The beaver's reconquest of Europe: the status, future and management of a conservation success

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Abstract
Overhunting reduced Eurasian beaver *Castor fiber* populations to c. 1200 animals, in eight isolated populations, around the end of the 19th Century. Protection, natural spread, and reintroductions led to a powerful recovery in both range and populations during the 20th Century, which continues at a rapid pace. The minimum current population estimate is 465000. There are also c. 12500 North American beaver *C. canadensis* established in Finland and Russian Karelia; however, other populations of *canadensis* introduced in Austria, Poland and France appear to be extinct. Populations are now established throughout Europe with the exception of the British Isles, Iberia, Italy, and the southern Balkans; reintroductions are continuing. Considerable further expansion in range and population, especially in western Europe and the lower Danube basin, can be expected. If current trends continue, *C. fiber* will within a few decades be a fairly common mammal in most of Europe. Expanding populations typically show a pattern of rapid range extension within a watershed, followed only later by rapid population growth; and a barrier effect of watershed divides, which can be strongly isolating where physical or habitat barriers (such as mountains or intensive farmland) intrude between watersheds. Management of beaver distribution should therefore operate at the watershed scale. The period of rapid population increase, if unchecked, leads to a phase of population decline as marginal habitats are occupied and exhausted. This coincides with a peak in conflicts with human landuse interests. A regulated hunting take of healthy beaver populations is recommended as the optimal management regime in managed landscapes. Early provision of interpretation and public viewing opportunities has been a feature of several recent reintroductions. This provides a benefit to the local economy through wildlife tourism, and helps foster positive attitudes to beavers.

INTRODUCTION
The Eurasian beaver *Castor fiber* was once one of – perhaps the - most widespread of Palaearctic mammals, distributed continuously across Eurasia from the British Isles to eastern Siberia, throughout the deciduous and coniferous forest zones, and extending in wooded river valleys far into the tundra of the north and the steppes of the south (Zharkov & Solokov 1967; Macdonald & Barrett 1993). Prized for its fur and castoreum, a glandular secretion used in territorial marking by beavers but valued by humans as a medicine and perfume base, overhunting eliminated *C. fiber* throughout most of its range by the middle 19th century. At the beginning of the 20th century about 1200 individuals remained in eight isolated populations (Nolet & Rosell 1998) (Figs. 1 & 2).

By the beginning of the 20th century the tide of decline had turned. Remnant populations received legal protection, and reintroductions began in 1922 (to Sweden from Norway). Early reintroductions were mainly motivated by fur harvesting prospects; later, conservation and ecosystem management reasons became more prominent. Remarkably little planning or monitoring of most earlier reintroductions was undertaken, the reintroduction method usually consisting of a "hard release", i.e. simply letting animals go, into likely-looking environments which had not been scientifically assessed for suitability. Later reintroductions have generally been more thoroughly researched beforehand. Despite this frequent lack of planning, a viable population has established in every country in which reintroduction has been attempted except perhaps Switzerland

(Winter 1997) (with the caveat that in Denmark and Romania, reintroduction is too recent to judge success or failure). The present minimum world population of European beaver, taking the most conservative estimates from each country, is 465000; the actual figure probably exceeds 500000.

The pace of reintroduction, and of population and range expansion, has probably never been more rapid than at the present time. Considerable expansions in range, and many new reintroductions, have taken place even since the mid-1990s (Nolet & Rosell 1998). An ambitious programme to recolonise the entire Danube basin is now underway, and there have been very recent reintroductions to Denmark and Belgium (below). Populations in some parts of Europe are now at a mature stage of development. This allows the whole process of recolonisation to be reviewed, and the management implications for what will be, in much of Europe, a common mammal of the 21st century, assessed.

HISTORY AND STATUS OF BEAVER POPULATIONS BY COUNTRY

Russia, Mongolia & Xinjiang (China)

West of the Urals, beavers survived in Russia in the Voronezh region (*C. f. osteuropaeus)* and on the border with Belarus (*C. f. belarusicus = vistulensis*) (Fig. 2). Reintroductions were conducted on an extensive scale between 1927 and 1964, over 10000 beavers (mainly *C.f. belarusicus*) being translocated. Little detailed information is available regarding distribution and numbers; however, the species seems to be widespread throughout the forest zone of European Russia (Lavrov 1983; Nolet & Rosell 1998). A population of c. 2000 *C. canadensis* is established in Russian Karelia, through immigration from Finland assisted by the introduction of 6 specimens near Lake Onega in 1964 (Danilov 1995; Nolet 1997).

East of the Urals, relict populations remain in the Konda-Sosva region (*C. f. pohli*), the upper Yenesei (*C. f. tuvinicus*), and along the Urungu river system in Mongolia and Xinjiang (China) (*C. f. biruli*), both close to the Russian border Some local translocations of *C. f. biruli* have taken place in west Mongolia. All of these relict populations remain low in numbers. Reintroduced beaver of mixed origin are found on the middle Yenesei, upper Ob, and tributaries of the Irtysh draining the eastern flank of the Urals. There are also isolate groups in the Baikal region (Fig. 2). There have also been reintroductions of both *C. fiber* and *C. canadensis* in the Russian far east on the Amur, in Kamchatka, and elsewhere (Saveljev 1997b), about which very little information is available.

The total Russian population was estimated in 1983 at 170000 (Lavrov 1983; Nolet & Rosell 1998); in recent years the population is said to have been on the increase (Andreyev *et. al.* 1997).

Ukraine

Beaver were widely translocated to the basin of the Dneiper river as part of the general Soviet era programme. In addition, populations are spreading into Ukraine from Russia and Belarus. The current population is estimated at 12500 (Nolet & Rosell 1998).

Belarus
A remnant population of beaver (*C.f. belarusicus)* survived in the Pripet marsh region of Belarus (Fig. 1), and was the source stock for widespread reintroductions to areas in the former eastern bloc throughought the 20th century. Little is known of the present status in Belarus, although the species is widespread except in the SW. No recent population estimate is available; the population in 1972 was estimated at 14000 (Nolet & Rosell 1998).

Estonia
Extinction of the original population occurred in 1841. Reintroduction began in 1957 with 10 *C. f. belarusicus* from Belarus, and beavers (*C. f. osteuropaeus)* appear to have spread from a reintroduction on the Russian shore of lake Peipus at about the same time. Population development has followed the usual pattern of lag phase and exponential increase (Hartman 1995). In 1970 the population was 50, in 1980 400-500, and in 1992 c. 4000 (Laahti 1995).

