

Population and Distribution of Eurasian Beaver (*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, Eurasian beavers (*Castor fiber*) have powerfully recovered in range and population, through widespread reintroductions, relaxation of persecution, and natural spread. Populations are now (2010) established in all countries within their former natural range in Europe except for Portugal, Italy, and the south Balkans (Greece, Albania, Bulgaria, Macedonia, Kosovo, Montenegro). In Asia, there are significant populations in West and Central Siberia; and small relict populations elsewhere in west and south Siberia, and in Xinjiang (China)/western Mongolia. The current minimum world population estimate for Eurasian beavers is 1.04 million, though this figure includes some populations of introduced North American beavers (*C. canadensis*) in the NW and Far Eastern Russian Federation, where the ranges of the two species occur in close proximity and to some extent overlap. Both populations and range are in rapid expansion, and in 2008 the species was reclassified by IUCN as **Least Concern**, though some subspecies remain threatened. We present maps summarizing current knowledge of the world distribution of Eurasian beaver and the Eurasian distribution of the introduced North American beaver, and tables of the most recent known population estimates for each country, broken down by region for the Russian Federation.

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

Introduction

Eurasian 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 recolonizing much of its range, including areas where it has not occurred for centuries or even millennia. The pattern of re-expansion 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, Nolet and Rosell 1998, Halley and Rosell 2002, 2003). 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. Periodic summaries and updates 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. In this paper, we present a summary of the information available on population and distribution up to the end of 2010, in a similar format to information presented in Halley and Rosell 2002, 2003 for ease of comparison.

Distribution and populations

Distribution in Europe is shown in Figure 1 and in Asia in Figure 2. The continuous population ranges from Germany through Poland, the Baltic States, Belarus, Ukraine, to central Siberia in the Russian Federation. 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

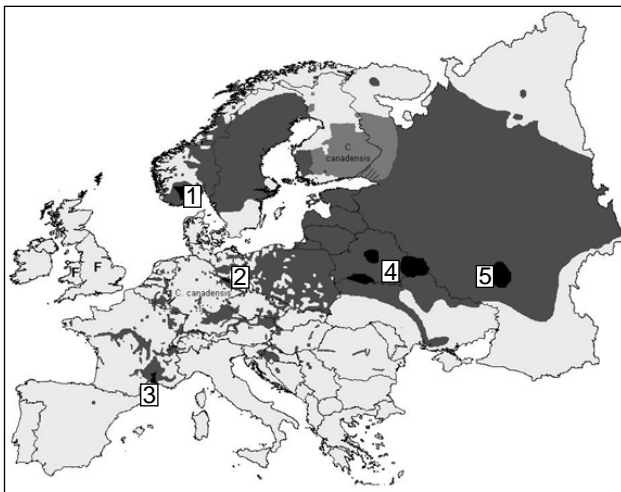


Figure 1. Distribution of both beaver species in Europe. Traditional subspecies designations: 1 – *Castor fiber fiber*; 2 – *Castor fiber albicus*; 3 – *Castor fiber galliae*; 4 – *Castor fiber belarusicus*; 5 – *Castor fiber osteuropaeus*. Dark grey shading represents the present range of *Castor fiber* (locations of relict populations are marked in black); light grey shading represents the range of *Castor canadensis*. Squares are reintroduction sites where range has not yet spread significantly



Figure 2. Distribution of both beaver species in Russia, Kazakhstan, Mongolia, and China. Traditional subspecies designations: 1 – *Castor fiber fiber*; 6 – *Castor fiber pohlei*; 7 – *Castor fiber tuvnicus*; 8 – *Castor fiber birulai*. Dark grey shading represents the present range of *Castor fiber* (relict populations are marked in black); light grey shading represents the range of *Castor canadensis*

periphery of the main Russian range, in central Asia, and on the Amur of 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 205 have been recorded to distinct locations outside the former Soviet Union (FSU) (Halley and Rosell 2002). Within the former

Soviet Union, almost 17000 beavers were translocated between 1927 and 2004, of which 12000 were to sites in Russia and the remainder to Ukraine, Belarus, Latvia, Estonia, Lithuania and Kazakhstan in decreasing order of numbers (Saveljev 2003).

