

COMEBACK OF THE BEAVER *Castor fiber*: AN OVERVIEW OF OLD AND NEW CONSERVATION PROBLEMS

Bart A. Nolet & Frank Rosell

Abstract

Due to over-hunting c. 1200 Eurasian beavers Castor fiber survived in eight relict populations in Europe and Asia at the beginning of the 20th century. Following hunting restrictions and translocation programmes in 15 countries, the Eurasian beaver became re-established over much of its former range, and presently numbers c. 430000. The translocated populations often consist of a mixture of geographical forms. Preservation of the original, unmixed populations has therefore top priority: all five in Europe have reached the assumed minimum viable population size of c. 1880 animals each, but the three in Asia are still endangered. Their protection should be carried out at the level of river catchments. Nowadays the main threats for beavers are habitat destruction and introduced North American beavers Castor canadensis. On the other hand, growing beaver populations cause increasing conflicts with man, and population and/or damage control may therefore be required. In view of these two very different problems, we conclude that the conservation of beavers is best served by preservation and restoration of riparian woods with intact natural water regimes.

Keywords: Conservation biology, reintroduction, translocation, population control and damage control.

INTRODUCTION

The Eurasian beaver *C. fiber* was once widespread in Europe and Asia, inhabiting the forest zones but also wooded river valleys reaching into the tundra and steppe zones (Zharkov and Sokolov, 1967; Djoshkin and Safonov, 1972). However, at the beginning of the 20th century only eight small populations with a total of c. 1200 beavers were left. The beaver was apparently first exterminated from the south of its range, since in

Portugal, Spain, Greece, Turkey, Azerbaijan and Iraq only sub-fossil finds have been recorded (Boessneck, 1974). The beavers subsequently disappeared from Italy and Britain in the 16th century. In most countries the last beaver was killed in the 19th century (Table 1).

The main cause for the near disappearance of the beaver was, without doubt, over-hunting. Beavers are easily located, especially in autumn when they fell trees and build or repair their lodges, dams and food caches, or during ice-cover in winter. The beaver was mainly hunted for its fur (pelt), the chemical substances from its castor sacs (castoreum, used as a medicine and a base aroma in perfume), and its meat (Djoshkin and Safonov, 1972). The tail was prepared like fish to be eaten on Fridays (Nolet, 1994).

Fortunately, a series of management measures led to a remarkable recovery of the beaver. At first, starting in 1845 in Norway, hunting was prohibited in all countries which still retained beaver populations, although in some cases (Finland, Sweden) the protection came too late (Table 1). Subsequently, many beavers were translocated to restock vacant areas. The first reintroduction took place in Sweden in the 1920s. Later reintroductions or translocations were conducted in (in chronological order) Norway, Russia, Latvia, Finland, Germany, Poland, Lithuania, Switzerland, Estonia, Mongolia, France, Austria, Netherlands, and the Czech Republic (Table 1). The early reintroductions were aimed at the re-establishment of a game species to be harvested for its fur. From the 1970s onwards, the animals were reintroduced more and more for ecological reasons, i.e. because of the significant impact beavers can have on their surroundings in being able to fell mature trees and modify water levels (Djoshkin and Safonov, 1972; Kollar and Seiter, 1990; Nolet, 1994). Although a number of these reintroductions failed because not enough animals were released, most gave rise to viable beaver populations (Macdonald *et al.*, 1995). However, because not much attention was paid to the origin of the founders, many of the translocations resulted in a mixture of beavers of different geographical forms.

Now the Eurasian beaver is slowly becoming re-established over much of its former range owing to two

Table 1. The history and present status of beavers (*C. fiber*) in Europe and Asia

Country	Extirpation		Protection	Reintroduction	Present population size	References
Austria	1869	—		1970-90	130	Sieber (1989); Kollar and Seiter (1990)
Betarus	Remnant	1922			14 000	Djoshkin and Safonov (1972)
Belgium	1848				1	Huijser and Nolet (1991)
Britain	16th century			Proposed	0	Macdonald <i>et al.</i> (1995)
Croatia	?	—		Under investigation	0	
Czech Republic				1991	6	Schwab <i>et al.</i> (1994)
Denmark	7	—		Under investigation	0	
Estonia	1841			1957	4000	Laanetu (1995)
Finland	1868	1868		1935-37	800	Ermala <i>et al.</i> (1989); Lahti (1995)
France	Remnant	1909		1959-95	5000	Richard (1985, 1986); Macdonald <i>et al.</i> (1995)
Germany	Remnant	1910		1936-40, 1966-89	4000	Heidecke (1984); Schwab <i>et al.</i> (1994); Macdonald <i>et al.</i> (1995)
Hungary	1865				30	Kollar and Seiter (1990)
Italy	1541				0	Djoshkin and Safonov (1972)
Latvia	1871			1927-52	50 000	Balodis (1992, 1995)
Lithuania	1938			1947-59	14 000	Palionene (1965); Mickus (1995)
Mongolia and China	Remnant			1959-85	800	Lavrov and Lu Hao-Tsuan (1961); Lavrov (1983); Stubbe and Dawaa (1983, 1986)
Netherlands	1826			1988-95	70	Stoltenkamp (1986); Nolet (1994, 1995)
Norway	Remnant	1845		1925-32, 1952-65	50 000	Djoshkin and Safonov (1972); Ermala and Lahti (1995); Rosell and Parker (1995, 1996)
Poland	1844	1923		1943-49, 1975-86	5000	Zurowski and Kasperczyk (1988); Zurowski (1992); Macdonald <i>et al.</i> (1995)
Russia	Remnant	1922		1927-33, 1934-41, 1946-64	170 000	Djoshkin and Safonov (1972); Safonov (1975); Lavrov (1983)
Slovakia	?					Kollar and Seiter (1990)
Sweden	1871	1873		1922-39	100 000	Freye (1978); Hartman (1994a, 1995b)
Switzerland	1820	?		1956-77	350	Stocker (1985); Macdonald <i>et al.</i> (1995)
Ukraine	Remnant	1922			12 500	Djoshkin and Safonov (1972); Lavrov and Lavrov (1986)

factors: (1) the natural habitat is still present in some areas, and (2) the beaver is so plastic that it can survive and reproduce in the cultivated landscape (Heidecke, 1992). The Eurasian beaver presently numbers an estimated 430 000 in Europe and Asia. In large parts of the continent, the number of beavers is still increasing, despite the fact that most of the natural habitat has disappeared: forests have been cleared or taken into production, many wetlands have been drained and water-courses regulated. The spread of beavers into this man-made landscape leads or will lead to conflict with man. In several countries the populations of beavers are strong enough to be harvested and hunting is again allowed. In other countries where hunting is not permitted, other measures to control the population and limit damage by beavers may have to be considered in order to keep public opinion in favour of beavers.

TAXONOMY AND SPECIES CHARACTERISTICS

The genus *Castor* consists of two species: the Eurasian beaver *C. fiber* and the North American beaver *C. canadensis* which have different numbers of chromosomes ($2N = 48$ and 40 , respectively), following Robertsonian fusion of eight chromosome pairs in *C. canadensis* (Lavrov and Orlov, 1973). The two species are very similar in appearance and behaviour, but they do not interbreed (Djoshkin and Safonov, 1972).

Based on differences in skull measurements Heidecke (1986b) distinguished eight subspecies which represent the eight relict populations in Europe and Asia. Whether the observed clinal differences (a general increase in size from east to west, and from north to south) have a genetical or ecological basis remains to be assessed (Frahner and Heidecke, 1992; Hartman, 1992). We therefore refer to these geographical forms by their common names (Rhone beaver, Elbe beaver, Scandinavian beaver, Belarussian beaver, Voronezh beaver, West-Siberian beaver, Tuvian beaver, and Mongolian beaver). These geographical forms are likely to be able to interbreed as has been experimentally shown for Elbe and Voronezh beavers, and Belarussian and Voronezh beavers (Heidecke and Zscheile, 1989; Zurowski, 1989).

The Eurasian beaver is the continent's largest rodent. Beavers have a semi-aquatic life-style and live in all kind of freshwater systems. They are strict herbivores and as a hindgut fermenter are able to live on very fibrous food. Water and trees are considered the essential features for beavers (Novak, 1987). It is unclear to what extent non-woody food plants are also required (Nolet *et al.*, 1995). Beavers are monogamous, living in small family groups. They produce only about 1-3 young per year in a single litter (Wilsson, 1971). On average, beavers live 7-8 years (Heidecke, 1991). The wolf *Canis lupus* is considered the beaver's main predator, but this species is so rare in Europe and Asia that it cannot be regulatory (Tyurnin, 1984). Dispersal usually takes

place at 1.5-2 years of age (Hartman, 1994b). The maximum distance recorded is 170 km (Heidecke, 1984). During colonisation, the spread is slowed by uplands between catchments (Hartman, 1995a). Reproduction, survival and dispersal are density dependent (Heidecke, 1991). Beavers use scent to mark their territories (Rosell and Nolet, 1997), and their territorial behaviour limits the population density (Nolet and Rosell, 1994). Beavers can have a major impact on their environment through their felling of trees and building of dams, dens, lodges, canals and food caches (Nummi, 1989, 1992; Nolet *et al.*, 1994b; Rosell and Parker, 1996). However, nearly all knowledge regarding this aspect stems from studies of *C. canadensis* in boreal forest systems in North America (e.g. Naiman *et al.*, 1986; Johnston and Naiman, 1990; Pastor and Naiman, 1992).

PAST AND PRESENT DISTRIBUTION

Relict populations

In the beginning of the 20th century only eight small populations remained in Europe and Asia (Figs 1 and 2): an estimated 30 individuals along the Rhone in France (Richard, 1985), 200 along the Elbe in Germany (Heidecke, 1986a), 100 in south Norway (Myrberget, 1967), 290 along the Neman and tributaries of the Dnepr in Belarus and the Ukraine (Lavrov and Lavrov,

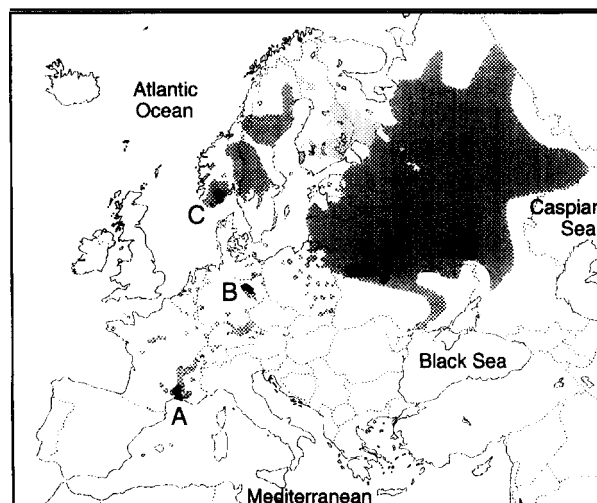


Fig. 1. The historic and present range of beavers in Europe. Black areas show populations remaining at the beginning of the 20th century, situated (A) along the Rhone, (B) along the Elbe, (C) in south Norway, (D) along the Neman and in the Dnepr basin (Beresina, Sosz, Pripjat, and Teterev), and (E) along the Don (Voronezh). The present range of *C. fiber* is depicted in dark gray; light gray marks the position of populations of *C. canadensis* (in Finland/Karelia and along the Seine in France). Based on maps given by Danilov (1995), Ermala *et al.* (1989), Hartman (1995b), Heidecke (1986b), Heidecke and Klenner-Fringes (1992), Kollar and Seiter (1990), Laanetu (1995), Lahti (1995), Macdonald *et al.* (1995), Myrberget (1967), Nolet (1995), Richard (1985), Rosell and Parker (1995), Schwab *et al.* (1994), Stocker (1985), Zharkov and Sokolov (1967), and Zurowski (1992).

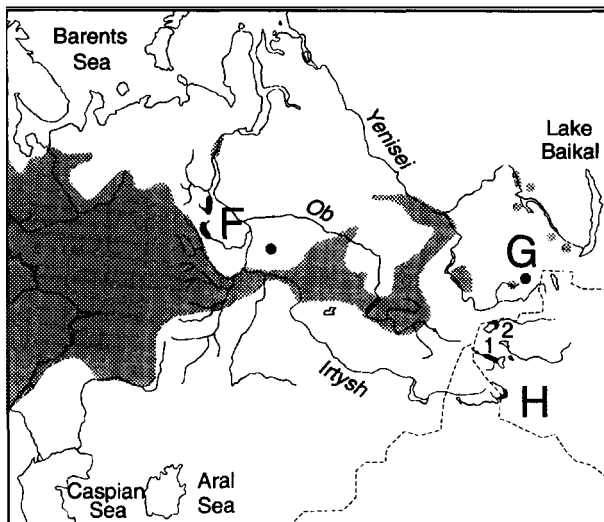


Fig. 2. The present range of beavers in Asia. In black the relict populations are shown which are situated (F) in the Konda-Sosva region in West-Siberia, (G) along the Upper Yenisei (Tuva mountains) in Middle Siberia, and (H) along the Urungu river and its tributaries in China and Mongolia (1 and 2 indicate the reintroduction sites along the Chovd-gol and Tes-gol, respectively). The present range of mixed geographical forms of *C. fiber* is depicted in gray (redrawn from Heidecke, 1986b).

1986), 70 along the Don (Voronezh) in Russia (Stubbe and Romashov, 1992), 300 along the Konda and Sosva in West-Siberia, 30-40 along the Upper Yenisei in the Tuva mountains of Middle Siberia (Lavrov and Lavrov, 1986), and presumably less than the 100-150 found along the Urungu in China in 1959 (Lavrov and Lu Hao-Tsuan, 1961).

The original populations in Europe have all increased considerably in the course of the 20th century. In France, hunting was prohibited in 1909 (and reinforced in 1972), and in 1928 a reserve was installed (Richard, 1985). During 1959-1995, 208 beavers were translocated within France (Richard, 1985; Macdonald *et al.*, 1995). Now (1995) there are *c.* 5000 Rhone beavers (Macdonald *et al.*, 1995).

In Germany, a hunting ban in 1910 led to an initial recovery (Heidecke, 1984). Between 1936 and 1940, a first translocation took place to the Havel basin. However, after the Second World War the population fell by more than half to again only 200 individuals (Heidecke, 1986a). Between 1973 and 1980, four beavers were translocated to the Havel watershed and 28 beavers to the Peene valley, and a reserve was established along the Elbe (Heidecke, 1983, 1984). In the 1980s and 1990s, small numbers were released elsewhere in Germany and about 70 in the Netherlands (Heidecke and Klenner-Fringes, 1992; Nolet, 1995). In 1991, the number of Elbe beavers was estimated at 2800 (Heidecke and Klenner-Fringes, 1992).

In Norway, the beaver was totally protected in 1845, 1899 and 1924 for 10, 19 and 1 year(s), respectively, which enabled the population to recover (Rosell and

Parker, 1995). Between 1922 and 1939 about 80 Scandinavian beavers were released at 19 sites in Sweden (Hartman, 1994a). In 1925-1932 and in 1952-1965, nine translocations with a total of 40 beavers were carried out within Norway, but most of them failed due to the small numbers (2-6) released (Myrberget, 1967). During 1935 and 1937, 17 Scandinavian beavers were released in Finland. Rough estimates of the present population sizes of Scandinavian beavers are about 50 000 in Norway, 100000 (1995) in Sweden, and only 800 (1990) at the one stronghold (Satakunta) in Finland (Ermala and Lahti, 1995; Hartman, 1995b; Lahti, 1995; Rosell and Parker, 1996).

In the former USSR, hunting was prohibited in 1922 and reserves were established along the Beresina, Voronezh, and Konda and Sosva rivers. Extensive translocation programmes were carried out between 1927 and 1964 (Djoshin and Safonov, 1972). In 1983, 30000 Belarussian beavers were present in Belarus and the Ukraine and *c.* 2000 Voronezh beavers in the Don basin (Lavrov, 1983).

In contrast, the relict populations of Asia are still rather small. According to the latest published information, only 200 West-Siberian beavers were living in the Konda-Sosva region in 1976-1979 (Heidecke, 1986b). The number of Tuvian beavers was even smaller with 50 animals present along the Upper Yenisei (Lavrov and Lavrov, 1986). Only the relict population of Mongolian beavers has increased and spread into Mongolia, where in 1965 a reserve was founded along the Bulgan-gol (the Mongolian part of the Urungu). In 1959 and 1960, four beavers were translocated to the Chovd-gol in west Mongolia, followed by 35 between 1974 and 1985. In 1985, another 10 were translocated to the Tes-gol in northwest Mongolia (Fig. 2; Stubbe and Dawaa, 1983, 1986). The most recent (1983) population estimate is 800 (Lavrov, 1983).

Mixed populations

In other parts of Europe and Asia beaver populations were founded by releasing beavers from different origins. In the water catchment of the Danube, beavers from Sweden, Poland, Russia and France (Richard, 1985) were released in Bavaria (120 animals) and in Austria (66, but see below) between 1966 and 1990. In Bavaria, this population numbers between 1000 and 1500 individuals (1994), and has reached the Czech Republic (Schwab *et al.*, 1994). Along the Inn and Salzach in Austria the maximum number present was still only 40 individuals in 1989, but around Vienna the reintroduction was more successful, and this population amounts to 120 individuals (1990), partly living in Hungary, the Czech Republic and Slovakia (Sieber, 1989; Kollar and Seiter, 1990).

Between 1956 and 1977, 141 beavers from France, Germany, Norway and Poland were reintroduced to 30 sites in Switzerland. Twenty of these reintroductions failed because of the low numbers released and the poor

habitat quality of the release sites (Stocker, 1985). In 1993, the Swiss population had nonetheless increased to c. 350 animals (Macdonald *et al.*, 1995).

Small reintroductions took place in other parts of Central Europe. In 1985, four Rhine beavers were released in the Rhine valley near Karlsruhe (Reider, 1985). Between 1981 and 1989, 12 beavers from Poland were reintroduced in the Eifel mountains in Germany; there are now (1995) about 60 (Schulte, 1995). In 1990, one of these crossed the border into Belgium (Huijser and Nolet, 1991). In 1991, three beaver pairs from Poland were reintroduced into the Czech Republic and further releases are planned (Schwab *et al.*, 1994).

Reintroductions also took place in Latvia between 1927 and 1952 (16 beavers from Norway and Russia), in north-east Poland between 1943 and 1949 (perhaps a few tens of Voronezh beavers), in Lithuania between 1947 and 1959 (78 beavers from Russia and Belarus), and in Estonia in 1957 (Palionene, 1965; Zurowski and Kasperczyk, 1988; Balodis, 1992; Laanetu, 1995). These population were boosted by immigration from Belarusian beavers which originated from the relict population along the Neman (Djoshkin and Safonov, 1972). In order to spread the populations, beavers were translocated within Poland (223 animals) and Latvia (145 animals) in the 1970s and 1980s (Balodis, 1992; Zurowski, 1992). In Poland, this included 31 captive-bred beavers from a farm where Belarussian and Voronezh beavers had been interbred (Zurowski, 1989). At present, the populations number 5000 in Poland (1995), 4000 in Estonia (1992), 50 000 in Latvia (1990), and 14 000 in Lithuania (1988) (Balodis, 1995; Laanetu, 1995; Macdonald *et al.*, 1995; Mickus, 1995).

In Russia, the first reintroductions took place between 1927 and 1933 (18 beavers including 10 *C. canadensis*), but were unsuccessful (Safonov, 1975). Between 1934 and 1941, > 300 beavers, mainly from the Voronezh region, were translocated to uninhabited areas. Between 1946 and 1964, > 10 000 beavers were translocated, most of them originating from Belarus (Djoshkin and Safonov, 1972; Safonov, 1975). According to the latest population estimate there are c. 170 000 beavers in Russia (calculated from Lavrov, 1983; this figure includes the original populations of Voronezh, West-Siberian and Tuvian beavers, but not the Belarussian beaver population).

Unfortunately, later releases of North American beavers *C. canadensis* were more successful than the one in Russia between 1927 and 1933 mentioned above. In the 1930s, a few beavers from Canada were released in Masuria (Poland). Their population numbered 100 at the end of the 1950s, but their present status is unclear (Djoshkin and Safonov, 1972). During 1935 and 1937, 7 *C. canadensis* from the USA were released in Finland together with the 17 Scandianvian beavers mentioned above. Descendants from the North American beavers at Sääminki were subsequently translocated to other places, including Lapland. At present, *C. canadensis*

numbers 3300-5200 in Finland (Lahti, 1995). North American beavers immigrated into Russia from Finland in the 1950s. This immigration was boosted with the release of six *C. canadensis* near lake Onega in 1964 (Safonov, 1975). Now (1989) their number in Karelia is c. 2000 (Ermala *et al.*, 1989). In 1969 and 1971, 54 *C. canadensis* were translocated to the Amur basin in the Far East (where earlier *C. fiber* had been released) (Safonov, 1975). In 1975, three beavers from Canada were set free near Paris, and in 1985, their number had increased to 50 (Richard, 1985). Another 15 beavers from Canada were released in the Danube in Austria between 1976 and 1990, and it is unknown how many of the beavers around Vienna are *C. canadensis* (Sieber, 1989; Kollar and Seiter, 1990).

CONSERVATION

Minimum viable populations

Although the taxonomy within *C. fiber* has still to be clarified using traditional biometrics and modern genetic methods, the biological diversity within the Eurasian beaver can best be preserved by maintaining viable populations in each of the eight areas in Europe and Asia where original, unmixed beaver populations are living (Fig. 1).

These populations should contain sufficient genetic variation to allow adaptation to future changes of the environment. An effective population size of 500 is suggested as a lower limit for this (Franklin, 1980). Using the formulas of Lande and Barrowclough (1987) and the data of Heidecke (1984), we calculated that this is equivalent to an actual population size of c. 1880 beavers. However, more knowledge is needed about how much genetic variation is still present within the populations. The first data suggest extremely low levels of genetic variation in the Swedish population, whereas the Voronezh population still seems to contain high levels of genetic diversity (Ellegren *et al.*, 1993; Milishnikov *et al.*, 1994).

Based on the above criterion, the original populations in Europe have reached their minimum viable population size, but the three Asian populations are still far from that. Given the minimum population size needed, the protection of the original populations should be executed at a larger scale than the present reserves, preferably at the level of river catchments.

Reintroduction

Reintroductions and translocations have played an important role in the recovery of the beaver in Europe and Asia. Given the growth of the present beaver populations, many parts of the continent will be naturally repopulated by beavers in the not-too-distant future. However, some isolated areas may not be reached, and we recommend examination of the feasibility of reintroductions of beavers in Britain, Denmark,

Italy (Po basin) and in the lower Danube. If conservationists wish to speed up the process in other areas in order to restore the ecological processes driven by beavers, surplus beavers could be relocated from elsewhere. Care must be taken to re-introduce only the nearest geographical form. When re-introducing beavers, the best strategy is to establish a network of interconnected populations within a water catchment (Zurowski and Kasperczyk, 1988; Nolet and Baveco, 1996).