Latvia
Beavers became extinct in Latvia in 1871. Reintroduction began in 1927 (2 pairs) and 1935 (1 pair), using *C.f. fiber* from Sweden. By 1950 this nucleus had increased to 78. In 1952, 10 *C.f. osteuropaeus* were reintroduced, and from the late 1950s *C.f. belarusicus* spread into Latvia from Belorussia. The characteristic pattern of slow increase followed by rapid exponential population growth (Hartman 1995) was exhibited: populations were estimated as 1400 in 1973, 50000 in 1990, and 70000 in 1997. Beaver are now found throughout the country, except for the NW corner (Balodis 1994, 1997).

Lithuania
Lithuania's dense network of watercourses and marshes is ideal habitat for beaver to live in - and to hide. The last beaver of the original Lithuanian stock was not killed until 1938 (Mickus 1995). Between 1947 and 1959 78 beavers were reintroduced. The first 8 were *C. f. osteuropaeus*, the remainder *C. f. belarusicus*. Subsequently, beaver immigrated from Latvia, Belarus and the Kaliningrad enclave of Russia. The whole country is now occupied, and the population is c. 10000 (Mickus 1995).

Poland
Beaver became extinct within the present borders of Poland in 1844. 3-4 pairs (*C. f. osteuropaeus*) were reintroduced to the NE in 1949, in addition to an unknown number of unclear origin during the German occupation in 1942-43. From 1975-86 223 individuals were released at various sites throughout the Vistula river system. 48 individuals, mainly *C.f. belarusicus* were released between 1974 and 1985 on the Oder. *C. f. fiber* from Norway have also been supplied to Poland for reintroduction purposes (T. Punsvik *pers. comm.*). Other, unofficial, reintroductions have also taken place, and there has been considerable immigration from Lithuania and Belarus. Further reintroductions are continuing. The present population is c. 17000 (A. Czech *pers. comm.;* Zurowski & Kasperczyk 1986; 1988).

C. canadensis was also introduced to Poland in the mid 20th century; however, the species appears not to have established in competition with *C. fiber*, and is now apparently extinct (A. Czech *pers. comm.*).

Romania

The last of the native Romanian beavers was apparently killed in 1824 (Nolet & Rosell 1998). 9 beavers were reintroduced to the Olt river near Brasov, in November 1998, as the first stage of a co-operative reintroduction project by ICAS Romania, WGM of Bavaria, WWF Austria and WWF International. Beavers were sourced from Bavaria, and so of mixed subspecific origin. 19 additional animals were released in the same area in 1999. A further reintroduction, to the Danube delta, will take place in 2000 (Troidl & Ionescu 1997; G. Schwab, *pers. comm*.).

Bulgaria

Bulgarian authorities, in cooperation with the WWF International and WWF Austria, are planning reintroductions to two sites in Bulgaria in 2001 and 2002. One of these will be in the Danube islands on the border with Romania; the second site has not yet been decided (G. Schwab, *pers. comm*.)

Croatia

Beavers became extinct in Croatia in the middle of the 19th century (Nolet & Rosell 1998), and were reintroduced to Croatia in a three year programme from 1996-1998. 29 were released at the Mura/Drava confluence near the Slovene/Hungarian border, and 56 at two sites on the Sava river and its Cesma tributary near Zagreb (M. Grubesic *pers. comm*). The source population was from Bavaria, and so of mixed subspecific origin. Both populations are now firmly established. Some beavers from the Drava site have moved into Hungary (O. Bozsér *pers comm*), and signs of beaver activity have been reported from Serbia (G. Schwab, *pers. comm*.). The population in early 2000 had increased to c. 150 animals (M. Grubesic *pers. comm*.)

Hungary

8 beaver were introduced in Gemenc National Park in southern Hungary in 1996 (since increased to 30), and to Tisa -Stausee in central Hungary in 1993. Beavers immigrated to the Szegetköz area from Austria in the late 1990s, and in April 2000 8 individuals were released at Fertõ-Hanság National Park. Both sites are in NE Hungary. Source stock for the Fertõ-Hanság reintroduction, from Bavaria, was of mixed subspecific origin. Individuals have also immigrated along the Drava river system from Croatia.

A further reintroduction on the Tisa in central Hungary is planned. The reintroduction programme is a collaboration between WWF Hungary and WWF Austria.

The present population is c. 70 animals. (O. Bozsér *pers comm*).

Slovakia

The species became extinct at some point in the 19th century (Valachovic 1997). Beaver immigrating from Austria were recorded as early as 1976; however, firm establishment

dates from the later 1980s (J. Sieber *pers. comm.*). Beaver are now well established on the lower Morava, and in the western foothills of the Malé Karpaty. The population is estimated at about 150 (Valachovic 1997). In 1995, 5 individuals from Poland (stated to be *C. f. beloruscius*) were reintroduced to Horná Orava in northern Slovakia. Breeding has been recorded (Dúha & Majzlan 1997).

Czech Republic
Beavers from the Austrian reintroduction reached the Czech Republic in the 1980s. By 1997 they had spread up the Morava river as far as Kromeriz (Valachovic 1997). Beaver have also recently reached southwestern Czechia from Bavaria in the Oberpfalz/Cesky Les region (G. Schwab *pers. comm.*). Beaver were directly reintroduced near Olomouc on the Morava in the mid 1990s. There is no estimate of population size available.

Austria
Beaver became extinct in Austria in 1869 (Nolet & Rosell 1998). 40 individuals were released between 1976 and 1985 to the Danube near Vienna, and to the Inn and Salzach on the border with Bavaria. Danube stock was sourced from Poland (70%), Russia, and Sweden, and so is of mixed subspecific origin, presumably mainly *C.f. beloruscius* with an admixture of *C.f. fiber* and possibly *C.f. osteuropaeus.* The Inn/Salzach population was initially *C. f. fiber* (but is now in contact with populations of mixed origin). Population increase was initially slow, but since 1994 has reached the rapid increase phase (Hartman 1995), the total population in 1999 being c. 1000, with a further 200 in adjacent parts of Slovakia and the Czech republic (q.v.) (J. Sieber *pers. comm.*). Range has expanded very rapidly along the Austrian Danube. Ranges of the two release populations are fused, and distribution is continuous with the Bavarian population.

The Vienna release also included 12 N. American beavers, *C. canadensis.* Fortunately, they do not appear to have established a competing population with *C. fiber* and are presumed extinct: of 100 live trapped or dead beaver examined since 1997, none were *C. canadensis* (J. Sieber *pers. comm.*).

Switzerland
Extinction 1820. 141 beavers (*C.f.fiber, galliae, beloruscius & osteuropaeus*) were reintroduced to 30 sites between 1956 and 1977; however, many of these sites were of unsuitable habitat in fast-flowing mountain rivers, and too few beavers were released for a viable population at each site. In addition, mountain barriers and habitat fragmentation have greatly restricted spreading, so that population growth has been much slower than in most countries. The population remains fragmented (Fig. 1), and the species on the Swiss Red Data List (Winter 1997). Beavers in the SW around Lake Geneva (upper Rhone watershed) are *C. f. galliae,* and may now be in contact with their parent population expanding up the Rhone; in the remainder of the country they are of mixed origin.

