Population and distribution of European beavers (*Castor fiber*)

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Abstract: After being reduced to about 1,200 animals in eight isolated populations by the beginning of the 20th century, European beavers (*Castor fiber*) have powerfully recovered in both range and population, through relaxation of persecution, natural spread, and widespread reintroductions. Populations are now (2003) established in all countries within their former natural range in Europe except for Britain, Portugal, Italy, and the south Balkans (Greece, Albania, Bulgaria, Macedonia; status in Bosnia-Herzegovina is uncertain). In Asia, there are significant populations in central Siberia, Kamchatka, and on the Amur; and small relict populations elsewhere in Siberia, and in Xinjiang (China)/western Mongolia. The current minimum population estimate is 639,000. Both populations and range are in rapid expansion. We present maps summarizing current knowledge of the world distribution of European beaver and the Eurasian distribution of the introduced American beaver (*Castor canadensis*), and tables of the most recent known population estimates for each country.

Keywords: beaver, *Castor fiber*, population, distribution, range, reintroduction.

Introduction

European beavers (*Castor fiber*) have, since the late 19th century, staged a remarkable recovery both in population and distribution. From being a critically endangered species reduced to about 1,200 animals in scattered enclaves, the species is now conservationally secure and, aided by widespread reintroductions, rapidly recolonising much of its range, including areas where it has not occurred for centuries or even millennia. The pattern of reexpansion is not only interesting in itself, but also offers valuable insights in the fields of population biology and conservation ecology. Until recently, this expansion has not been well documented, but since the latter part of the 20th century increasing amounts of information have become available, allowing the preparation of reviews summarizing the then current status of the species (Macdonald et al. 1995, Halley & Rosell 2002). However, both population and distribution continue to expand rapidly, both through natural spread and new reintroductions, so that these reviews rapidly become overtaken by events. Regular summaries of the most recent population and distribution data are therefore of use, both to current researchers and managers seeking an overview of the many, widely scattered, papers on the subject, and for future biologists interested in following in detail a remarkable case study in conservation biology.

Distribution

Population distribution is best known in western and central Europe (figure 1), less so for European Russia and Asia (figure 2). The continuous population ranges from eastern Poland through the Baltic States and European Russia to central Siberia. There is a large disjunct population in Norway and Sweden, and smaller scattered disjunct populations through the rest of mainland Europe. Disjunct reintroduced populations are also found on the periphery of the main Russian range, on the Amur watershed in eastern Siberia,

