

REVIEW

Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia

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ABSTRACT

1. A century ago, overhunting had reduced Eurasian beaver *Castor fiber* populations to c. 1200 animals in scattered refugia from France to Mongolia. Reintroductions and natural spread have since restored the species to large areas of its original range. Population has more than tripled since the first modern estimate in 1998; the minimum estimate is now c. 1.5 million.
2. Range expansion 2000–2020 has been rapid, with large extensions in western and south-central Europe, southern Russia, and west and central Siberia. Beavers are now re-established in all countries of their former European range except for Portugal, Italy, and the southern Balkans; they occur broadly across Siberia to Mongolia, with scattered populations further east. About half of the world population lives in Russia. Populations appear to be mature in much of European Russia, Belarus, the Baltic States, and Poland.
3. There is a significant population of North American beaver *Castor canadensis* in Finland and north-west Russia. Most other 20th-Century introductions of this species have become extinct or been removed.
4. Recent DNA studies have improved understanding of *Castor fiber* population prehistory and history. Two clades, east and west, are extant; a third ‘Danube’ clade is extinct. Refugial populations were strongly bottlenecked, with loss of genetic diversity through genetic drift.
5. Future range extension, and large increases in populations and in impacts on freshwater systems, can be expected. Beavers are now recolonising densely populated, intensely modified, low-relief regions, such as England, the Netherlands, Belgium, and north-west Germany. They will become much more common and widespread there in coming decades. As beavers are ecosystem engineers with profound effects on riparian habitats, attention to integrating beaver management into these landscapes using experience gained in other areas – before the rapid increase in population densities and impacts occurs – is recommended.

INTRODUCTION

This paper is the third review – including short updates the fifth paper – intended to summarise Eurasian beaver *Castor fiber* distribution change and population development (Nolet & Rosell 1998, Halley & Rosell 2002, 2003,

Halley et al. 2012; a population estimate for Europe was also recently presented in a short communication, Wrobel 2020). The status of the North American beaver *Castor canadensis* in Eurasia is also reviewed. Information available is copious, but very widely scattered. Some is available in peer-reviewed papers, but most is in national- or

regional-level reports, popular articles, and other sources not searchable in scientific databases.

The Eurasian beaver is on the threshold of large extensions in geographic range, and exponential growth in population, in many parts of western and south-central Europe, including some of the most heavily populated and human-modified regions of the world. This, the amount of information relevant to understanding beaver population development accumulated since the last review, and the large changes in population and distribution since the last update, make a new review timely.

METHODS

We collect sources on the Eurasian population and distribution of both species of beaver, and patterns of population development, on an ongoing basis. Principal sources are searches of Internet science literature databases, general Internet searches, grey literature, conferences, and personal correspondence. Maps of beaver distribution and the population table are updated as new information is received.

Beaver populations develop on watersheds (Hartman 1994a, 1994b, 1995) and should ideally be considered on a watershed scale. However, almost all information is available at a national or sub-national scale. Here, we present data by country, following the structure of Halley and Rosell (2002) for ease of comparison. ‘Beaver’ means the Eurasian beaver unless otherwise stated.

TAXONOMY, GENETICS, AND REINTRODUCTIONS

Recent advances in DNA studies have deepened and modified understanding of the species’ post-Ice Age and bottleneck period population histories.

Previously, eight subspecies, one for each 19th to early 20th-Century refugium, were identified (see, e.g. Lavrov 1983, Nolet & Rosell 1998). The reality of this subdivision has long been doubted (e.g. Halley & Rosell 2002, Halley 2011, Rosell et al. 2012, Horn et al. 2014), and it is no longer tenable in the light of modern genetic studies. For example, “Ancient British beavers ... formed part of a large, continuous, pan-Western European clade that harboured little internal substructure” (Marr et al. 2018). Senn et al. (2014) considered that “A likely suggestion is that divergence in mtDNA haplotypes (into ‘western’ and ‘eastern’ phylogroups) did indeed arise following population retreat into glacial refugia during the last glacial maximum (~25000 ya), but that introgression following secondary contact of re-emergent populations caused subsequent mixing of divergent haplotypes in contact regions”. This agrees with genetic evidence from a wide range of other species indicating recolonisation of Europe from two

main Ice Age refugia in the Balkans and southern France/Iberia (e.g. Hewitt 2000).

In addition, Durka et al. (2005) identified an extinct ‘Danube’ clade, neither ‘western’ nor ‘eastern’, while both Biedrzycka et al. (2014) and Munclinger et al. (in preparation) identify DNA markers apparently present in no known refugial population. These are likely to be explained (though other explanations are possible) by the survival of one or more populations in north-central Europe in addition to the eight known. Saveljev et al. (2011) also found genetic differentiation in beavers from the Pripet refuge, corresponding to different rivers in which beavers survived, flowing separately from the Pripet Marshes area.

Further genetic research deepening or modifying understanding of *Castor fiber* population history can be expected. We name, as appropriate below, the refugia reintroduction stock came from. This allows assignment to the earlier ‘subspecies’ if so desired.

HISTORY AND STATUS OF BEAVER POPULATIONS BY COUNTRY

Halley and Rosell (2002) provide information on beaver source populations, and details of location and size of reintroductions, before 2002. European distribution in 2002 is shown in Fig. 1; current distribution in Fig. 2. Asian distribution in 2002 is shown in Fig. 3, and current distribution in Fig. 4. Dates of extinction, legal protection, and reintroductions, and current population estimates for each country are given in Table 1. Fig. 5 shows the minimum population estimates from 1998 to 2019.

Austria

In Austria, 40 Eurasian beavers were reintroduced (several sites) in 1970–90 (Halley & Rosell 2002). Beavers have also immigrated to Austria from Bavaria, Germany, in large numbers. Beavers from Austria have colonised adjacent regions of Slovenia, Hungary, Slovakia, the Czech Republic, Switzerland, and Italy. The Universität für Bodenkultur, Wien, maintains a website on beavers in Austria (<https://www.dib.boku.ac.at/iwj/forschung/projekte-aktuelle-informationen/der-biber-castor-fiber-in-oesterreich/>). The population was estimated as 7600 in 2017. The latest available map (Appendix S1 and see website) dates from 2012. Nine North American beavers were also introduced in the 1980s, but no beaver carcasses examined in later years have been of this species; it appears to have become extinct (Sieber 2000).

Belarus

Beavers survived in the Pripet, Berezina, and Neman Rivers, Belarus, and were reintroduced widely in the Soviet period.

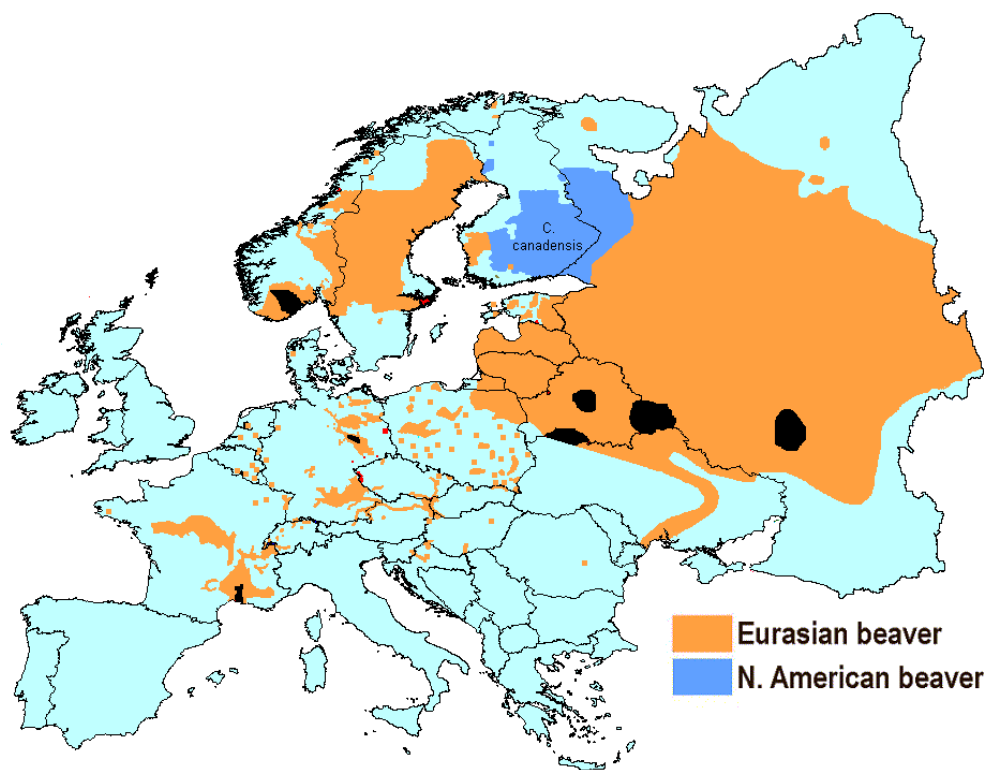


Fig. 1. Beaver distribution in Europe in 2002. Black = refugia where Eurasian beaver was never extinct.

Beavers from these three populations differ significantly from one another in morphological and biological characters (Samusenko & Fomenkov 1983). Recent genetic data indicate that combining all beavers of Belarus stock into one subspecies, *Castor fiber belorussicus*, is not valid (Saveljev et al. 2011).

Beavers are now distributed throughout Belarus. The National Statistical Committee (<http://www.belstat.gov.by/en/>) publishes annual population figures in English. The figure for 2017 was 51100. Figures suggest a peaking and decline in population in recent years (2011: 60500; 2012: 64400; 2013: 62000; 2014: 63400; 2015: 58300; 2016: 51300).

Litvinov et al. (2012) describe the modern populations of beavers. Belarus is developing a national management strategy, aimed at achieving more intensive hunting and use of beaver derivatives – meat and castoreum (G. Yanuta personal communication).

Belgium

Although vagrants from German reintroductions occurred previously, beavers in Belgium descend mainly from unofficial releases of 101 individuals in 1998–2000 to several sites, mainly in the Ardennes, and an unofficial release in the Dijle and Laan Rivers of Flanders in 2003

(all openly publicised). Other beavers have spread into Flanders from the Netherlands, also in 2003. All source to the mixed stock population in Bavaria (Verbeylen 2003).

The Flanders population in 2018 was c. 155 territories, minimum 400 beavers (J. van den Bogaert, and Belgium Beavers Working Group, personal communications); in Wallonia c. 650 territories or 1800–2000 beavers (Bernaerts 2016; J.-P. Facon, Gouvernement Wallonie, and Belgium Beavers Working Group, personal communications). Distribution in 2016 is shown in Appendix S2.

Bosnia and Herzegovina

Forty beavers were released on the Semešnica and Sokočnica Rivers, south of Banja Luka, Bosnia and Herzegovina, in 2005 and 2006 (Trbojević & Trbojević 2016). Beavers have also spread throughout the Sana and parts of the Korana and Una rivers in north-west Bosnia from Croatia, to the lower Drina River in the east from Serbian reintroductions, and along the Bosnian side of the Sava River, from Croatia and Serbia. Trbojević and Trbojević (2016) estimated the 2016 population at c. 140. Population growth rates, and the scattered distribution away from the reintroduction sites (Appendix

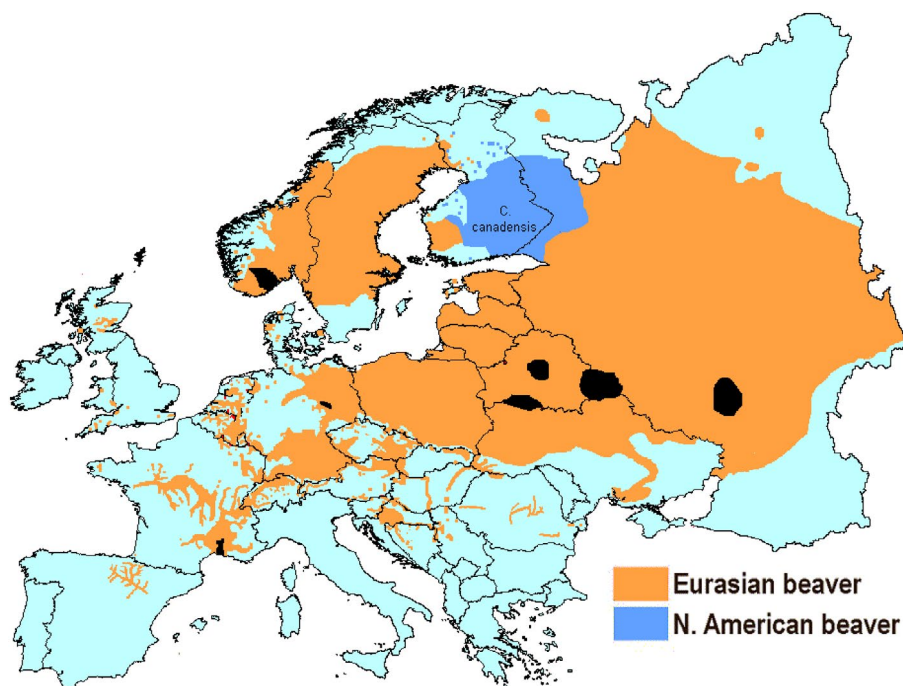


Fig. 2. Beaver distribution in Europe in 2020. Black = refugia where Eurasian beaver was never extinct.

S3; Trbojević & Trbojević 2016; Figs 1 and 2), suggest that beavers are still in the ‘establishment’ phase (Hartman 1994a, 1994b, 1995, Halley & Rosell 2002). Rapid increases on all of these rivers can be expected.

Bulgaria

A recent study (Boev & Spassov 2019) documents former beaver presence throughout Bulgaria and extinction in 1750–1850. Spread from Romania is likely in the near future.

China

A native population is found in Xinjiang in the far north-west, in the upper part of the Ulungur (Wulungu) river (upper Ob watershed; Lavrov & Lu 1961). Beavers also live on the partly Mongolian Chinge and Bulgan River tributaries. These populations are threatened by unsustainable water and soil exploitation, forest destruction, and agricultural expansion. There are more than 60 irrigation dams on the Ulungur River. The dam closest to the Mongolian border completely isolates Mongolian from Chinese subpopulations.

50 km of the Bulgan was designated as the Bulgan River Beaver Reserve in 1980. In 1992, beavers were translocated from the Bulgan to the Irtysh River to reduce risks of genetic bottlenecks, but results were

unsatisfactory (Huang 1993). A 2007 survey on the Bulgan showed 145 families with 508–645 beavers (Chu & Jiang 2009).

Beavers are Critically Endangered in China (Jiang et al. 2016). The population is estimated as <600.

Croatia

Beavers were reintroduced to Croatia from Bavaria in 1996–98. Forty-eight were released on the Sava River near Ivanic Grad and 29 on the Drava at Legrad. Nine were released on the Česma, a Sava tributary near the main release site (Grubesić et al. 2001, Cavric 2016). Beavers are now widespread in the Croatian Drava and Sava River basins and have spread into Slovenia, Bosnia and Herzegovina, Hungary, Slovenia, and Austria (on the Mura, via Slovenia). The population in Croatia is estimated at 10000 (Tomljanović et al. 2018).

Czech Republic

History and status of beavers in the Czech Republic are reviewed by Vorel et al. (2012) and Vorel and Korbela (2016). Recolonisation from Austria on the Morava River (Danube watershed) began in 1988 and from Germany on the Elbe in 1992. There has also been recolonisation in the south-west Czech Republic from Bavaria since 1993. These movements were supplemented by reintroductions

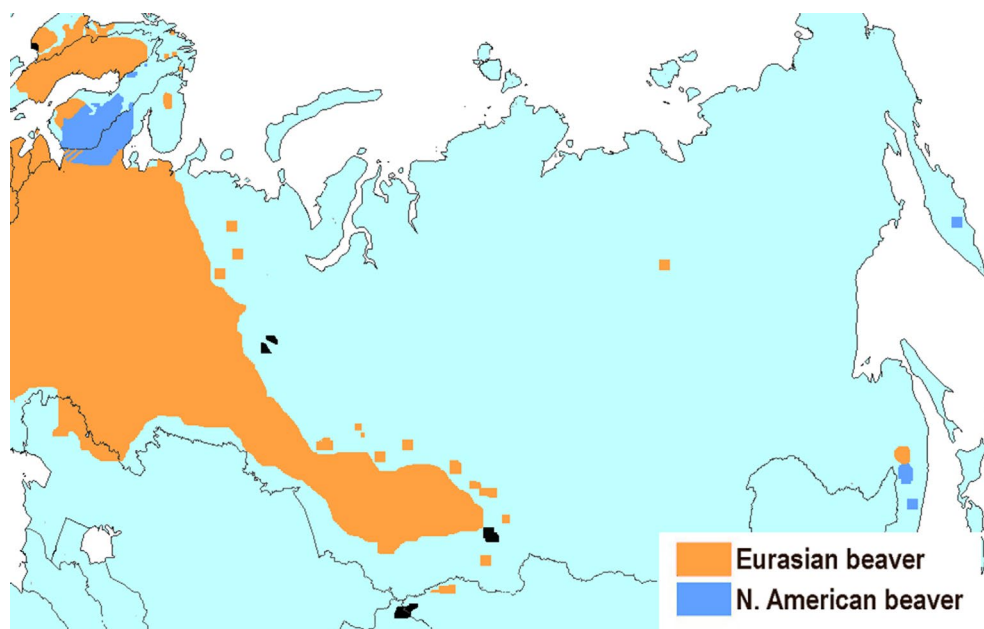


Fig. 3. Beaver distribution in Asia in 2002. Black = refugia where Eurasian beaver was never extinct.

in the 1990s (Halley & Rosell 2002). Beavers are now widespread in Moravia and appear near to capacity on the Morava watershed, which drains most of the region (Vorel & Korbelova 2016). They are also widespread in the south-west, with scattered populations in central and north-western regions (Appendix S4). Population size for the Czech Republic is estimated at >6000. Rapid spread and linkage of populations are predicted in the coming decade (Vorel & Korbelova 2016). Development has conformed to the typical pattern: rapid spread within a watershed to high-quality sites, with infilling of steadily less optimal habitat thereafter (John et al. 2010, Barták et al. 2013). The rate of spread into unoccupied stretches of main rivers approximates 20 km/year during the rapid expansion phase (John et al. 2010, Barták et al. 2013).

A national management plan was adopted in 2003 (Vorel & Korbelova 2016). Natura 2000 sites, 1.2% of the Czech Republic, are completely protected; in most of the country (86%), management measures are permitted as necessary; and the 'south Bohemian fishpond basin' (13%) with large numbers of earth retention dykes is zoned as incompatible with beaver settlement.

Denmark

Elbe beavers were reintroduced at Klosterheden in Jylland, Denmark, in 1999, and at Sjælland near Copenhagen in 2009–11. In Jylland (Appendix S5; Elmeros 2017), the population has spread to a number of stream systems in the northern and central peninsula. The beaver population

in Jylland numbered 98 territories, or an estimated 166–202 animals, in 2017 (Elmeros 2017). Taidal (2018) reported 13 territories (c. 50 individuals) in Sjælland.

England

A number of releases inside enclosures in England have been made since 2002. Beavers have been living wild on the River Otter in Devon, south-west England, since at least 2008, where breeding is confirmed from 2014. Their origin was unknown, and the government initially planned to remove them. This changed, partly as a result of electoral politics (the government wished to avoid controversies that might lose votes in an election), and the proposal of the Devon Wildlife Trust for a five-year 'trial' of the beavers' effects on the landscape was accepted in 2015 (Crowley et al. 2017). This involved supplementing the population with further releases. Thirteen family groups are now established (Devon Wildlife Trust 2016, Brazier et al. 2020). Brazier et al. (2020) provide a comprehensive report on the population, its development, and impacts.

In 2018, it became clear that beavers were living wild elsewhere in England: on the Tamar River, the Kent Stour, and the Wye on the Welsh border, and in the Somerset levels (Swaile et al. 2018; Appendix S6). Most are Bavarian stock (Campbell-Palmer et al. 2020), though the Kent Stour animals appear to be descended from enclosed Norwegian beavers at Ham Fen. Ten populations living in enclosures, and 13 projects in development, fenced and free-living, were identified (Campbell-Palmer et al. 2020; Appendix S6).

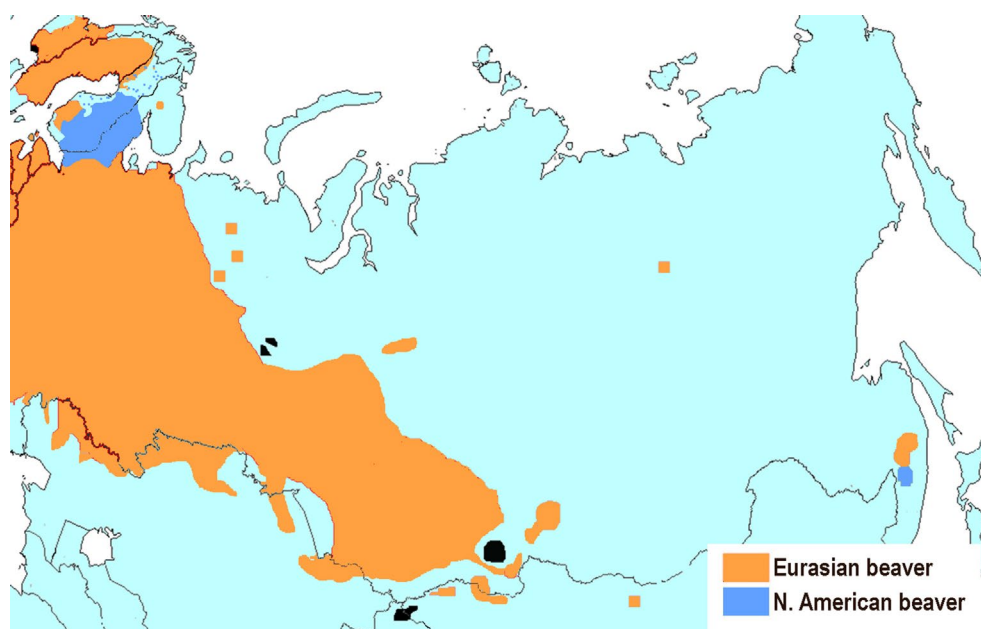


Fig. 4. Beaver distribution in Asia in 2020. Black = refugia where Eurasian beaver was never extinct.

Natural England is reviewing evidence from the River Otter trial and will make a recommendation on the desirability of further reintroduction (Campbell-Palmer et al. 2020).

Estonia

Beavers were reintroduced to Estonia in 1957 and spread naturally from releases in Russia and Latvia. They are now present throughout the country, except for parts of the Baltic islands. The harvest has increased steadily to 2017 (7038 animals), and the number of families increased from 2256 in 2012 to 2494 in 2015 (Veeroja & Männil 2018). Hunters' estimates of the population, however, declined from a peak of 20000 in 2008 to 14000 in 2016 (Veeroja & Männil 2018). The most recent estimate is 12–13000 individuals in 2016 (Sjöberg & Belova 2020). Beavers were the Hunting Association's 'animal of the year' for 2019 (<http://www.ejs.ee/aasta-loom-2019-kobras/>).

Finland

The government of Finland collects high-quality data on beaver populations, available online in English (LUKE 2019); see also Fig. 6. Eurasian beavers from Norway, and North American beavers from the USA, were released in 1935–37 (Lahti & Helminen 1969). The North American beaver population is most dense in Pohjois-Karjala, Etelä-Savo and Pohjois-Savo, but the species also occurs in other parts of eastern and central Finland, and sporadically in Lapland (Fig. 6). It is spreading westwards in southern

Finland, and there is a risk that it will spread further into areas populated by the Eurasian beaver. At present, in south-west Finland, the two species are in contact in western parts of Pirkanmaa Province. North American beavers have also spread eastward from Finnish Lapland into Murmansk region, Russia (Fyodorov & Krasovsky 2019).

Eurasian beavers have recently invaded Finnish Lapland (Finland north of roughly 66°N) from Sweden though the border Tornä watershed (Tornionjoki). Sixty-two beavers were reintroduced, mainly as widely scattered pairs, from 1960 to 1993 on Swedish tributaries (Mangi 2008). They remained uncommon until the 1990s, when the rapid increase phase of population development commenced. Beavers are now strongly established on the lower and middle Tornä in Finland and on the adjacent lower Kemi (Kemijoki) watershed. A few groups are established on the upper Ounas tributary of the River Kemi (Fig. 4).

The Kemi is the longest river in Finland, c. 550 km for the main course. The watershed drains central and southern Finnish Lapland from 66 to 68°N and a small area of Russia (Fig. 6), an area of about 55000 km². The climate is harsh, but the topography is largely flat or gently undulating. Rivers are tortuous and lakes abundant; the amount of suitable habitat for beavers is very large. More or less simultaneously, the North American beaver has colonised the upper watershed in the east and south-east, though established groups are widely scattered. Also, there are, or appear to be, a few groups of North American beavers remaining in the Tornä and Ounas rivers from

Table 1. Dates of extinction (extirpation), legal protection, reintroductions or translocations, and most recent population estimates for Eurasian beavers *Castor fiber* by country.

Country	Extirpation	Protection	Reintroduction and/or translocations	Most recent population estimate	Source/comments
Austria	1869	–	1970–90	7600	Kollar and Seiter (1990), Univ. für Bodenkultur Wien
Belarus	Remnant	1922	1948	51100	National Statistical Committee of the Republic of Belarus (2018)
Belgium	1848	–	1998–99	2200–2400	Dewas et al. (2012), www.beverwerkgroep.be 2019
Bosnia and Herzegovina	?	?	2006	140	Trbojević and Trbojević (2016)
Bulgaria	1750–1850	?	–	–	Boev and Spassov (2011)
China	Remnant	1991	–	600	Chu and Jiang (2009), Jiang et al. (2016)
Croatia	1857?	–	1996–98	10000	Grubestic et al. (2001), Kralj (2014), Cavric (2016), Tomljanović et al. (2018)
Czech Republic	Mid 18th Century; 1876*	–	1800–10, 1991–92, 1996	>6000	Jitka Uhlikova pers. comm., Vorel et al. (2012), Vorel and Korbelova (2016)
Denmark	c.500 BC [†]	–	1999, 2009–11	216–252	Asbirk (1998), Elmeros (2017), Taidal (2018)
England	18th Century?	–	2016 [†]	c. 150 [†]	Coles (2006), D. Gow pers. comm. (2019)
Estonia	1841	–	1957	18000	Timm, Estonian Environmental Information Centre pers. comm., Estonian Hunter's Association (2019), Veeroja and Männil (2018)
Finland	1868	1868	1935–37, 1995	3300–4500 [‡]	Lahti and Helminen (1969), Natural Resources Institute Finland (Luke) (2019)
France	Remnant	1909	1959–95	>14000	Dewas et al. (2012), ONCFS (2018)
Germany	Remnant	1910	1936–40, 1966–89, 1999–2000	35000	Schwab et al. (1994), G. Schwab pers. comm. (2018)
Hungary	1865	–	1980–2006	14600–18300	Bajomi (2011), Čanády et al. (2016), Bajomi et al. (2016)
Italy	1541	–	proposed	1	Nolet (1996), Messagero Veneto 30/11/2018
Kazakhstan	1915	–	1963–86	5500	Saveljev (2005)
Latvia	1870s	–	1927–52, 1975–84	100000–150000	Belova et al. (2016)
Liechtenstein	?	?	–	50	Fasel (2018)
Lithuania	1938	–	1947–59	121000	A. Ulevicius pers. comm. (2019), Belova et al. (2016)
Luxembourg	?	?	–	c. 75	Herr et al. (2018)
Moldova	?	?	–	?	Status uncertain
Mongolia	Remnant	?	1959–2002; 2012, 2018	800	Samiya (2013), Saveljev et al. (2015), Adiya et al. (2015)
Netherlands	1826	–	1988–2000	2300–3800	Kurstjens and Niewold (2011), Dijkstra et al. (2018), Dijkstra (2019)
Norway	Remnant	1845	1925–32, 1952–65	>80000	Rosell and Pedersen (1999), Parker and Rosell (2003), F. Rosell pers. comm. (2020)
Poland	1844	1923	1943–49, 1975–2000	124622	Janiszewski and Misiukiewicz (2012), Rozkrut (2018)
Portugal	c. 1450	–	–	0	Antunes (1989)
Romania	1824?	–	1998–99	2145–2250	Ionescu et al. (2010), Pașca et al. (2018)
Russian Federation	Remnant	1922	1927–33, 1934–41, 1946–2005	700000	Ognev (1963), Federal State Statistics Service, Russian Research Institute of Game Management and Fur Farming (2019); see text
<i>North-West Federal District</i>				152800§	Russian Fur Union (2016)
<i>Central FD</i>				153750	Russian Fur Union (2016)
<i>Volga FD</i>				168070	Russian Fur Union (2016)
<i>South FD</i>				7660	Russian Fur Union (2016)
<i>Ural FD</i>				58100	Russian Fur Union (2016)
<i>Siberian FD</i>				80780	Russian Fur Union (2016)
<i>Far Eastern FD</i>				800§	Russian Fur Union (2016)

(Continues)

Table 1. (Continued)

Country	Extirpation	Protection	Reintroduction and/or translocations	Most recent population estimate	Source/comments
Scotland	16th Century	–	2009	c. 319–547	Coles (2006), Campbell-Palmer et al. (2018)
Serbia	1903?	–	2003–4	240	Ćirović pers. comm. (2012), Smeraldo et al. (2017)
Slovenia	1750?	?	–	300–400	Grubešić pers. comm. Jursic et al. (2017)
Slovakia	1858	–	1995	7700–9600	Čanády et al. (2016)
Spain	17th Century	1980s	2003	450–650	Cena et al (2004), Sáenz de Buruaga (2017)
Sweden	1871	1873	1922–39	130000	Hartman (1994a, 1995), Belova et al. (2016)
Switzerland	1820	–	1956–77	2800	C. Angst pers. comm. 2012, BAFU (2016)
Ukraine	Remnant	1922		46000	Safonov and Pavlov 1973, Matsiboruk (2013a), Matsiboruk (2013b)
Wales	16th Century	–	Feasibility study completed	c. 15	Coles 2006; Jones pers. comm. (2009), D. Gow pers. comm. (2019)
Minimum Population Estimate				1,487,000§	

*1876 extirpation of animals descended from 1800–10 reintroduction in S Bohemia (Vorel & Korbelova (2016).

||Based on subfossil remains. Philological evidence from place names suggests a remnant may have survived as late as the 11th Century.

†First licensed release, to River Otter; to supplement a population apparently deriving from escapes. Populations on other rivers are apparently the result of escapes from fenced enclosures. Population figure is for wild-living beavers only.

‡Also c. 10300–19100 *Castor canadensis*. Source: <https://www.luke.fi/en/natural-resources/game-and-hunting/beavers/>.

§Population estimate includes some *Castor canadensis*; Russian North-west FD < 20000, Far East FD < 200.

||Navarra only, see text.

an earlier introduction. Whether these are genuinely North American beavers or Eurasian beavers settled at old North American beaver sites is unclear. DNA testing is underway (K. Kauhala, personal communication).

The scene seems set for rapid increase of both species, eventually meeting along a front within the Kemi basin

somewhere in central Lapland. *Castor canadensis* is classified as an invasive species in Finland’s National Strategy on Invasive Alien Species, so a logical strategy would be to attempt to eliminate, or at least reduce, North American beaver on the Kemi, to favour recolonisation by Eurasian beaver (Parker et al. 2012). Strategic reintroductions of

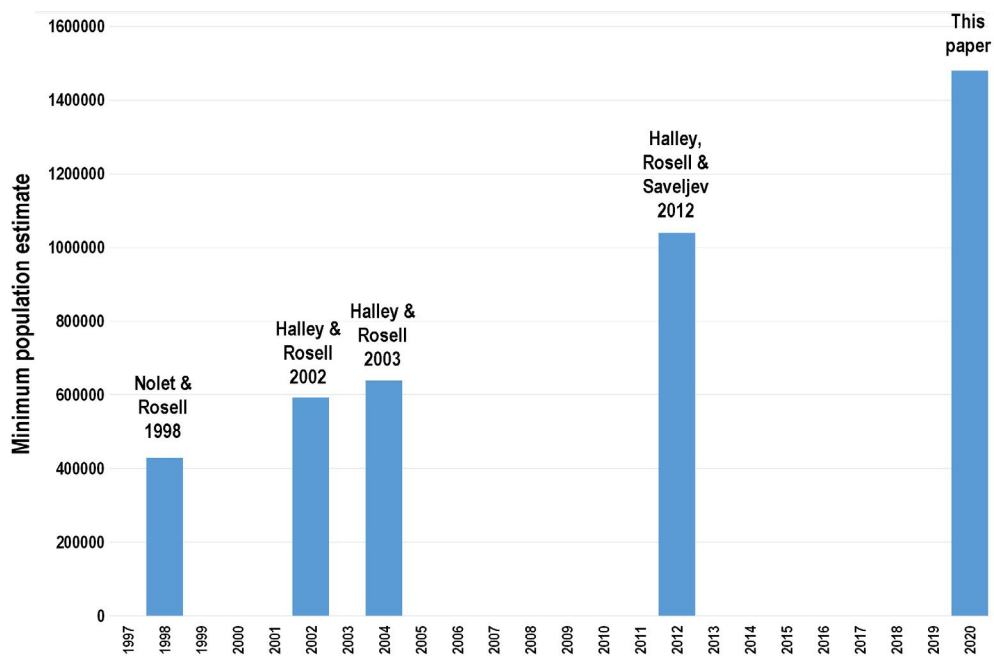


Fig. 5. Minimum total Eurasian beaver *Castor fiber* population estimates 1998–2020. The sources are indicated.

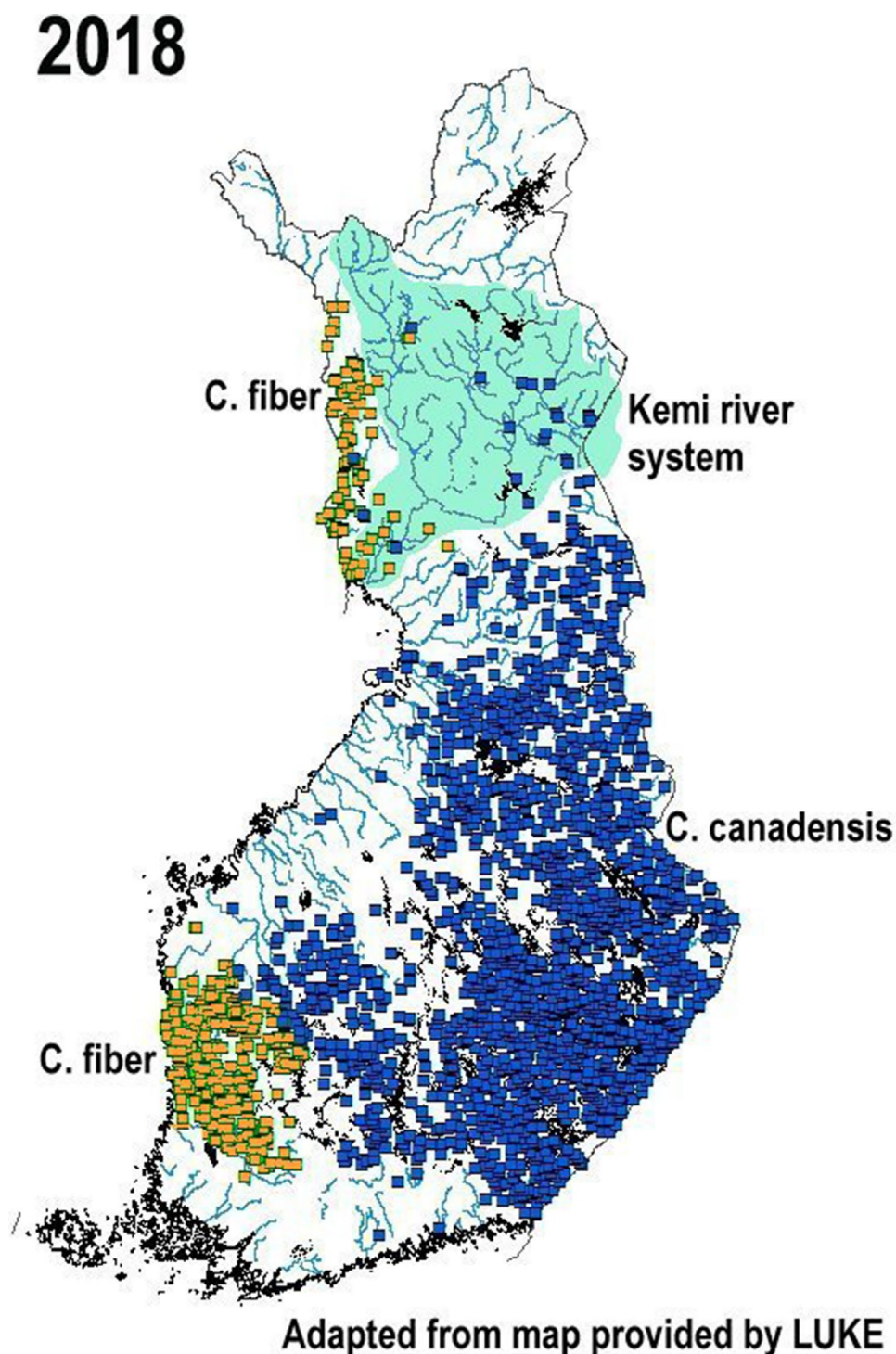


Fig. 6. Distribution of Eurasian beavers *Castor fiber* and North American beavers *Castor canadensis* in Finland in 2018. The catchment of the Kemi watershed is indicated. Adapted with permission from LUKE (2019).

Eurasian beavers to sites in the Kemi basin would assist this process.

This would be technically straightforward, and much cheaper than managing a later situation resembling that

in south-west Finland. Finland is legally required to (at least) contain the spread of North American beaver when feasible. Article 19 of the European Union Regulation on the Prevention and Management of the Introduction and

Spread of Invasive Alien Species states that measures must be taken ‘aimed at the eradication, population control or containment of a population of an invasive alien species’ (Genovesi & Shine 2003, European Union 2014). Human social and regulatory factors are the main barrier to management (K. Kauhala, personal communication).

France

Beavers survived in very small numbers in the Rhone delta, France. There have been 26 reintroductions (273 individuals) from this source within France (Dubrulle & Catusse 2012). The most recent accounts of population and distribution are Dewas et al. (2012), Dubrulle and Catusse (2012) and ONCFS (2018). ONCFS (now Office français de la biodiversité) publishes a regularly updated distribution map (Appendix S7) online at <http://carmen.carmencarto.fr/38/Castor.map>.

The current population estimate for France is > 14000, in effect unchanged from the 10–15000 reported by Halley et al. (2012). A new population estimate based on a 2019 survey will be published in 2020 (ONCFS 2018) and will be significantly higher. Range has extended significantly on most occupied watersheds. In 2009, 10500 km of watercourse was permanently occupied; in 2018, 15000 km (ONCFS 2018); in 2019, 16500 km (Yoann Bressan, Office français de la biodiversité, personal communication). On much of the Rhone the population is mature; some marginal sites have been abandoned (Dewas et al. 2012).

Small populations are now established on the Saône and Doubs (major northern tributaries of the Rhone) and on the Garonne (84811 km²), ‘certainly’ to a 25 km stretch of the Tarn tributary downstream of Albi, 55 km north-east of Toulouse, and ‘probably’ to a 20 km reach above Rabastens, a further 40 km downstream. These are below the hydro-barrages on the upper Tarn, which until recently restricted spread (ONCFS 2018). A population was recently discovered on the lower Vère, a small side tributary of the Aveyron tributary of the Garonne west of Mountauban (ONCFS 2017). Large-scale colonisation of both the Saône and Doubs, and the Garonne above the barrage at Golfech (65 km north-east of Toulouse), should occur over the next 20 years (Dewas et al. 2012, ONCFS 2017). Colonisation of the city of Lille and the Avesnois in Nord Pas de Calais, NW France, was confirmed in 2020 (<https://ofb.gouv.fr/actualites/le-castor-deurope-de-retour-dans-le-departement-du-nord>).

Eleven beavers from north-east France, and 101 from throughout France, were genetically tested in 2011 and 2018, respectively. All were *Castor fiber*, and all except one of Rhone stock. The exception was an animal tested in 2018, descended from Elbe beavers, found on the Saar in extreme north-eastern France (Bressan et al. 2018).

An adult beaver was filmed on the River Nive near Ustaritz in south-west France in late 2018 (*Onda* newspaper, 11 January 2019; <https://www.liguria.com/repere-un-castor-sur-les-bords/>). It may have been from the Ebro, which would involve a crossing of the (formidable) foothills of the Pyrenees.

Germany

Beavers on the River Elbe, Germany, descend from the refugium on that river system. The population in Bavaria, now found throughout the state, is of highly mixed origin, but not including Elbe beavers (see Halley & Rosell 2002). Bavaria has been the source for most reintroductions throughout Europe since the 1970s, including to the remainder of Germany. The current population is estimated at 35000.

Beavers are now found throughout most of eastern and southern Germany, with strongly established disjunct populations in the west (Appendix S8; Stolz 2017). Rapid expansion in range, followed by rapid population increase, will almost certainly take place in western Germany, and into remaining unoccupied areas of the south and east, over the next 2–3 decades.

A comprehensive website on beavers in Germany and central Europe is available at <http://www.bibermanagement.de/>.

Greece

Government organisations have suggested a beaver reintroduction feasibility study in Greece (Alexandros Karamanlidis, personal communication).

Hungary

Beavers immigrated to Hungary from Austria from the 1990s, along the River Danube (Boszér 2000). In 1996–2008, more than 200 beavers were reintroduced in the areas of Gemenc and Hanság, on the River Tisza (the main watershed of eastern Hungary, entering from Transcarpathian Ukraine and exiting to Serbia) and on the River Dráva (which forms part of the border with Croatia). Reintroduction history is described by Bajomi (2011) and Bajomi et al. (2016). Most were sourced from Bavaria. Beavers are now found along the entire course of the Hungarian Danube, and most of the Tisza and some of its tributaries. The population is estimated at 14600–18300 (Čanády et al. 2016).

Italy

In 2018, a beaver settled on the Gailitz, a Danube head-stream (via the Austrian Drava), at Tarvisio in extreme

north-east Italy, the first Italian record for 450 years (*Messaggero Veneto* newspaper, 30 November 2018). The Alps are a formidable barrier to spread into the rest of Italy, as for other populations established around the land border of Italy.

Kazakhstan

Beavers were part of the Kazakh fauna until the early 20th Century. The modern population spread into the lower Ural watershed from 1963, from reintroductions upstream near Orenburg, Russia (Karagoyschin 2000). A second population in eastern Kazakhstan descends from migration and translocation from the Russian Altai in the 1980s (Berber 2008). In 1996, beavers were removed from the Kazakh Red Data Book. The current range is an almost continuous strip of northern Kazakhstan. Population and distribution are increasing; hunting has been permitted since 2009 (Baytanaev et al. 2012).

Latvia

Beavers are present throughout Latvia, as a result of reintroductions from Norway and Russia. The population estimate peaked at 89474 in 2009–10 and declined to 58000 by 2017–18 (Zemkopibas Ministrija 2018). Estimated population size in 2016–17 was 58000 (State Forest Service 2018) but, according to expert opinion, the actual population size could be as high as 150000 (J. Ozolins, cited in Sjöberg & Belova 2020). See Lithuania for a likely cause of the discrepancy.

Liechtenstein

Beavers spread from Switzerland in 2008. In 2017–18, the population was estimated at 50 (Fasel 2018).

Lithuania

Beavers descended from reintroductions from Russia are present throughout Lithuania. The official population estimate is 40600 (Lietuvos Respublikos Aplinkos ministerija 2017, Raskauskaite & Simkevicius 2017), but this is a hunters' association estimate, reported to the game and wildlife authorities. Hunting associations (which have the hunting rights) must pay landowners on a population basis if they do not ensure the population is 'optimal'. This provides a motive for underestimating population size. The real population appears to be roughly stable, with local declines and increases observed, and is estimated at c. 100000 (A. Ulevicius, personal communication) and 101265 (Sjöberg & Belova 2020).

Luxembourg

Herr et al. (2018) review population history and current distribution of beavers in Luxembourg. Groups of North American beavers, established in the early 21st Century, apparently from zoo escapes in German Saarland, have been removed. There are currently c. 20 established Eurasian beaver territories, or about 75 individuals (Appendix S9), mainly descended from immigrants from Belgium; but also Germany and possibly France.

Mongolia

A small population of Sino-Mongolian beavers survived on the Bulgan River in the extreme west of Mongolia and neighbouring Xinjiang in China. Local translocations of Bulgan beavers have taken place, to the Khovd (1959–85, 39 animals), the Tes (in 1985, 1988 and 2002, 37 animals), and to Voronezh (four, in 1962; Stubbe & Dawaa 1983, Samiya et al. 2012, Saveljev et al. 2015).

Native beavers are today found in three isolated populations: Bulgan, Khovd, and the Uvs Lake basin (includes the Tes River and adjacent small rivers in Mongolia and Russia). The total population is estimated at 600, of which the Tes population is the largest (Samiya 2013, Saveljev et al. 2015).

Fourteen beavers from Bavaria, Germany, and 27 from Kirov, Russia, were brought to Ulaanbaatar, Mongolia, in 2012 (Samiya et al. 2012, Adiya et al. 2015), to improve water retention in regional rivers, and 16 Kirov beavers (9 males, 7 females) from seven families were released on the Zaan (Tuul River tributary, Selenga basin). From 2012 to 2019, 38 beavers from a captive breeding facility (containing Kirov and Bavarian animals) were released into the wild on the Zaan and Tuul. The facility contained 44 individuals in 20 family groups in 2019 (S. Shar, personal communication). Further releases in north and east Mongolia are planned.

Monitoring attempts have not produced useable estimates of the wild-living population in Mongolia.

Netherlands

The current status of beavers in the Netherlands is reported by Dijkstra (2019). The population is estimated at 3500. Beavers continue to expand in both population and range, by expansion from reintroductions, immigration from Belgium (mainly along the River Maas), and from Germany in the Drenthe Province. In 2012–14, the range increased by 30% per year in terms of 5x5 km squares occupied. In 2015–17, this slowed to 11% per year (Dijkstra et al. 2018). Distribution (Appendix S10) is mapped in the

National Flora and Fauna Database at <https://www.verspreidingsatlas.nl/8496057>.

Norway

Beavers survived in Telemark in south-east Norway and were reintroduced at numerous sites from the 1920s to the 1990s (Rosell & Pedersen 1999). The species now occupies the entire country south of Saltfjellet (an ocean-edge tundra/ice cap plateau) on the Arctic Circle, and east of the mountain chain dividing Atlantic from Skagerrak watersheds south of Trondheim (Appendix S11).

Populations reintroduced north of Saltfjellet in the 1960s and 1970s at Rago National Park in Nordland, and in the Porsanger/Tana region of Finnmark, are now extinct. Occasional vagrants, probably from Sweden, are reported in the area.

Four small populations have become established by natural spread on Atlantic-draining rivers in the south-west fjord region of Norway. This must have involved overland travel across the watershed divide. In the long term, beavers will probably establish themselves in pockets of suitable habitat in much of fjordland Norway. Beavers are also advancing slowly into the region along the coast, both from the south and north. Colonisation patterns indicate dispersal through brackish and salt water, especially where it is sheltered (Halley et al. 2013).

In Norway, beavers are hunted as small game. Hunting rights are owned by the landowner; there is no system of 'compensation' for beaver impacts. This and that beavers are not highly prized as a hunting object, in combination, renders the species of low salience, underlining the large human social factors involved in 'wildlife-human conflicts' (Parker & Rosell 2003). In consequence, there are no full-time beaver managers in Norway and no funding for monitoring. The population estimate (80000) is, in these circumstances, an educated guess.

Poland

Beavers were widely reintroduced in Poland from the Soviet Union, mainly from 1975, with internal translocations from 1990 to 2000. They are now found throughout Poland. The population shows signs that it may be leaving the rapid increase phase of development, from 500 animals in 1975 to 125000 in 2017. Figures in Rozkrut (2018) show a levelling off of population in 2015–17. In the Vistula Delta, where beavers reappeared in the mid-1990s, studies indicate suitable habitat is now saturated and the population stable (Zwolicki et al. 2019). While a longer series is needed to confirm the trend, it is likely that populations may decline moderately over the next 20 years.

A Polish website offering beaver management services claims annual damage to private landowners of €6.6 million (<https://swiatrolnika.info/publicystyka/firma-bobry-odlawianie>). However, despite the 23% population increase since 2015, there has been an 11% decrease in reported conflicts, and Ministry of Environment compensation payments totalled a modest €5192 in 2017 (Wróbel & Krysztofiak-Kaniewska 2020). The reason for the discrepancy is unclear. Wróbel and Krysztofiak-Kaniewska (2020) suggest that the decrease in reported conflicts may be due to landowners becoming used to beavers and developing better management skills. Use of flow devices is now widespread (Wróbel & Krysztofiak-Kaniewska 2020).

The Polish Union of Hunters does not want to hunt beavers, apparently because the obligation to compensate for damage would pass to them (Saveljev et al. 2020). Nevertheless, looking ahead, Polish specialists have already published a guide to the integrated use of beaver resources and hunting products (Misiukiewicz 2018).

Romania

The most recent source on beavers in Romania is Paşca et al. (2018). Reintroductions from Bavaria were carried out from 1998 to 2003. Ninety-one beavers were released in the Olt River, 56 in the Mureş and 35 in the Ialomiţa (Ionescu et al. 2010). In 2014–17, populations were estimated at 1565 on the Olt, 330 on the Mureş, and 214 on the Ialomiţa. In 2010, beavers, presumably from the Ialomiţa, colonised the upper Danube Delta near Tulcea, and later the main delta. In the north, beavers colonised Maramureş in 2008, from the Hungarian Tisza via Ukraine (Chiş 2015). There were six active territories in 2017 (double the 2015 figure), or c. 25–30 animals. (V. Chiş, personal communication). The Romanian population is estimated at 2145–2250 (Paşca et al. 2018). Signs of vagrants have also been recorded on the Someş and Criş Rivers of western Transylvania, tributaries of the Tisza; colonisation can be expected in the short to medium term.

Russian Federation

Although greatly reduced in numbers and very patchily distributed, in the 19th Century beavers survived in the Russian Federation in the forest zone at least as far east as the easternmost tributaries of the River Lena, and along many rivers in the steppe zone (Ognev 1963). It has been suggested that beavers did not live in rivers draining to the Sea of Okhotsk or the Pacific, except the upper Amur (Ognev 1963). However, beaver remains at human sites dated from 800 to 1500 years ago in the Ussuri headwaters about 50 km north of modern Vladivostok (Kuzmin 1995, 1997) indicate they were naturally present in that region.

Population and distribution are expanding. A map is available at <http://rusmam.ru/atlas/map>. While previously, range expansion was most active in the mountains of southern Siberia (Saveljev 2003), recent major expansion has shifted to southern European Russia, and the northern periphery in Siberia.

In European Russia, beavers have expanded down the Volga to Volgograd. Range has significantly expanded in the Rostov region along the River Don, to its mouth. Most inhabit the northern Rostov region, on the Seversky Donets, Kalitva, and Chir, and the middle Don. Population increases are expected on the lower Don, as well as colonisation of rivers around the Sea of Azov. Previously, beavers swimming in the sea were recorded only in the Dnieper estuary (Igor Sheygas, personal communication), but dispersing beavers have recently been recorded in the Sea of Azov. Migrants emerge from the mouth of the Don and have settled south along the coast (Valery Stakheev, personal communication).

The Don River delta and Tsimlyansk area may also be colonised by beavers from Ukraine (see below). The Rostov region population is estimated at >2300 (Stakheev et al. 2018). Beavers have also spread to the northern part of Kalmykia (a typical steppe region between the Rivers Don and Volga).

Beavers have begun to settle in large cities (St. Petersburg, Kazan, Kirov and others). At least 20 beaver territories are recorded in Moscow (see <http://rusmam.ru>).

In the western Urals, beavers have settled almost to the mountain headwaters of the Rivers Pechora, Ilych and Vishera. Permanent settlement on the Vishera River can be found up to 555 m above sea level, near the transition to alpine tundra (Saveljev et al. 2011).

Large-scale expansion is occurring in Siberia. Beavers from the Ob have penetrated northwards to the Taz basin in recent years. Average annual movement of the expansion front was about 40 km per year (Yan Kizhevato, personal communication).

On the Yenisei watershed, the northernmost stable population is found in the Yeloguy. Beavers are regular in the lower reaches of the Podkamennaya Tunguska. To the south, the entire middle and upper Yenisei basin is now inhabited, with increasing density upstream, both in protected and in hunting areas (Trenkov 2015). Beavers also live in the upper Angara in Irkutsk Region, and in Buryatia. An isolated population of Belarusian origin has existed in the Amur basin near Khabarovsk for 55 years; population and range are increasing. In contrast, the nearby population of *Castor canadensis* on the Obor is in decline (Oleinikov 2013).

In northern European Russia, range dynamics are less active. Interesting changes have occurred in the contact zone of the two species. Eurasian beavers have displaced

North American beavers in areas of southern Karelia inhabited by *Castor canadensis* since their release there in the late 1960s. The closest distance between colonies of different species is 10 km. Conversely, in north-eastern Karelia (Kemsky District), North American beavers have penetrated 70 km into Arkhangelsk region and are colonising areas inhabited by Eurasian beavers (Danilov & Fyodorov 2016). *Castor canadensis* from Finnish Lapland are moving east into Murmansk region (Kataev 2018, Fyodorov & Krasovsky 2019).

Between 2005 (Saveljev 2005) and 2015, the number of beavers in Russia increased annually, although growth rates gradually decreased. Borisov (2011) estimated populations as 528900 in 2008, 611800 in 2009, and 628300 in 2010. In 2015, the population was estimated at 622000 (Russian Fur Union 2016). See Table 1 for a breakdown by Federal District.

According to the Russian Research Institute of Game Management and Fur Farming, the population of both beaver species together reached 696070 in 2018. The Federal State Statistics Service (<https://www.gks.ru/folder/11194>) reported 24342 beavers harvested in the hunting season 2017–18.

Given the general trend, and that the number of North American beavers in the north-western regions does not exceed 20000, and in the Russian Far East no more than 200, the total population of the Eurasian beaver in Russia in 2020 can be estimated as at least 700000, about half of the world population.

Scotland

Detailed investigation of reintroduction began in Scotland in 1993, resulting ultimately in a ‘trial’ reintroduction of Norwegian beavers on the Knapdale Peninsula in western Scotland from 2009, at a site with strong natural barriers to spread. In the same year, however, it became clear that a wild population was established on the Rivers Tay and Earn, the largest watershed in Scotland. The source appears to have been escapes from enclosures, and beavers are of Bavarian origin (Campbell-Palmer et al. 2020). The first beaver observed and photographed in the wild was at the Tay/Earn confluence in April 2001 (Hugh Chalmers, personal communication). However, the territory at Rannoch/Dunalastair on the upper river (Territory 49 in Appendix S12), separated from the main population by three large hydroelectric dams along 25 km of river unoccupied by beavers despite much high-quality habitat, is unlikely to have resulted from natural spread from the lower river, where all fenced enclosures were located (Campbell et al. 2012).

Entrenched controversy surrounding land use in Scotland has strongly influenced both the official beaver

reintroduction and management issues. It has also led to much detailed research and review on various aspects of beaver biology, particularly on issues of local controversy such as beaver damming and migratory fish (Kemp et al. 2012, Beaver-Salmonid Working Group 2015). There has also been comprehensive monitoring (Campbell-Palmer et al. 2018); see also Gaywood (2018) for review.

The Knapdale population remains restricted in range and numbers. In 2019, it was augmented by seven animals translocated from the Tay (Scottish Natural Heritage 2020). The Tay and Earn population has continued to expand in range, and especially in population (Appendix S12), despite 82% of individuals being as closely related as first cousins, presumably due to small numbers of founding animals (Campbell-Palmer et al. 2020), and significant numbers being legally killed by landowners, as they were unprotected. Beavers have also colonised the Forth watershed to the south, where they are widely but thinly spread in high-quality habitat (Appendix S12). The watershed is small, and considerable growth in population can be expected in the near future. The 2017–18 population on the Tay/Earn and Forth was estimated at 114 active territories, or 319–547 individuals (Campbell-Palmer et al. 2018).

A small population in Beauy, near Inverness, descended from escapes, remains present despite the removal of five individuals in 2018. Tay beavers have recently spread west to rivers north of Knapdale (R. Campbell-Palmer, G. Dowse, Scottish Beavers, personal communications).

Beavers were given European Protected Species status in Scotland from 1 May 2019, and “the species will be allowed to expand its range naturally” (Scottish Natural Heritage, press release, February 2019). From that date to 31 December 2019, 87 beavers were killed under government licence (Scottish Natural Heritage 2020).

Serbia

Seventy-five beavers from Bavaria were reintroduced to Serbia, at Obedska Bara and Zasavica nature reserves on the lower Sava River, in 2004–2005. Both have established local populations. Smeraldo et al. (2017) report spread upstream to the Bosnia–Croatia border and to the lower Drina on the Bosnia–Serbia border. There appears to have been little downstream spread into the Danube, though habitat and hydrology appear suitable for transit and settlement; possibly Belgrade city (at the Sava–Danube confluence) has hindered spread in that direction. In recent years, the species has spread into northern Vojvodina from Hungary along the Tisza (Appendix S13). From 2004–2013, expansion of range was very rapid, 70.9 ± 12.8 km/year (mean \pm standard deviation, $n = 10$; Smeraldo et al. 2017), typical of the early expansion phase on large river systems

(Hartman 1995, Fustec et al. 2001, Halley & Rosell 2002). The population is estimated at c. 240. Rapid increase in population and range can be expected in the next 20–30 years.

Slovakia

Recent history and status of beavers in Slovakia are reviewed by Čanádý et al. (2016). Slovakian rivers drain southwards to the Danube in, or on the border with, Hungary. Beavers immigrated to Slovakia along the Danube from Austria from 1977 and from Poland to north-east Slovakia from 1993 (Valachovič 2012). Populations are concentrated in the west and north-east, with recent establishment from the Hungarian Tisza on its Hornád tributary in south-east Slovakia (Appendix S14). Central Slovakia remains uncolonised, but contains much suitable habitat. The population is estimated at 7700–9600 (Valachovič 2012).

Slovenia

Beavers from the Croatian reintroduction reached the Krka tributary of the River Sava, Slovenia, in 1998 (Vochl & Halley 2017, Jursic et al. 2017). Later, beavers entered the southern Dravinja (Drava) river from Croatia (downstream) and the north of the same river from Austria (upstream; Deberšek 2012). Hydro-barrages have so far prevented colonisation of the middle course. Since 2003 beavers have colonised the whole of the Slovene Mura, a Drava tributary, from Croatia (Deberšek 2012). The national population was estimated in 2015 as “at least 60 families with 300 to 400 individuals” (Ministry of Environment, quoted in *Dnevnik* newspaper, 29 March 2018) and “70 families” (*Slovenske Novice* newspaper, 10 April 2018). However, a detailed survey of the Krka estimated the population on that river alone at 50 active territories, 168–392 individuals (Jursic et al. 2017).

Spain

Eighteen individual beavers of Bavarian origin were released in Spain, near the confluence of the Ebro and its Aragon River tributary in 2003 (Cena et al. 2004). The release was unofficial, and Spanish authorities obtained a written derogation from the European Union Habitats Directive which allowed them to attempt extermination (albeit on the incorrect grounds that the species was ‘outside its natural distribution’ on the Ebro).

The issues both of the release and the attempts to remove the animals generated considerable heat, but little light on population status. The political geography of the Ebro is complex, and the environment is the

responsibility of the regions. Information obtained by conservation groups through Freedom of Information laws revealed that in La Rioja, 26 males and eight females were trapped in 2010, in Navarra 20 males and 16 females in 2008–2009, and in Aragon 10 males and five females (all older than three years old) in 2009–2010, using Bailey live traps and humane snares. A male in his second year was captured by the firemen of Zaragoza during the same period. The reason for the bias in the sex ratio is not clear. Later, a similar request to the European Commission revealed these figures were incomplete: from 2008–2017, 102 beavers were trapped in La Rioja, 83 in Navarra and 31 in Aragon (total 216; European Commission Environment Directorate 2018, Annexe, Echegaray et al. 2018).

The Ebro River basin contains a great deal of high-quality habitat, in which beavers can live unobtrusively. Trapping never extended to Euskadi (the Basque country), in which beavers were already present. As predicted (see <http://www.iberianature.com/spainblog/tag/beavers-in-spain/>), the trapping attempt failed, and little attempt was made after 2014 (16 animals trapped 2015–17, Echegaray et al. 2018). The environmental economics journal *Ballena Blanca* (No 6, April 2016) reported 100 individuals trapped (an underestimate based on then released figures) at a total cost of €131000. The population in Navarra alone was estimated in 2014 as 450–650 (Government of Navarra 2015, unpublished report). If this is correct, the population on the entire Ebro system must now be in excess of 1000 individuals.

The main text of the European Commission Environment Directorate (2018) letter reversed the European Union's position and stated beavers were a “historically autochthonous and renaturalised species in Spain”, and that Spain “must adopt the necessary actions to comply with the provisions of the (Habitats) Directive”, legally protecting the species. This decision is not as yet integrated into regional law.

Distribution in Spain (Appendix S15) is better known than population. Beavers are now found from Miranda de Ebro to Caspe on the main river, a straight-line distance of over 300 km through which the river meanders strongly. Beavers are established throughout the main Ega, Arga, Irati and Aragon tributaries and their side streams in Navarra (G. Berasategui, personal communication) and Euskadi (Sáenz de Buruaga 2017). Newspaper reports, trapping locations (Echegaray et al. 2018, Fig. 2), and Internet videos indicate beavers are also present on the Jalon (as far upstream as Arcos de Jalon), Alama, Cidaco, Iregua, Najarilla, and Cicados tributaries. Signs of dispersing individuals have been noted in several places on the lower River Ebro in Catalonia. Genetic studies indicate the population is of mixed genetic origin (Põdra & Aguilar Gómez 2015).

Sweden

Beaver reintroductions in Sweden commenced in the 1920s and were widespread except in the south (Hartman 1994a, 1994b, 1995). Recent expansion includes colonisation of the region around Uppsala, and the lower Tornë watershed on the border with Finland, the latter the result of many but mostly very small (one pair) reintroductions, 1960–1993, on the Swedish side of the watershed (Mangi 2008). Range expansion on the southern margins has been slow. Beavers now occupy the whole of Sweden apart from the far north (roughly, north of 67°N) and the south (roughly, south of 58°N); the population is estimated at 130000 (Belova et al. 2016).

A searchable mapping database of the Swedish distribution is available (Shah & Coulson 2019); however, the range mapped (largely through citizen science reports) is an underestimate, particularly in the sparsely inhabited north, where there is an observer bias near towns with academic institutions (G. Hartman, personal communication).

Switzerland

Online maps of beaver distribution in Switzerland are available at <https://lepus.unine.ch/carto/index.php?nuesp=70807> (Appendix S16), with a comprehensive website at <http://www.cscf.ch/cscf/home/biberfachstelle.html>

Minnig et al. (2016) provide a detailed account of reintroduction history, 141 individuals at 30 sites in 1956–77. Population was estimated at 2800 in 2015 (BAFU 2016). Beavers are now distributed widely on the Rhine and Rhone watersheds, with recent settlement on the Inn (Danube basin) from populations in Austria.

Ukraine

In the late 1930s, fewer than 100 Eurasian beavers survived in the Pripet Marshes. In the Rovno region, there was a colony of North American beavers brought from Poznań, Poland, in 1933 and 1934, but by the mid-1950s, this population had disappeared (Marin 1954). All beavers in Ukraine today are *Castor fiber*.

20th-Century restoration is well documented (Safonov & Pavlov 1973). Recent expansion has been rapid. From 2001 to 2010, the number of beavers in Ukraine increased by more than three times and in some areas up to 7.3 times (Matsiboruk 2013a). Average annual population growth was 24% (Matsiboruk 2013b). Beavers have begun to colonise both eastern Ukraine (Tokarsky 2009, Brusentsova & Ukrainskiy 2015) and southern Ukraine (Volokh 2011).

The beaver's geographic range now occupies half of Ukraine, including areas of intensive human activity (Tokarsky et al. 2012). By 2011, the population was close to 50000 (official statistics have not been published since then).

The population in Transcarpathian Ukraine, derived from the Hungarian Tisza reintroduction, is in rapid growth. Beavers reached the region in 2003 and doubled in population from 25 to 50 territories from 2009 to 2012 (Bashta & Potish 2012), with further expansion later (Barkasi 2016). Populations on the upper Dniester, on the eastern slope of the Ukrainian Carpathians, were expanding in the same period (Barkasi 2016).

Recent summers in Ukraine have been very arid, and the winter of 2019/20 was snowless. This affected habitat quality in beaver-inhabited rivers. Predation patterns have also changed: in the Chernobyl Exclusion Zone, wolf *Canis lupus* excrement was formerly dominated by the remains of wild boar *Sus scrofa*, but now it is almost entirely composed of beaver hair (V. Smagol, Institute of Zoology, NAS Ukraine, personal communication).

Wales

The history of beavers in Wales is reviewed by Coles (2019). Reintroduction was assessed as feasible in 2009 (Halley et al. 2009, Jones et al. 2011). There were four known fenced populations in 2018 (Swail et al. 2018), with field signs in the wild on the River Dyfi in west Wales; beaver signs are widespread on the River Wye on the English border, though a 2018–19 survey found no strong evidence of beavers living in established territories (R. Campbell-Palmer, A. Leow-Dyke, personal communication). Population size is unknown.

POPULATION DEVELOPMENT

Beaver populations have continued to spread and grow in size, confirming the prediction (Halley & Rosell 2002) that the species will, within a few decades, be a fairly common animal throughout most of its former range. The current 'minimum population estimate' is 1479863 (which can be rounded as 1.5 million), 3.5 times the 1998 estimate (Nolet & Rosell 1998), and 2.5 times the 2002 estimate (Halley & Rosell 2002), using the same methods of adding together the estimates for each country and using the lower limit where a range is given. This is not meant as anything other than a general guide.

Population development during recolonisation was reviewed by Halley and Rosell (2002). Developments since have followed the same general pattern (e.g. John et al. 2010, Bártak et al. 2013, Zwolicki et al. 2019): colonisation of new watersheds by natural spread or reintroduction;

a period of relatively slow population growth, but rapid range extension, followed by a phase of rapid population increase; then a period of population decline as habitat not capable of supporting beavers permanently is inhabited and temporarily exhausted; and finally, rough stability. The size of the watershed influences the length of these stages, which are shorter in smaller watersheds; as do human interventions, in particular hunting and the pattern of hunting (Parker & Rosell 2003, 2012).