The total Swiss population is c. 350 (Winter 1997; S. Capt, Centre Suisse de Cartographie de la Faune, *pers. comm.*)

Italy
Extinction 1541. Reintroduction to the Po basin has been recommended in a European Union / Bern Convention Nature and Environment Series document (Nolet 1997).

Germany
A relict population of beavers survived on the Elbe river, numbering about 200 animals in 1950 (Heideke & Hörig 1986). This population has since increased greatly in numbers and in range and now occupies much of the Elbe river system.

From 1966, beaver were reintroduced to Bavaria, mainly on the Danube and lower course of the Inn. Due to the Cold War tensions of the time, Elbe beavers (*C.f. albicus*) from East Germany were not made available and the reintroduction stock was of very mixed origin: *C. f. fiber, belarusicus, galliae,* and probably also *osteuropaeus.* In the 1970s, a population of *C.f. belarusicus* was reintroduced to the Eifel from Poland; *C.f. albicus* was reintroduced to the Peene river in NE Germany, in the 1980s *C.f. albicus* to Hesse, and; and in 1994 *C.f. albicus* to Saarland. The reintroduced population in Baden-Wurtemburg / Rhine close to Karlsruhe is *C.f. galliae*.

The Bavarian reintroductions, in particular, have been successful in establishing a strong population, now continuous with the expanding Austrian reintroduction. Bavarian beavers have been the source population for many recent reintroductions into the lower Danube basin, and to Belgium (G. Schwab *pers comm*; Macdonald *et al* 1995).

The total population is now 8000-10000 animals (G. Schwab *pers. comm.*). A very comprehensive beaver website concentrating on the central European population, especially Bavaria (in German, with an English version planned) is available at: http://www.bibermanagement.de/

Denmark
The most recent known subfossil remains in Denmark are well over 2000 years old; however, place-name evidence suggests that beavers probably survived to about 1100 AD (Klein 1999).

Reintroduction was recommended in a document published by the European Union / Bern Convention in 1997 (Nolet 1997). 18 beavers (*C. f. albicus*) were reintroduced to a network of small streams and ponds in the Klosterheden, NW Jutland, in October 1999. The area lacks a major river system. One family has since built 3-4 small dams (c. 1m wide).

Public viewing of the beavers is encouraged and has been described as ”a great success” (Skov- og Naturstyrelsen 1999). A website (in Danish) giving full details of the reintroduction, where to see beavers, and contacts for further information, is available (http://www.sns.dk/natur/baever/index.htm).

A further reintroduction, to Lake Silkeborg in central Jutland, is planned for October-November 2000 (S. Asbirk, *pers. comm.*).

Finland
Extinction 1868. 17 *C. f. fiber* from Norway, and 7 *C. canadensis*, were released in 1935-37 (Eurasian and North American beavers were then thought to be a single species).

In contrast to Poland and Austria, where *C. fiber* appears to have competitively displaced *C. canadensis* (see below for discussion), *canadensis* spread much more quickly than *fiber*, and ousted *fiber* from many areas where the two species came into contact. The two species do not appear to coexist sympatrically except in the very short

term. Outside the main range of *C. fiber* in the southwest, a small population of European beavers persists in Norra Tavastaland in the south (Fig. 1; Ermala *et al* 1999).

Heavy harvesting (c. 20% of the population each year (Hartman 1999); 18% of the *C. canadensis* population and 9% of the *C. fiber* population in 1998 (Ermala *et al* 1999)) appears to be the cause of the very slow population growth observed up until recent years. In 1985 there were c. 3000 *C. canadensis* and c. 500 *C. fiber* in Finland. In 1998, however, a survey produced a figure of 10500 *C. canadensis* and 1500 *C. fiber*. Given the abundant habitat available in Finland, the population nevertheless remains at only a fraction of carrying capacity.

In Finnish Lapland, the population of *C. canadensis* now abuts that of the expanding Swedish *C. fiber* population, which is now established along the Torne river on the Finnish border. This is a matter of considerable concern to Swedish nature managers (G. Hartman *pers comm*). Attempts are being made to eliminate *C. canadensis* from Lapland; by 1999 the remaining population was only c. 40 animals. (Rosell & Pedersen 1999; Ermala *et al* 1999).

Sweden

The last undoubted Swedish beaver was killed in 1871, although occasional sightings were reported later in that decade. Legal protection was enacted in 1873 (Hartman 1994; Rosell & Pedersen 1999).

Reintroduction, entirely of *C. f. fiber* from Norway, commenced in 1922. Beaver were released at 19 sites. 11 of these, at most 47 individuals, bred successfully. Reintroduction sites were well spread from south-central to northern Sweden, mainly in the western mountains near the Norwegian border.

The geography of Sweden is well suited to beaver range expansion. Major river systems run in parallel west-east; except for the mountain spine on the Norwegian border, the topography is largely flat, and the landscape heavily wooded. Isolating barriers between river systems are therefore low.

Beaver populations spread rapidly in range, with a long lag phase before populations exploded in the 1970s and later (see Discussion). In 1940, there were about 400 animals; in 1961 2200; in 1969 7500; in 1977 c. 40000; and in the early 1990s populations were estimated at over 100000 (Hartman 1994a, b; 1999). Populations are either completely protected, or open for unrestricted hunting (no quota limits) in season. Beaver are protected in the northernmost province, Norrbotten; in Uppsala and Stockholm provinces in the east; and the south. Elsewhere, the hunting season is from 1st October - 10th/15th May (depending on locality); the actual harvest is about 6% per annum (Hartman 1999).

As late as the early 1990s, the beaver population in Sweden was divided into two main ranges in west-central and north-central Sweden (Hartman 1994a, b; Nolet & Rosell 1998). Major range expansion has continued. The two main ranges are now continuous, and beavers now occupy the whole country apart from the south, the far northwest, and the region around Uppsala north of Stockholm (Hartman 1999 & *pers. comm*; Fig. 1). With the Norwegian population, the range is now continuous from the Baltic to the Atlantic.

Norway

A population of c. 100 beaver survived in southwest Norway (Fig. 1), and has provided the source stock for all modern populations of *C. f. fiber*.

The spread of beavers in Norway is worth examining in some detail. Information is more complete than for most counties, and in many areas the population has passed through all stages from recolonisation to maturity. The following account is summarised from a recent detailed review of the Norwegian literature by Bevanger (1996), where not otherwise indicated.

