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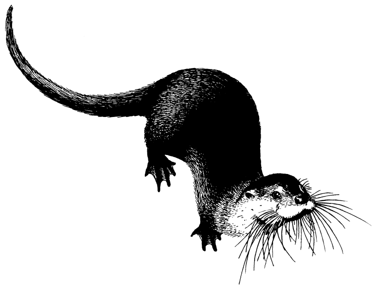

Beavers

A conference is always a good opportunity to meet old friends and to make some new ones, but the main goal is of course to exchange knowledge. This year the Third International Beaver Symposium was held in Arnhem, the Netherlands. The Symposium was hosted by the Society for the Study and Conservation of Mammals (VZZ), and was attended by 123 beaver researchers from 23 countries.

Subjects of presentations and posters ranged from genetics and autecology to distribution, population development and effects of the European beaver (*Castor fiber*) and the American beaver (*Castor canadensis*) on ecosystems. We know that beaver specialists nowadays mostly prefer other common names, i.e. the Eurasian beaver and the North American or Canadian beaver, but in this issue we use the generally accepted common names, i.e. as given in 'The atlas of European mammals' by Mitchell-Jones et al. (1999). We propose that the possible change of the common names of the two beaver species be discussed at the Fourth International Beaver Symposium (to be held in Freising, Germany in 2006).

This Lutra beaver special is the outcome of our invitation to the presenters of papers and posters to submit their contributions to the symposium as an article for Lutra. In this way we could look forward to the acquisition of a respectable number of manuscripts. We have screened them thoroughly on scientific quality, using the review reports provided by a large number of referees. We now proudly present the articles that met our scientific standards.

As the beaver is now again expanding its range, both with and without human help, it is not surprising that a lot of research still focuses on monitoring population development and optimising reintroductions. Halley & Rosell present a new overview of the situation in Europe and Hartman presents some interpretations in the long-run development of populations after reintroduction. Also more detailed overviews are given of population development and changes in distribution in several regions: the Loire basin (Fustec & Cormier), Wallonia (Van den Bergh & Manet), Flanders (Verbeylen) and the Netherlands (Sluiter). Reinhold presents a short case study about the development of a small beaver population in the polder area of Flevoland, the Netherlands, a large-scale agricultural region often seen as a 'desert' in terms of native wildlife.

There are quite a lot of papers with descriptive ecological research. Busher provides us with some data about the intriguing, but still not completely understood aspects of food caching. An interesting case study is presented by Kurstjens & Bekhuis about beaver behaviour in the case of extreme low or high water in the Gelderse Poort area (visited during the symposium excursion) along the river Rhine.

Also more synecological oriented research is presented. As a keystone species, beaver have a huge effect on ecosystem functioning and biodiversity. Some preliminary data are presented on the influence of recently reintroduced beavers on their surroundings in Denmark (Elmeros et al.) and in an enclosed area in Scot-

Photograph: Rollin Verlinde.

land (Jones et al.). The influence of heavy browsing by beavers and their competitors is brought up by Baker.

As populations settle and start expanding, beavers may come close to civilisation. Their ability to change the hydrodynamics of rivers and lakes by building dams sometimes causes severe damage due to flooding. Consequently, an increasing amount of attention is being paid to the impact of beaver on abiotic processes in ecosystems. John & Klein give some interesting outcomes of research on the effects of beaver dams on hydrogeomorphology of a river basin and Gorshkov reports about the effects of beaver on the sedimentation in rivers.

Research of a complete different nature is presented by Ulevičius & Paulauskas, who discuss the genetic and morphological diversity in beavers in different parts of Lithuania.

Quite a lot of research is focused on the management problems caused by planned or unplanned beaver expansion towards more populated areas. Should nature managers choose to actively control population size (i.e. to start hunting or trapping beavers again), to capture and relocate, or to minimise the problems by using flow devices or financial compensation for the damage incurred by landowners? The contributions of Lisle, Hadidian, and Parker & Rosell each highlight these problems and various possible solutions. The philosophy behind prescribed fires in relation to beaver is presented by Hood & Bayley. Baskin & Göran bring up the rear with an overview of questions, hypotheses and possible research projects concerning beaver management based on the experiences with beavers in Northern Europe.

In the last few years a lot has been published about beavers. We therefore finish this special with two reviews of publications we think are most interesting. Furthermore, we have included a preview of observations of beaver in their lodge based on video recordings by the late Donald Griffin.

It seems that a more quantitative, experimental approach is still rare in beaver research, even though many interesting questions need a non-descriptive approach to be answered. One could mention here the composition and energetic value of the chosen food items, assessments of carrying capacity of areas based on habitat quality, or research into the thresholds for viable (meta)populations of beaver, including the resemblances and differences between regions where beaver currently live.

The compilation of this special issue of Lutra would not have been possible without the aid of the peer reviewers. Because of the ‘sudden’ high number of papers about beavers and the limited number of experts on this species, some even reviewed more than one paper for this issue. We are grateful to all of them for their enormous help. We are also grateful to the World Wildlife Fund for subsidising this special issue. We hope the articles of this special issue of Lutra reflect the broad scope of beaver studies and will help to achieve the goal of the conference: spreading knowledge about this fascinating rodent!

Meanwhile we have strengthened the editorial team once again: starting with this issue Jan Piet Bekker has stepped in. We hope authors and readers of Lutra can take advantage of his thorough knowledge of mammals, in particular about their ecology and distribution, both within and outside Europe.

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

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

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

Introduction

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

Distribution

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

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

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

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

Discussion

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

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

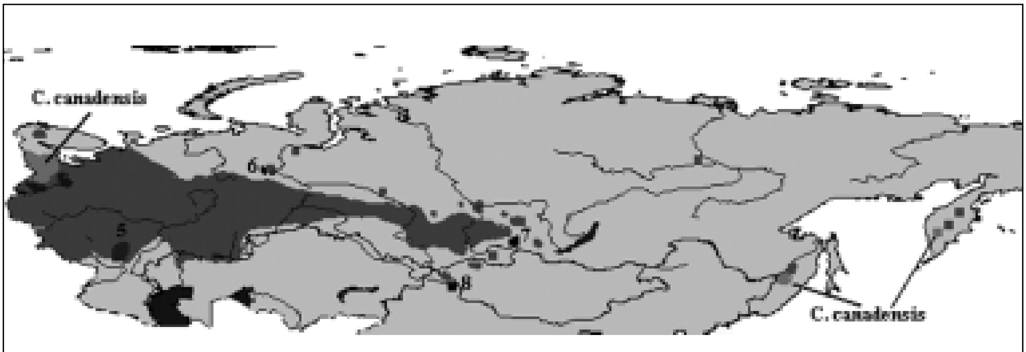

Figure 2. Distribution of beavers in Russia, Mongolia, Kazakhstan and Xinjiang (China). Locations of relict populations are marked in black. Traditional subspecies designations: 5 = *Castor fiber osteuropaeus*; 6 = *Castor fiber pohlei*; 7 = *Castor fiber tuvinicus*; 8 = *Castor fiber biruli*; 5-8 are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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Afterword: The authors would be grateful, on a continuing basis, for any corrections and/or updates to the information we have regarding the progress of reintroduction, range expansion, and population development of European beavers. All contributions will, of course, be acknowledged in any resulting publications.

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Samenvatting

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

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

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Irruptive population development of European beaver (*Castor fiber*) in southwest Sweden

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Abstract: European beavers (*Castor fiber*) have been reintroduced to many areas within their former range. The resulting populations are still in a phase of population growth and range expansion. From a management point of view it is of interest to understand the pattern of population development that these populations are, or will be, exhibiting. Based on data from two surveys of a province in southwestern Sweden, I have earlier proposed that reintroduced beaver populations may exhibit an irruptive pattern of development, possibly as a result of overutilization of resources and lack of predators. The aim of this study was to see if a repeated study, twelve years after the previous, would support or question the proposed pattern of population development. Data from three surveys of the same province were used. The overall population density for the total area had increased from 0.10 colonies/km^2 in 1976, to 0.19 in 1987, and to 0.21 in 1999. However, when population density of local areas with time passed since colonisation was related, a peak in density (mean: 0,34 colonies/km^2) after 25 years was revealed. Dividing the data into groups, areas colonised more or less than 25 years ago, and beaver population density decreased or increased since the previous survey (1987), showed that a negative change in population density was significantly more common in areas colonised more than 25 years ago. The results support the proposed pattern of population irruption in the studied beaver population.

Keywords: Castor fiber, reintroduction, population irruption.

Introduction

The European beaver (*Castor fiber* L., 1758) was historically found from England in the west across the whole Eurasian continent, and from the Mediterranean Sea in the south to the tundras in the north. Mainly due to overhunting, the beavers disappeared from most of Eurasia and at the beginning of the 20th century only eight remnant populations with a total of about 1200 beavers were left. The reintroduction of a Norwegian beaver pair to Sweden in 1922 was the first of a large, and still increasing, number of reintroductions and translocations to many areas within the beavers' former range in Eurasia (Nolet & Rosell 1998).

The resulting populations are still in a phase of population growth and range expansion. From a management point of view, whether it is a question of conservation, hunting, or reduction of damage, it is of great interest to understand the pattern of population development that these populations are, or will be, exhibiting. The main conceptual model of a successful reintroduction would be that the population development is in line with the classic sigmoid growth curve. If, on the other hand, the population would be limited by its food resources and the population itself influences the standing crop of available food, the eventual development would be a population irruption (Caughley 1970, Caughley 1976).

Being the result of the oldest reintroduction of beavers, the Swedish population may give insight into long-term development of reintroduced beaver populations. By comparing survey results, eleven years apart, from the two Swedish provinces of Värmland and Västernorrland, with beaver populations dating back to the 1920s, I have earlier proposed that these populations showed patterns of development similar to what could be predicted by the Riney-Caughley model for irruptive ungulate populations (Riney 1964, Caughley 1970, Caughley 1976, Hartman 1994). The aim of this study was to see if a repeated study of the Värmland-population, twelve years after the previous, would support or question the proposed pattern of population development.

Materials and methods

In 1976, Lavsund (1979) performed a beaver survey in the province of Värmland, based on questionnaires sent to moose-hunting license areas. The administration of moose hunting in Sweden is based on a system of license areas that consist of land of one or several landowners or are part of larger property where hunting is rented by a hunting team. The information used in this article is based on answers to the following questions in these questionnaires: 1. What is the size of your area? 2. What year was the first beaver settlement observed in the area? 3. Give a rough estimate of how many occupied beaver settlements there are in the area. 4. How many beavers were shot last year?

A description of how to define an active settlement was enclosed with the questionnaire. I conducted similar surveys in 1987 (Hartman 1994) and 1999. Pearson correlation and Chi-square tests were used to analyse the data.

Study area

The province of Värmland is situated in southwestern Sweden. It has an area of approximately 17,600 km^2. Roughly 75% is covered by boreal forest. Altitudes vary from 40 to 690 m, but only 23% of the area is higher than 200 m. The last beavers of the original population were probably killed during the 1830s (Ekman 1910). In 1925, two beaver pairs were imported from southern Norway and reintroduced to the eastern parts of the province. This first reintroduction was followed by another two pairs at the same site in 1927. Other introductions at a site 40 km southeast of the first site, took place in 1928 (one pair) and 1930 (one pair), but no offspring was observed (Fries 1940). In 1961/1962 the population was estimated at about 1000 individuals, and in 1976 at 7500-9500 individuals (Lavsund 1979).

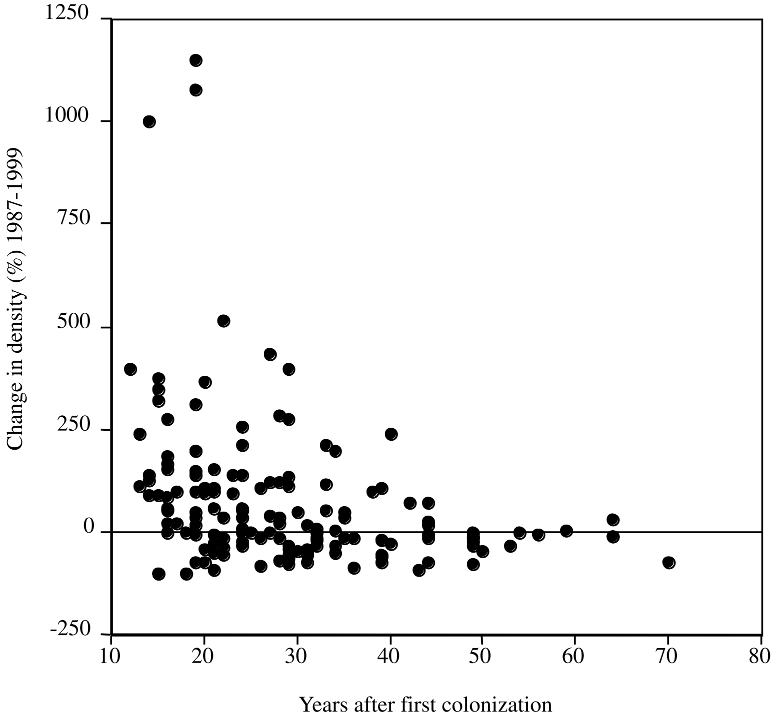
Results

Questionnaires were sent to 315 moose-hunting areas in 1976, to 426 areas in 1987, and to 475 in 1999 (table 1). The percent of hunting areas not yet colonized by beavers decreased from 45% in 1976, to 17% in 1987, to 6% in 1999. Expressed as percent uncolonized area this yields 35% in 1976, 17% in 1987, and 3.5% in 1999. This, in addition to the fact that answers were often incomplete, is the reason why *n*-values vary between analyses. The overall percent of areas with negative population development had increased from 23% during the period 1976-1987, to 40% during the period 1987-1999.

According to an estimate calculated as the sum of all found colonies divided by the sum of all surveyed areas, the beaver population density of the whole province increased from 0.10 colonies/km^2 in 1976 (n=192), to 0.19 colonies/km^2 in 1987 (n=356), and then levelled at 0.21 colonies/km^2 in 1999 (n=248).