In 2009, beavers were reintroduced to Knapdale in western Scotland and near Copenhagen in Denmark. In 2010 the existence of a wild- living population on the Tay watershed in Scotland, probably resulting from escapes of captive animals, became public. Sightings of free living animals on the Tay date from 2001 (H. Chalmers pers. comm.). Breeding has been confirmed in at least two locations and suspected in at least six others; but both the size and status of the population is unclear. This population was not established by the licensing process required in Scotland, and the authorities are currently (December 2010) attempting removal by live trapping at some of the known sites on the river.

Introduced populations of North American beaver are established in Finland and northwest Russia, and the Russian Far East (Savelyev and Safanov 1999; Safonov and Saveljev 1999). In 2009 a small population was discovered in Luxembourg, apparently as a result of escapes from a wildlife park just across the border in Germany (Table 1).

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

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

Of recent reintroductions, that to the Ebro/Aragon watershed of Spain, which is considered illegal by the regional authorities affected, is the most poorly documented. Current distribution and populations are unknown, though probably rather wider and larger than mapped and given in the table, given known patterns of dispersal and population growth (Halley and Rosell 2002; Discussion) and the large amount of high quality habitat available; breeding and the occupation of new territories is known to have occurred. Trapping and removal is apparently underway in one (possibly two) of the four Spanish regions affected, but neither systematically or widespread enough to have any realistic chance of substantially affecting the population. There are reports of beaver signs found recently (autumn 2010)

downstream on the Ebro at Caspe, c.200 km SE of the known range (I. Jimenez pers. comm.), but this may represent a wandering individual rather than establishment.

The status in Turkey remains uncertain. Reports of an observation on the Yumurtalik marshes (Adana province) in the 1970s (Boessneck 1974, Kumerloev 1975, Veron 1995, discussed in Savelyev 2000) were discounted by Turkish wildlife experts (Özgün Emre Can, Turkish Society for the Protection of Nature, pers. comm.; Halley and Rosell 2002). However, further sightings have been alleged (Dr. Yüksel Coşkun, Univ of Dulche, pers. comm.), but their reliability is unclear and requires confirmation. If the species is still extant in Turkey, clearly it would represent an additional surviving subspecies (and ESU), a significant addition to the genetic diversity of the species, and is probably critically endangered. Establishing the status, and, if extant, population and distribution, in the area should clearly be priority.

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

Discussion

Populations of the eight refugia in which Eurasian beavers survived the 19th century are currently each described as separate subspecies. Recent mtDNA studies (Ducroz et al. 2005) indicate that extant populations of the species divides into at least two Evolutionary Significant Units (ESUs). The western ESU comprises the traditional subspecies *C.f. fiber*, *albicus*, and *galliae*; the eastern *C.f. belarusicus*, *osteuropaeus*, *pohlei*, *tuvinicus*, and *birulai*. While western ESU populations show very little differentiation and are clearly a single ESU, eastern populations are more diverse and may be considered to be several ESUs. These findings should be taken into account by managers seeking reintroduction stock in line with IUCN guidelines.

Eurasian beaver families consist of, on average, about four 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 and 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 serious breeding problems in this species, but 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). Recently other fuller and interesting research of the major histocompatibility complex, MHC, of the aboriginal beavers of Eurasia (*albicus*, *galliae*, *fiber*, *tuvinicus*, *birulai*, *pohlei*) has been carried out (Babik et al., 2005), using the same samples as used in Ducroz et al., 2005 and Durka et al., 2005. In all the relict populations except *pohlei*, the MHC on the DRB gene is specific and monomorphic, one form only in each relict population and a different one for each. Only West Siberian beavers *C.f.pohlei* show any variation of the immune system (4 variants of the DRB gene). The current minimum world population estimate of 1 036 226 given here is conservative, calculated by adding together the lowest estimates for each country. Note, however, that the population figures for the North West Russian and Far East Federal Districts of the Russian Federation are for Eurasian and North American beavers combined (those for Finland do not include *C. canadensis*).