Although earlier attempts at legislation were made as early as 1845, effective legal protection dates from 1899. By 1910 the population had increased to c. 1000, with a marginal increase in range to the southeast. In 1919, the population was estimated at 7000, and limited hunting was again permitted. Limited range expansion in the southwest continued. In the later 1930s, population growth was halted and even reversed owing to (often illegal) overhunting; during the war years 1940-1945 the population sharply declined, apparently due to the reappearance of subsistence hunting as a motive (Myrberget 1967). A small population reintroduced at Songli west of Trondheim in 1929 seems to have disappeared around this time. However, in 1942-43 the first beaver from the reintroduced population in Sweden immigrated to eastern Norway on the Trysil watershed.

From 1925-1965 reintroductions also took place (all of *C.f. fiber*), 40 animals to 8 sites from the south to the extreme north. The population in 1965 stood at 5-10000 – effectively unchanged from the 1919 figure. There were further reintroductions in Trøndelag and northern Norway in the following decade.

In 1975 the range in southern Norway remained substantially unchanged, but a major new feature appeared in the form of large scale immigration from the burgeoning Swedish population. In Hedmark and North-Trøndelag provinces immigrant beavers colonised large new areas. Beaver also spread into SE Sør-Trøndelag at this time. Reintroductions were made on the Orkla in western Sør-Trøndelag (near the site of the failed Songli reintroduction) and in northern Norway. Between 1975 and 1985, beaver reached the large Glomma watershed (42000 km^2) in eastern Norway, by natural spread, and colonised throughout. Further reintroductions took place in the far north.

In the decade to 1996, beaver continued to increase in both numbers and range, though populations in the north remain small and fragmented. There are now two major disjunct populations (Fig. 1), in the southeast wholly descended from natural spread, and in eastern Norway continuous with and largely derived from the Swedish population, supplemented by reintroduced animals. The population derived from the Orkla reintroduction in the 1970s is now continuous with a population of Swedish origin spreading down the Orkla watershed (*pers. obs.*).

The current population is estimated at >50 000 (Rosell 1999). Beaver are protected in areas with low, or newly colonising, populations; a hunting season with a variable quota (depending on the local population size) is permitted elsewhere. About 10% of the population is harvested annually (Hartmann 1999). In some areas, guided ”beaver safaris” generate additional income (Rosell & Pedersen 1999).

There seems to be no barrier to continued rapid expansion in Trøndelag, where beaver are common on the Namsen and small populations are established on all other major river systems. Significant spread may also be expected in south-central Norway, where beaver have reached the main Gudbrandsdal watershed (17500 km^2) running

NNW from the Oslo area. North of Trøndelag, except in Finnmark, watersheds are small and isolating barriers high, and the climate very harsh, so that population expansion will probably continue to be slow.

Netherlands
Extinction of the original population occurred in 1826. Following a very thorough prestudy, a total of XX *C. fiber albicus* were reintroduced to two sites in the Rhine delta, Biesbosch and Geldersee Poort, from 1988-1997. Reproductive success has been lower than in most populations. The reasons for this are unclear, but may be due to relatively poor habitat quality, or cadmium pollution from contaminated river sediments (Nolet *et. al.* 1994). Nevertheless, the population has increased to c. 120 (Rosell & Pedersen 1999).

Belgium
Beavers became extinct in 1848. The current reintroduction is a co-operative programme run by Rangers, a youth environmental group, and Castors, an environmental NGO. 40 beavers of mixed subspecific origin from Bavaria were released at several sites in the Ardennes in 1998, supplemented by 12 additional animals in 1999. Reproduction has been recorded (R. Dennis *pers. comm;* G. Schwab *pers. comm.*). Public viewing opportunities and "beaver safaris" are available; there is a website (in French) at: http://www.castor.be

France
A relict population of 30 individuals (*C. f. galliae*) survived in the lower Rhone and has formed the source population for all reintroductions within France. 16 reintroductions have been made, of which 11 are reported as successfully increasing in population. In addition, the Rhone population has expanded greatly in numbers and in range. The current population is c. 5000.

A population of *C. canadensis,* established for some years on a reservoir near Paris, has been removed from the wild (J.-C. Jacob *pers comm*).

Scotland
Fur taxation records indicate that beavers remained relatively common in Scotland into the mediaeval period. Documentary evidence suggests the species persisted in the Loch Ness area until c. 1550 (Kitchener & Conroy 1997).

Reintroducing beaver to Scotland has been mooted in conservation circles for many years, and reintroduction to Britain was specifically recommended in a document published by the European Union/Bern Convention in 1997 (Nolet 1997). However, the current reintroduction initiative dates from 1994. T.C. Smout and M. Magnusson, then respectively vice chairman and chairman of Scottish Natural Heritage, initiated formal studies following a suggestion (to TCS) from the present author.

Studies of the feasibility and desirability of reintroduction have been co-ordinated by M. Cooper at SNH. Investigation of the history of beaver in Scotland was studied by A.C. Kitchener and J. Conroy (Kitchener & Conroy 1997), and a comprehensive survey of relevant scientific knowledge was compiled by D. Macdonald, F. Tattersall, and others (Macdonald *et al* 1995). A recent simulation study concluded that a reintroduction of 20

animals to any one of a number of defined release sites would have a high probability of successfully establishing a viable population (South *et. al.* 2000).

In 1997, a full public consultation was held by SNH. Results indicated strong support from the general public, including in rural areas where beaver were likely to be released, but reservations were voiced by many landowners and strong opposition was registered by some angling interests, who feared beaver dams would damage salmon stocks (Scottish Natural Heritage 1998; M. Cooper *pers. comm.*) despite scientific evidence to the contrary (see, e.g., Bergstrom 1985; Macdonald *et al* 1995 for review). A final decision to reintroduce beavers in a seven year trial reintroduction was made in March 2000; however, this decision is dependent on the designation of a suitable reintroduction site, and on securing part funding from outwith SNH (Scottish Natural Heritage 2000).

England

Extinction appears to have occurred by the 12th century (Macdonald *et al.* 1995). Reintroduction to Britain has been recommended in a document published by the European Union / Bern Convention (Nolet 1997). English Nature have formally investigated reintroduction possibilities. No decision has been taken, and it seems likely that any English reintroduction will await the results of the trial reintroduction to Scotland.

MANAGEMENT ISSUES

Interspecific competition

Evidence from Finland, Austria and Poland suggests that *C. fiber* and *C. canadensis* competitively exclude one another. In Finland, *C. fiber* appears to lose out to *C. canadensis*, while in Austria and Poland the converse has been the case; in both the latter countries *C. canadensis* appears to have become extinct.