Using areas that provided data both in 1987 and 1999, and plotting relative changes in density between the two surveys against year of colonization, shows a rapid increase in roughly the first 25 years after colonization, but then a levelling out or decrease (figure 1). By dividing the data into groups, areas colonized more or less than 25 years ago, and beaver population density decreased or increased since the previous survey, and after excluding areas colonized between surveys, a negative change in population density was shown to be significantly more common in areas colonized more than 25 years ago. During the period 1987-1999, 24% of the areas showed a decrease in density in the more recently colonized group, and 58% in the >25 year group (n=155, *Chi-Square*=18.0, P=0,0001). The same type of plot, using data collected 23 years apart in time

Figure 1. Relative changes in local beaver population densities in the province of Värmland during a twelve-year period, related to time since colonization (*n*=155).



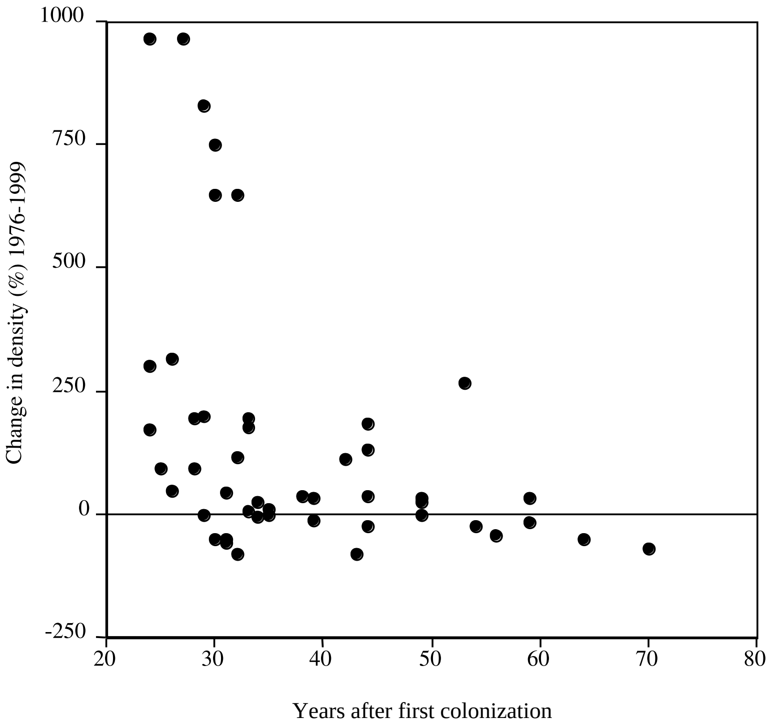


Figure 2. Relative changes in local beaver population densities in the province of Värmland during a 23-year period, related to time since colonization (*n*=47).

Table 1. The response to questionnaires sent to moose-hunting areas in 1976, 1987, and 1999, and the area of moose-hunting areas involved.

Year	Number sent	Number of answers	Total area (km^2)	Mean area (km^2)	SD	Min. (km^2)	Max. (km^2)
1976	315	192	6,533	36	36	5	38
1987	426	356	10,359	29	29	4	313
1999	475	248	6,632	27	26	2	240

(1976 and 1999), yields a similar pattern (figure 2, *n*=47). In this case 19% of the 37 more recently colonized areas showed a decrease in density, while this was found in 50% of the 10 in the >25 year group. However, low expected frequencies preclude further statistical analysis here.

As expected, the magnitude of change in population density between surveys (1987-1999) is negatively correlated to the size of survey areas (*n*=155, *r*=-0.172, *P*=0,03). By pooling data from all three surveys, and excluding areas without beavers and areas colonized less than one year ago, and by grouping the data by time since colonization into five-year periods, and plotting the average densities against period, a peak in density 25 years after colonization was found (figure 3, *n*=574).

Mean hunting pressure in 1999 was rather low (0.51 animals/colony, *sd*=0.44). Hunting pressure was not significantly correlated to current population density (*n*=179, *r*=0.01, *P*=0.22) or change in population density between 1987 and 1999 (*n*=122, *r*=0.38, *P*=0.68). There was, however, a negative correlation between time since colonization and hunting pressure (*n*=169, *r*=-0.22, *P*=0.003).

Discussion

Temporal variability in size of the entire population should be less than temporal variability in population size within local populations, provided that factors that affect population size on a large spatial scale, e.g. weather, are less important than local ecological factors. Hence, local rapid population increase will be compensated for by equally rapid population decrease in another local population. This is the reason why there is a negative correlation between the magnitude of change over time and the size of surveyed areas. It also explains why the total density has increased between the surveys in spite of an increased percent of local areas with negative population development. The time of the observed density peak (after 25 years) is, consequently, also related to the average size of moose-hunting areas in the province, and the large range of sizes of these areas will make the results less distinct.

The results of this study correspond to my previous study of the beaver population in Värmland (Hartman 1994) and support the conclusion that it exhibits dynamics of an irruptive nature. Hunting has not likely affected the pattern of population development, considering the low hunting pressure and the fact that it seems to decrease in time since colonization, possibly indicating a decreasing interest in beaver hunting in time. Predation can also be eliminated as an important factor because the first wolves (*Canis lupus*) did not reappear in Värmland until the beginning of the 1980s. A rough estimate of the current wolve population is 50 individuals.

The most plausible explanation to the observed pattern of population development is that food availability decreases over time. The decrease will be because local beaver populations have come to a point where they utilize food resources faster than they are renewed. This is the most common explanation to population irruptions. It has been shown that food availability determines local population dynamics in beavers (Fryxell 2001). If overutilization is the sole factor, the reduction in food abundance is reversible. It might, however, also be that beavers by consuming favoured tree species induce a change in succession towards less palat-

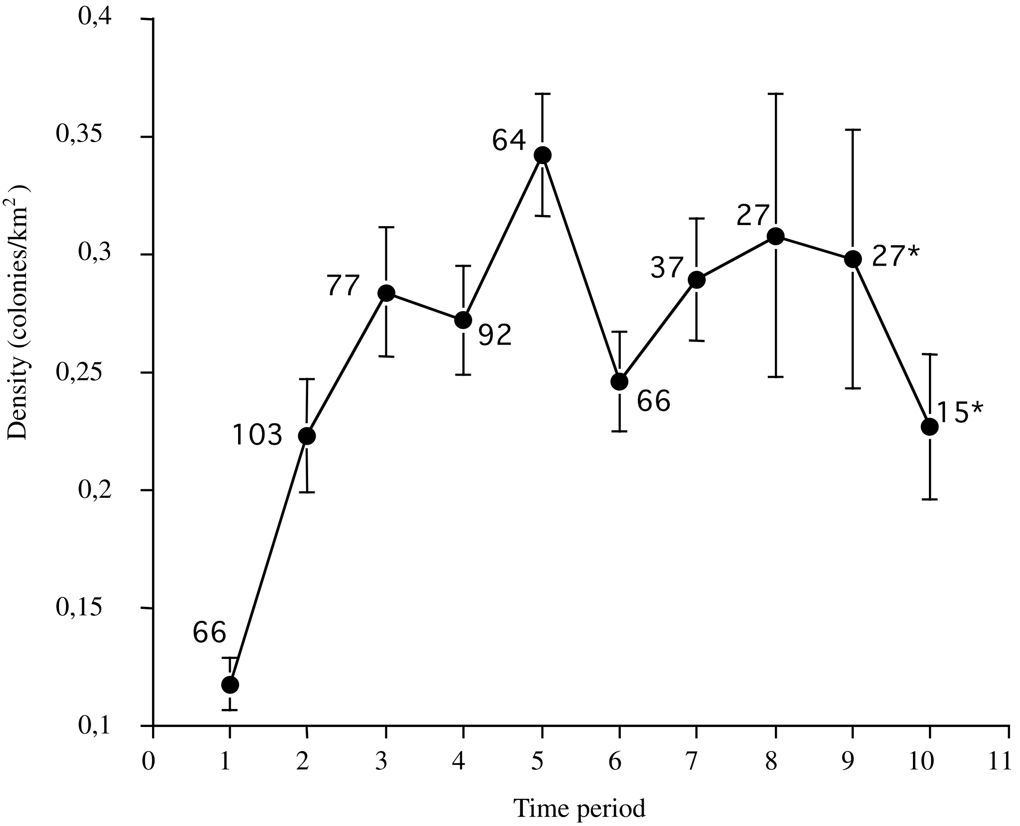


Figure 3. Average density of local beaver populations in relation to time since colonization (*n*= 574). 'Time' is divided into five-year periods. Data from three surveys (1976, 1987, 1999) of the province of Värmland are pooled. Periods 9 and 10, marked *, are not five-year periods but denote 41-50 and 51-70 years since colonization. Vertical bars show standard errors. Numbers are *n*-values.

able species (Fryxell 2001). If this is the case, major disturbance, e.g. forest fire, will be necessary to restore degraded areas. These factors are of course not mutually exclusive so a combination of overutilization and induced succession may be the underlying cause. Similar patterns of population irruption in American beaver (*Castor canadensis*) populations have been found in North America (Busher & Lyons 1999). Notable in their study is that the Prescott peninsula population peaked after 30 years and the size of the study area is 50 km^2, which is very similar to what is presented in this study. Busher & Lyons (1999) suggest that grazing by white-tailed deer (*Odocoileus virginianus*) will inhibit regeneration of woody species, which might be an additional explanatory factor to the observed decline in beavers. The abundance of moose (*Alces alces*) in Värmland (more than 9,000 were shot in 2002) might accordingly have an affect on beaver food abundance.

There are two management consequences of the results of this study. First, monitoring of an introduced beaver population has to be performed at a geographical scale small enough to detect the different phases of population development in the irruptive process. Second, if management authorities wish to reduce the phase in which densities peak, and for example the strong impact beavers have on their surroundings, hunting should be allowed during the rapid increase phase when the population is able to sustain a higher harvest rate than during the post-irruptive decline. From a strictly conservational point of view there might also be a reason to try to level the population development, considering that demographic instability may jeopardize the survival of local populations.

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Samenvatting

Explosieve populatieontwikkling van Europese bever (*Castor fiber*) in zuidwest Zweden

De Europese bever (*Castor fiber*) is in grote delen van zijn vroegere verspreidingsgebied geherintroduceerd. De populaties die het gevolg zijn van deze uitzettingen, vertonen nog steeds groei en areaaluitbreiding. Gezien vanuit het beheer van deze populaties, is het belangrijk de achterliggende processen van de populatieontwikkeling te begrijpen. Eerdere studies in 1987, in het zuidwesten van Zweden, leidden tot de voorspelling dat de beverpopulaties een explosieve groei zouden vertonen. De verwachting was dat dit samenhing met overexploitatie van het gebied, alsmede met het ontbreken van predatoren. Om te zien of de eerdere voorspellingen ondersteund worden door de huidige ontwikkelingen, is het onderzoek twaalf jaar later, in 1999, herhaald met gegevens uit hetzelfde gebied. De dichtheid over het hele onderzoeksgebied bleek te zijn toegenomen van 0,10 kolonies/km^2 in 1976, tot 0,19 in 1987 en 0,21 in 1999. Er zijn echter grote lokale verschillen. Het beeld is daarom anders wanneer dichtheden van lokale populaties in de loop der jaren worden uitgezet: na 25 jaar blijkt een maximum bereikt te worden van 0,34 kolonies/km^2. Negatieve populatiegroei sinds 1987 kwam vaker voor bij populaties die meer dan 25 jaar geleden waren gekoloniseerd. De resultaten van het onderzoek ondersteunen het eerder voorspelde model van explosieve populatiegroei.

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The habitat potential of the downstream Loire River for European beavers (*Castor fiber*)

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Abstract: During the 19th century the European beaver (*Castor fiber*) disappeared from most parts of France, except for the Rhône Valley. In the 1970s, beavers caught from the river Rhône were released in the Loire River, near the city of Blois. While this reintroduction was successful and led to the progressive recolonisation of the Loire River and its tributaries, the density of beaver colonies has remained low. Furthermore, habitat quality has decreased in the downstream part of the Loire, and beavers might not find enough suitable sites to settle. This study was designed to estimate the number of suitable places for beaver settlement in a downstream segment of the Loire River, which is still uncolonised, but already explored by pioneer individuals. For this purpose, we searched for relationships between signs of beaver presence (lodges, cut trunks, and remains of browsed plants) and vegetation features, bank characteristics, and human disturbance in a presently colonised region of the Loire River. Beavers selected sites dominated by 10-15 m tall trees to build lodges, irrespective of the tree species. Sites with cut trees were dominated by Salicaceae. Beavers fed on Salicaceae and numerous herbs. Based on these findings, vegetation features in the uncolonised stretch of the river are expected to be favourable to beaver settlement and feeding. However, beavers will have to face river bank protections and more intense levels of human activity in most of the uncolonised area. These factors may dramatically limit the number of sites suitable for lodge building.

Keywords: Castor fiber, France, Loire, habitat selection, river colonisation, Salicaceae, diet, aquatic mammal.

Introduction

The European beaver (*Castor fiber* L., 1758) had all but disappeared from France at the end of the 19th century because of human persecution. The sole exception was the Rhône Delta where small populations remained (Halley & Rosell 2002). After their protection in the Rhône Valley in 1909, their populations expanded along the river Rhône and its tributaries. In 1968, the species came under protection throughout France, and about 250 individuals from the Rhône Valley were caught and released at different sites across the country (Rouland 1991, Halley & Rosell 2002, Anonymous 2003; figure 1).

In the Loire River, 13 individuals were released near the city of Blois between 1974 and 1976 (figure 1). Reintroductions along this river were successful, and beavers settled in more than 80 sites over 25 years; they now occupy 25% of the Loire River system (Fustec et al. 2001). However, beaver density along the Loire River is approximately 0.125 colonies/km, which is lower than densities estimated in other European countries (Hartman 1994, Ulevicius 1999, Fustec et al. 2001).