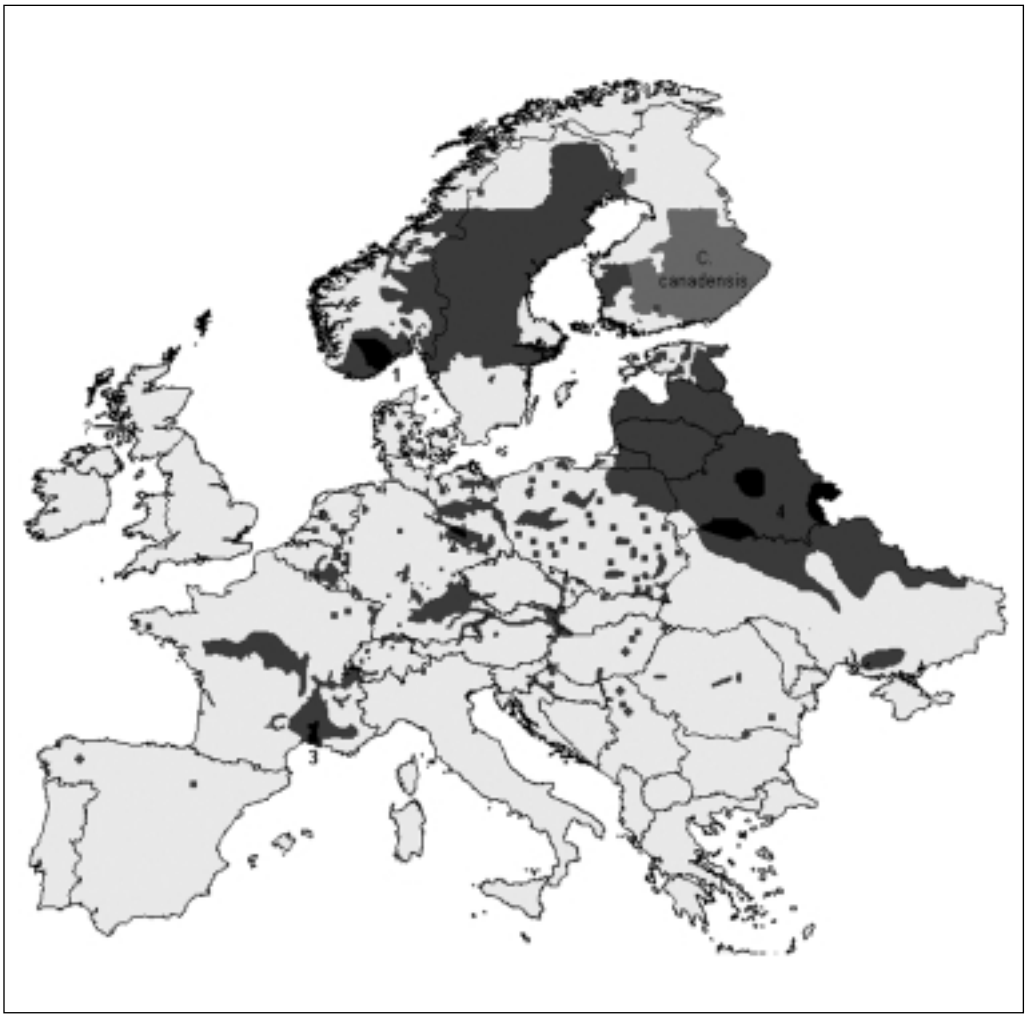

Figure 1. Distribution of beavers in Europe, excluding Russia. Locations of relict populations are marked in black. Traditional subspecies designations: 1 = *Castor fiber fiber*; 2 = *Castor fiber albicus*; 3 = *Castor fiber galliae*; 4 = *Castor fiber belarusicus*. 1-3 are all *Castor fiber fiber*, 4 is *Castor fiber vistulanus* in DuCroz's reclassification (J.-F. DuCroz, personal communication; see Discussion). Dark shading represents the present range of *Castor fiber*; light shading represents the range of *Castor canadensis* in Finland. Squares are reintroduction sites where range has not yet spread significantly; crosses represent planned reintroductions (sources: Andersen 2002, P. Asbirk, personal communication, Balodis 1994, O. Boszér, personal communication, Bevanger 1995, O. Capt, personal communication, A. Czech, personal communication, Danilov 1995, Dúha & Majzlan 1997, Ermala et al. 1999, Fustec et al 2001, M. Grubesic, personal communication, Hartman 1999, G. Hartman, personal communication, Heideke & Ibe 1997, G. Ionescu, personal communication, Laanetu 1995, H. Lea, personal communication, V. Kostkan, personal communication, Mickus 1995, Niewold & Lammertsma 2000, F. Niewold, personal communication, Nolet & Rosell 1998, Office Nationale de la Chasse 1997, Pachinger & Hulik 1999, J. Ramon, personal communication, J. Reinhold, personal communication, Richard 1986, Rosell & Pedersen 1999, A.P. Saveljev, personal communication, G. Schwab, personal communication, J. Sieber, personal communication, H. Sluiter, personal communication, Troidl & Ionescu 1997, Ulevicius et al. 1999, A. Ulevicius, personal communication, D. Valachovic 1997, A. Vorel, personal communication, Winter 1997).