All surviving European populations have grown in numbers beyond the point where further loss of genetic diversity through drift might be a conservation problem. The status of some of the Asian relict populations is unclear and would merit investigation.

In most countries of the western and central European mainland, beavers occur 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 and Rosell (2002); the most detailed case study of range and population expansion is found in Hartman (1995). 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. The furthest known dispersal known, 500km, was registered in 1958 in the Irtysh watershed, in the Omsk region of the USSR (Lavrov 1980 quoted in Saveljev et al. 2002); and a dispersal of 200 km involving crossing a watershed divide has also been re-

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

Country	Extirpation	Protection	Re-introduction and/ or translocations	Present population size	References/comments
1	2	3	4	5	6
Austria	1869	-	1970-90	3 000	Sieber (1989), Kollar and Seiter (1990), Parz-Gollner and Vogl (2006); Parz-Gollner and Hülzler (conf. pres. Dubingiai)
Belarus	remnant	1922	1948	65 400	Djoshkin and Safonov (1972), Belarus Ministry of Statistics (2008)
Belgium	1848	-	1998-99	800-1000	Rubbers and Van den Boegert (2006); Dewas pers comm.
Bosnia and Herzegovina	?	?	2006	60	Kunovac (pers. comm. 2009)
China	remnant	1991	-	700	Sheng et al.(1990), Smith (1999)
Croatia	1857?	-	1996-98	600	Grubestic et al (2006); Grubestic (pers. comm. 2009)
Czech Republic	17th century	-	1991-92, 1996	2 000-2 500	Kostkan and Lehká (1997), Kostkan (2001), Vorel et al. (2008)
Denmark	c.500 BC ¹	-	1999	121	Skov- og Naturstyrelsen (1999); Klein (1999); Elmeros et al. (2007, 2009)
England	18th century?	-	Feasibility study completed	0 ²	Coles 2006; Gow (pers. comm.)
Estonia	1841	-	1957	16 300-17 500	Laanetu (1995), Ulevicius (pers. comm.), Timm (Estonian Environmental Information Centre) (pers. comm.)
Finland	1868	1868	1935-37, 1995	1 500-2 500	Ermala et al.(1999), Lahti (1995), Härkönen (1999),EU ⁶
France	remnant	1909	1959-95	10 000-15 000	Richard (1985, 1986), Office Nationale de la Chasse (1997), Dewas (in press)
Germany	remnant	1910	1936-40, 1966-89, 1999-2000	8 000-10 000	Schwab et al. (1994), Macdonald et al. (1995), Schwab (pers. comm. 2009).
Hungary	1865	-	1980-2006	492	Kollar and Seiter (1990), Bozsér (pers. comm.); Gruber (pers.comm.); EU ⁶
Italy	1541	-	proposed	0	Nolet (1996)
Kazakhstan	1915	-	1963-1986	5 500	Karagoishin (2000), Saveljev (2005), Berber (2008)
Latvia	1830s	-	1927-52, 1975-84	100 000 – 150 000	Balodis (1992, 1994, 1995, 1997, 1998); Ozolins and Baumanis (2000)
Lithuania	1938	-	1947-59	86 000-121 000	Palionene (1965), Mickus (1995), Balciauskas et al. (1999); Ulevicius (2000); Ulevicius (pers.comm. 2009)
Luxembourg	?	?	-	0 ³	Schley et al. (conf. pres. Dubingiai)
Moldova	?	?	-	?	Status uncertain

¹ Based on subfossil remains. Philological evidence from placenames suggests a remnant may have survived as late as the 11th century.

² Reintroductions to fenced enclosures at Ham Fen, Kent, 2001 (6); Cotswolds Water Park in 2005 (6) (2009 at population least 10, Rodell pers. obs.); and Martin Mere in 2007 (4). Enclosures are large enough that animals live an essentially wild existence, but dispersal is prevented.

³ C. 15 *C. canadensis* established, probably escaped from zoo in Saarland (Schley et al pers. comm)

⁴ Current population of the official trial reintroduction in Knapdale. A small feral population of beavers, of unknown size, is established in the wild on the Tay river system (see text).