In previous studies focusing on the Loire River downstream from Blois, we have shown relationships between home-range size and the canopy cover by white willows (*Salix alba*) and black poplars (*Populus nigra*) (Fustec et al. 2001). Nevertheless, we have also shown that bank characteristics, human disturbance, and vegetation structure may be more important than a high density of Salicaceae for lodge site selection (Fustec et al. 2003). Further information about cut trees and feeding sites would provide a more complete understanding of habitat utilisation.

In the downstream parts of the Loire River, pioneer individuals are just beginning to explore

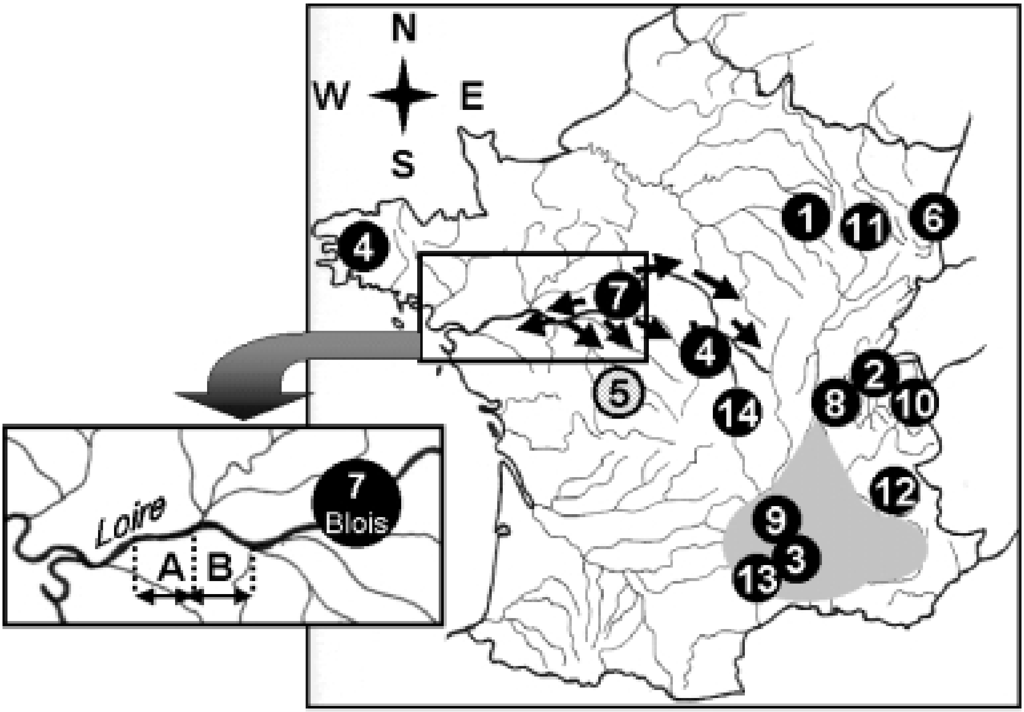

Figure 1. Distribution map of beaver colonies in France after reintroductions (modified from Rouland 1991). Grey area = populations of the Rhône Valley; black circles = areas with one or several successful reintroductions; dotted circle = unsuccessful reintroduction; black arrows = colonisation of the Loire River valley by beavers; numbers indicate successive reintroductions; A = uncolonised stretch, and B = colonised stretch of the Loire River.

a developed part of the river that is equipped for fluvial traffic. It is unclear whether this stretch of the river contains sufficient suitable sites for settlement of the beavers. This study, of an already colonised part of the river, was designed to identify the characteristics of sites where beavers fell trees, and sites where they browse cut branches and herbs (refectories). Our aims were (1) to compare site selection to the various animal needs, and (2) to estimate the habitat potential of the uncolonised stretch of river.

Material and methods

Study area

The Loire Valley (France) is a vast alluvial plain composed of sand and clay interspersed with limestone and loess. The study area was located in this valley, about 127 km downstream from Blois (47°45' N, 0°75' E; figure 1). Two river sections were distinguished: (1) the A-stretch, which is not yet colonised but occasionally explored by beavers, and (2) the B-stretch, colonised by beavers since 1983. The Loire River bed is some 200-300 m wide and the stream carries huge quantities of sand and gravel that form numerous islands held by riparian woods, or continuously shifting sandbanks (figure 2). With little precipitation in the summer, the Loire River has its lowest flow in September (160-180 m^3s^{-1} at Saumur Montjean), while riparian forests are flooded in winter (maximum 1320-1500 m^3s^{-1} in January-February). Riparian woods are characterised by three main woody plant communities: the pioneer willow grove, the tall willow grove, and the ash-elm community (figure 2). The humid and mild climate is favourable to the growth of numerous herbs that colonise banks and sandbanks at-periods of low flow. Banks and islands are sometimes protected from erosion by ripraps. Only the very downstream part of the Loire River (from the A-stretch to the estuary) is modified and equipped for fluvial traffic.

Data collection

The field study has been conducted over four consecutive years (2000-2003). The riverbanks were surveyed for signs of beaver presence by canoe and on foot from June to September, when low water levels allow better access to sandbanks in order to search for signs of beaver activity. The surveys included both sides of the Loire River and island banks (88 km of shoreline in the A-stretch and 105 km in the B-stretch). The whole bankside was divided into 10 m wide and 0.6 to 1.5 km long contiguous plots. Borders between plots corresponded with obvious changes in plant community (structure and/or species composition), or river bank characteristics. In each plot (n=89 in A-stretch, n=104 in B-stretch) human activity was qualitatively assessed using a scale ranging from 1 (low disturbance) to 5 (very high disturbance), and the bank slope was classified as (1) <20%, (2) 20-50% or (3) >50%. Woody plants were classified in three categories based on plant morphology: tall trees (10-15 m), small trees (5-10 m), and tall bushy plants (>5 m). In our classification, a 'tree' was defined as a plant with a trunk and no basal branches touching the water at flood time, 'bushy' qualified plants without a main trunk, but with basal branches accessible to beavers even at low water levels. In each plot, the canopy cover for each plant morphological category was

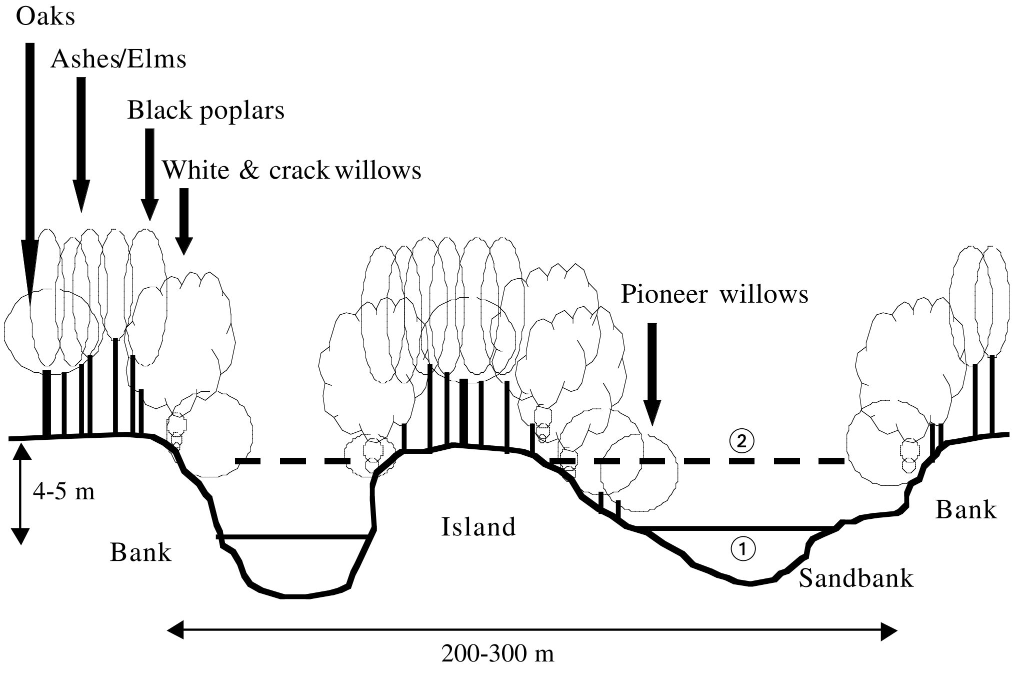

Figure 2. Woody plant communities of the minor bed of the Loire River. The pioneer willow grove is dominated by purple osiers (*Salix purpurea*), common osiers (*Salix viminalis*), and almond-leaved willows (*Salix triandra*). The tall willow grove is dominated by white willows (*Salix alba*), crack willows (*Salix fragilis*), and black poplars (*Populus nigra*) with some hybrids (*Populus* x *canadensis*). The ash/elm community is dominated by narrow-leaved ashes (*Fraxinus angustifolia*), smooth-leaved elms (*Ulmus minor*) and common oaks (*Quercus robur*). (1) low water level reached in September, (2) high water level reached in February.

estimated for each woody and herbal plant species, using an Abundance-Dominance scale (AD) ranging from 1 to 5: (1) <5%, (2) 5-25%, (3) 25-50%, (4) 50-75%, (5) 75-100%, and (+) isolated plants (Guinochet 1973). In each plot, we recorded beaver signs: lodges (burrows and hut-burrows) and tree-felling (hereafter stump sites). We discovered 28 sites with remains of browsed twigs and herbs in the water (hereafter refectories). Plant species found in the 28 refectories were identified, but the characteristics of the plant community covering the bank were recorded in only 17 of these sites. Neither dams, nor huts were found on the Loire River.

AD-values were transformed into mean canopy cover values: (1) 2.5%, (2) 12.5%, (3) 37.5%, (4) 62.5%, (5) 87.5%, (+) 0.5%. In earlier work (Fustec et al. 2003) we compared plots with and without lodges using the non-parametric Mann-Whitney test, which is based on medians equality and does not assume a Gaussian distribution or equal standard deviations. The same method was used here to compare plots without beaver signs with stump plots. Comparisons were also made between refectory plots and those without beaver signs. Plots combining lodges and stumps (n=3) were not included in the analysis.

Results

In the colonised part of the river, stump sites were strongly characterised by a canopy cover of tall Salicaceae (table 1). Crack willow (*Salix fragilis*) cover was markedly higher in stump plots than in those without beaver signs (U=1519, P=0.001; table 1), and a similar trend was found for *Populus nigra* and *Populus* x *canadensis* (U=863, P=0.011). There was no difference between these plots in the canopy cover of white willows, pioneer Salicaceae, and non-Salicaceae trees (table 1). Cover by bushy plants and bushy Salicaceae was higher in stump plots than in plots without beaver signs (U=817, P=0.046 and U=800, P=0.035; table 1). No difference was found between the two types of plots in mean cover of tall or small trees (table 1). Beavers fell trees on plots with steep banks (U=1416, P=0.011), and low human activity (U=742, P=0.005; table 1).

Occurrence of refectories did not depend on the bank slope (U=676, P=0.303), or on human disturbance level (U=622.5, P=0.174). Only one significant difference in vegetation structure and species composition was found between refectory plots and plots without beaver signs, that of cover by small Salicaceae trees: mean 0.26% (n=17) in refectory plots and 0.75% (n=36) in plots without beaver signs (U=1249, P=0.002). Eighty-two percent of the refectories examined (n=28) contained young twigs removed from Salicaceae (poplars, white willows, and crack willows; table 2). Browsed herbs belonged to various locally abundant species, particularly Monocotyledons. Five species of Poaceae and Cyperaceae were found in 49% of the refectories (table 2).

Discussion

Lodge sites in the colonised part of the Loire River

European beaver and American beaver (*Castor canadensis* Kuhl, 1820) are known to be able to live in places without Salicaceae, but when available, they prefer plants from this family as both food and building material (Nolet & Rosell 1998, Donkor & Fryxell 1999, Parker et al. 2001). Previously, Fustec et al. (2001) showed that on the Loire River, the home range size of the European beaver varied from 4.2 to 7.4 km, and was inversely correlated with the canopy cover of white willows and black poplars. However, vegetation is not homogeneous throughout a given home-range, and despite Salicaceae occurrence, lodges are sometimes built on sites where this plant family is poorly represented. According to Fustec et al. (2003), woody plant morphology seems to be a more important determinant of lodge site selection than Salicaceae abundance: beavers build lodges in sites with more than 37.5% canopy cover by 10-15 m tall

Table 1. Comparison of habitat variables between stump sites (with cut trees) and sites without beaver signs in the colonised part of the Loire River (B-stretch). Values are means (median / min-max). *U*-values are based on Mann-Whitney tests. *P*-values are two-tailed: ** = significant at the 0.01 level, * = significant at the 0.05 level.