and on the Kamchatka peninsula in the Russian Far East. Although natural spread has contributed significantly to range and populations, most of the expansion is due to reintroductions, of which at least 157 have been recorded outside the former Soviet Union (FSU) (beaver were also extensively translocated within the FSU, but details are not available) (Halley & Rosell 2002). In 2003, beavers were reintroduced to the Ebro in Spain, with plans for further reintroductions to the Guadalquivir, Guadiana, and Tajo (Tagus) river systems (H. Lea, personal communication); reintroductions to Serbia at Obedska Bara and at Zasavica, on the Sava west of Belgrade, took place in spring 2004, and a later release to Ola Becej on the Danube north of Belgrade is planned (G. Schwab & D. Cirovic, personal communication). In Siberia there have been recent reintroductions (2001-2003) on the lower Ob and on the middle Lena (A.P. Saveljev, personal communication). Introduced populations of American beaver (*Castor canadensis*) are established in Finland and northwest Russia, on the Amur, and in Kamchatka (Saveljev & Safonov 1999, A.P. Saveljev, personal communication).

Available information on relict population sizes is given in table 1, and data on date of extinction, legal protection, reintroduction, and current population size in table 2.

Discussion

Populations of the eight refugia in which beavers survived the 19th century are currently each described as separate subspecies. However, recent mDNA testing indicates clearly that only two subspecies are justifiable (*Castor fiber fiber = Castor fiber fiber, albicus* & *galliae*, and *Castor fiber vistulanus = Castor fiber belarusicus, osteuropaeus, pohlei, tuvinicus* & *birulei*) (J.-F. DuCroz, personal communication). This finding should be taken into account by managers seeking reintroduction stock in line with IUCN guidelines.

European beaver families consist of, on average, about five individuals, of which only the adult pair breeds. The minimum populations quoted should be interpreted in this light; the Rhône remnant population, for example, would seem to have been reduced to about six breeding pairs at minimum, well below the 25 pairs often quoted as a minimum viable population (MVP). (That evidence on the ground indicates that this rule-of-thumb is generally too pessimistic, is fortunate for conservation; see Caughley & Sinclair (1994) for review of this issue). The small size of remnant populations, and resultant inbreeding and loss of genetic diversity, does not seem to have led to breeding problems in this species, but

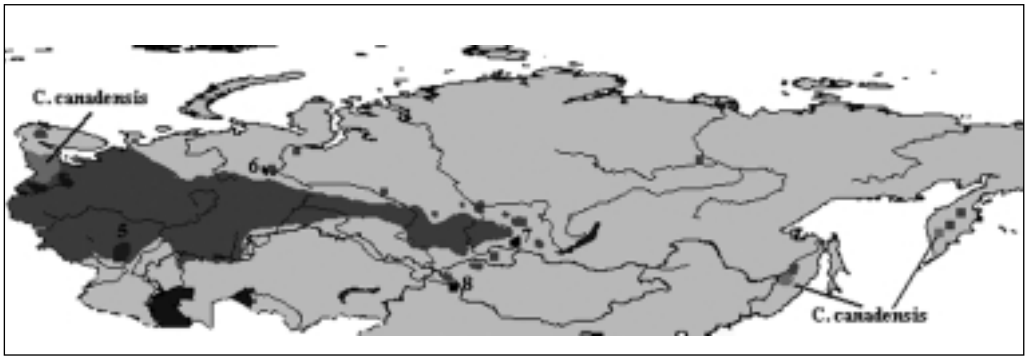

Figure 2. Distribution of beavers in Russia, Mongolia, Kazakhstan and Xinjiang (China). Locations of relict populations are marked in black. Traditional subspecies designations: 5 = *Castor fiber osteuropaeus*; 6 = *Castor fiber pohlei*; 7 = *Castor fiber tuvinicus*; 8 = *Castor fiber biruli*; 5-8 are all *Castor fiber vistulanus* in DuCroz's reclassification (J.-F. DuCroz, personal communication; see Discussion). Dark shading represents the present range of *Castor fiber*; light shading represents the range of *Castor canadensis* (figure adapted from Nolet & Rosell 1998 and A.P. Saveljev, personal communication).

Table 1. Location and estimated minimum population sizes of relict populations of European beaver (*Castor fiber)*.

Population	Minimum population size	References
Lower Rhône, France	30	Richard 1985
Telemark, Norway	60-120	Collet 1897
Elbe, Germany	200	Heideke & Hörig 1986
Pripet marshes, Belarus/Ukraine/Russia	<300	Zharkov & Solokov 1967
Voronezh, Russia	70	Lavrov & Lavrov 1986
Konda-Sosva, Russia	300	Lavrov & Lavrov 1986
Upper Yenesei, Russia	30-40	Lavrov & Lavrov 1986
Urungu, Mongolia/China	<100-150	Lavrov & Hao-Tsuan 1961

suggests that populations descended solely from some of the smaller surviving populations may be more susceptible as a population to epidemic disease, due to lack of diversity in immune systems (Ellegren et al. 1993). In this connection, recent evidence that only two subspecies of European beaver can be justified (J.-F. DuCroz, personal communication; see above) suggests that managers may consider mixing individuals from the various refugia of each subspecies. This would broaden the genetic diversity within reintroduced populations somewhat without compromising subspecific integrity, as IUCN guidelines recommend.

The current world population estimate of 639,000 given here is conservative, calculated by adding together the lowest estimates for each country (rounded to the nearest thousand). All surviving European populations have grown in numbers beyond the point where further loss of genetic diversity through drift might be a conservation problem, though the status of some of the Siberian relict populations is unclear in this respect and would merit investigation.

The actual population is probably considerably higher than the figure given above. Assuming, for example, the higher end of the range estimates, and that populations estimated at 'greater than' were 10% above the figure given, yields a population estimate of just below 742,000. In some cases the population estimates given are several years old, so that, allowing in addition for natural increase, the true population may be closer to the higher of these figures. However, the limitations in data available make all estimates beyond stating the minimum population speculative.

In most countries of the western and central European mainland, beavers exist at relatively low numbers for the present, and there is much unused suitable habitat. The range maps presented here are therefore probably conservative, as newly colonising beavers tend to select prime habitat requiring little alteration, where their presence may not immediately be noted by non-specialists. Very considerable expansion in both populations and range can be expected in the coming decades, especially in western Europe and the Danube watershed. A typical pattern of population development on a watershed following natural or artificial recolonisation has become evident in recent years, the evidence for which is reviewed in Halley & Rosell (2002); the most detailed case study of range and population expansion is found in Hartman (1995; personal communication.). At first, range expansion through the watershed is rapid, but population expansion is relatively slow. This seems to be because beavers select the best habitat available, rather than settling close to their natal territory. It is also difficult to find a mate in the vast, unoccupied stretches of a large watershed, and it appears that beaver will wander widely while searching. Extreme figures of movements of 500 km (Lavrov 1980 quoted in Saveljev et al. 2002), and 200 km involving crossing a watershed divide (Saveljev et al. 2002), have been reported, both of animals moving into uncolonised waters.

Table 2. The history and present status of European beavers (*Castor fiber*).

Country	Extinction	Protection	Reintroduction and/or translocations	Present population size	References
Austria	1869	–	1970-1990	>1300	Kollar & Seiter 1990 Sieber 1999 J. Sieber, pers. comm.
Belarus	remnant	1922	–	24,000	Djoshkin & Safonov 1972 Safonov & Saveljev 1999
Belgium	1848	–	1998-2000	200-250	Van den Bergh & Manet, pers. comm.
Bosnia-Herzeg.	?	–	-[1]	0[1]	M. Grubesic, pers. comm.
Bulgaria	?	–	planned	0	G. Schwab, pers. comm.
Croatia	1857?	–	1996-1998	c.180	M. Grubesic, pers. comm.
Czech Republic	17th century	–	1991-1992 1996	c.500	Kostkan & Lehky 1997 Kostkan 1999
Denmark	c.500 BC[2]	–	1999	60-70	Skov- og Naturstyrelsen 2000 Berthelsen & Madsen 2003 J. Berthelsen, pers. comm.
England	<12th century	–	–	0[3]	Macdonald et al. 1995 Campbell & Tattersall 2003 F. Tattersall, pers. comm.
Estonia	1841	–	1957	11,000	Laanetu 1995 U. Timm, pers. comm. A. Ulevicius, pers. comm.
Finland	1868	1868	1935-1937 1995	2000[4]	Lahti 1995 Ermala et al. 1999 A. Ermala, pers. comm.
France	remnant	1909	1959-95	7000-10,000	Richard 1985, 1986 Fustec et al. 2001 R. Dennis, pers. comm. P. Rouland, pers. comm.
Germany	remnant	1910	1936-1940 1966-1989 1999-2000	8000-10,000	Schwab et al. 1994 Macdonald et al. 1995 G. Schwab, pers. comm.
Hungary	1865	–	1991-1993 1996-2003	>400	Kollar & Seiter 1990 O. Bozsér, pers. comm. G. Schwab, pers. comm.

Table 2 *(continued)*. The history and present status of European beavers (*Castor fiber*).

Country	Extinction	Protection	Reintroduction and/or translocations	Present population size	References
Italy	1541	–	proposed	0	Nolet 1996
Kazakhstan	?	–	–	1000	Djoshkin & Safonov 1972 Safonov & Saveljev 1999 Saveljev & Safonov 1999
Latvia	1830s	–	1927-1952 1975-1984	>100,000	Balodis 1992, 1995, 1997, 1998 Ozolins & Baumanis 2000
Lithuania	1938	–	1947-1959	50,000-70,000	Palionene 1965 Mickus 1995 Balciauskas et al. 1999 Ulevicius et al. 1999 Ulevicius 2000 A. Ulevicius, pers. comm.
Luxembourg	18th century?	–	2000	1[5]	Schley et al. 2001
Mongolia/China	remnant	–	1959-1985	800	Lavrov & Hao-Tsuan 1961 Lavrov 1983 Stubbe & Dawaa 1983, 1986
Netherlands	1826	–	1988-2000	177-227	Nolet 1994, 1996 J. Reinhold, pers. comm. H. Sluiter, pers. comm.
Norway	remnant	1845	1925-1932 1952-1965	c.70,000	Djoshkin & Safonov 1972 Bevanger 1995 Rosell & Pedersen 1999 Andersen 2002 H. Parker, pers. comm.
Poland	1844	1923	1943-1949 1975-1986	18,000-23,000	Zurowski & Kasperczyk 1986, 1988 Zurowski 1992 Macdonald et al. 1995 Czech 1999 Dzieciolowski & Gozdziewski 1999 A. Czech, pers. comm.
Romania	1824?	–	1998-1999	>170	Troidl & Ionescu 1997 G. Schwab, pers. comm.

Table 2 *(continued)*. The history and present status of European beavers (*Castor fiber*).

Country	Extinction	Protection	Reintroduction and/or translocations	Present population size	References
Russia	remnant	1922	1927-1933 1934-1941 1946-1964	232,000-300,000	Djoshkin & Safonov 1972 Lavrov 1983 Dezhkin 1999 Safonov & Saveljev 1999 Saveljev & Safanov 1999
Scotland	16th century	–	?	0[6]	Kitchener & Conroy 1997 Scottish Natural Heritage 2000
Serbia	1903?	–	2004	30	G. Schwab, pers. comm.
Slovenia	?	?	1999	<6[7]	M. Grubesic, pers. comm.
Slovakia	1851	–	1995	>500	Dúha & Majzlan 1997 Valachovic 1997 Pachinger & Hulik 1999
Spain	17th century	1981	2003	18	H. Lea, pers. comm.
Sweden	1871	1873	1922-1939	>100,000	Freye 1978 Hartman 1994, 1995
Switzerland	1820	–	1956-1977	>350	Stocker 1985 Macdonald et al. 1995 Winter 1997 S. Capt, pers. comm.
Ukraine	remnant	1922	–	6000	Djoshkin & Safonov 1972 Lavrov & Lavrov 1986 Safonov & Saveljev 1999
Wales	12th century	–	–	0	Macdonald et al. 1995

[1] Spread into Bosnia-Herzegovina along the Sava river (from the Croatian reintroduction) is likely to have occurred, but no data.
[2] Based on subfossil remains. Philological evidence from placenames suggests a remnant may have survived as late as the 11th century.
[3] Five animals reintroduced to a fenced enclosure at Ham Fen, Kent, 2003.
[4] Finland also has a population of 14,000 American beavers (*Castor canadensis*).
[5] Natural spread from Belgium.
[6] Scottish Natural Heritage has applied to the Scottish Executive for permission to conduct a trial reintroduction in Knapdale, west Scotland. A decision is pending.
[7] Natural spread from Croatia.

However, the longest distance *colonisation* to have been reported is apparently Hartman's (1995) record of colonisation of an area about 70 km away from the nearest other occupied area. Some time later, depending on the size and topography of the watershed but often after about 10-25 years, populations reach a critical density for encountering a mate, and the population then increases very rapidly. This is followed (on average 25-34 years after watershed colonisation in Hartman's (1995; personal communication) study) by a phase of population decline as marginal habitats become exhausted; and then by rough stability.

While in established populations average dispersal distance is usually much less than the extremes mentioned above, 3.9 km on the Azas river in Siberia, individuals disperse much further, one subadult male being found 85 km upstream (Saveljev et al. 2002). This implies the potential for considerable gene flow within continuous populations.

Incidences of beaver conflicts with humans tend to intensify during the later stages of the rapid increase phase, in part because then beaver more often take into use more marginal sites requiring more beaver engineering, dams, canals, etc, which may conflict with human landuses. In many countries, this phase of population development has been accompanied by the introduction of hunting, aimed at least in part at addressing conflict issues (Halley & Rosell 2002).

Conversely, while beavers can and do cross land, and have been found up to 11.7 km away from the nearest water body (Saveljev et al. 2002) watershed divisions do show a clear barrier effect for beaver expansion, which can be strongly isolating where natural or artificial habitat barriers, such as high mountains or intensive farmland, intrude between watersheds. Depending on the management strategy, therefore, this suggests a policy of many reintroductions to many watersheds, or, conversely, the early removal of colonising individuals on watersheds where their presence is considered undesirable. Given the pattern of range expansion within watersheds, confining beaver populations to a particular stretch within a watershed will be impractical unless there are strong artificial barriers to expansion, such as man-made river barrages, or a heavy and directed hunting or trapping effort (Halley & Rosell 2002). Beaver populations should therefore be managed on a watershed scale.

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Samenvatting

Populatie en verspreiding van Europese bevers (*Castor fiber*)

Na een afname in het begin van de twintigste eeuw tot ongeveer 1200 dieren in acht verschillende populaties, hebben de Europese bevers (*Castor fiber*) zich krachtig hersteld, zowel in verspreiding als populatiegrootte, door vermindering van de jacht, natuurlijke verspreiding en op veel plaatsen uitgevoerde herintroducties. Populaties hebben zich nu (2003) gevestigd in alle landen binnen hun voormalige natuurlijke verspreidingsgebied met uitzondering van Groot Britannië, Portugal, Italië en de zuidelijke Balkanlanden (Griekenland, Albanië, Bulgarije, Macedonië; de status in Bosnië-Herzegovina is onzeker). In Azië zijn er aanzienlijke populaties in centraal Siberië, Kamchatka en de Amur en kleine relict-populaties elders in Siberië en in Xinjiang (China) / west Mongolië. De huidige minimum schatting van de populatieomvang is 639.000. Zowel de populaties als het verspreidingsgebied breiden zich snel uit. We presenteren kaarten die beknopt de huidige wereldverspreiding van de Europese bever weergeven, en de Europees-Aziatische verspreiding van de uitgezette Amerikaanse bever (*Castor canadensis*). Verder laten we tabellen zien met de meest recente populatieschattingen voor elk land.

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