Chance factors may have been the crucial influences on the eventual winner of the conflict in each case. However, the two species are rather different in a number of ecological characteristics. *C. canadensis* breeds at a younger age, has much larger litters, and lives in larger colonies than *C. fiber* (Danilov 1995). In terms of r-K selection theory (MacArthur & Wilson 1967) it is relatively more r-selected, and *C. fiber* relatively more K-selected. R-selection appears to be an adaptation to a usually unsaturated environment where mortality is dominated by periodic or irregular non density-dependent dieoffs caused by, e.g., extreme climatic events. K selection invests more resources in fewer offspring to maximise their chances of success in a stable environment, where mortality and reproduction is dominated by interspecific competition between individuals. It is possible that the harsh environment of Finland, and the early inception of a heavy hunting take (Hartman 1999), favoured rapidly reproducing, r-selected *canadensis*, and the more temperate climate and minimal or absent hunting offtake of Poland and Austria favoured the reproductive strategy of *C. fiber*, when the two species were brought into direct competition.

Clearly, as a non-native, *C. canadensis* populations should, where possible, be removed; and where not possible, their spread restricted. In France, management authorities have removed the small *C. canadensis* population established near Paris; and

in Finland an attempt to eliminate the Lapland population of *C. canadensis*, which is now in contact with *C. fiber* along the Swedish border, is in progress.

Patterns of spread and barriers to range expansion

Following reintroduction to a river system, or release from hunting and trapping pressure on river systems where beavers survived, extension in range is very much faster than expansion in population. This appears to be due to the fact that beavers will move a long way through unsuitable or less suitable habitat to ”cherry pick” the best habitat available within a river system, before filling in less favourable habitats in between. This phenomenon has been noted on the Danube river system (J. Sieber *pers. comm*; G. Schwab *pers. comm*); the Glomma in Norway (Bevanger 1995); and has been studied in detail on a number of river systems in Sweden (Hartman 1994a, b). The exception to this rule is that large man-made dams appear to act as quite effective barriers to population spread, in some cases at least (see below).

The downside of this pattern of re-establishment, from a population increase point of view, is that pairs of animals may not find each other in the vast, unoccupied stretches of a large river system when populations are low. This appears to be the cause of the characteristic lag phase in population development, which may be as long as 20 or 30 years, before a population reaches the phase of rapid population growth (Hartman 1994a,b; 1995).

The spread of beavers within a river system cannot, in practice, be constrained without a heavy, and constant, directed hunting or trapping effort. Wildlife managers need therefore to be clear that introducing beavers to a river system is to reintroduce them to the entire river system, and that beavers will not necessarily remain in the vicinity of the reintroduction location if the habitat is less favourable than elsewhere on the river system. In Switzerland, a number of reintroductions failed for this reason, and in another cases beavers moved out of the reintroduction site to more favourable habitat on flatter ground downstream (Macdonald *et al* 1995; Czech 1997). However, in Poland, recent evidence suggests that beaver can be behaviourally ”acclimatised” to mountain conditions; such populations may be a better source stock for mountain area reintroductions than animals from plains habitats (Czech 1997).

Movement between watersheds is much more restricted. Even where good beaver habitat occurs on headwaters on both sides of a watershed, population spread is significantly slowed. This effect was studied in detail by Hartman (1994a,b; 1995) in Sweden (Fig 3). A small scale example of the same process can be seen in the Trondheim Bymarka, a small peninsula west of the city of Trondheim in Norway (Fig. 4). The Bymarka is hilly (0-600m) and heavily wooded, drained by a number of small stream systems which empty separately into the fjord or the river Nidelva in Trondheim city. Beavers were directly reintroduced to this area in 1975, to Theisendammen in the NE. By 1999, beavers were well-established on the Lierelva stream system, where 5 colonies had been established, two on marginal sites later abandoned. Beaver had also moved down Lierelva, through several kilometres of suburban housing, to establish a colony on the Nidelva river within Trondheim city. Further expansion on the river has so far been curtailed by a hydroelectric dam immediately upstream, and tidal water downsteam. Beaver, probably also from Lierbekken, have also colonised two sites on the Ristbekken

in the west. However, 25 years after re-establishment, and with all suitable sites at Theisendammen and Lierelva occupied, beaver have still not succeeded in crossing the watershed to any of the remaining main stream systems, the largest three of which each contain sufficient suitable habitat for several colonies. This is despite the fact that clearly marginal sites on the occupied stream systems have been occupied, and although beaver-navigable streams on each watershed come within a few hundred metres of one another (*pers. obs.*).

Where beaver habitat is separated by serious natural or man-made barriers, the isolating affect appears to be very strong. A remnant beaver population survived in Telemark in south Norway, and has expanded only slowly in range (though greatly increased in numbers) since the turn of the century. This appears to be due to the mountainous terrain (especially in the west) and lack of unifying river systems locally. Meanwhile, c. 80 beaver originating from this population were introduced to the flat ground and large river systems of Sweden from 1927, of which a maximum of 47, at 11 sites, bred successfully (Ellegren *et. al.* 1993). All of the beavers of Sweden and almost all in the contiguous range in Norway (>125000 animals) are derived from these individuals, mainly through natural spread.

In much of western Europe suitable beaver habitat is fragmented, and isolated by large stretches of man-made unsuitable habitat. Where the region is also one of small, isolated river systems, this can prove an effective barrier to range expansion. For example, 10 beaver were reintroduced to the Elez river in Brittany (Bretagne) in 1969, and rapidly expanded to a population of c.40. The population has remained stable at this level ever since. Downstream migration has been inhibited by a manmade dam. Only one beaver has ever been found on an adjacent watershed, and no breeding colonies have been established (Lafontaine 1990 and *pers. comm.*; Gillie 1996; *pers. obs.*).

The lesson for nature managers, especially in areas such as the British Isles or Denmark where watersheds are numerous and relatively small and isolating barriers generally strong, is that, if desired, beaver expansion between watersheds can be contained relatively easily. Depending on the desired goal, this may indicate a strategy of many reintroductions to many river systems, or conversely of the rapid removal of any pairs which do manage to establish naturally on watersheds where their presence is considered undesirable, before they have the chance to spread their progeny widely within the river system.

In most parts of Europe beaver are in either the lag phase or the rapid increase phase of population expansion. However, ”mature” populations are found in Russia, Belarus, parts of the Baltic states, and parts of Scandinavia. In Sweden, it has been possible to follow population development in detail from initial establishment on a watershed to population maturity. Results show that beaver populations exhibit a classic ”irruptive” pattern, with a slowdown in population increase after the rapid expansion phase, occupation of marginal habitat not capable of sustaining beavers permanently, and a consequent decline in population as the ”capital” of these marginal areas is depleted. In 58 areas studied in Sweden, population growth turned negative on average 34 years after the first appearance of beavers (Hartman 1994a, b; 1995).

The marginal areas which cannot sustain permanent beaver occupation tend to be those which require most beaver engineering in the form of dam construction and the felling of large trees (as more energetically profitable saplings and bushes are depleted),

and are the source of most of the conflicts reported between beavers and man. Formerly, wolves may have played an important role in regulating beaver populations below this level (Hartman 1994b). However, wolves are now absent or uncommon throughout the beaver's range (except perhaps in parts of Russia). The scientific advice in Sweden to managers interested in minimising conflicts between human land use interests and beaver is "reasonably heavy harvesting during the rapid increase phase" (Hartman 1994b). A short-term alternative might be to live trap beavers for restocking populations elsewhere.

Taxonomy, genetics and reintroductions

While it is clear from chromosome number differences, failed crossbreeding attempts, and the lack of observations of hybrids in the wild that *C. fiber* and *C. canadensis* are distinct species (Lavrov 1983), the status of the various subspecies, and even the number of acceptable subspecies, is far from clear (Saveljev 1997a). Apart from the refuge of Rhone beavers *C.f. galliae* in southern France, the refugia in which beavers survived in the 19th century must all have been colonised post Ice-Age. It seems a suspicious coincidence that each of the populations of these refugia are described as distinct subspecies. All except *belarusicus* and *osteuropaeus* (both, incidentally, disputed taxons (Savalyev 1997)) derive from tiny populations of under 200 animals, and the small differences in average morphology (mainly of the skull) which are the basis of the current classification might plausibly be ascribed to founder effects and to local adaptations to prevailing conditions. *C. f. fiber* from Scandinavia is known to be of extremely low genetic variability (Ellegren *et al* 1993).

Several authors consider the maintenance of the "genetic integrity" of the various subspecies when planning new reintroductions to be important, and that the nearest surviving geographical form should be used in reintroductions (e.g. Savalyev 1997; Nolet 1997; Nolet & Rosell 1998). In most of mainland Europe, however, populations are of highly mixed origin. Translocations on a vast scale were carried out in the former Soviet Union throughout much of the 20th century, and stocks in Poland, the Danube, and Rhine are all descendants of two or more of the currently accepted subspecies. *C.f. albicus* on the Elbe will soon be (as they were in the fairly recent past) in contact with populations in Poland and, later, in Bavaria. Genetic introgression is inevitable. As the Elbe beavers in the Netherlands and Saarland share the Rhine watershed with Rhone beavers *C.f. galliae* (Karlsruhe) and Polish beavers (probably mainly *C.f. beloruscius*) (Eifel), this leaves only the *C. f. albicus* Danish reintroductions, and the reintroduction in Hesse in NW Germany, as relatively safe from genetic introgression in this subspecies. In the long term, most of the populations of mainland Europe seem likely to be in genetic contact one with another. This implies that, if maintaining completely unmixed stocks of each of the presently described subspecies (except perhaps *C.f. fiber* and *C. f. galliae*) is a management goal, attention should be given to establishing populations of each in natually isolated locations.

Inbreeding does not seem to be a problem. Recent population bottlenecks are known to have sharply reduced genetic variability in *C. f. fiber*, which is monomorphic at many genetic loci and in general of very low genetic variability (Ellegren *et. al.* 1993). Nevertheless, the Scandinavian population has increased from c. 100 a century ago to over 150000 today.

BEAVERS IN THE 21ST CENTURY
Population development and range expansion

In the next 30 years the major locus of population increase and range expansion seems set to be the Danube river system. The Danube is the second most extensive river system in Europe (after the Volga), draining 817,000 km^2, and contains a great deal of suitable habitat. Beaver are already firmly established on the upper reaches in Bavaria and Austria. In recent years reintroductions have been or will be made at the mouth of the Danube, at several sites along its main course, on the central sections of main tributaries such as the Morava, Sava, Drava, Tisa and Olt, and on the upper Orava/Váh. While the early reintroductions were made by local groups primarily concerned with the local or regional environment, recent re-establishments have been part of a co-ordinated international strategy aimed at the recolonisation the entire watershed, organised by WWF (Austria, International), the Munich Wildlife Society, and authorities and NGOs in the various counties (G. Schwab, *pers. comm.*).

Major expansions can also be expected along the Loire and Rhine, although pollution in the latter may have affected reproductive success in the Netherlands (Nolet *et al* 1994). Further expansions can be expected throughout Scandinavia, particularly in southern Sweden and in south-central Norway, where beavers have reached the main Gudbrandsdal watershed (Bevanger 1996). Assuming the planned removal of the remaining *C. canadensis* pocket in Finnish Lapland is successful, there seems to be no barrier to major expansion of the Swedish population of *C. fiber* into northern Finland. Considerable increases in range and population can also be expected in Poland in particular.

Management

Human population densities are high, and the landscape intensively managed, in much of the area which beavers are now recolonising. In the Netherlands, beavers coexist with one of the densest human populations on earth. In some ways, this is a cause for optimism, as it demonstrates clearly that beavers do not, as sometimes alleged, require large areas of wild country in which to survive. The former association with remote areas was a function of those areas also being remote from hunting and trapping pressures.

Conversely, populations in areas of high human densities inevitably come more often into contact with human activities. Reintroducing beavers into a managed landscape necessarily implies management of, or at the least affected by, beavers. A typical trajectory of landowner attitudes to recolonising beavers has been described by Rosell and Pedersen (1999). Appearance of the first individuals is a source of curiosity, and often pride. At this stage, beaver are ”cherry picking” the best habitat, in which damming, or frequent felling of large trees, is not usual. In the second phase (typically about 20 years later), complaints start to increase and the beaver’s image turns negative. This is largely due to increase in populations and occupation of more marginal habitat. These typically require more habitat alteration on the beavers’ part, and so greater potential conflict with habitat alterations perpetrated by humans. The third stage is reached when beavers are no longer a novelty and have again become an accepted part of the local scene. Management is continued, but conflicts are local, solutions well-tried, and the landowner view generally more balanced, with the benefits of beaver populations (e.g.

deacidification and purification of water, hunting opportunities, maintenance of ponds which act as habitat for duck and drought refugia for fish, etc – Macdonald *et al* 1995 for review) better appreciated.

Most beaver conflicts with man occur in a very narrow riparian zone: 75% within 20m (Nolet 1997), and almost all within c. 100m, of the water's edge. Current moves throughout Europe to conserve and regenerate the riparian zone around rivers, for other conservation and flood control motives, have the side effect of both creating beaver habitat, and reducing the scope for conflict with many human activities.

In the Nordic countries, which have the most developed beaver populations outside Russia and the Baltic states, management is through directed hunting (Rosell & Petersen 1999; Moe 1996; Ermala *et. al.* 1999). This approach has several advantages. It allows management of the beaver population in a way which minimises conflicts; it gives landowners a direct incentive to have, and manage, beavers as an integral part of their land management practices; and it is self financing. Other methods, such as culling or translocation by the authorities directly, or payment of compensation, are both expensive and self-defeating, in that they reinforce the mental habit of viewing beavers as "a problem", and so entrench conflict. Some care must be exercised in setting hunting regulations, however, as the species has shown itself historically to be highly vulnerable to overhunting.

Ethically, it is difficult to see why healthy populations of beavers should be regarded as any different to other game species which can be managed, in part, with a view to a hunting take. In the absence of significant predation pressure from wolves, not a practical proposition in most of Europe, the alternative agent of population regulation to hunting or culling is starvation, either directly or through increased susceptibility to disease. This is arguably the less ethical (albeit passive) management option.

An important additional benefit of beaver reestablishment is public enjoyment. Beaver lead fascinating lives, and are easy to observe in daylight in summer. They can live in peri-urban, and even quiet urban, locations, and can become very tame. For example, in Trondheim in Norway (*pers. obs.*), one well known family group has a dam anchored on one side to the embankment of a main road, directly overlooked from the pedestrian walkway. A housing subdivision is 150m away and the home range largely bounded by the road and a sports arena car park. The beaver ignore passersby and observers on the walkway, or elsewhere more than c. 20m distant. "Beaver safaris" are a small, but significant, feature of the tourist industry in Norway (Rosell & Pedersen 1999); the scope for similar operations in more heavily populated areas of Europe would be correspondingly greater.

In Denmark, SNS (the government nature conservation and forestry body) actively promotes viewing of the very first beaver reintroduced there in 1999. "Beaver safaris" are offered to observe beavers in Norway, Sweden, and at the recent reintroduction in Belgium. In any case, as beaver leave very obvious signs, attempting to conceal reintroduction locations is a largely futile exercise; public viewing and interpretation both increases tourism income (and so local support), and helps to shape a positive public attitude from the outset.

Populations of beavers are now established or establishing in most regions of their former European range, the main exceptions to date being Iberia, Italy, the south Balkans and the British Isles. There seems little doubt that populations will increase both in

numbers and in range until beaver are again a tolerably common species in suitable habitat over much of Europe. In an era of ever-increasing pressure on wild nature, this is an encouraging indicator of the scope for many wild species to coexist with developed human economies, given sufficient vision and tolerance.

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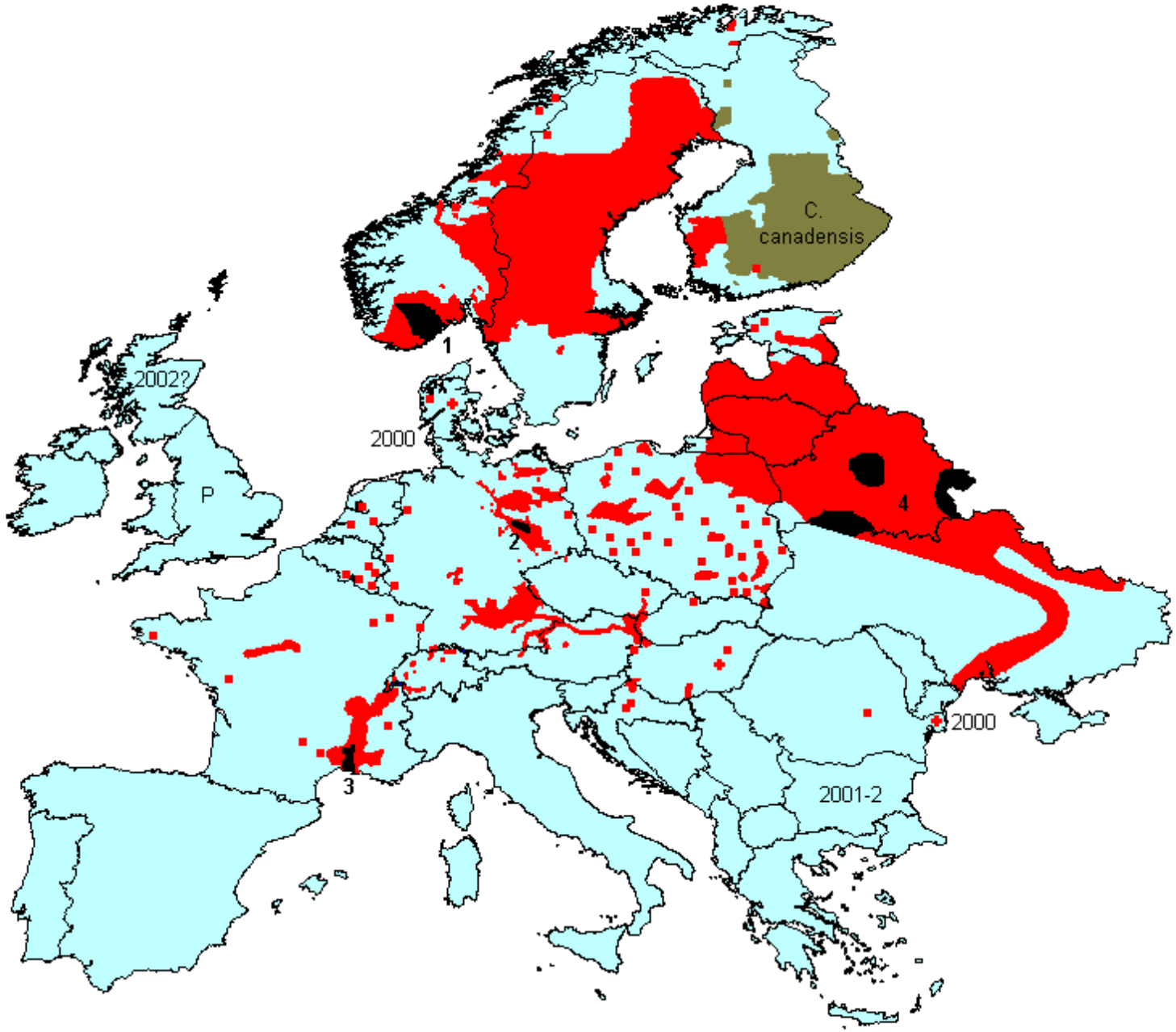
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Figure 1. Distribution of beavers in Europe, excluding Russia. Locations of relict populations are marked in black: 1 *Castor fiber fiber*; 2 *C. f. albicus*; 3 *C. f. galliae*; 4 *C. f. belarusicus*. Red shading represents the range of reintroduced beavers of mixed origin; green shading represents the range of *C. canadensis* in Finland. Red squares are reintroduction sites where range has not yet spread significantly; red crosses represent planned reintroductions, with date. Other dates refer to planned reintroduction dates to countries where the reintroduction location is not yet determined; ”P” countries where reintroduction has been formally proposed but no decision made. (Sources: S. Asbirk *pers. comm.*; Balodis 1994; O. Boszér *pers. comm.*; Bevanger 1996; S. Capt (Centre Suissse de Cartographie de la Faune) *pers. comm.*; A. Czech *pers. comm.*; Danilov 1995; Dúha & Majzlan 1997; Ermala *et. al.* 1999; M. Grubesic *pers. comm.*; Hartman 1999 & *pers. comm.*; Heideke & Ibe 1997; Lahti 1995; Mickus 1995; Nolet & Rosell 1998; Richard 1985; Rosell & Pedersen 1999; G. Schwab *pers. comm.*; J Sieber *pers. comm.*; Troidl & Ionescu 1997; Valachovic 1997; Winter 1997.)