	Stump sites (*n*=60)	No beaver signs (*n*=36)	*U*	*P*
Species mean cover (%)				
Salicaceae				
Populus alba	0.13 (0 / 0-2.5)	0.11 (0 / 0-2.5)	1104	0.752
Populus nigra & *P.* × *canadensis*	3.42 (12.5 / 0-62.5)	7.01 (2.5 / 0-37.5)	1400	0.011*
Salix alba	3.04 (0.5 / 0-37.5)	5.29 (0.5 / 0-37.5)	1025	0.658
Salix fragilis	2.90 (2.5 / 0-37.5)	1.51 (0 / 0-12.5)	1519	0.001**
Salix purpurea	0.09 (0 / 0-0.5)	0.07 (0 / 0-0.5)	1128	0.574
Salix triandra	0.29 (0 / 0-12.5)	0.04 (0 / 0-0.5)	1189.5	0.176
Salix viminalis	0.17 (0 / 0-2.5)	0.11 (0 / 0-0.5)	1082	0.983
Main other woody species				
Fraxinus angustifolia	8.05 (2.5 / 0-37.5)	10.83 (2.5 / 0-62.5)	1056.5	0.851
Quercus robur	0.88 (0 / 0-37.5)	0.18 (0 / 0-2.5)	1244	0.135
Sambucus nigra	0.06 (0 / 0-0.5)	1.09 (0 / 0-37.5)	1052.5	0.717
Ulmus minor	2.51 (0.5 / 0-37.5)	3.25 (0.5 / 0-37.5)	1105	0.840
Bank characteristics				
Slope (1-3 increasing scale)	2.85 (3 / 1-3)	2.50 (3 /1-3)	1416	0.011*
Human disturbance (1-5 increasing scale)	1.50 (1 / 1-3)	1.97 (2 / 1-4)	742.5	0.005**
Mean cover by different plant structure (%)				
10-15 m tall trees	23.96 (12.5 / 0-87.5)	19.23 (12.5 / 0-62.5)	1193	0.372
10-15 m tall Salicaceae trees	8.04 (2.5 / 0-62.5)	5.41 (2.5 / 0-37.5)	1298	0.082
5-10 m small trees	12.79 (2.5 / 0-62.5)	10.62 (7.5 / 0-62.5)	1147	0.829
5-10 m small Salicaceae trees	4.14 (0 / 0-37.5)	1.58 (0.3 / 0-12.5)	1135	0.648
>5 m bushy plants	15.75 (12.5 / 0-87.5)	12.03 (2.5 / 0-37.5)	817	0.046*
>5 m bushy Salicaceae	6.02 (2.5 / 0-37.5)	4.67 (2.5 / 0-37.5)	800.5	0.035*
Herbs	25.80 (12.5 /0.5-87.5)	31.38 (12.5 / 2.5-87.5)	884	0.432

trees, with about 33% Salicaceae. As is the case on the river Rhône, the beavers along the Loire River dig burrows or hut-burrows on steep banks (slope >50 %), rather than building huts (Richard 1973, Erome 1984, Fustec et al. 2003). Since the Loire River banks have a sandy substrate that is prone to collapse beavers require the strong root system of a 10-15 m tall tree as a burrow frame, irrespective of the plant species. They avoid sandbanks and most kinds of ripraps, but select quiet places, such as islands, to build lodges (Fustec et al. 2003).

Stump sites in the colonised part of the Loire River

On the Loire River, European beavers mainly fell poplars and willows, and to a lesser extent non-Salicaceae species (Fustec et al. 2001). These results concur with other studies conducted in areas where Salicaceae are available (Gorshkov et al. 2002). However, several authors report that both European and American beavers do cut numerous non-Salicaceae species such as Ulmaceae, Oleaceae, Aceraceae, Betulaceae, Rosaceae, and

Table 2. Occurrence of plant species identified from remains of browsed branches and herbs in refectory sites (n=28).

Plant species	Occurrence in refectories (%)
Salicaceae (4 sp.)	**82.3**
Populus nigra	32.1
Salix fragilis	21.6
Populus x canadensis	14.3
Salix alba	14.3
Other woody species (3 sp.)	**14.3**
Ulmus minor	7.1
Fraxinus angustifolia	3.6
Prunus laurocerasus	3.6
Monocotyledons (5 sp.)	**49.5**
Carex riparia	21.0
Paspalum paspalodes	10.7
Echinochloa crus-gallii	7.1
Phalaris arundinacea	7.1
Cyperus esculentus	3.6
Dicotyledons (13 sp.)	**82.2**
Xanthium orientale	17.8
Artemisia vulgaris	10.7
Calystegia sepium	10.7
Polygonum amphibium	7.1
Conyza sp.	7.1
Cirsium sp.	3.6
Arctium lappa	3.6
Bidens frondosa	3.6
Lycopus europaeus	3.6
Rorippa sylvestris	3.6
Rorippa palustris	3.6
Ludwigia grandiflora	3.6
Erysimum cheiranthoides	3.6

Pinaceae (Nolet et al. 1994, Hartman 1996, King et al. 1998). In some cases, non-Salicaceae species are positively selected, even when they are uncommon compared to Salicaceae (Nolet et al. 1994, Collen & Gibson 2001). The differential use of woody species, either for construction or for food has implications for preference indices (Doucet et al. 1994). For instance, branch or trunk diameter may influence the selection of woody species for construction purpose (Barnes & Mallik 1997). According to our results, European beavers in the Loire River fell trees in plots with a high Salicaceae cover, in particular poplars and crack willows. This concurs with the findings of Fustec et al. (2001) that beavers of the Loire River use 4 cm mean diameter branches of willows and 6 cm of poplars for construction. Such branches (1.5-2.5 m length) can be commonly found in the roof frames of hut-burrows, where they are covered with either willow or non-Salicaceae twigs (ashes and elms; J. Fustec & J.P. Cormier, unpublished data). Because of the specific development traits of trees, beavers from the Loire River can only get frame branches, of these characteristics, from Salicaceae (poplars, white willows, and crack willows), whatever their morphological category. The rodent either cuts the trunk of trees to get the required branches, or directly removes basal branches of bushy plants. Plant morphology therefore appears to be less important in plant selection by beavers, although the abundance of bushy plants varies significantly between plots with and without beaver activity. Nevertheless, this result must be considered with some caution, as willows naturally tend to form bushes, and poplars have a high potential to resprout from the stump after being felled by beavers. This result may be simply linked to the high Salicaceae cover observed in stump plots.

Refectory sites in the colonised part of the Loire River

As discussed previously, Salicaceae twigs are, when available, the main food of the European beaver (Nolet et al. 1994, Barnes & Mallik 1997, Dzieciolowski & Misiukiewicz 2002). As this study shows, the beavers of the Loire River mainly use the same species for food as for construction, but have a preference for 5-10 m trees. Nolet et al. (1994) suggested that beavers positively select non-Salicaceae woody species, such as ash. In the Loire valley, ash is rarely eaten, even though it is very common. By contrast, various herbs are frequently used as food by beavers, when they are available, and it is likely that these provide important nutrient complements (Nolet et al. 1994, Nolet et al. 1995, Ganzhorn & Harthun 2000).

The habitat potential of the uncolonised stretch of the Loire River

In the uncolonised river stretch, canopy cover by poplars, white willows, and crack willows is markedly higher than in the colonised stretch, particularly for 10-15 m tall trees (P=0.0009). Canopy cover by 5-10 m trees (P<0.0001) and herbs (P<0.0001) is also higher (Fustec et al. 2003). Therefore, vegetation in the uncolonised stretch of the Loire River seems more favourable for feeding than in the colonised stretch. On the basis of a minimum cover of tall trees of more than 37.5%, we have identified 28 suitable sites for settlement along the 88 km surveyed in the uncolonised stretch, compared to 12 in the colonised stretch (Fustec et al. 2003). Unfortunately, the uncolonised stretch has been developed and equipped for fluvial navigation, which means that beavers will have to face a significantly more intense level of human activity (P=0.016; Fustec et al. 2003). Another factor is that river banks in the uncolonised stretch have been extensively altered: 78% of the bank length is protected by ripraps, and groynes have been built along the riversides to retain sand and maintain a channel for boats in the middle of the river. Taking these factors into account, only three of the 28 sites might be suitable for beaver settlement. It is possible that the beavers may adapt to this altered part of the Loire River. Alternatively they may find better living conditions along the tributaries.

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Samenvatting

De vestigingsmogelijkheden voor de Europese bever (*Castor fiber)* in het benedenstroomse deel van de Loire, Frankrijk

In de jaren '70 vond een herintroductie plaats van de bever (*Castor fiber*) in de Loire, dichtbij de stad Blois. De dieren waren afkomstig uit de Rhône, waar zich lange tijd de enige overgebleven beverpopulatie van Frankrijk ophield. De introductie bij Blois was succesvol; de dieren verspreidden zich langzaam maar zeker over dit deel van de Loire en haar zijrivieren. Het was echter de vraag in hoeverre de bever zich ook meer stroomafwaarts zou kunnen vestigen. Om hierover een uitspraak te kunnen doen is allereerst in een door bevers bewoond deel van de Loire de relatie onderzocht tussen het voorkomen van beversporen (burchten, vraatsporen) en kenmerken van de vegetatie, de rivieroever en menselijke verstoring. Bevers bleken hun burchten bij voorkeur te bouwen op plaatsen die gedomineerd worden door 10-15 meter hoge bomen, ongeacht de boomsoort. Het voedsel bestond in hoofdzaak uit wilgen en populieren (Salicaceae) en een aantal soorten kruidachtige planten. De gevonden resultaten, alsmede de uitkomsten uit eerder onderzoek, zijn vergeleken met de eigenschappen van een naburig, meer stroomafwaarts gelegen traject van de Loire. Dit deel van de rivier was niet gekoloniseerd, maar wel zijn hier geregeld bevers waargenomen, mogelijk op zoek naar geschikte vestigingsplaatsen. Uitgaande van de vegetatie, bleek dit gebied enkele tientallen gunstige vestigingsplaatsen te herbergen, zelfs meer dan in het onderzochte bewoonde traject. Echter, het onbewoonde traject is grotendeels ontwikkeld voor de scheepvaart. Op vele plaatsen zijn stroomdammen aanwezig en is het oevertalud verstevigd. Als deze factoren in aanmerking worden genomen, blijven er naar verwachting slechts drie plaatsen over met goede kansen voor vestiging van de bever.

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The European beaver (*Castor fiber* L.) in Wallonia (southern Belgium): the set-up of an afterthought management programme

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Abstract: The beaver (*Castor fiber*) returned to Wallonia mostly due to clandestine reintroductions of 100 Bavarian beavers between 1998 and 2001. Beaver settlements are now present in most of the river basins, sometimes in seemingly unsuitable areas or in highly urbanised zones. Beavers spread widely during the two years following the reintroductions. The Walloon authorities instituted proceedings against the perpetrators of these releases and, at the same time, instigated a survey and a structure for managing possible conflicts. Forest, fishing and muskrat trapping agents conduct the field survey work and transfer information to the Research Centre for Nature, Forests and Wood (CRNFB) and the Biernausaut Association. With this set-up, a new beaver site can be detected within one month. About 200-250 beavers are now present in Wallonia, at about 60 sites. Only small problems have occurred until now, but they are expected to increase as the beaver population grows and spreads. Thus, beaver management has to continue, to prevent conflicts with human activities but also in accordance with nature conservation objectives such as the implementation of the Natura 2000 programme. A future trans-border co-ordination for surveying beavers should be developed.

Keywords: beaver, *Castor fiber*, monitoring, management, Belgium.

Introduction

As in other Western European countries, numbers of the European beaver (*Castor fiber*) declined from the Middle-Ages onwards. The species finally became extinct in Belgium during the 19th century as a result of habitat degradation (habitat fragmentation, agricultural and sylvicultural intensification) and, more especially, excessive hunting (Hallet & Libois 1982). The last beaver was reported in Brabant in 1848 (van Wijngaarden 1966).

After one century of absence, the beaver's return was expected. The first observation was made on the river Ruhr, near the German border (near Kückelscheid) in 1990 (Huijser & Nolet 1991, Libois 1993). This beaver most likely originated from the German North Eifel. But the real comeback of the beaver to Wallonia took place in 1997, when several individuals settled in de Ruhr valley (see figure 1).

Having noted the wide spread of beavers in Europe, especially in nearby countries, the Walloon authorities considered that this species would be able to naturally recolonise Wallonia in the medium to long term (e.g. about thirty years, Stein 1999). The beaver is no longer threatened on a European scale. Wildlife policy gave priority to seeking to preserve some really endangered species and habitats, rather than encouraging a reintroduction of beaver populations.

Beaver bombing

A few months after this first sighting, in the autumn of 1998, some beaver traces were found in the Ourthe basin, near Hotton and Houffalize. Similar traces were found in the Houille valley in

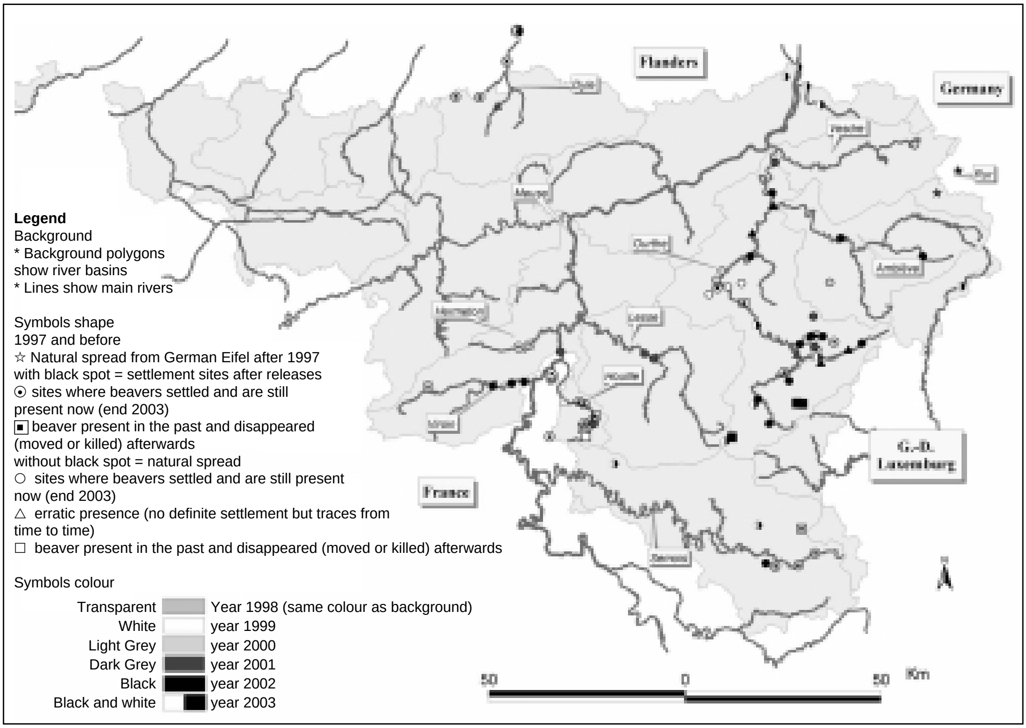

Figure 1. Distribution of the European beaver in Wallonia by river basin (end 2003). *Carthography: ASBL Biernasaut 2003. Fonds Cartographiques: MRW-DGRNE.*

spring 1999. In view of the long distance from the nearest population these beavers obviously came from clandestine releases.

At the end of 1999, and in the beginning of 2000, more releases were made in the Middle Ourthe basin, in the Upper Meuse basin and in some tributaries of these rivers. New settlements were found in the Hermeton and Meuse and in a nature reserve in Virelles, in the upper part of the Eau Blanche basin (tributary of the Viroin). At the beginning of 2001, further new releases were made in the Semois basin, near Arlon, and in the Dyle basin, near Wavre (south of Brussels). Around the same time, some first dispersals were observed from different locations, as some pregnant females were released in the previous years.

Corroborated information from different sources has established that approximately 100 beavers were released in six areas over three years. There were probably no more releases in Wallonia after 2001. The released animals mainly originate from Bavaria, and a few from the Elbe (Schwab & Schmidbauer 2002). The number of reintroduced beavers is, relative to Belgium's small area, higher than for any other reintroduction carried out in Europe.

Releases were made without any serious study of habitat suitability, except in some places where a quick evaluation of food resources was probably carried out. Beavers were often released near to roads or bridges and sometimes in highly urbanised areas (even near a town centre). A few beavers were found shot by rifle, or disappeared suddenly from some problematic sites (about six individuals). This was probably a consequence of the negative perceptions of some landowners towards beavers. As the releases were clandestine landowners did not receive any information prior to the reintroduction and were therefore unprepared for the presence of beavers and unaware of how to prevent conflicts. In other cases, some beavers were released at sites where food resources were limited. In a natural dispersal situation, such 'second-choice' basins would have been last to be colonised. Fortunately, the beaver shows an extraordinary capability to adapt, and these reintroductions have led us to reconsider the theoretical habitat suitability criteria. Some of the reintroduced beavers seem content with limited food resources (and a limited availability of willow or poplar) and very small streams.

After the events

The Walloon authority instituted proceedings (which are still running) against the perpetrators of these clandestine releases and, having identified the supplier, requested that no more beavers be delivered. The first concern of nature managers was to find out the origin of beavers, in order to confirm whether the released animals were *Castor canadensis* or *Castor fiber*. Skull measurements and DNA analyses of five dead beavers indicate that all the dead beavers found so far are *Castor fiber*. Information from the beaver provider indicates that, at least most of, the released beavers are *Castor fiber*. Another problem is the lack of knowledge about the total number, health, sex and age of the released animals and the location of their release.

A first survey was done in winter 2000-2001 by the CRNFB in collaboration with the Forestry Service and the muskrat trappers (Manet & de Crombrugghe 2002). The main goal was to determine population size and its geographical extent before the first sub-adult dispersal. This survey also provided information on reproduction. A total of 47 habitation sites were found, inhabited by one or more beavers and at least 15 of these sites showed signs of reproduction as early as from the first year of occupation.

Survey and conflict management structure set-up

The Biernausaut Association has been authorised to collaborate with the relevant services (i.e. Nature and Forests Division, Watercourses Division, CRNFB) to address the problems resulting from these clandestine releases. The tasks of the Biernausaut Association are to inform and mediate with landowners, set up communication tools for the public, and develop international and trans-border contacts for information and co-ordination. It has also been asked to adapt existing habitat suitability criteria to the Walloon landscape, to identify release sites for problem beavers that are recaptured elsewhere and to set up a recapture procedure. Finally, the association has to give technical and specialised information to forest and fishing agents and muskrat trappers (who do the main field survey work) and to help information transmission and co-ordination between the different services involved. Some external observers have joined the network. These observers transmit the information to the CRNFB and the Biernausaut Association. With this structure, new beaver settlements are supposed to be detected within one month.

When a beaver settlement is detected, Biernausaut Association collects information about the site, and contacts landowners. Information on beaver biology, legal status and ways of preventing damage is given to the landowner. A report is made at least every three months, to the Nature Direction and the Minister's Cabinet, and they are responsible for deciding what action to take. Beavers are protected under Walloon legislation and some compensation can be made for the damage that they cause. However, the cost of preventing damages falls to the landowner. No compensation is given for this, nor for the damage itself, except when the damaged property is used for a main professional activity and the costs are above 125 Euro.

The clandestine character of reintroduction, and the slowness of proceedings against the perpetrators, have made mediation with many landowners more difficult. Many consider the beaver as an 'illegal pest' for which no damage compensations is given, and they sometimes need 'strongly persuasion' not to shoot beavers.

Survey results

By 2003, beavers had permanently settled in about 60 Walloon sites, and about seven areas show occasional traces of beaver (stray beavers or dispersal paths). None of these sites can be considered highly problematic now, although nine sites show some slight problems: four with beaver holes in pond banks, three with beaver dams and two with landowner hostility towards beavers. Since the last releases, dispersals have been observed in most basins (see figure 1), and sometimes (three cases to date) across the basin sources to another basin.

In 2001, very few new sites were occupied. However, in the context of the clandestine reintroductions, each new site seemed suspect, even though beavers are dispersing naturally from the German Eifel to the Vesdre, Our and maybe Amblève rivers, and maybe also from the Lower Meuse in the Netherlands.

In 2002, 19 new sites were listed, mainly in the Ourthe basin. These sites are located upstream as well as downstream, sometimes at quite a long distance from a release site (50-80 km). These settlements generally correspond to optimal habitat according to a progression of despotic distribution (Nolet & Rosell 1994). In 2003 (i.e. from January to July), the dispersal pattern corresponds closely to an, apparently preferred type of chosen habitat.

Some beavers (2-3 families) have dispersed from Belgium to France along the Upper Meuse, and are tracked by the French ONCFS. In the same way, some beavers went to the Dyle Basin in Flanders, where their numbers were recently (April 2003) added to by clandestine restocking of about another 20 Bavarian beavers. These beavers have to be monitored and managed by the Flemish Nature Administration. Currently, the total number of beavers in Wallonia is estimated to about 200-250 individuals.

Discussion

Every reintroduction programme needs a general discussion that includes all concerned interest groups. Species reintroduction must remain a justified and well-prepared action and cannot be improvised, nor be a promotional action for a few people's benefit. Reintroduction projects need to include surveys and a public information campaign, especially in the case of a damage-causing species like beaver. The export of animals designed for reintroduction should require official acknowledgement from the destination country's authorities. The suppliers should be obliged to satisfy themselves about the validity of this acknowledgement.

It is very likely that the Belgian beaver population will grow in size in the future, as many river basins are still to be colonised. Moreover, the Belgian population can be expected to provide a link between the French population in the Moselle, those in the Eifel in Germany and the recently reintroduced populations in Dutch Limburg.

Thanks to its extraordinary adaptation capabilities, the beaver has succeeded in settling in many different types of sites, including in some less suitable basins where it was released. The theoretical dispersal pattern for the beaver should be adjusted to local topographic and hydrographic characteristics. Even if dispersal along watercourses remains the main case, we should not ignore terrestrial dispersal over crests and through source areas, which have appeared more frequent than expected.

Until now beaver activities pose no severe problem. Nevertheless, these problems are expected to increase as the beaver populations grow in a densely populated country, particularly in urbanised areas like the Escaut basin. To limit these conflicts, a survey and proper beaver management must be maintained.

Beside the usual damages a particular problem arises in beaver management. As the beaver uses similar habitats to the muskrat (*Ondatra zibethicus*), muskrat trapping with Conibear traps and poisoned carrots (chlorophacinone) can be a risk, mainly for young beavers. In France (Loire and Alsace), it has been observed that coypu (*Myocastor coypus*) trapping with larger Conibear traps and another type of poison (bio-accumulating bromadiolone) seems to have a significant influence on some local beaver populations (P. Rouland and J.-C. Jacob, personal communication). There are not many coypu present in Wallonia, so their trapping is not systematically organised. Instructions have been given to muskrat trappers to pay attention to the trap systems that they use in beaver territories during critical months for young beavers, while maintaining the efficiency of muskrat trapping.

Another question is the impact of beaver dams' on fish migration. Some dams make it impossible for fish to migrate upstream, even in winter. In such cases, when some important fish breeding sites may become impossible to reach from downstream, a beaver dam can cause a serious problem and may have to be removed. Beside this, thought should be given to the use of pipe systems in beaver dams, which have been proved to be efficient in preventing flooding in several other countries. This may allow an accommodation to be made, one which will maintain beaver habitat, reduce flood risks and provide passage to migrating fish species.

Beaver management can also be linked to the improvement of valley habitats, particularly through the restoration of bank vegetation and flood zones between the river and cultivated areas. The recently established Natura 2000 programme may be useful in this regard.

Acknowledgements: We would like to thank the forest and fishery agents, muskrat trappers and other people who provided data on beaver presence in Wallonia.

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Samenvatting

De Europese bever (*Castor fiber* L.) in Wallonië (zuid België): opzet van een reactief beheerprogramma

De bever (*Castor fiber*) keerde in Wallonië in hoofdzaak terug door clandestiene herintroducties van 100 bevers uit Beieren tussen 1998 en 2001. Vestigingen van bevers zijn nu aanwezig in de meeste stroomgebieden, soms in ogenschijnlijk niet geschikte of in sterk verstedelijkte gebieden. De bevers verspreidden zich verder gedurende de twee jaar volgend op de herintroducties. De Waalse autoriteiten startten de vervolging van de uitvoerders van deze vrijlatingen. Tegelijkertijd werd een onderzoek- en managementstructuur opgezet voor mogelijke conflicten. Organisaties voor bos, visserij en muskusrattenbestrijding voerden het veldonderzoek uit en brachten de informatie over aan het Research Centrum voor Natuur, Bossen en Hout (CRNFB) en de Biernausaut Associatie. Met deze opzet

kan een nieuwe bevervestiging binnen een maand worden ontdekt. Nu zijn ongeveer 200-250 bevers aanwezig in Wallonië op ongeveer 60 plaatsen. Tot nu toe hebben zich alleen kleine problemen voorgedaan, maar te verwachten is dat het aantal problemen zal toenemen als de beverpopulatie groeit en zich verder zal verspreiden. Het beverbeheer moet dus doorgaan om conflicten met menselijke activiteiten te voorkomen, maar het moet ook in overeenstemming zijn met natuurbehouddoelstellingen zoals de implementatie van het programma Natura 2000. Een toekomstige grensoverschrijdende coördinatie voor beveronderzoek zou moeten worden ontwikkeld.

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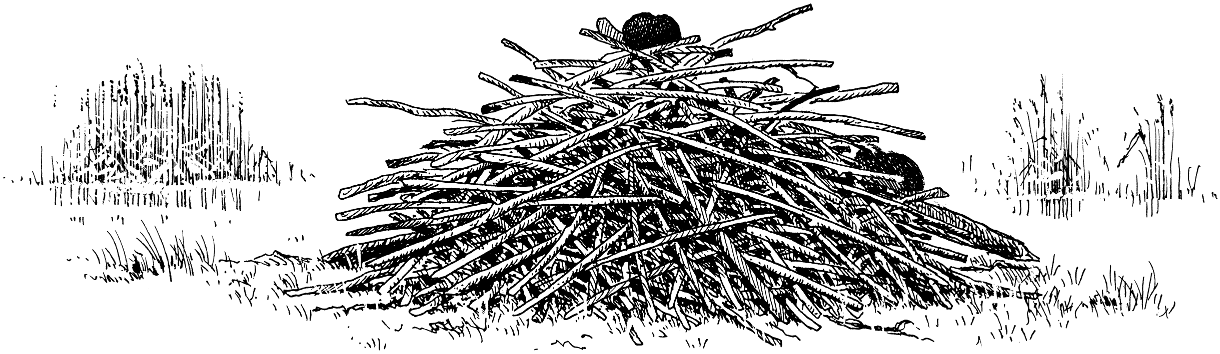

The unofficial return of the European beaver (*Castor fiber*) in Flanders (Belgium)

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Abstract: After a long period of absence, beavers (*Castor fiber*) reappeared in Flanders in the spring of 2000, first in the province of Vlaams-Brabant and in 2002 also in Limburg. The beavers originate from the unofficially reintroduced Walloon population. With a view to a future reintroduction project to restock this not yet reproducing Flemish beaver population, a feasibility study was conducted at the request of AMINAL Nature Division (Ministry of the Flemish Government). This study concluded that the basins of the rivers Schelde and Dijle could carry a viable beaver population of at least 40 families that were all expected to stay in the same area and cause no problems in the wide vicinity. Even before the Flemish government had decided whether or not to proceed with the preparation of an official reintroduction, 20 Bavarian beavers of unknown age and sex were released on 11 April 2003 along the rivers Dijle and Laan. This happened unofficially, without any scientific follow-up and without preparing or informing the local population or other interest groups. Scarcely two months later at least two beavers had already crossed the city of Leuven. Beavers are now permanently present along the rivers Dijle and Laan south of Leuven. Some traces have also been found on the IJse. Complaints are coming in about damage to private as well as to public property and an adaptation of rat control methods is required. Since in the densely populated Flanders many human-beaver conflicts can be expected, the pros and cons of beaver presence in Flanders should be weighed up carefully, taking all interest groups into account.

Keywords: European beaver, *Castor fiber*, Flanders, illegal introduction, human-beaver interactions.

Introduction

The European beaver (*Castor fiber*) was originally distributed from Britain to Mongolia but disappeared due to hunting for fur and meat and for the medical and cosmetic properties of the castoreum (Nolet & Rosell 1998). The decline was accelerated by the destruction of its habitat as a result of the canalisation of large watercourses. In Belgium the beaver probably started to decline in the 16th century, and finally became extinct in 1848 in Flanders and in 1890-1900 in Wallonia, according to data from Lorraine (Born 2002). The abolition of beaver hunting almost everywhere in Europe and the numerous reintroductions have allowed the species to resettle in a large part of its original northern and eastern European distribution area.

The presence of beavers in all countries surrounding Flanders made us believe that the beaver would naturally recolonise Flanders. This article describes what happened in contrast with our expectations and how we plan to handle problems arising from this situation in the future.

Where did we expect beavers to invade Flanders from?

Wallonia

In Wallonia a beaver was sighted for the first time again in 1990, in the basin of the river Roer in the Hautes Fagnes (see figure 1) (Huijser & Nolet 1991, Born 2002). This animal originated from the German Eifel area, where Polish beavers were introduced between 1981 and 1989 (figure 1). In 1997 a beaver family settled on the Belgian part of the river Roer. A further spread to the rest of Belgium was thought unlikely in the short term, since the river Roer belongs to the basin of the river

Rhine (figure 1). But it was also estimated that the expansion to another basin would not be a problem in the long run, once the population was sufficiently large (after 20-30 years or even earlier). In 1998 suddenly beavers started to appear everywhere in Wallonia, mainly in the Ardennes and the surroundings of Namur (figure 1). These animals originated from an unofficial release of 101 beavers (4 from the Elbe and 97 from Bavaria) in Wallonia, spread over three years (1998-2000). In some cases the animals were released close to urban centres, leading to several traffic victims. Ten of the 101 beavers were released in 1999 in a pond next to the river Argentine south-east of Brussels, just across the Flemish border in Wallonia (Rixensart, see figure 2, point 1) (Niewold & Rossaert 2002, Niewold 2003). Since then the Walloon beaver population has expanded considerably (several animals have been found tens of kilometres from the release site) and probably consists of about 150-200 individuals, but an exact estimate is difficult to make.

The Netherlands

Besides the three Dutch beaver populations in the Biesbosch, the Gelderse Poort, and the Flevopolder, in 2002 at least seven beavers, originating from the river Roer in the German Eifel area, were present along the river Maas in the Dutch province of Limburg (see figure 2, point 2) (Niewold & Rossaert 2002, Niewold 2003). Since no reproduction took place, this population was restocked with another ten beavers from the Elbe in fall 2002, as part of an official reintroduction project in which a total of ten beaver families will be released between 2002 and 2005. One of the released animals died in traffic. The population was restocked again in October 2003 in Thorn (see figure 2, point 3), just across the Flemish border (but without any consultation with the Flemish governmental services). In the following few months this already resulted in immigration of several beavers into Flanders from this side.

Where do the 'Flemish' beavers originate from?

Immigration from Wallonia

In spring 2000 the beaver returned to Flanders for the first in a very long time, originating

Figure 1. Location of the different countries, provinces, regions and rivers mentioned in the article.

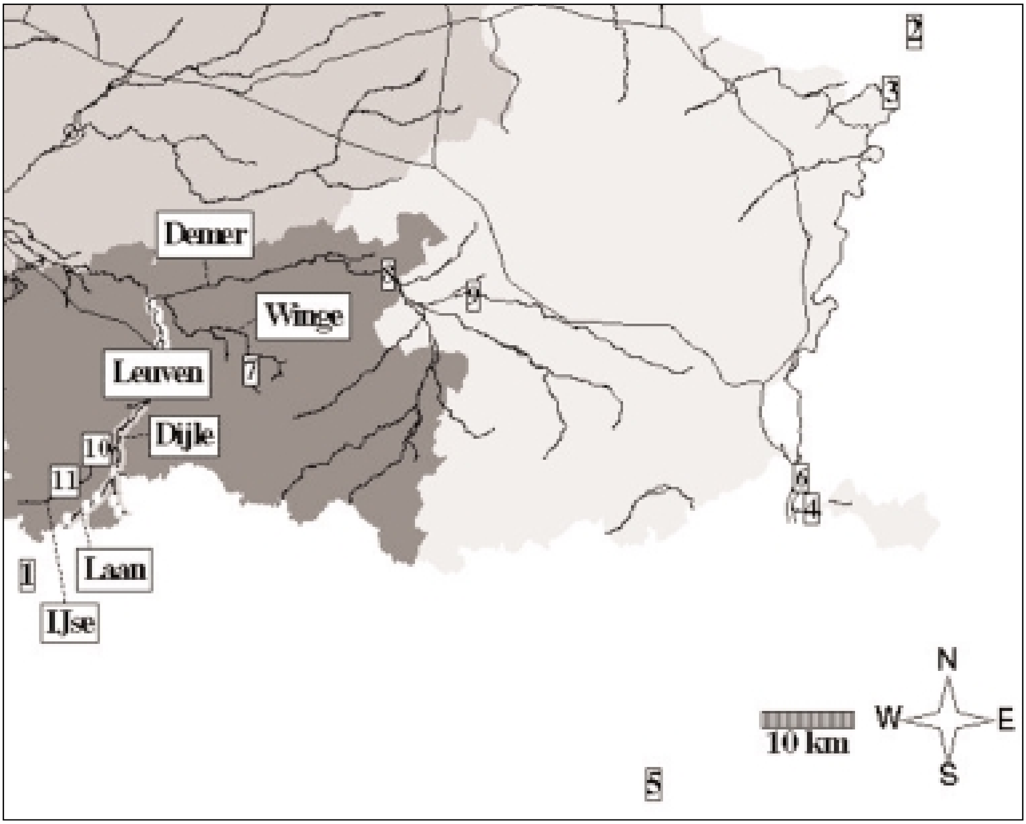

Figure 2. Distribution of the European beaver in Flanders. Grey part of the river Dijle and Laan = permanent presence since 11 April 2003; white part of the river Dijle = presence in May-June 2003; white dots on the grey part of the river Dijle and Laan = release-sites on 11 April 2003; numbers = beaver sightings, see text.

from the above-mentioned unofficially introduced population in Rixensart (Niewold & Rossaert 2002, Niewold 2003). Since then, an increasing number of beaver traces have been observed along the rivers Dijle and Laan south of the city of Leuven in the Flemish province of Vlaams-Brabant (figure 2). The number of beavers was believed to be three to five individuals that had settled in relative isolation, for the time being without any signs of reproduction.

Also in the Flemish province of Limburg there are occasional sightings of beavers, probably originating from the Walloon population. In the period from September 2002 till the end of the winter of 2002-2003 beaver traces, probably from one animal, were found at two locations on the river Berwijn (Voeren, figure 2, point 4), about 50 km from the nearest Walloon release-site in Durbuy (figure 2, point 5). At the end of the winter of 2002-2003 this animal was probably disturbed and disappeared until August 2003, when again signs of beaver (feeding damage in a cornfield and a small dam partly built with corn plants) were seen. A beaver, possibly the same one, was also sighted on an isle in the river Maas in Lanaye (Visé, figure 2, point 6) at the end of April 2003.

A feasibility study

As part of a future reintroduction project to restock this not yet reproducing Flemish beaver population, a 'feasibility study for the recolonisation by beaver of the basin of the rivers Schelde and Dijle' was conducted by the Dutch research institute Alterra, at the request of AMINAL Nature Division (Ministry of the Flemish Government) (Niewold & Rossaert 2002, Niewold 2003). This study concluded that the area could carry a viable beaver population of at least 40 families (about 160 animals). Only the city of Leuven was thought to be an important dispersal barrier, although other studies show that comparable barriers are easily crossed, especially downstream. In the Gelderse Poort (in the Netherlands) beavers swim almost daily through a flooded tube of 100 m and there are also several beavers that were able to pass an old water mill when going from the river Argentine (Wallonia) to Flanders. This makes us suspect that beavers have a higher dispersal ability than previously thought. According to the feasibility study there will be almost no bottlenecks and it is expected that the released animals will all stay in the same area and cause no problems in the wide vicinity. The view is taken that the different interest groups (like rat control organisations, hunters, fishermen, farmers, and the local population) will adapt to the presence of beaver without any problems.

Unofficial release of Bavarian beavers

Even before the Flemish government could make a decision based on the feasibility study whether or not to proceed with the preparation of an official reintroduction, 20 Bavarian beavers of unknown age and sex (believed to include 2 pregnant females and 1 beaver family) were released on 11 April 2003 in at least 6 locations along the rivers Dijle and Laan (see figure 2, white dots). This happened unofficially, without any scientific follow-up and without preparing or informing the local population and other interest groups. A German beaver biologist, who was given to understand that it concerned an official release (everything happened in broad daylight), transported the beavers into Flanders from Bavaria (Germany). In Flanders this is considered an illegal action, since it is forbidden to possess and transport protected animals, which the beaver has been since 2001, without a permit from the government (Flemish Decree 13/7/01). Some of the animals were released in an artificial lodge to decrease stress, but several of the release-sites were located close to roads, not taking into account the possibility of traffic victims. According to the German beaver biologist who imported the beavers into Flanders, the beavers were checked genetically (at least 1 animal per family) to make sure that no American beavers (*Castor canadensis*) were amongst them.

Scarcely two months after the release at least two beavers had already crossed the city of Leuven. One (possibly a pregnant or nursing female) was mistaken for a coypu (*Myocastor coypus*) and shot on 12 June 2003 in Lubbeek, at least 30 km from the release site (measured along the rivers Dijle, Demer and Winge, see figure 2, point 7). Early in July 2003 a burrow (with obvious beaver hairs) was found in the dyke of the river Demer near Diest (at more than 45 km along the rivers Dijle and Demer, see figure 2, point 8), but the beaver that had made the burrow had again disappeared. In October 2003 again signs of beaver activity (damage to corn), from probably the same animal, were found on the river Demer in Lummen (12 km further upstream, see figure 2, point 9). The traces found in May and June 2003 on the river Dijle north of the city of Leuven to where the river joins the river Demer possibly originate from these animals. Since summer 2003 no fresh beaver signs have been found along this transect (see figure 2, white part of the river Dijle). Apart from these, beaver traces have been found everywhere along the rivers Dijle and, to a lesser extent, Laan south of Leuven since summer 2003 (see figure 2, grey part of the river Dijle and Laan). Some traces have also been found on the IJse, another tributary of the river Dijle, since September 2003 in the surroundings of Neerijse (see figure 2, point 10) and just upstream from the centre of Huldenberg (see figure 2, point 11).

How can we switch from a bad start to a good situation?

In countries where the reintroduction of beavers took place officially, preparing and informing the different interest groups usually took several years. In some countries the preparation period was even so long that the population started to ask when the introduction would finally take place. This is of course an ideal situation. In Flanders we have been confronted with a sudden presence of beavers that was unexpected and therefore often regarded in a negative light. We do not yet have an adequate system for damage prevention and compensation. Complaints are coming in about damage to private as well as to public property (feeding, burrowing and damming damage). Besides feeding on natural vegetation, mainly willow (*Salix* spp.) but e.g. also alder (*Alnus glutinosa*) and butterbur (*Petasites hybridus*), there are reports of damage to poplar (*Populus* x *canadensis*), fruit trees, Norway spruce (*Picea abies*) and agricultural crops (mainly corn, but also beets and grains). Since dykes are sufficiently steep in Flanders, most beavers make burrows. So far at least three sites with burrows have been found in the dyke of the river Dijle and two on the river Demer. Lodges have only been built on two ponds along the river Dijle and lairs have been made in high bank vegetation, such as Japanese knotweed (*Fallopia japonica*) and butterbur. In Flanders most rivers are also sufficiently deep, so probably not many dams will be built. Only on the smaller tributaries is damming activity already taking place, often with the use of corn as building material. In some places dams have been removed by muskrat (*Ondatra zibethicus*) trappers employed by the Flemish government to prevent flooding, but they have immediately been rebuilt by the beavers. We know from experience that it is useless to remove a dam when the owners are still present, so in the future some problems with beavers are only likely to be solved by removing the animals. Another problem that is likely to arise is the interaction between efficient control of muskrats and coypus and the attempt to avoid unintended captures of beavers. Changing rat control methods will require more personnel and thus more money, and it is now up to the Flemish government to set their priorities.

If the Flemish government gives its approval, beavers in Flanders will be monitored intensively starting in 2004. A careful consideration of the pros and cons of beaver presence in Flanders, based on both a population viability analysis and a cost-benefit analysis, and taking all interest groups into account, will show whether or not the densely populated Flemish region is suitable for the development of a viable beaver population, and if so, at what costs.

Conclusion

By the end of 2004, we hope to have a better picture of what the presence of a beaver population in Flanders will mean in terms of extra costs for human activities that are considered important in Flanders, such as water management (e.g. repair of dykes, removal of fallen trees) and rat control (e.g. removing some traps during periods when there are young beavers around, using time-consuming live-traps). Up to now it has been rare to estimate in advance all costs associated with beaver reintroduction. This is probably due to the fact that most beaver reintroductions took place in countries where there are still large amounts of nature present, where interactions between beavers and humans are less obvious. Flanders however, is so densely populated by humans that one might expect many human-beaver conflicts. Hence preventive measures should be taken, not only to avoid hindrance to human activities but also to allow this native animal to regain its place in Flanders without being regarded negatively by humans.

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Samenvatting

De officieuze terugkomst van de Europese bever (*Castor fiber*) in Vlaanderen (België)

Na een lange tijd van afwezigheid, werden sinds de lente van 2000 opnieuw bevers (*Castor fiber*) gesignaleerd in Vlaanderen, eerst in Vlaams-Brabant en vanaf 2002 ook in Limburg. De bevers zijn afkomstig van de niet-officieel geïntroduceerde Waalse populatie. Met het oog op een toekomstige aanvulling van deze nog niet reproducerende Vlaamse beverpopulatie, liet AMINAL afdeling Natuur (Ministerie van de Vlaamse Gemeenschap) een haalbaarheidsstudie uitvoeren. De studie concludeerde dat er in het bekken van Schelde en Dijle ruimte is voor een levensvatbare beverpopulatie van minstens 40 families, die naar verwachting allemaal ter plaatse zouden blijven en geen problemen zouden veroorzaken. Nog vóór de Vlaamse overheid op basis hiervan kon beslissen om al dan niet verder te gaan met de voorbereiding van een officiële herintroductie, werden op 11 april 2003 twintig Beierse bevers van onbekende leeftijd en geslacht losgelaten langs de rivieren Dijle en Laan. Dit gebeurde op een niet-officiële wijze, zonder enige wetenschappelijke begeleiding en zonder voorbereiding of informatie naar de verschillende belangengroepen toe. Amper twee maanden later waren al minstens twee van deze dieren Leuven gepasseerd. Bevers zijn nu permanent aanwezig langs de Dijle en de Laan ten zuiden van Leuven. Beversporen zijn ook gevonden langs de IJse. Klachten van schade aan privé- en openbare eigendommen beginnen binnen te komen en aangepaste rattenbestrijdingsmethoden dringen zich op. Omdat in het dichtbevolkte Vlaanderen vele interacties kunnen worden verwacht tussen mens en bevers, is de ontwikkeling van een realistische visie op de toekomst van de bever in Vlaanderen noodzakelijk, waarbij rekening wordt gehouden met alle belangengroepen.

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The reintroduction and the present status of the beaver (*Castor fiber*) in the Netherlands: an overview

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Abstract: The beaver (*Castor fiber*) was reintroduced to the Netherlands in 1988, in the Biesbosch National Park. In the following years beavers were also introduced in several newly developed nature areas, including the Gelderse Poort, a natural area 100 km upstream from the Biesbosch. Fifteen years later, we see a steadily growing beaver population, living in a still expanding ecological network of traditional nature reserves and newly developed nature areas, especially along the rivers Rhine, Meuse and IJssel. The number of beavers in the Netherlands is estimated at about 200-250 individuals.

Keywords: core area, dispersal, ecological network, population, numbers.

Introduction

The beaver (*Castor fiber*) became extinct in the Netherlands, due to extensive hunting for its fur. Legend has it that the last beaver was killed by a fisherman in 1826; he mistook the beaver for an otter (*Lutra lutra*) trying to take fish from his nets and clubbed it to death (Belonje 1988). Sometimes a species will return on its own accord, when habitat conditions improve. This was impossible for the beaver as the nearest core population of beavers is in the river Elbe (Sachsen-Anhalt) in Germany. Reintroduction was the only possibility to get the beaver back in the Netherlands.

The discussion on the reintroduction of the beaver started in the early 1950s. The main argument in favour of reintroduction was that hunting had been responsible for the extinction of the beaver. Good quality habitats were still to be found in several parts of the country, for example in the Weerribben and the Biesbosch (van Wijngaarden 1959).

In 1985 the Dutch Government officially granted permission to reintroduce the beaver in the Biesbosch National Park. Permission was granted for a five-year period, under the condition that this reintroduction should be surveyed intensively. Farmer organisations were strongly opposed to this experiment due to bad experience with the muskrat (*Ondatra zibethicus*) which caused a lot of damage by burrowing holes in dikes (van der Ouderaa 1984).

Over a period of three years (1988-1991) a total of 42 beavers from the Elbe region were released in the Biesbosch. Niewold and Lammertsma (2000) considered the reintroduction a success. The beaver had again become an indigenous species and was added to the ‘Red List of endangered and vulnerable species’ (c.f. Lina & van Ommering 1994), i.e. as a vulnerable species. The beaver was also legally protected in the same year by the ‘Natuurbeschermingswet’ – the Nature Conservation Act (Lina & van Ommering 1994). This article presents an overview of the developments in the Biesbosch in the years after 1994, as well as other (re-)introductions and developments of beaver populations in the Netherlands.

The beaver in National Park the Biesbosch: from start to present

The Biesbosch area was once part of the beaver’s historical range (van Wijngaarden 1966). The area still satisfies the habitat and landscape requirements of the beaver and is expected to continue to do so in the foreseeable future (van Wijngaarden 1966). The Biesbosch is large enough, and of good enough quality, to provide a natural habitat for a viable and free ranging population.

Data on dispersion are rare. The first beaver known to migrate was in 1995. This individual drifted some 65 km downstream of the Biesbosch and built a lodge in a small nature reserve near Rhoon. In 1998 and 1999 beavers were also observed upstream near Stolwijk and the Kil van Hurwenen (figure 1). In 1996 an adult beaver, with the same earmarks used in the Gelderse Poort (see next section) was seen close to the Biesbosch. This could be the first case of immigration into the Biesbosch (Niewold & Lammertsma 2000).

In the first years following reintroduction only 31% of the adult pairs had young. In 1994 this figure had risen to 57%, though it fell again in 1999 to only 40% (Nolet 1994, Niewold & Lammertsma 2000, Dijkstra 2001). The percentage of adult pairs with young is somewhat lower than populations in Norway (Rosell et al. (1998) give 50%) and the same as the population in Sachsen-Anhalt in Germany (Heidecke & Langer 1998).

The territories of the beaver in the Biesbosch National Park are vast. Their winter territory consists of approximately twelve kilometres of banks, three kilometres of which are overgrown with willows and other trees and bushes (Rosell & Nolet 1997). A territory is occupied by a family group with an average of 2.9 adult and young beavers (Niewold & Lammertsma 2000).

Taking all the data on reproduction, mortality and dispersion into account, we see an annual growth of 7% in the beaver population in the Biesbosch during the period 1988-2001 (Dijkstra 2002).

In 1993 a minimum viable population analysis (Nolet 1993) indicated that in the short term (20 years) the chance of extinction was 20%. Over

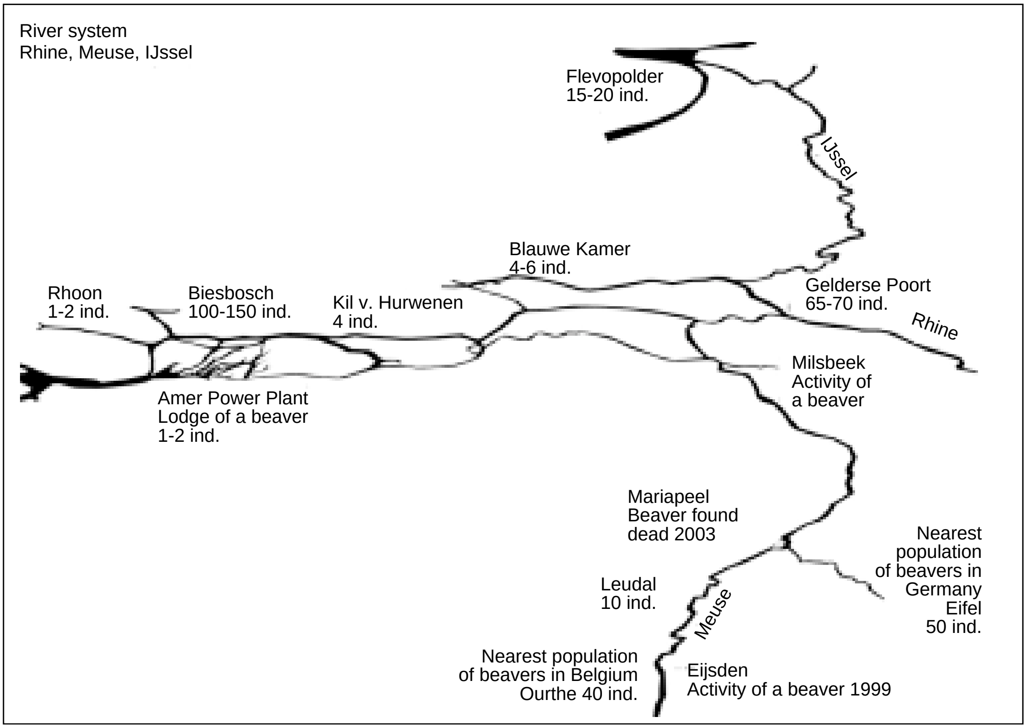

Figure 1. Distribution of beavers in the Netherlands in 2003.

the long term (100 years) the population of beaver was at greater risk, with a 60% chance of extinction. For the time being, Staatsbosbeheer (the Dutch Forestry Commission) is optimistic about the viability of the beaver population in the Biesbosch. Fourty-five lodges were counted in 2002 and, in 2003 sixteen new lodges appeared. The number of beavers in the Biesbosch is now estimated at between 100-150 individuals. From the Brabantse Biesbosch the beaver now colonises parts of the national park on the opposite side of the Nieuwe Merwede (i.e. the Dordtse and Sliedrechtse Biesbosch). The beaver also colonises the area with willow coppices (so-called “grienden”) downstream, along the Hollands Diep and the Oude Maas. Using newly developed nature areas along the rivers upstream as stepping stones, beavers from the Biesbosch should be able to migrate to other core areas, for example the Gelderse Poort population, and vice versa.

The Gelderse Poort: a second core population

The reasonably successful development of the beaver population in the Biesbosch paved the way for the reintroduction of the beaver in the Gelderse Poort, approximately 100 km upstream of the Biesbosch. A study of the results in the Biesbosch (Niewold 1995) was used for the reintroduction of beavers in the Gelderse Poort.

In this recently developed nature reserve, a total of 54 beavers were released in 1994 (figure 1). Losses were high (51%) during the reintroduction period. In March 2000 it was estimated that 37 beavers lived in the Gelderse Poort (Niewold & Müskens 2000a). A similarly high mortality was also found in the Biesbosch in the first years (BHB 1994). In 2000 the mor-tality rate was less than 10% (J. Rouwenhorst, personal communication).

In the period between reintroduction in 1994 and the year 2000, 20 young have been raised. At present, there are 65-70 beavers in the Gelderse Poort. This area has a great potential as habitat for the beaver. According to carrying capacity calculations from Niewold & Müs-kens (2000b) the beaver population in the Gelderse Poort could grow to 210 individuals. This model also indicates that, even with 15 individuals, the beaver population in the Gelderse Poort is out of the danger zone, Staatsbosbeheer still closely monitors the development of numbers. Annual counts over the whole area should continue to give insights into the growth of the population.

Recently an appeal has been made for robust natural rivers in the Netherlands (Anonymous 2003): rivers that have sufficient capacity to retain water in dry periods, to store it in wet periods and at the same time offer species such as the beaver the ecological network they require. At present the country accommodates two strong core beaver populations, in the Biesbosch and the Gelderse Poort. The beaver has the potential to spread from these core areas over the entire river system (see figure 1). In the near future, one could envisage not two separate core populations but one in which beavers have access to the entire river area.

The Leudal: an important stepping-stone in the Meuse estuary

Beavers have been observed over a longer period in the tributaries and streams of the Meuse (Kurstjens 2003). They probably originated from the Eifel in Germany. At the initiative of Province Limburg, at least ten beavers were released along the Meuse in 2002. Half of these animals were released in the Leudal (figure 1). The existing nature reserves and nature development areas along the Meuse form a potential habitat for beavers. Despite the fact that there are core populations of the beaver across the border in Belgium (Ourthe) and Germany (Eifel), Province Limburg was of the opinion that the beaver needed a helping hand to colonise these new nature areas.

Other locations in the Rhine and Meuse estuary and elsewhere

Very different from the reintroduction programme is the development of some small beaver populations along the rivers Rhine, Meuse and IJssel (figure 1). For example, some individuals from the Biesbosch population colonised small nature areas along the river, approximately 10 km from the core population. They now live there in newly made lodges and may have young in the near future.

Following the escape of a sub-adult beaver from the zoo “Dierenpark Ouwehand”, one subadult settled some kilometres further away in the Blauwe Kamer (figure 1); presumably the escaped individual. The next winter this beaver remained in this nature reserve. Apart from the development in the river estuary in the Netherlands, some isolated observations have also been made. In the Mariapeel a beaver was found dead. This individual probably used small ditches and canals to reach the Mariapeel, which is approximately 10 km from the Meuse. In Flevoland a small group of beavers escaped from a zoo and had young in the forests and swamps of the Oostvaardersplassen. This population is now estimated at 15-20 individuals (figure 1).

Conclusion

Fifteen years after the reintroduction of the beaver in the Netherlands its population and distribution are both still growing. Beavers are now living in an ecological network of traditional nature reserves and newly developed nature areas along the rivers Rhine, Meuse and IJssel. There are now two core populations: in the Biesbosch and the Gelderse Poort. It is likely that in the near future contact will be established between the Dutch beaver population and the core populations in Belgium and Germany. The number of beavers in the Netherlands in 2003 is estimated at 200-250 individuals (see table 1 and also figure 1).

Table 1. Estimated number of beavers in the Netherlands in 2003.

Location	Number
Biesbosch	100-150
Gelderse Poort	65-70
Leudal	10
Flevopolder	15-20
Blauwe Kamer	4-6
Kil van Hurwenen	4
Rhoon	1-2
Total	200-250

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Samenvatting

De herintroductie en de tegenwoordige status van de bever (*Castor fiber*) in Nederland: een overzicht

De bever (*Castor fiber*) werd in Nederland in 1988 geherintroduceerd in het Nationale Park de Biesbosch. In de navolgende jaren zijn er ook bevers uitgezet in verschillende natuurontwikklingsgebieden, waaronder de Gelderse Poort, een gebied met veel natuurterreinen, 100 km stroomopwaarts gelegen van de Biesbosch. Op dit moment, 15 jaar na de eerste herintroductie, is er sprake van een gestaag groeiende beverpopulatie binnen een zich nog steeds uitbreidend ecologisch netwerk bestaande uit 'oude' natuurgebieden en recent tot ontwikkeling komende natuurgebieden, met name langs de Rijn, de IJssel en de Maas. Het totale aantal omstreeks 2003 in Nederland voorkomende bevers wordt geschat op 200-250 individuen.

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The beaver (*Castor fiber*) in Flevoland, The Netherlands

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Abstract: Thirteen years after an unintended introduction, there is a growing beaver (*Castor fiber*) population in the province of Flevoland, The Netherlands. The population was estimated to be at least 15 animals in 2003. It is assumed that the number of potential settlements is the limiting factor for the beaver population in Flevoland. At three locations in the canal Hoge Vaart, an opening in the sheet-pile walls was made to allow beavers to build a lodge behind these concrete canal bank stabilization measures. These actions illustrate the positive attention the beaver currently receives from the administration of the province.

Keywords: beaver, *Castor fiber*, Flevoland, bank construction.

History

After more than 150 years of absence, the successful reintroduction of the beaver (*Castor fiber*) in the Netherlands has been a fact for over a decade now. Forty-two beavers of Elbe origin (Germany) were reintroduced in the Biesbosch in the period 1988-1991 (Nolet 1993). To guarantee additional animals to strengthen the reintroduced population and to give people the opportunity to meet this new Dutch species, a breeding group of beavers was started in Nature Park Lelystad.

Nature Park Lelystad is located in the province of Flevoland. It is a wildlife park where threatened European mammals and birds are bred for reintroduction purposes. There are, for example, breeding groups of red deer (*Cervus elaphus*), otter (*Lutra lutra*), European bison (*Bison bonasus*) and white stork (*Ciconia ciconia*). The park is open to visitors. In 1988 two beavers arrived at Nature Park Lelystad from the Elbe-region (Germany). The animals were kept in a fenced-in semi-natural area. Soon after their arrival, two other beavers from the Elbe-region were brought into another fenced area.

In December 1990 the first successful escape was a fact: one of the first beavers was found swimming in a nearby pond. Armed with brooms, the park guards could force the beaver back into the park. A few days later, however, a gnawed tree again marked the escape of one or more beavers from the park. These animals started a successful but unintended introduction of beavers in Flevoland.

Population development

Thirteen years after the first beavers escaped from Nature Park Lelystad, the population is still free-living and growing. Since 1999, a census is carried out yearly by volunteers of the Landscape Management Foundation Flevoland (LBF) and members of the Dutch Society for the Study and Conservation of Mammals (VZZ). Every February new as well as known lodges are visited to determine if lodges are still used by beavers and to assess the best locations for a population count in the summer. At one night in June and one night in July beavers are counted near the lodges from 8-11 pm. Both young, subadult and adult beavers at each lodge are registered. The maximum of both counts is seen as a minimum estimate of the number of beavers per lodge for each age category.

The minimum number of beavers in Flevoland increased from 11 in 2000 to 15 in 2003 (Van der

Photo 1. Typical canal in Flevoland with a bank construction of sheet-pile walls. *Photograph: Jeroen Reinhold.*

Bend & Reinhold 2003; figure 1). Supplementary counts showed that the volunteers miss animals during their counts. The actual population in Flevoland in 2003 is therefore assumed to be larger, i.e. about 30 animals.

Adapted canal banks

The province of Flevoland was formerly part of Lake IJssel. The land was reclaimed in the period 1942-1966. Villages, waterways, nature

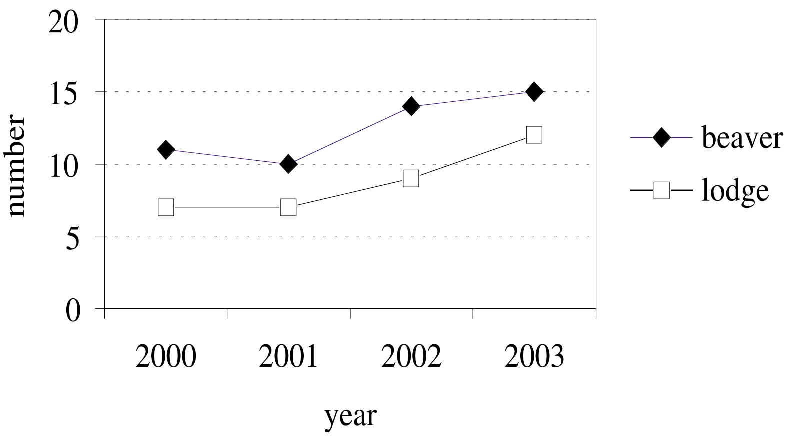

Figure 1. The number of beaver lodges and the minimum number of beavers counted in 2000-2003 in the province of Flevoland, The Netherlands.

areas, and agriculture in this province are all strictly planned. Large natural areas were planned at the borders of the province. The central part is mainly agricultural land. Large canals were made to transport water out or into the province. Canal banks had no ecological function and were mainly constructed of concrete sheet-pile walls (photo 1).

These canals potentially interconnect important nature areas; a function considered of no importance 50 years ago. Nowadays, ecologists and the government see the canals as ecological 'highways' for migrating animals. The beaver is one of the species that profit from these ecological corridors. The beaver dispersed in Flevoland from Nature Park Lelystad to other parts of the province, mainly in the western and southern parts of the island, using large canals as corridors. Five out of seven lodges outside Nature Park Lelystad are situated close to one of the main canals (figure 2). Because of the bank construction used, beavers seldom use the canals themselves to build lodges. It is assumed that the number of potential areas for settlements is the limiting factor for the beaver population in Flevoland.

Fortunately, the Flevoland administration, who owns the canals, has planned to replace the mono-functional sheet-piles into a multi-functional bank construction with passage possibilities for animals like beaver. In 2002, the Flevoland administration seeked advice by LBF to alter the canal banks of concrete sheet-piles into a beaver-friendly bank enabling beavers to build lodges (Reinhold 2002). In 2003 the advised construction was made at three locations in the canal Hoge Vaart (photo 2). Sheet-pile walls with a total width of 1 m were pushed 0.5 m under the water surface, and behind these walls a beaver pool of 5x5 m with a depth of 0.75 m was made. One of the banks in the pool has a steep slope, next to which a willow was planted.

Photo 2. An adapted bank construction with possibilities for beavers to build a lodge. *Photograph: Jeroen Reinhold.*

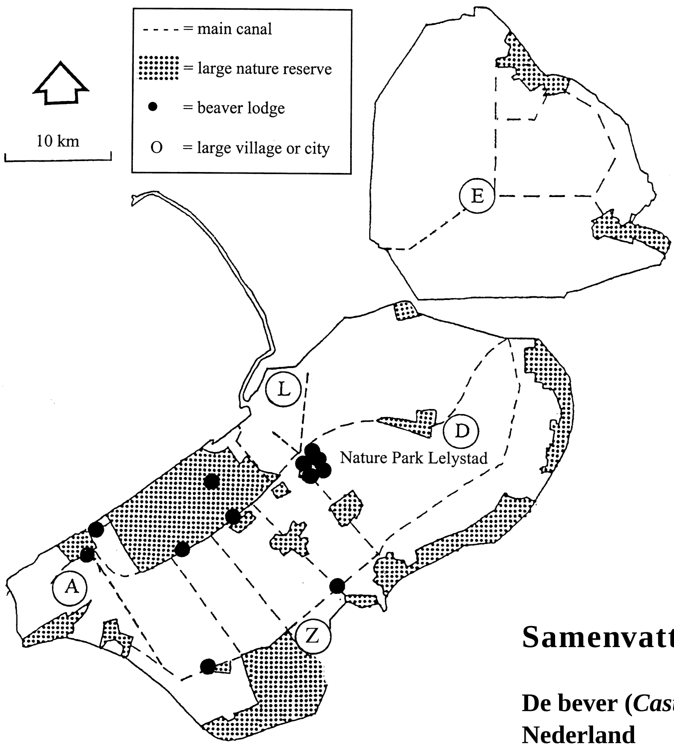

Figure 2. The locations of beaver lodges in relation to the locations of nature areas and main waterways in Flevoland (2003). The letters indicate large villages or cities: A = Almere; D = Dronten; E = Emmeloord; L = Lelystad; Z = Zeewolde.

The willow stabilizes the bank and is expected to provide shelter to beaver. Future surveys will show if and when the beavers start using these bank constructions.

Acknowledgements: I would like to thank all volunteers who count the beavers in Flevoland, the Nationale Postcodeloterij for their financial support, and the administration of Flevoland for the realization of the beaver-friendly canal banks. Furthermore, I thank two anonymous referees. Their useful comments helped improve the paper.

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Samenvatting

De bever (*Castor fiber*) in Flevoland, Nederland

Dertien jaar na een succesvolle ontsnapping uit Natuurpark Lelystad is de populatie bevers (*Castor fiber*) in Flevoland gestaag gegroeid. Vrijwilligers van Landschapsbeheer Flevoland en de Beverwerkgroep Nederland van de Vereniging voor Zoogdierkunde en Zoogdierbescherming tellen jaarlijks het minimum aantal dieren per burcht. In 2003 werden 15 dieren geteld. Het werkelijke aantal ligt hoger en wordt geschat op circa 30 dieren. Uitbreiding van de populatie wordt waarschijnlijk beperkt door het aantal plekken waar burchten gegraven kunnen worden. De Provincie Flevoland heeft daarom in 2003 op een drietal plaatsen langs de Hoge Vaart bevervriendelijke oevers aangelegd, die bevers de mogelijkheid bieden om achter de oeverbeschoeiing van het kanaal een burcht te graven. Daarmee nemen de vestigingsmogelijkheden voor de bever in Flevoland toe.

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Food caching behaviour of the American beaver in Massachusetts

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Abstract: At northern latitudes in North America beavers (*Castor canadensis*) store branches of woody plants in caches during the autumn. The food cache provides food for the beaver family during the winter when plant productivity is low and snow and ice restrict beaver movements. I examined the initiation and development of food caches and physical aspects of food cache locations at eight sites during autumn 2001 and autumn 2002 in western Massachusetts. Construction of caches began on September 28 (week 39) in 2001 and September 18 (week 38) in 2002. Median start date for caches was during week 41 (October 9-10) both years. Mean cache volume was 60.4 m^3 in 2001 and 72.1 m^3 in 2002. Change per week in cache volume was 8.9 m^3 in 2001 and 9.2 m^3 in 2002. Water depths where caches were constructed ranged from 1.00-2.05 m (mean = 1.31 m) during 2001 and 0.75-1.85 m (mean = 1.26 m) during 2002. These observations of caching behaviour in the American beaver offer a means of comparison with the caching behaviour of the European beaver (*Castor fiber*).

Keywords: American beaver, *Castor canadensis*, food caching, initiation date, temporal change, environmental cues.

Introduction

Both species of beaver, the American beaver (*Castor canadensis*) and the European beaver (*Castor fiber*), are choosy generalist herbivores and at northern latitudes and high elevations (regardless of latitude) they are long term food cachers who engage in communal food caching (Jenkins 1975, Vander Wall 1990). Food caches are initiated in the autumn and branches of woody species are placed in the water usually near the winter lodge (Novakowski 1967, Aleksiuk 1970, Slough 1978, Busher 1991). Evidence exists that the two species are different in the construction of caches and that the cause may be related to environmental factors (Hartman & Axelsson, in press). North American beavers living in areas that are not subject to long periods of cold when the ponds freeze may not built food caches (Hill 1982, Echternach & Rose 1987). However, in areas where freezing of the ponds is common 100 percent of beaver families do construct a cache (Yeager & Rutherford 1957, Busher 1991, Busher 1996).

While species composition and location in a cache have been examined (Slough 1978, Busher 1991) no present study has fully documented the temporal development of the food cache. In this paper I report the development of food caches during the autumn comparing both intrafamily and interfamily behaviours. I designed the study to test the hypothesis that food caching behaviour will intensify as the autumn progresses. Specifically, once food caching is initiated (late September to early October) the beaver families should store food at a lower rate early in the autumn and increase their hoarding activity in late autumn (November). This hypothesis is reasonable since the food cache represents the primary food source during the energetically stressful period of cold and restricted movement in winter. Food caching behaviour may be tied to environmental cues such as air temperature, which in turn would influence water temperature. Increasing hoarding behaviour in response to increasing cold may represent an evolutionary strategy ensuring an adequate, high quality food supply for the winter. An inadequate food supply could cause reduced reproduction and increased mortality, which would reduce fitness.

Methods

Study Area

Research was conducted on the Prescott Peninsula, Quabbin Reservation, located in west-central Massachusetts (42° 25' N, 72° 20' W) (figure 1). The Quabbin Reservation, which contains the watershed and major reservoir for the drinking water supply for the metropolitan Boston area, was created in 1939 by damming the Swift River and Beaver Brook. The reservation's area is 335 km^2 and the reservoir is 100 km^2. The climate consists of warm, usually moist summers and cold winters with major periods of snow. The construction of the reservoir and creation of the watershed area caused the relocation of 2500 people and the complete destruction of three towns (Hodgdon 1978, Lyons 1996). The reservoir was filled to maximum capacity by 1946. The Prescott Peninsula has an area of 50 km^2, is 16 km long and narrows from north to south (4.8 km to 0.6 km). The peninsula is heavily forested (approximately 92%) with dominant deciduous trees being red maple (*Acer rubrum*), oak (*Quercus* spp.), ash (*Fraxinus* spp.), and birch (*Betula* spp.). Eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and hemlock (*Tsuga canadensis*) are the most common conifers on the peninsula (Hodgdon 1978).

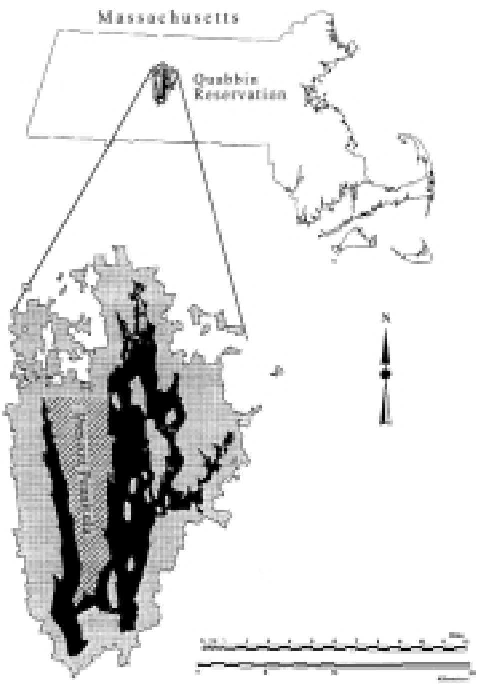

Figure 1. Location of the Quabbin Reservation, Massachusetts, USA. The research site is approximately 130 km (80 miles) west of Boston, Massachusetts.

The Quabbin Reservation is managed as a watershed by the Metropolitan District Commission (MDC); an agency of the Commonwealth of Massachusetts. In addition to serving as the water supply for approximately 3 million people in eastern Massachusetts, the reservation provides forest products, recreational opportunities, wildlife observation and research, and cultural resource protection. One of the unique features of the watershed and reservoir is that human use has been strictly controlled since its inception. Until recently, there has been a complete prohibition of trapping and hunting of all wildlife species on the reservation and, especially on the Prescott Peninsula, wildlife populations have been allowed to exist with little human interference. Beavers on the Prescott Peninsula are found on small streams, larger streams, ponds and along the shore of the reservoir.

Food cache analysis

In the autumn of 2001 a random sample of known active beaver family areas was selected for study. Eight beaver family areas were surveyed each year and six of the eight areas were occupied both years. