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 founds 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>
<thead>
<tr>
<th>Country</th>
<th>Extirpation Protection</th>
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<th>References</th>
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<tr>
<td>Austria</td>
<td>1869</td>
<td></td>
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<td></td>
<td>1959-95 5000</td>
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<td>?</td>
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<td>Under investigation 0</td>
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<td>Denmark</td>
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<td>1868, 1868</td>
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<td>1935-37 800</td>
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<td>1865</td>
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<td>1909-95 5000</td>
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<td>Remnant</td>
<td></td>
<td>1909-95 5000</td>
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<td></td>
<td>1947-59 14 000</td>
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<td>Remnant</td>
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<td>1988-95 70</td>
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<td>1925-32, 1952-65</td>
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<td>1844</td>
<td>Remnant</td>
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<td>1943-49, 1975-86 50000</td>
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<tr>
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<td>1927-33, 1934-41, 1946-64</td>
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<td>Immigration from Austria</td>
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<td>Sweden</td>
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<td>1922-39 100 000</td>
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<td>Ukraine</td>
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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 (Frahmert 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 kinds of freshwater systems. They are strict herbivores and as hindgut fermenters 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


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 Teterew), 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 (1993b), Heidecke (1986b), Heidecke and Klenner-Fringes (1992), Kollar and Seiter (1990), Laanetu (1995), Lahti (1995), Macedonald 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 (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 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 Rhone 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 (Palinene, 1965; Zurowski and Kaspereczyk, 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 Belarusian 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 Scandinavian 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 mimimum 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 µg 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 (Muller-Schwarze and Heckman, 1980; Welsh and Muller-Schwarze, 1989). Engelhart and Muller-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.

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