1935, "more than 400 animals" (cf. p. 4), and are probably too conservative.

In 1957 about 500 animals were reported from Ångermanland and a local census in Värmland resulted in about 550 animals (Lundberg, 1958).

In 1959 local estimations in the Fax river system gave about 250 beavers (Wilson, 1959), to which about 600 individuals from other areas in Angermanland, several hundred pairs in Värmland and scattered populations in other areas have to be added. All together this gives a total population of much more than 1000 beavers (Curry-Lindahl, 1960).

Gradually as the beaver increased considerably it became difficult to follow the situation in detail. Therefore, in 1960 the author suggested to the Swedish Society for Conservation of Nature to undertake a census of the beaver in Sweden in cooperation with the Royal Board for Crown Lands (Kungl. Domänstyrelsen) and the Swedish Sportsmen's Association (Svenska Jägareförbundet). This proposal was carried out in 1961 except in Medelpad and Ångermanland where it was done in 1962—1963. Preliminary counts were made during the spring and summer but the main census was made in the autumn (October and November), when the beavers are busy getting and storing food for the winter and therefore concentrated to their home ponds.

The material of the census has been compiled by Lundberg, Pettersson & Weinberg (1965). The figures obtained must be interpreted as indicative, due to the difficulties of making exact counts of an aquatic mammal dispersed over vast areas. According to the census there

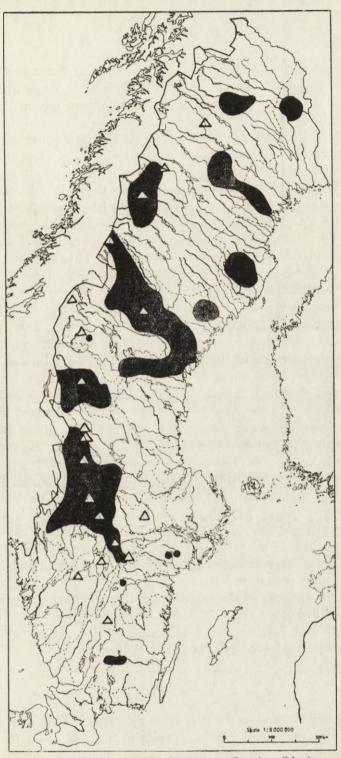


Fig. 2. The present distribution of the beaver in Sweden (black areas and dots). Triangles indicate localities where beavers have been introduced during the period 1922—1940.

are 2,206 beavers in Sweden. The map shows that there are two major concentrations, a northern one in the provinces of Ångermanland (871 beavers) and Jämtland (438 beavers) and a southern one in the province of Värmland (654 beavers) — Fig. 2.

The present distribution of the beaver in Sweden is, of course, partly determined by the location of previous introductions. Most of the introduced beavers were released in localities situated rather far away from the main river courses but connected with them by the same water system. The dispersal from the original areas has generally followed the rivers downwards. Colonies have first been established along smaller tributaries but as the expansion continued, beavers settled along larger tributaries, and finally in the main rivers. An outstanding example of this dispersal pattern is what happened in Ångermanland. In 1925 two beavers were introduced in the vicinity of Görvikssjön in eastern Jämtland. Five years later beavers were discovered in the river Fråstan in western Ångermanland, about 20 km as the crow flies from the site of introduction. If the beavers moved direct from one area to another they must have travelled about 10 km on land. If they followed the water courses, they must have made a big detour of about 60 km.

The Fråstan river is a tributary to the Fax river which in its turn is the main tributary to the Angerman river. Having colonized the Fråstan river, beavers moved down to the Fax river to settle there and later to move on to the Angerman river (cf. p. 4). As soon as the major rivers were reached, the beavers did not show any tendencies to occupy minor tributaries which they met during their dispersal downwards. This means that in Angermanland the colonization concentrates along the shores of large rivers even close to human settlements. Today this area is the centre of beavers occurring in Sweden. Thus one pair of beavers introduced in 1925 has 38 years later increased to a population of about 871 individuals. Some beavers may have arrived to Angermanland from other areas which may reduce the figure given above, but on the other hand the increase of the beaver in eastern Jämtland is also the result of the two beavers introduced there in 1925. Already 14 years later the population in that area had increased to about 100 individuals (Brehm & Ekman, 1955), an incredibly rapid multiplication.