Habitat management

Riparian (willow *Salix* spp.) woods are the prime habitat for beavers. Here beavers attain a higher fecundity than elsewhere (Heidecke, 1991), and at the same time cause relatively little conflict with man (Heidecke and Klenner-Fringes, 1992). Thus, intact riparian forests are of crucial importance to the conservation of healthy beaver populations. Unfortunately, some flood-plains for instance along the Elbe and Loire, which support important beaver populations, are threatened by dam-building and canalisation.

On the other hand, riparian habitat is being restored for instance along the Rhine. A case study for the rehabilitation of the Lower Rhine showed that the best prospects for beavers were where river dynamics were given more room within the flood-plains (Reijnen *et al.*, 1995). If safe dry places are not sufficiently available in a floodplain, so-called beaver hills can be created which have proved to function along the Elbe (Hinze, 1953).

The flood-plains should not only contain sufficient food, but also have a natural water regime, and man-made dams can have serious consequences for beavers by changing this. Especially in northern regions, where beavers build food caches, water regimes with high levels in summer and low levels in winter may cause the food cache to be washed away (with the sudden water draw-down) or become dry and useless (Wilsson, 1971; Nault and Courcelles, 1984; Smith and Peterson, 1991). In areas with wolves, the beavers may also become more vulnerable to predation when the entrance to their lodge is no longer covered with water (Nault and Courcelles, 1984; Smith and Peterson, 1991). As a result, beavers move more frequently, lose body weight (Smith and Peterson, 1991), and in some cases drown or starve to death (Wilsson, 1971). Periodic floods at the right time of the year are also crucial to the rejuvenation and thus persistence of riparian willow forests (Nolet *et al.*, 1994b).

Water quality does not seem to be critical to beavers. However, some aspects need further investigation. High nutrient and herbicide loads have as yet unknown effects on the food supply of beavers. In addition, beavers may have a relatively high exposure to cadmium because their main food, willows, tends to accumulate cadmium (Nolet, 1994). The mean cadmium concentration in kidneys of beavers from the Mulde river in Germany ($467 \mu\text{g g dry wt}^{-1}$) is the greatest reported in free-ranging herbivores and about five times above the

critical concentration at which kidney damage has been shown in mammals and birds (Nolet *et al.*, 1994a).

CONTROL

Population control

Beaver populations have recovered so well in Belarus, Estonia, Finland, Latvia, Lithuania, Norway, Russia, Sweden and Ukraine, that shooting is again allowed in these countries, though restricted to the autumn, winter and spring. Damage control is becoming an increasingly important objective rather than hunting as a sport or for pelts.

In the absence of natural predators in most of Europe and Asia, beaver populations grow until they are limited by their food supply. Population regulation by hunting should aim to keep densities which allow for rapid growth. However, as history shows, beavers are very easily over-hunted. Population control by hunting should therefore only be undertaken if it is accompanied by a sound population census and harvest scheme. In North America, different culling schemes are presently in use, but in Europe and Asia there is much less experience in the use of culling (see review by Rosell and Parker, 1995).

Killing or relocating beavers is at best a temporary solution to human-beaver conflicts, because other beavers will occupy the vacant territories. A more sophisticated way to reduce damage is fertility control. Beavers might be exceptionally suited for such an approach since they live in stable, territorial family groups in which only the adult pair breeds. By sterilising one of these adults without disrupting the family group, the reproduction might cease in the territory. Tests performed in North American beavers proved successful provided that the animals were not castrated, i.e. their hormone system was kept intact (Brooks *et al.*, 1980). Hormone implants are now being tested (Tippie, 1993).

North American beavers are more fecund than Eurasian beavers: they produce about 3-4 young per year and a larger proportion of two-year-olds reproduce (Hill, 1982). As a result, *C. canadensis* out-competed *C. fiber* in Finland (Ermala *et al.*, 1989). In Eurasia, therefore, local populations of *C. canadensis* should be exterminated before they start to grow, whereas large established populations should be prevented from spreading into areas inhabited by *C. fiber*. Mixed populations are not easily freed of *C. canadensis* because live specimens of the two species can only be identified with certainty by examination of the chromosomes.

Damage control

Nearly all beaver damage is related to their feeding on cultivated plants (crops, trees) and dam-building (Richard, 1986; Heidecke and Klenner-Fringes, 1992; Rosell and Parker, 1995). In a far smaller number of cases beavers cause problems by digging in dikes and

banks (Mickus, 1995). Most of the damage (>75%) is reported from within a distance of 20 m from the water's edge (Heidecke and Klenner-Fringes, 1992). Restoration of at least 20 m wide zones of natural vegetation along the banks of waterways (not accessible to cattle and horses) is therefore probably the best durable solution to the problem of beaver damage.

Alternatively, feeding damage can be reduced by fencing or using wire around individual trees (Richard, 1986). Flooding can in some cases be prevented by putting overflow-pipes through the dams (Heidecke and Klenner-Fringes, 1992). Prevention of damage by using chemical repellents may be a promising method but needs more research. The regular application of beaver scent has experimentally been shown to prevent colonisation in the North American beaver (Müller-Schwarze and Heckman, 1980; Welsh and Müller-Schwarze, 1989). Engelhart and Müller-Schwarze (1995) showed that predator odours, especially of coyote *Canis latrans*, lynx *Lynx canadensis* and river otter *Lutra canadensis*, could be used as feeding repellents for the North American beaver. Richard (1986) mentions the successful use of slaked lime, quick lime and linseed oil.

Another approach would be to introduce a compensation scheme for farmers and foresters. Beaver damage is easily recognised. Moreover, damage is often thinly spread over a large number of land owners, and the prevention of damage may be costly.

ACKNOWLEDGEMENTS

The Council of Europe funded the writing of a report (Nolet, 1996) which formed the basis of this paper. We thank Erik Wessel for technical advice during preparation of the figures. This is publication 2236 of the Netherlands Institute of Ecology, Centre for Limnology.