Table 2.
(continued)

	1	2	3	4	5	6
Mongolia	remnant	?	1959-2002		800	Lavrov (1983), Stubbe and Dawaa (1983, 1986), Stubbe et al. (1991), Shar (2005)
Netherlands	1826	-	1988-2000		300-350	Nolet (1994, 1996), EU ⁶
Norway	remnant	1845	1925-32, 1952-65		>70 000	Rosell and Pedersen (1999); Parker and Rosell (2003)
Poland	1844	1923	1943-49, 1975-2000		31 000 – 41 000	Zurowski and Kasperczyk (1986, 1988), Zurowski (1992), Macdonald et al. (1995), Dzieciolowski and Gozdziwski 1999, Czech (pers. comm.); EU ⁵
Portugal	c. 1450	-	-		0	Antunes 1989
Romania	1824?	-	1998-99		610-690	Troidl and Ionescu (1997), Schwab (pers. comm.); Ionescu et al. (2006); G. Herlo (pers. comm. 2009); G. Ionescu et al. (pers. comm. 2009)
Russian Federation	remnant	1922	1927-33, 1934-41, 1946-2005		495 700 ⁶ (by Federal District see below)	Djoshkin and Safonov (1972), Lavrov (1983), Saveljev and Safonov (1999), Safonov and Saveljev (1999), Dezhkin (1999); Saveljev 2003; Lomanova 2009
North-West Federal District					120 500 ⁷	Lomanova 2009
Central FD					126 000	Lomanova 2009
Privolzhsky FD					138 600	Lomanova 2009
South FD					7 500	Lomanova 2009
Ural FD					31 500	Lomanova 2009
Siberian FD					70 800	Lomanova 2009
Far Eastern FD					800 ⁷	Saveljev 2003; Lomanova 2009
Scotland	16th century	-	2009		12 ⁴	Scottish Wildlife Trust (pers. comm. 2009) ⁴
Serbia	1903?	-	2003-4		150	Cirović 2006; Cirović (pers. comm. 2008)
Slovenia	?	?	1999		20 ⁵	Grubesić (pers. comm.); EU ⁵
Slovakia	1851	-	1995		520-700	Pachinger and Hulik (1999); Valachovic (1997), Dubha and Majlan (1997); EU ⁵
Spain	17 th century	1980s	2003		>40	Cena et al (2004); Cena (pers. comm.)
Sweden	1871	1873	1922-39		>100,000	Freye (1978), Hartman (1994, 1995)
Switzerland	1820	-	1956-77		1600	Stocker (1985), Macdonald et al. (1995), Winter (1997), S. Capt, Centre Suisse de Cartographie de la Faune (pers. comm. 2007); Angst (conf. pres. Dubingiai)
Ukraine	remnant	1922			35 420	Safonov and Saveljev (1999) Ukrghosstatistika (2008)
Wales	16th century	-	Feasibility study completed		0	Coles 2006; Jones (pers. comm. 2009)
Minimum Population Estimate					1 044 000	(using lowest estimate from each country; final figure rounded to nearest thousand)

⁵ Natural spread from Croatia.

⁶ EU: European topic centre on biodiversity <http://biodiversity.eionet.europa.eu/article17/>

⁷ Both species (*C. fiber* and *C. canadensis*).

ported (Saveljev et al. 2002). Both were animals moving into uncolonised waters. However, the longest distance colonisation (i.e., settlement and breeding) has been reported is apparently Fustec et al.'s (2001) record of colonisation of an area about 80 km away from the nearest other occupied area, on the Loire in France.

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) 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 south 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 and 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 and Rosell 2002). Beaver populations should therefore be managed on a watershed scale.

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Afterword

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References

- Babik, W., Durka, W. and Radwan, J. 2005. Sequence diversity of the MHC DRB gene in the Eurasian beaver (*Castor fiber*). *Molecular Ecology* 14: 4249-4257.
- Balčiauskas, L., Trakimas, G., Juskaitis, R., Ulevicius, A. and Balčiauskiene, L. 1999. Atlas of Lithuanian mammals, amphibians and reptiles. Akstis Publications, Vilnius, Lithuania. (In Lithuanian with English summary).
- Balodis, M. 1992. Die Biber in Lettland (The beaver in Lithuania). In: R. Schröpfer, M. Stubbe and D. Heidecke (eds.). Materialien des 2. Internationalen Symposiums Semiaquatische Säugetiere: 121-129. Martin-Luther-Universität, Halle/Saale, Germany.
- Balodis, M. 1994. Beaver population of Latvia: history, development and management. *Proceedings of the Latvian Academy of Sciences, section B*. 7-8: 122-127.
- Balodis, M. 1995. Beavers in Latvia. In: A. Ermala and S. Lahti (eds.). Proceedings of the Third Nordic Beaver Symposium, 1992, Finland: 6-9. Finnish Game and Fisheries Research Institute, Helsinki, Finland.
- Balodis, M. 1997. Recovery of the beaver in the inconstant Latvian landscape. In: K. Pachinger (ed.). Proceedings European Beaver Symposium, 15-19 September 1997: 3. Comenius University, Bratislava, Slovakia.
- Balodis, M. 1998. Beavers in the Gauja national park, Latvia. *Proceedings of the Latvian Academy of Sciences* 52: 49-53.
- Berber, A.P. 2008. Game animal resources of Kazakhstan. TaiS Print. House, Karagandy. 1-456. (in Russ.).
- Boessneck, J. 1974. Ergänzungen zur einstigen Verbreitung des Bibers, *Castor fiber* (Linné, 1758). Säugetierkundliche Mitteilungen (München). 22. 83-88.
- Caughley, G. and Sinclair, A.R.E. 1994. Wildlife ecology and management. Blackwell Science, Cambridge, UK.
- Dewas, M. in press. The situation of native and introduced beavers (*Castor* spp.) in France and neighbouring countries. *Mammal Review*.
- Dezhkin, V. 1999. Beaver in the modern world: necessity of the population management on the national and the international level. In: Proceedings of the First European-American Beaver Congress, Volga-Kama National Nature Preserve, 24-28 August 1999: 43-47. Special Publication of the Volga-Kama National Nature Preserve, Tatarstan, Russia
- Djoshkin, W.W. and Safonov, W.G. 1972. Die Biber der alten und neuen Welt (The beaver in the Old and new world). A. Ziemsen Verlag, Wittenberg, Germany.