V. ECOLOGY

The ecology and biology of the beaver in Sweden do not in general differ from what is known for this species in the coniferous forest region of northern Europe. Works by Gisler (1756), Wibeck (1928), Fries (1940; 1944; 1947; 1953), Brehm & Ekman (1955), Curry-

-Lindahl (1955; 1963; 1965), von Post (1958), Wilsson (1960; 1961; 1962; 1964) have deal with the ecology and biology of the beaver in Sweden.

Wooded areas within the coniferous forest region but with foliferous trees, particularly with *Populus tremula*, *Salix caprea* and *Betula pubescens*, surrounding slowly running watercourses are habitats frequented by the beaver. However, lodges are usually built beside a pond with stagnant water, which may have been dammed up by the beavers.

At present no beaver colonies in Sweden are known from the subarctic birch forest region, but many geographic names bear witness that in the past and before the extermination during the 18th century beavers occurred also above the conifer tree limit. One of the introductions in 1924 was made in what had the reputation to be an ancient beaver land near the Lake Tärna, situated in the subarctic belt of southern Swedish Lapland. In 1935 about 50 beavers were reported from that area (E k m a n, 1944), but during the following five years the whole population disappeared by unknown reasons. No signs of emigration were observed. Severe winters may have wiped out this population entirely.

The food of the Swedish beavers is chiefly fresh bark of foliferous trees, especially of Populus tremula, Salix caprea, S. aurita, S. cinerea, S. glauca, S. lapponum, S. pentandra and Betula pubescens. They also eat buds, shoots, twigs and leaves of these trees as well as roots, stems and leaves of grass and flowering plants like Epilobium angustifolium, Filipendula ulmaria, Geranium silvaticum, Rumex acetosa, Comarum palustre, Lysimachia vulgaris and several aquatic species. Own excreta are regularly eaten.

Beavers greatly affect the environment of their habitats by constructions of dams and canals, irrigations and tree cutting. The cutting operations are mostly made close to the shores but in some areas as far as about 100 m from the nearest water.

The predation on beavers by carnivores is without doubt negligible. The lynx (Lynx lynx) is, of course, a potential predator on beavers, but usually it does not frequent aquatic and swampy habitats. Man is the beaver's worst enemy. Though totally protected, beavers are locally threatened by extensive water regulations of rivers and lakes for hydroelectricity, which interfere violently with the activities of the species. Beavers are almost every year caught in fish-traps and gill-nets, and in this way drowned.

VI. BIOLOGY

The beaver is chiefly nocturnal, but in areas where it is not disturbed it may be active by day as well. I have watched beavers in clear sunshine

while they were cutting trees, feeding and repairing barrages. If the wind did not carry warning smells to the beavers they continued to work without being disturbed. Several observations have given me the impression that by day the beavers chiefly rely on their olfactory sense and do not react very much to what they may see or hear. However, by night the beavers react to strange sounds. By day, sudden movements of foreign objects, for instance human beings, may scare them, but human sounds may be ignored. Once in Jämtland while watching two swimming beavers I shouted. The beavers reacted in different ways. One sank deeper down in the water, changed its direction and swam straight on towards the shore where it disappeared. The other one continued to swim slowly in the middle of the stream as if nothing unusual had happened. None of them gave any warning signals by tail clapping.

This latter behaviour is characteristic for beavers. The movement is so swift that it is rather difficult to observe in detail how it is performed. Initially there is an upward movement of the tail, so that its upper side may clap the water at the same time as the animal starts diving. By several observations of wild beavers I had got the impression that it was always the dorsal side of the tail that produces the blow against the water surface. However, by later observations I found that there are three different ways in which the tail claps against the water, though the movements are invariably the same (Curry-Lindahl, 1955). Most often it is the underside of the tail that claps the water, but claps of only the upper side or both sides in succession may also occur (Curry-Lindahl, 1963). This variation depends on the body's position in the water at the moment when the animal dives and simultaneously performs the tail clapping. These movements have been illustrated by Wilsson (1964), but he does not describe either the double-clapping or the single one by the upper side of the tail (Fig. 3).

The tail clapping is the most often heard sound from beaver colonies, but the adult animals also produce growling, hissing and grunting sounds. Kittens have a rather rich vocabulary.

Swedish beaver lodges vary greatly both in shape and size. There are three types of beaver cabins: 1. Houses or lodges of poles, sticks, twigs, slices of bark, turf and mud, sometimes also flat stones and in winter snow, which the beaver carries to the house. 2. Holes or cavities in river banks overbuilt with branches and having an underwater entrance. 3. Similar holes but with the entrance above the water surface.