In much of European Russia, Belarus, Ukraine, Poland, Latvia, and Lithuania, populations appear to be nearing maturity, with increases peaking in Poland and declines reported in Belarus according to official statistics. However, these trends are general, and the accuracy of the statistics and the potential influence of biasing factors are open to question. Nevertheless, there is a general consistency across the region which indicates that the period of rapid population growth has probably now ended.

In the Nordic countries, range expansion has slowed in recent years (though not stopped), and the population is mature in many areas. The main exception is Finnish Lapland, currently under invasion from the west by *Castor fiber* and from the south and east by *Castor canadensis* (Fig. 4). In Norway, reintroduced populations of *Castor fiber* north of the Arctic Circle are now apparently extinct. Habitat patches are in general small and, except in Finnmark, the terrain is very rugged, inhibiting dispersal. At present, the northern limit of both *Castor fiber* and *Castor canadensis* coincides roughly with 67°N all the way from the Norwegian Sea to the White Sea, even the populations of both species colonising the Kemi watershed in Finnish Lapland are mostly south of this limit or very close to it. The only established population to the north is in central Murmansk Oblast at about 68°30'N, the status of which is little known.

Castor canadensis is present to the shore of the Arctic Ocean on the Mackenzie Delta, Canada, and in the adjacent Alaskan north slope at 69°N (Tape et al. 2018), in a winter climate much more severe than similar latitudes in the Gulf-Stream influenced Nordics. In climatically modern times (subfossils dated to c. 1350 before present), beavers occurred to at least 70°N at Varanger in extreme north-east Norway (Horn et al. 2014). Therefore, it seems unlikely that climate is limiting beaver populations in the north. The current populations all derive from refugia much further south and have limited genetic diversity, which may influence their ability to adapt to the extreme conditions of the Arctic. However, the apparent pattern may be a temporary effect of reintroduction history. The Kemi watershed extends through most of Finnish Lapland from 65°30'N to 68°30'N in largely flat terrain, with no

barriers to dispersal (Fig. 6), so whether there is a real climatic effect limiting northern distribution at around 67°N will soon become evident.

In the south, the Mediterranean Sea forms a natural southern limit to the range in the west; it has formed an effective barrier to most mammal dispersal for at least 5.5 million years (Groves & DiCasta 1991). Beavers formerly occurred in steppe and desert regions south to the Tigris/Euphrates (Legge & Rowley-Conwy 1986), where rivers flowing in from the north provided a dispersal route and riparian vegetation permitted. River systems populated by crocodiles or alligators – north to the Yangtze, Indian subcontinent, and Nile – would presumably be unsuitable for beavers.

INTERSPECIFIC COMPETITION

Differences in chromosome number (*Castor fiber* 48, *Castor canadensis* 40), anal gland secretion differences, failed crossbreeding attempts, and lack of observations of hybrids in the wild all confirm that *Castor fiber* and *Castor canadensis* are distinct species which cannot hybridise (Lavrov & Orlov 1973, Lavrov 1983, Rosell & Sun 1999).

Because of the early history of *Castor fiber* and *Castor canadensis* in Finland and north-west Russia, it has sometimes been assumed that the relationship is one of straightforward dominance of *canadensis* over *fiber*. Recent data suggest that this is an oversimplification, without identifying a general pattern which would allow prediction of the outcome. In some places, such as France and Luxembourg, wild-living *Castor canadensis* populations have been removed (Dewas et al. 2012, Herr et al. 2018). However, *Castor canadensis* were also introduced in the Styr River (Dnieper watershed) in north-west Ukraine in 1924 and to East Prussia (now Poland) in 1926. Beavers of unknown origin were also released here in 1942–43 (Panfil 1971) and four Voronezh *Castor fiber* in 1961 (Klarowski 1983). In 1979, a survey revealed that all animals in the region were now *Castor fiber* (Zurowski 1980, cited in Saveljev 1989). In 1933–34, seven North American beavers were released in the Rovno region, then in Poland (now in Ukraine), and survived to 1956 but then died out (Dezhkin 1960). A similar decline in the *Castor canadensis* colony in the Russian Far East (see above) is currently evident. In Austria, 12 individuals of *Castor canadensis* were reintroduced, along with 40 Eurasian beavers, in the 1980s (Sieber 2000). In each of these cases, *canadensis* has disappeared, apparently through intraspecific competition with *fiber* in the latter case at least (Sieber 2000).

The species meet at the eastern and western edges of the Finnish – north-west Russian range of *Castor canadensis*. At present, *fiber* is slowly losing ground to *canadensis* in south-west Finland (LUKE 2019), and on the line of

contact between the White Sea and Lake Onega, but *canadensis* has lost ground to *fiber* by c. 50 km on the Karelian isthmus north of St. Petersburg (Saveljev 1989, Danilov et al. 2011, Danilov & Fyodorov 2015, 2016). We agree with Danilov and Fyodorov (2015, 2016) that the factors which can ‘tip the balance’ are likely to be complex and may include local biotic conditions and the provenance and genetic diversity of founder populations. The results of interspecific competition are also likely to be influenced by the relative sizes of each population, and so by the number of dispersers, once beavers have spread throughout a river system and begin to compete for space (Parker et al. 2012).

For management, a policy of active preference for *Castor fiber* over *Castor canadensis*, especially where populations are not yet ‘consolidated’ (such as on the Kemi, see Fig. 6 and section on Finland), is clearly preferable, rather than hoping that *fiber* will prove to be the dominant species. European Union member states are required to exterminate, control or contain North American beaver and other invasive species (European Union 2014).

BEAVERS IN THE MID-21ST CENTURY

Recolonisation of the beaver’s former range and, to a lesser extent, re-establishment of the population in Europe north and east of Poland–Ukraine inclusive is, with exceptions, substantially complete; and within a few decades it will be complete. In Fenno-Scandia, spread into southern Sweden, western Norway, and north of the Arctic Circle can be expected.

In contrast, in most of continental Europe west of Poland – Ukraine, and in Great Britain, populations are in the early colonisation or rapid increase phases, though they are at or near maturity in some regions such as Bavaria and the lower Rhone. Both range and population size will increase rapidly in this region in coming decades, roughly one third of the land mass of Europe with well over two thirds of its human population.

Beavers remain absent from most of their former range in southern Europe – Portugal, Spain excepting the Ebro, Italy, and the Balkans from Bulgaria – Montenegro southwards.

In Asia, there are extensive regions of Russia, especially eastern Siberia, where beavers remain absent; scope for further increases in range and population is correspondingly large. Beavers of Voronezh/Belarus origin released in Siberia are now in contact with native populations in Western Siberia (*Castor fiber pohlei*) and the upper Yenisei (*Castor fiber tuvunicus*). Management may be necessary if maintenance of unmodified forms of the two autochthonous gene pools is to be maintained.

The Danube basin is the world's most international watershed, draining part or all of 19 countries. Thirty years ago, beavers were confined to the upper reaches from Bavaria to Vienna. As a result of reintroductions and natural spread, the species is now present and rapidly increasing on the main river as far as the Hungarian–Serbian border near Mohacs, and on the main tributaries Morava, Tisza, Sava, Drava, and Mures. There are no serious barriers to further spread on the Danube basin above the Iron Gates barrages, on the Serbia–Romania border about 150 km south-east of Belgrade. There are many rapidly expanding beaver populations, increasingly linked. Downstream of the Iron Gates, the Olt and Ialomița populations are also in rapid expansion, and a population is now established in the Danube Delta. Populations are relatively small at present, about 1800 animals in 2017 (Pașca et al. 2018), and the area of unoccupied habitat is very large. Absent further reintroductions, it will take rather longer for populations in the lower basin to expand throughout, but, as with the upper basin, there are few barriers to spread.

The western extremity of the North European Plain – northern France, Benelux, north-west Germany and England – is one of the most densely populated, human-modified regions in the world. The terrain is flat or low relief. Beaver populations are now widely established in the region, and the period of rapid population increase is under way or about to commence. Management is likely to become an increasingly salient issue in coming decades. Other than in the Netherlands, there is little sign at present that it will be other than reactive.

“How will the increasing beaver populations across Europe, and their associated impacts on flow regimes, water quality and biodiversity, affect river catchment restoration?” was recently identified as a ‘priority question’ for landscape restoration in Europe (Ockendon et al. 2018). Understanding, adapting to, and utilising these impacts should be a priority for river catchment management in general. Attention to this and to framing public debate, on the basis of the detailed information and experience already available (Thompson et al. in press), would be both wise and cost-effective. As most large watersheds, and most beaver populations, in central and western Europe are international, European Union mechanisms for research and development of management methods would perhaps be most appropriate.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Beaver distribution in Austria in 2012.

Appendix S2. Beaver distribution in Belgium in 2016.

Appendix S3. Beaver distribution in Bosnia & Herzegovina in 2015.

Appendix S4. Beaver distribution in the Czech Republic in 2015.

Appendix S5. Beaver distribution in Jylland, Denmark in 2017.

Appendix S6. Beaver distribution in England and Wales in 2018.

Appendix S7. Beaver distribution in France in 2019.

Appendix S8. Beaver distribution in Germany in 2017.

Appendix S9. Beaver distribution in Luxembourg and adjacent regions.

Appendix S10. Beaver distribution in the Netherlands in 2017–19.

Appendix S11. Distribution of beavers in Norway in 2019.

Appendix S12. Distribution of beaver territories in Scotland, Tay and Forth watersheds.

Appendix S13. Beaver distribution in Serbia in 2015.

Appendix S14. Beaver distribution in Slovenia in 2015.

Appendix S15. Distribution of beavers in Spain (Ebro watershed) in 2019.

Appendix S16. Distribution of beavers in Switzerland in 2019.