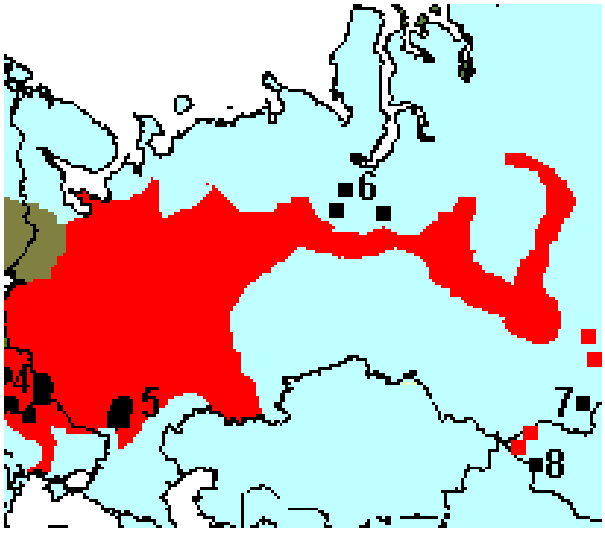

Figure 2. Distribution of beavers in European Russia, western Siberia, Mongolia and Xinjiang (China). Locations of relict populations are marked in black: 4 *Castor fiber belarusicus*; 5 *C. f. osteuropaeus*; 6 *C. f. pohlei*; 7 *C. f. tuvinicus*; 8 *C. f. biruli*. Red shading represents the range of reintroduced beavers of mixed origin; green shading represents the range of *C. canadensis* in Russian Karelia and adjacent regions of Finland (Redrawn from Nolet & Rosell 1998).

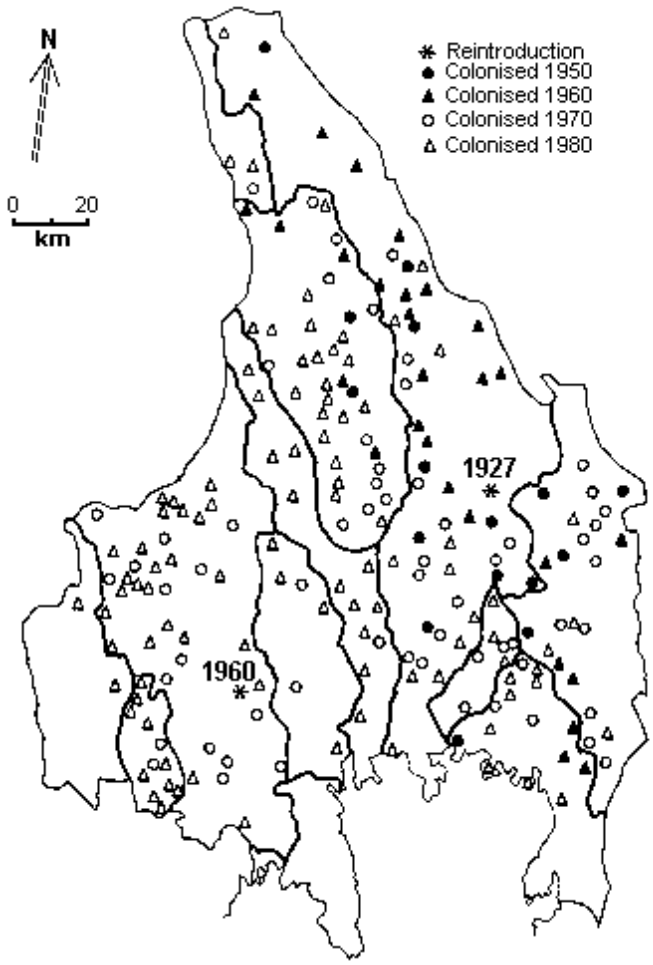

Figure 3. Patterns of spread of beavers recolonising Varmland province, Sweden. Watershed divides are shown by bold lines. Dates of reintroductions are indicated. Beaver spread very rapidly throughout watersheds after initial recolonisation, with infilling thereafter. Watershed divides, however, significantly slowed range expansion. Figure adapted from Hartman (1994b).

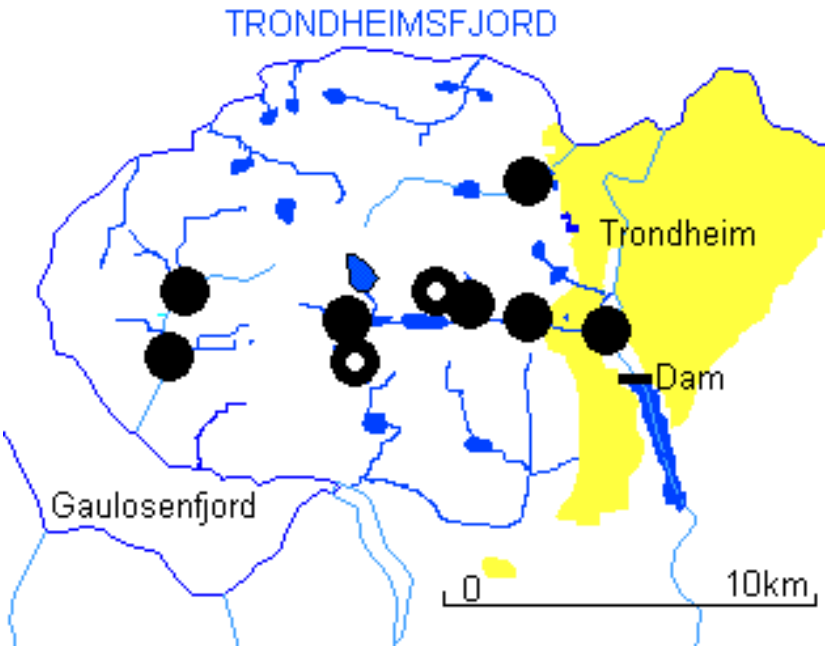

Figure 4. Distribution of beavers in Trondheim Byneset in 1999. Filled black circles represent the centres of active home ranges; hollow circles indicate abandoned home ranges. Beaver were reintroduced to Theisendammen (top right home range) in 1975. They have since colonised two adjacent stream systems. Each of the three largest uncolonised stream systems contain sufficient habitat for several beaver colonies, but as yet remain unoccupied.