REFERENCES

- Balodis, M. M. (1992) Die Biber in Lettland. In *Materialien des 2. Internationalen Symposiums Semiaquatische Säugetiere*, ed. R. Schröpfer, M. Stubbe and D. Heidecke, pp. 121-129. Martin-Luther-Universität, Halle/Saale.
- Balodis, M. M. (1995) Beavers in Latvia. In *Proceedings of the 3rd Nordic Beaver Symposium*, ed. A. Ermala and S. Lahti, pp. 6-9. Finnish Game and Fisheries Research Institute, Helsinki.
- Boessneck, J. (1974) Ergänzungen zur einstige Verbreitung des Bibers, *Castor fiber* (Linné, 1758). *Säugetierkundliche Mit* 22, 83-88.
- Brooks, R. P., Fleming, M. W. and Kennelly, J. J. (1980) Beaver colony responses to fertility control: evaluating a concept. *Journal of Wildlife Management* 44, 568-575.
- Danilov, P. I. (1995) Canadian and European beavers in Russian North-west (distribution, number, comparative ecology). In *Proceedings of the 3. Nordic Beaver Symposium*, ed. A. Ermala and S. Lahti, pp. 10-16. Finnish Game and Fisheries Research Institute, Helsinki.
- Djoshkin, W. W. and Safonov, W. G., (1972) *Die Biber der alten und neuen Welt*. A. Ziemsen Verlag, Wittenberg.
- Ellegren, H., Hartman, G., Johansson, M. and Andersson, L. (1993) Major histocompatibility complex monomorphism and low levels of DNA fingerprinting variability in a reintroduced and rapidly expanding population of beavers. *Proceedings of the National Academy of Sciences of the USA* 90, 8150-8153.
- Engelhart, A. and Müller-Schwarze, D. (1995) Responses of beaver (*Castor canadensis* Kuhl) to predator chemicals. *Journal of Chemical Ecology* 21, 1349-1364.
- Ermala, A., Helminen, M. and Lahti, S. (1989) Some aspects of the occurrence, abundance and future of the Finnish beaver population. *Suomen Riista* 35, 108-118.
- Ermala, A. and Lahti, S. (eds.) (1995) *Proceedings of the 3rd Nordic Beaver Symposium*. Finnish Game and Fisheries Research Institute, Helsinki.
- Frahnert, S. and Heidecke, D. (1992) Kranio-metrische Analyse eurasischer Biber, *Castor fiber* L. (Rodentia, Castoridae)-Erste Ergebnisse. In *Materialien des 2. Internationalen Symposiums Semiaquatische Säugetiere*, ed. R. Schröpfer, M. Stubbe and D. Heidecke, pp. 175-189. Martin-Luther-Universität, Halle/Saale.
- Franklin, I. R. (1980) Evolutionary change in small populations. In *Conservation Biology: An Evolutionary-ecological Perspective*, ed. M. E. Soule and B. A. Wilcox, pp. 135-149. Sinauer Associates, Sunderland, MA.
- Freye, H. A. (1978) *Castor fiber* Linnaeus, 1758-Europäische Biber. In *Handbuch der Säugetiere Europas*, ed. J. Niethammer and F. Krapp, pp. 184-200. Akademische Verlagsgesellschaft, Wiesbaden.
- Hartman, G. (1992) Age determination of live beaver by dental X-ray. *Wildlife Society Bulletin* 20, 216-220.
- Hartman, G. (1994a) Long-term population development of a reintroduced beaver (*Castor fiber*) population in Sweden. *Conservation Biology* 8, 713-717.
- Hartman, G. (1994b) Age of dispersal of European beaver (*Castor fiber*) in an expanding population. In *Ecological studies of a reintroduced beaver (Castor fiber) population*. pp. 71-81. Ph. D. thesis, Swedish University of Agricultural Sciences, Uppsala.
- Hartman, G. (1995a) Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. *Wildlife Biology* 1, 97-103.
- Hartman, G. (1995b) Population development of European beaver in Sweden. In *Proceedings of the 3rd Nordic Beaver Symposium*, ed. A. Ermala and S. Lahti, pp. 21-22. Finnish Game and Fisheries Research Institute, Helsinki.
- Heidecke, D. (1983) Biber-Wiederansiedlungen auf populationsökologischer Grundlage. *Säugetierkundige Informationen* 7, 19-29.
- Heidecke, D. (1984) Untersuchungen zur Ökologie und Populationsentwicklung des Elbebibers, *Castor fiber albicus* Matschie, 1907. Teil 1. Biologische und populationsökologische Ergebnisse. *Zoologische Jahrbücher Abteilung Systematik* 111, 1-41.
- Heidecke, D. (1986a). Bestandssituation und Schutz von *Castor fiber albicus* (Mammalia, Rodentia, Castoridae). *Zoologische Abhandlungen (Dresden)* 41, 111-119.
- Heidecke, D. (1986b). Taxonomische Aspekte des Artenschutzes am Beispiel der Biber Eurasiens. *Hercynia NF* 2, 146-161.
- Heidecke, D. (1991) Zum Status des Elbebibers sowie etho-ökologische Aspekte. *Seevögel* 12, 33-38.
- Heidecke, D. (1992) Protokoll zum Biber-Workshop. In *Materialien des 2. Internationalen Symposiums Semiaquatische Säugetiere*, ed. R. Schröpfer, M. Stubbe and D. Heidecke, pp. 461-464. Martin-Luther-Universität, Halle/Saale.

- Heidecke, D. and Klenner-Fringes, B. (1992) Studie fiber die Habitatnutzung des Bibers in der Kulturlandschaft. In *Materialien des 2. Internationalen Symposiums Semiaquatische Säugetiere*, ed. R. Schröpfer, M. Stubbe and D. Heidecke, pp. 215-265. Martin-Luther-Universität, Halle/Saale.
- Heidecke, D. and Zscheile, D. (1989) Erfolgreiche Kreuzung von Elbe- und Woroneshbiber im Zoologischen Garten Schwerin. *Säugetierkundige Informationen* 13, 105-107.
- Hill, E. P. (1982) Beaver *Castor canadensis*. In *Wild Mammals of North America: Biology, Management, and Economics*, ed. J. A. Chapman and G. A. Feldhamer, pp. 256-281. The John Hopkins University Press, Baltimore and London.
- Hinze, G. (1953) *Unser Biber*. Die Neue Brehm-Bücherei, Akademische Verlagsgesellschaft Geest and portig K.-G., Leipzig.
- Huijser, M. P. and Nolet, B. A. (1991) Eerste waarneming van een bever *Castor fiber* in België na 1848. *Lutra* 34, 43-44.
- Johnston, C. A. and Naiman, R. J. (1990) Browse selection by beaver: effects on riparian forest composition. *Canadian Journal of Forest Research* 20, 1036-1043.
- Kollar, H. P. and Seiter, M. (1990) *Biber in den Donau-Auen östlich von Wien. Eine erfolgreiche Wiederansiedlung*. Verein für Ökologie und Umweltforschung, Wien.
- Laanetu, N. (1995) The status of European beaver (*Castor fiber* L.) population in Estonia and its influence on habitats. In *Proceedings of the 3rd Nordic Beaver Symposium*, ed. A. Ermala and S. Lahti, pp. 34-40. Finnish Game and Fisheries Research Institute, Helsinki.
- Lahti, S. (1995) Bäckerns utbredning i Finland från 1980-talet fram till idag. In *Proceedings of the 3rd Nordic Beaver Symposium*, ed. A. Ermala and S. Lahti, pp. 41-43. Finnish Game and Fisheries Research Institute, Helsinki.
- Lande, R. and Barrowclough, G. F. (1987) Effective population size, genetic variation, and their use in population management. In *Viable Populations for Management*, ed. M. E. Soule, 87-124. Cambridge University Press, Cambridge.
- Lavrov, L. S. (1983) Evolutionary development of the genus *Castor* and taxonomy of the contemporary beavers of Eurasia. *Acta Zoologica Fennica* 174, 87-90.
- Lavrov, L. S. and Lavrov, V. L. (1986) Verteilung und Anzahl ursprünglicher und aborigener Biberpopulationen in der UdSSR. *Zoologische Abhandlungen (Dresden)* 41, 105-109.
- Lavrov, L. S. and Lu Hao-Tsuan (1961) Present conditions and ecological peculiarities of beaver (*Castor fiber* L.) in natural colonies in Asia. *Vestnik Leningradskogo Universiteta* 9, 72-83.
- Lavrov, L. S. and Orlov, V. N. (1973) Karyotity i taksonomija sovremennich bobrov (*Castor*, Castoridae, Mammalia). *Zoologische Zhurnal* 52, 734-742.
- Macdonald, D. W., Tattersall, F. H., Brown, E. D. and Balharry, D. (1995) Reintroducing the European beaver to Britain: nostalgic meddling or restoring biodiversity? *Mammal Review* 25, 161-200.
- Mickus, A. (1995) The European beaver (*Castor fiber* L.) in Lithuania. In *Proceedings of the 3rd Nordic Beaver Symposium*, ed. A. Ermala and S. Lahti, pp. 44-45. Finnish Game and Fisheries Research Institute, Helsinki.
- Milshnikov, A. N., Likhnova, O. P., Nikonova, O. A., Larvov, V. L. and Orlov, V. N. (1994) Allozyme variability in the European beaver (*Castor fiber* L., 1758; Castoridae, Rodentia) from the Voronezh State Nature Reserve. *Russian Journal of Genetics* 30, 468-473.
- Müller-Schwarze, D. and Heckman, S. (1980) The social role of scent marking in beaver (*Castor canadensis*). *Journal of Chemical Ecology* 6, 81-95.
- Myrberget, S. (1967) The Norwegian population of beaver, *Castor fiber*. *Meddelelser fra Statens viltundersøkelser* 2, 26.
- Naiman, R. J., Melillo, J. M. and Hobbie, J. E. (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67, 1254-1269.
- Nault, R. and Courcelles, R. (1984) *La Grande River Hydroelectric Complex: Beaver Behavior During the Exploitation of la Grande 2 and Opinaca Hydroelectric Reservoirs*. Societe d'energie de la baie James and Societe des travaux de correction du complexe la Grande, Montreal, Quebec, Canada.
- Nolet, B. A. (1994) Return of the beaver to the Netherlands: viability and prospects of a reintroduced population. Ph. D. thesis, Rijksuniversiteit Groningen, Groningen.
- Nolet, B. A. (1995) Verspreiding en aantalsontwikkeling van de bever *Castor fiber* in Nederland in de periode 1988-1994. *Lutra* 38, 30-40.
- Nolet, B. A. (1996) Management of the beaver (*Castor fiber*): towards restoration of its former distribution and ecological function in Europe? Report Council of Europe, Strasbourg.
- Nolet, B. A. and Baveco, J. M. (1996) Development and viability of a translocated beaver *Castor fiber* population in the Netherlands. *Biological Conservation* 75, 125-137.
- Nolet, B. A. and Rosell, F. (1994) Territoriality and time budgets in beavers during sequential settlement. *Canadian Journal of Zoology* 72, 1227-1237.
- Nolet, B. A., Dijkstra, V. A. A. and Heidecke, D. (1994a) Cadmium in beavers translocated from the Elbe river to the Rhine/Meuse estuary, and the possible effect on population growth rate. *Archives of Environmental Contamination and Toxicology* 27, 154-161.
- Nolet, B. A., Hoekstra, A. and Ottenheim, M. M. (1994b) Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. *Biological Conservation* 70, 117-128.
- Nolet, B. A., Van der Veer, P. J., Evers, E. G. J. and Ottenheim, M. M. (1995) A linear programming model of diet choice of free-living beavers. *Netherlands Journal of Zoology* 45, 317-335.
- Novak, M. (1987) Beaver. In *Wild Furbearer Management and Conservation in North America*, ed. M. Novak, J. A. Baker, M. E. Obbard and B. Malloch, pp. 283-312. Ministry of Natural Resources, Ontario.
- Nummi, P. (1989) Simulated effects of the beaver on vegetation, invertebrates and ducks. *Annales Zoologica Fennica* 26, 43-52.
- Nummi, P. (1992) The importance of beaver ponds to waterfowl broods: an experiment and natural tests. *Annales Zoologica Fennica* 29, 47-55.
- Palionene, A. (1965) The beaver in the Lithuanian S. S. R. *Acta Theriologica* 10, 111-116.
- Pastor, J. and Naiman, R. J. (1992) Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139,690-705.
- Reider, N. (1985) Erste Versuche zur Wiedereinbürgerung des Bibers, *Castor fiber* in Südwestdeutschland. *Zeitschrift für Angewandte Zoologie* 72, 181-189.
- Reijnen, R., Harms, W. B., Foppen, R. P. B., de Visser, R. and Wolfert, H. P. (1995) *Rhine-Econet. Ecological Networks in River Rehabilitation Scenarios: a Case Study for the Lower Rhine*. Report No. 58-1995, RIZA, Lelystad.
- Richard, P. B. (1985) Peculiarities on the ecology and management of the Rhodanian Beaver (*Castor fiber* L.). *Zeitschrift für Angewandte Zoologie* 72, 143-152.
- Richard, P. B. (1986) The status of the beaver in France. *Zoologische Abhandlungen (Dresden)* 41, 121-130.
- Rosell, F. and Nolet, B. A. (1997) Factors affecting scent marking behavior in the European beaver. *Journal of Chemical Ecology* 23, 673-689.
- Rosell, F. and Parker, H. (1995) *Forvaltning av bever: dagens tilstand og fremtidig behov*. Høgskolen i Telemark, Avdeling for økonomi-, miljø- og idrettsfag, Bø.

- Rosell, F. and Parker, H. (1996) Beverens innvirkning på økosystemet—en nøkkelart vender tilbake. *Fauna* 49, 192-211.
- Safonov, V. G. (1975) Ergebnisse der Wiedereinbürgerung des Flussbibers (*Castor fiber* L.) in der UdSSR. *Beitrage zur Jagd und Wildforschung* 9, 397-405.
- Schulte, R. (1995) Die Verbreitung des Bibers (*Castor fiber* L.) in Deutschland und angrenzenden Gebieten. *Säugetierkundliche Mitteilungen* 36, 13-27.
- Schwab, G., Dietzen, W. and Von Lossow, G. (1994) Biber in Bayern: Entwicklung eines Gesamtkonzeptes zum Schutz des Bibers. *Schriftenreihe Bayerische Landesamt für Umweltschutz* 128, 9-31.
- Sieber, J. (1989) Biber in Oberösterreich: eine aktuelle Bes. *Jahrbücher Oberösterreichischer Museum-Verein* 134, 277-285.
- Smith, D. W. and Peterson, R. O. (1991) Behavior of beaver in lakes with varying water levels in northern Minnesota. *Environmental Management* 15, 395-401.
- Stocker, G. (1985) Biber (*Castor fiber* L.) in der Schweiz. *Probleme der Wiedereinbürgerung aus biologischer und ökologische Sicht*. Berichte nr. 274 Eidgenössische Anstalt für das forstliche Versuchswesen, Birmensdorf.
- Stoltenkamp, H. (1986) Over de bever (*Castor fiber* L.). Deel 2: de bever in Nederland. *Natura*, 292-298.
- Stubbe, M. and Dawaa, N. (1983) Akklimatisation des Zentralasiatischen Bibers—*Castor fiber birulai* Serebrennikov, 1929—in der Westmongolei. *Erforschung biologischer Ressourcen der Mongolischen Volksrepublik* 2, 3-92.
- Stubbe, M. and Dawaa, N. (1986) Die autochtone zentralasiatische Biberpopulation. *Zoologische Abhandlungen (Dresden)* 41, 93-103.
- Stubbe, M. and Romashov, V. A. (1992) Zum Gedenken an den russischen Biberforscher Leonid Sergeevic Lavrov (1911-1992). In *Materialien des 2. Internationalen Symposiums Semiaquatische Säugetiere*, ed. R. Schröpfer, M. Stubbe and D. Heidecke, pp. 465-467. Martin-Luther-Universität, Halle/Saale.
- Tippie, S. (1993) Alternatives in beaver management. *Humane Innovations and Alternatives*, 530-533.
- Tyurnin, B. N. (1984) Factors determining numbers of the river beaver (*Castor fiber*) in the European North. *Soviet Journal of Ecology* 14, 337-344.
- Welsh, R. G. and Müller-Schwarze, D. (1989) Experimental habitat scenting inhibits colonization by beaver, *Castor canadensis*. *Journal of Chemical Ecology* 15, 887-893.
- Wilsson, L. (1971) Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). *Viltrevy* 8, 115-260.
- Zharkov, I. V. and Sokolov, V. E. (1967) The European beaver (*Castor fiber* Linnaeus, 1758) in the Soviet Union. *Acta Theriologica* 12, 27-46.
- Zurowski, W. (1989) Wiederaufbau des Biberbestandes in Polen—Vorteile und Gefahren der Zucht. In *Die Illusion der Arche Noach: Gefahren für die Artenhaltung durch Gefangenschaftszucht*, ed. E. Schneider, pp. 219-235. ECHO Verlag, Göttingen.
- Zurowski, W. (1992) European beaver reintroduction into lowland and mountain tributaries of the Vistula river. In *Global Trends in Wildlife Management* (Transactions of the XVIIIth Congress of the International Union of Wildlife Biologists), ed. B. Bobek, K. Perzanowski and W. L. Regelin, pp. 163-166. Swiat Press, Krakow.
- Zurowski, W. and Kasperczyk, B. (1988) Effects of reintroduction of European beaver in the lowlands of the Vistula basin. *Acta Theriologica* 33, 325-338.