- Dubha, J. and O. Majzlan, O.** 1997. The first reintroduction of beaver in Horna Orava in Slovakia. In: K. Pachinger (ed.). Proceedings European Beaver Symposium, 15-19 September 1997: 7. Comenius University, Bratislava, Slovakia.
- Ducroz J.-F., Stubbe M., Saveljev A.P., Heidecke D., Samjaa R., Ulevicius A., Stubbe A., and Durka W.** 2005. Genetic variation and population structure of the Eurasian beaver *Castor fiber* in Eastern Europe and Asia. *Journal of Mammalogy* 86 (6): 1059-1067.
- Durka W., Babik W., Ducroz J.-F., Heidecke D., Rosell F., Samjaa R., Saveljev A., Stubbe A., Ulevicius A., and Stubbe M.** 2005. Mitochondrial phylogeography of the Eurasian beaver *Castor fiber* L. *Molecular Ecology* 14 (12): P. 3843-3856.
- Dzieciolowski, R. and Gozdziwski, J.** 1999. The reintroduction of the European beaver *Castor fiber* in Poland: a success story. In: P. Busher and R. Dzieciolowski (eds.). Beaver protection, management and utilization in Europe and North America: 31-35. Kluwer Academic/Plenum Publishers, New York, USA.
- Ellegren, H., Hartman, G., Johansson, M. and Andersson, L.** 1993. Major histocompatibility complex monomorphism and low levels of DNA fingerprinting variability in a reintroduced and rapidly expanding population of beavers. *Proceedings National Academy Science USA* 90: 8150-8153.
- Ermala, A., Lahti, S. and Vikberg, P.** 1999. Bäverstammen ökar fortfarande – fangsten redan närmare 2500 bävvar (The beaver population increases – trapping numbers near 2500 beavers). *Jägaren* 4: 28-31.
- Freye, H.A.** 1978. *Castor fiber* Linnaeus, 1758 – Europäische Biber. In: J. Niethammer and F. Krapp (eds.). Handbuch der Säugetiere Europas: 184-200. Akademische Verlagsgesellschaft, Wiesbaden, Germany.
- Fustec, J., Lode, T., Le Jacques, D. and Cormier, J.P.** 2001. Colonization, riparian habitat selection, and home range size in a reintroduced population of European beavers in the Loire. *Freshwater Biology* 46: 1361-1371.
- Halley, D.J. and Rosell, F.** 2002. The beaver's reconquest of Eurasia: Status, population development, and management of a conservation success. *Mammal Review* 32: 153-178.
- Halley, D.J. and Rosell, F.** 2003. Population and distribution of European beavers *Castor fiber*. *Lutra* 46: 91-102.
- Hartman, G.** 1994. Long-term population development of a reintroduced population in Sweden. *Conservation Biology* 8: 713-717.
- Hartman, G.** 1995. Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. *Wildlife Biology* 1: 97-103.
- Karagoishyn, Z. M.** 2000. Ecology of beaver (*Castor fiber* L., 1758) in Western Kazakhstan and its practical importance. Unpubl. PhD Inst. of Zoology; Almaty, 1-119. (in Kazakh., with Russ. and Engl. summary)
- Kollar, H.P. and Seiter, M.** 1990. Biber in den Donau-Auen austlich von Wien. Eine erfolgreiche Wiederansiedlung (Beaver in the Danube wetlands east of Vienna. A successful reintroduction). Verein für Ökologie und Umweltforschung, Wien, Austria.
- Kostkan, V.** 2001. The European beaver (*Castor fiber* L.) population growth in the Czech Republic. *Saugetierkundliche Informationen (Jena)*, Band 5. 25: 69-72 (Proc. 3.Symp. Semiaquatic Mammals and their Habitats)
- Kostkan, V. and Lehky, J.** 1997. The Litovleske Pomorave floodplain forest as a habitat for the reintroduction of the European beaver *Castor fiber* into the Czech Republic. *Global Ecology and Biogeography Letters* 6: 307-310.
- Kumerloeve, H.** 1975. Die Säugetiere (*Mammalia*) der Türkei (The Mammals of Turkey). *Veruff. zool. Staatssamml. (München)*. 18. 113-114.
- Laanetu, N.** 1995. The status of European beaver *Castor fiber* L. population in Estonia and its influence on habitats. In: A. Ermala and S. Lahti (eds.). Proceedings of the Third Nordic Beaver Symposium, 1992, Finland: 34-40. Finnish Game and Fisheries Research Institute, Helsinki, Finland.
- Lavrov, L.S.** 1980. Beaver. In: Sokolov, V.E. and V.V.Kucheruk, Eds. Results of tagging animals: 140-146. Nauka Publ., Moscow. (In Russian)
- Lavrov, L.S.** 1983. Evolutionary development of the genus *Castor* and taxonomy of the contemporary beavers of Eurasia. *Acta Zoologica Fennica* 174: 87-90.
- Lavrov, L.S. and Hao-Tsuan, L.** 1961. Present conditions and ecological peculiarities of beaver in natural colonies in Asia. *Vestnik Leningradskogo Universiteta* 9: 72-83. (In Russian).
- Lavrov, L.S. and Lavrov, V.L.** 1986. Verteilung und Anzahl ursprunlicher und aborigener Biberpopulationen und den USSR (Distribution and number of aboriginal origin beaver populations in the USSR). *Zoologische Abhandlungen Dresden* 41: 105-109.
- Lomanova, N.V. (Ed.)** 2009. Sostojanie resursov ohotnichyih kopytnyh zhyvotnyh, medvedej, sobolya, bobra, vydry i ih dobycha v Rossijskoj Federacii v 2003-2008. – CentrOhotKontrol, Moscow. 1-96. (in Russ.) (Status of resources of game ungulates, bears, sables, beaver, otters, and their game bag in the Russian Federation in 2003-2008).
- Macdonald, D.W., Tattersall, F.H., Brown, E.D. and Balharry, D.** 1995. Reintroducing the European beaver to Britain: nostalgic meddling or restoring biodiversity? *Mammal Review* 25: 161-200.
- Mickus, A.** 1995. The European beaver *Castor fiber* L. in Lithuania. In: A. Ermala and S. Lahti (eds.). Proceedings of the Third Nordic Beaver Symposium, 1992, Finland: 44-45. Finnish Game and Fisheries Research Institute, Helsinki, Finland.
- Nolet, B.A.** 1994. Return of the beaver to the Netherlands: viability and prospects of a re-introduced population. PhD-thesis. Rijksuniversiteit Groningen, Groningen, The Netherlands.
- Nolet, B.A.** 1996. Management of the beaver *Castor fiber*: towards restoration of its former distribution and ecological function in Europe. Council of Europe/Convention on the Conservation of European Wildlife and Natural Habitats Bern Convention Nature and Environment series 86. Council of Europe Publishing, Strasbourg, France.
- Nolet, B. and Rosell, F.** 1998. Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. *Biological Conservation* 83: 165-173.
- Office Nationale de la Chasse 1997. Le castor dans le sud-est de la France (The beaver in southwestern France). Office Nationale de la Chasse, Paris.
- Ozolins, J. and Baumanis, J.** 2000. The current beaver status in Latvia. In: A. Czech and G. Schwab (eds.). The European beaver in a new millenium. Proceedings of the 2nd European Beaver Symposium, 27-30 September 2000, Bialowieza: 29. Carpathian Heritage Society, Krakow, Poland.
- Pachinger, K. and Hulik, T.** 1999. Origin, present conditions, and future prospects of the Slovakian beaver population. In: P. Busher and R. Dzieciolowski (Eds.). Beaver protection, management and utilisation in Europe and North America: 43-52. Kluwer Academic/Plenum Publishers, New York, USA.