By the census 1961—1963 data were also obtained concerning the various types of beaver cabins. There were 455 used sites of category 1, 126 of category 2 and 28 of category 3. 180 lodges of category 1 were not inhabited.

The population of 871 beavers in Ångermanland corresponds to 173 houses (= 5 beavers per site), the one of 654 beavers in Värmland to 204 houses and holes (= 3.2 beavers per site) and the 438 beavers in Jämtland to 140 houses and holes (= 3.1 per site).

These figures have to be considered with care, but it is interesting to compare them with what we know about litter sizes and numbers of beavers inhabiting a cabin. There are usually 1—3, seldom up to 5, young in a litter. They are born in May—June, when the male and the young from the previous years temporarily leave the cabin. They soon return which means that a beaver family occupying a cabin is mostly composed of two adults and two litters, e.g. usually 3—5 individuals. This figure corresponds rather well with the average figures mentioned above for cabins in three Swedish provinces.

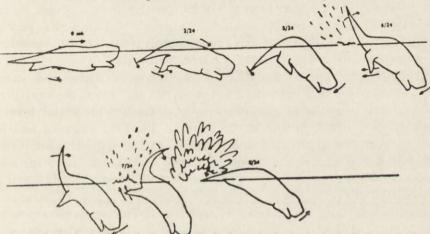


Fig. 3. The tail clapping movements in the beaver when diving after having been alarmed. The figures indicate the time in seconds. After L. Wilsson (1964).

Copulation in Swedish beavers takes place during the late winter, presumably in February and March. The gestation period in Castor fiber is reported to be either 6—9 weeks or 3—4 months. This difference suggests a delayed implantation. In Swedish beavers the gestation period is about 105 days. The kittens may be born either with open eyes or blind. In the latter case they open within 8 days. The young leave the cabin temporarily already at an age of one month and undertake regular feeding excursions at an age of $1^{1/2}$ —2 months. Hence they can swim at an early stage, but during their first months the fur becomes wet in the water and it takes a considerable time before it dries. Therefore the kittens are sensible to low temperatures and mostly remain in the cabin during the critical period.

The young remain with their parents in the same cabin until they are two years old. Apparently two-year-old beavers quit the lodge by innate urge or are driven forcibly from it by the parents. Whatever the direct reason may be it certainly is of survival value. It prevents over-browsing and overpopulation within a limited area, thus adjusting the population to the carrying capacity of the vegetation and avoiding a rapid depletion of the food resources.

The female is sexually mature at least at an age of $2^{1/2}$ years but pair formation may take place somewhat earlier. Probably the sexes keep together for lifetime. At an age of 3 years the beaver is fullgrown and weighs more than 20 kg. The maximum weight is 33 kg.

Cabins usually consist of one, two or three compartments: a "dining room" with water basin, a "living room" and a "bedroom". The latter two may be combined. Each family has its own territory, though several families use the same feeding grounds and have unrestricted passage along the water ways. The lodges vary in length from 5 to 10, sometimes 15 m. with a width of 2—3 m. and a height of 1—2 m.

The material for the construction of barrages of dams and canals consists of tree trunks, branches, twigs, earth and mud. Several dams can be created by the same family in order to control the water level in relation to the cabin entrance, the shores, the food storages and the canals used for transports of trunks. The length of the barrages differs widely in relation to the topography. Longer barrages than 15 m. seem to be uncommon in Sweden. The height is isually about 1 m. but can be considerably higher.

As mentioned above the beaver is territorial. Though both sexes are equipped with anal glands containing castoreum, it seems according to Wilsson (1962) that only females inspect and mark the territories with castoreum and defend them against trespassers.

In Sweden beavers are obliged to gather and accumulate food for later consumption during the winter. This work is done during the late summer and the autumn months by collecting branches and twigs, which are stored inside and outside the cabin. In the latter case the stored food is anchored in the bottom of the dam, lake or river.

VII. PROTECTION

In Sweden the beaver is totally protected. People's attitude to this species is friendly and there is hardly any illegal hunting or damage to beaver constructions, though there are occasional complaints concerning damage to forests by water logging. The reintroductions in 1922—1940 were in many cases results of private initiatives through collecting of money.

As mentioned earlier in this paper the most serious threat to the beaver comes from the destruction of habitats, cabins, dams and food storages by water regulations for hydroelectric purposes which may comprise extensive parts of a water system.

All beavers in Sweden and Norway belong to the species Castor fiber (Linnaeus, 1758). Due to numerous introductions of C. canadensis (Kuhl, 1820) in Finland and the U.S.S.R. this species may be expected to reach Scandinavia in the future. In the long run this would be the end of a pure Scandinavian population of C. fiber. Even if this species and C. canadensis are closely related and even may be conspecific, it would scientifically be a pity to mix the two forms which have been separated during so long a time, particularly since it is only the small populations of C. fiber in Scandinavia, central Germany, Poland, Switzerland and southern France which represent this species outside the European areas, where C. canadensis has been introduced or is advancing westwards.

In 1965 the author suggested to the State Game Research Institute of Finland that the introduction of *C. canadensis* in northern Finland should not be allowed in order to avoid immigrations of this species into Scandinavia.

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БОБР, CASTOR FIBER LINNAEUS, 1758 В ШВЕЦИИ — ИСЧЕЗНОВЕНИЕ И ВОЗРОЖДЕНИЕ

Резюме

Бобр заселил Швецию около 6000 лет до н. э. На протяжении последующих тысячелетий вид расселился по подходящим местообитаниям по всей стране. Во время климатических изменений, которые имели место около 500 лет до н. э., бобр оказался приуроченным к болотистым залесненным местам. Вплоть до XIII или XIV века бобр все еще встречается по всей Швеции, но уже к этому времени он становится все более редким в трех южных провинциях. В других частях Швеции бобр остается обычным в XV и XVI веках, но к XVII веку количество экспортируемых шкур резко пошло вниз. За последующие два столетия численность бобра подвергается выстрому сокращению и, наконец. в 1871 г. был добыт последний зверь. Ряд реинтродукционных мероприятий был начат в 1922 г., которые продолжались до 1940 г., когда 80 бобров, происходящих из Норвегии, были

расселены в различных частях Швеции. Эти мероприятия оказались успешными. Таксация 1961—1963 гг. показала, что численность животного возрасла до 2206 экз. Вид находится под полной охраной. Распространение вида из мест, куда он был первоначально вселен, в основном, идет вниз по рекам. В некоторых местах были обнаружены факты переселения. Подводятся итоги изучения экологии и биологии шведского бобра. Единственным отрицательно влияющим фактором на бобровое население является зарегулирование стока озер и рек. Продолжающееся переселение Castor canadensis из Финляндии может сказаться на чистоте скандинавской популяции С. fiber.

Kai CURRY-LINDAHL

BOBR W SZWECJI — WYNISZCZENIE I REAKLIMATYZACJA

Streszczenie

Bobry pojawiły się w Szwecji około 6 000 lat p.n.e. W ciągu następnych tysiącleci rozprzestrzeniły się w odpowiednich biotopach na terenie całego kraju. Zmiany klimatu jakie zaszły około 500 lat p.n.e. spowodowały wytworzenie się dużych obszarów wilgotnych lasów, co sprzyjało bytowaniu bobrów. Aż do XIII i XIV w. bóbr spotykany był w całej Szwecji, lecz w tym czasie wydaje się być rzadszy w trzech najbardziej południowych prowincjach. W pozostałych częściach Szwecji bobry były pospolite jeszcze w wieku XV i XVI, ale już w XVII w. ilość eksportowanych skórek ulega obniżeniu. W ciągu dwóch następnych stuleci liczebność bobra szybko spada a w roku 1871 zabity został ostatni osobnik. Reaklimatyzacja, rozpoczęta w 1922, kontynuowana była jeszcze w 1940 roku, kiedy to wypuszczono w różnych częściach Szwecji 80 bobrów pochodzących z Norwegii. Zabiegi te zostały uwieńczone sukcesem. W latach 1961—1963 stwierdzono, że populacja wzrosła do 2206 osobników. Bobry pozostają pod całkowitą ochroną. Obserwuje się, że bobry zasadniczo rozchodzą się z terenów gdzie były wypuszczone, w dół rzek. Opanowują one też tereny gdzie nie były wypuszczane. Przedstawiono dane o biologii i ekologii bobrów w Szwecji. Jedyna obecnie groźbą dla populacji bobrów jest szybka regulacja jezior i rzek. Przyszła imigracja Castor canadensis z Finlandii może stanowić niebezpieczeństwo dla czystości skandynawskiej populacji C. fiber.