- Palionene, A.** 1965. The beaver in the Lithuanian S.S.R. *Acta Theriologica* 10: 111-116.
- Richard, P.B.** 1985. Peculiarities of the ecology and management of the Rhodanian beaver *Castor fiber* L. *Zeitschrift für angewandte Zoologie* 72: 143-152.
- Richard, P.B.** 1986. The status of the beaver in France. *Zoologische Abhandlungen Dresden* 41: 121-130.
- Rosell, F. and Pedersen, K.V.** 1999. Bever. Landbruksforlaget, Oslo, Norway. (In Norwegian)
- Safonov, V. and Saveljev, A.** 1999. Beavers in CIS: resources, translocation and trapping. In: P. Busher and Y. Gorshkov (eds.). Proceedings of the First European-American Beaver Congress, 24-28 August 1999: 22-39. Volga-Kama National Nature Preserve, Kazan, Russia.
- Saveljev, A.P.** 2000. Are there any non-described autochthonous European beavers in Asia? Abstracts 2nd Eur. Beaver Symp., Białowieża, Poland. 37.
- Saveljev, A.P.** 2003. Biological peculiarities of aboriginal and artificially created beaver populations in Eurasia and their significance for the resource management strategy. Dissertation, Dr. of Biol. Sci. – Russian Res. Inst. of Game Management and Fur Farming of RAAS. Kirov. 1-201. (in Russ.).
- Saveljev, A.P.** 2005. Beavers in Asia: status, conservation, and management. Abstr. IX Intern. Mammal. Congress. July 31 – August 5, 2005. Sapporo, Hokkaido, Japan. 310.
- Saveljev, A.P. and Safonov, V.G.** 1999. The beaver in Russia and adjoining countries. Recent trends in resource changes and management problems. In: P. Busher and R. Dzieciolowski (Eds.). Beaver protection, management and utilization in Europe and North America: 17-24. Kluwer Academic/Plenum Publishers, New York, USA.
- Saveljev, A.P., Stubbe, M. Stubbe, A., Unzhakov V.V., and Kononov S.V.** 2002. Natural movements of tagged beavers in Tyva. *Russian Journal of Ecology* 33: 434-439.
- Schley, L., Schmitz, L. and Schank, C.** 2001. First record of the beaver *Castor fiber* in Luxembourg since at least the 19th century. *Lutra* 44: 41-42.
- Schwab, G., Dietzen, W. and Von Lossow, G.** 1994. Biber in Bayern: Entwicklung eines Gesamtkonzeptes zum Schutz des Bibers [Beaver in Bavaria: development of an overall concept for the protection of the beaver]. *Schriftenreihe Bayerische Landesamt für Umweltschutz* 128: 9-31. (In German)
- Shar, S.** 2005. Distribution of beavers (*Castor fiber*) in the Hovd river. Environment, history and culture of Western Mongolia and adjacent regions. Toms. 49-53. (In Russian)
- Sheng, H., Xu, H. and Zhang, E.** 1990. Xinjiang beaver and castoreum. *Acta Theriologica Sinica* 10(4): 263-267.
- Skov- og Naturstyrelsen Denmark.** 2000. Det første bæverunge i 1000 år [The first beaver young for 1000 years]. Press release, 6/8/00.
- Smith, A.T.** 1999. Family Castoridae. In: The Mammals of China. Eds. Sheng H., Noriyuku O., Lu H. - China Forestry Publishing House, Beijing: 197-198.
- Stocker, G.** 1985. The beaver in Switzerland: biological and ecological problems of re-establishment. Report 242. Swiss Federal Institute of Forestry Research, Berne, Switzerland.
- Stubbe, M. and Dawaa, N.** 1983. Akklimatisation des Zentralasiatischen Bibers – *Castor fiber birulai* Senbrennikov 1929 – in der Westmongolei [Acclimatisation of the Central Asian beaver *Castor fiber birulai* Senbrennikov 1929] in western Mongolia]. (In German) *Erforschung biologischer Ressourcen der Mongolischen Volkrepublik* 2: 3-92.
- Stubbe, M. and Dawaa, N.** 1986. Die autochthone zentralasiatische Biberpopulation (The aboriginal central asian beaver population). *Zoologische Abhandlungen Dresden* 41: 91-103.
- Troidl, C. and Ionescu, G.** 1997. Beaver project Romania – a reintroduction with special focus on anthropic factors. In: K. Pachinger (Ed.). Proceedings European Beaver Symposium, 15-19 September 1997: 29. Comenius University, Bratislava, Slovakia.
- Ulevicius, A.** 2000. Temporal changes in an abundant beaver *Castor fiber* population. In: A. Czech and G. Schwab (eds.). The European beaver in a new millennium. Proceedings of the 2nd European Beaver Symposium, 27-30 September 2000, Białowieża: 55. Carpathian Heritage Society, Krakow, Poland.
- Valachovic, D.** 1997. Distribution of the beaver in Zohorie region west Slovakia. In: K. Pachinger (Ed.). Proceedings European Beaver Symposium, 15-19 September 1997: 31. Comenius University, Bratislava, Slovakia.
- Winter, C.** 1997. Reintroduction of the beaver in Switzerland – a temporary or lasting success? In: K. Pachinger (Ed.). Proceedings European Beaver Symposium, 15-19 September 1997: 33. Comenius University, Bratislava, Slovakia.
- Zharkov, I.V. and Solokov, V.E.** 1967. The European beaver in the Soviet Union. *Acta Theriologica* 12: 27-46.
- Zurowski, W.** 1992. European beaver reintroduction into lowland and mountain tributaries of the Vistula river. In: B. Bobek, K. Perzanowski and W.L. Regelin (eds.). Global trends in wildlife management transactions of the 16th Congress of the International Union of Wildlife Biologists: 163-166. Swiat Press, Krakow, Poland.
- Zurowski, W. and Kasperczyk, B.** 1986. Characteristics of the European beaver population in the Suwalski lakeland. *Acta Theriologica* 31: 311-325.
- Zurowski, W. and Kasperczyk, B.** 1988. Effects of reintroduction of European beaver in the lowlands of the Vistula basin. *Acta Theriologica* 33: 325-338.

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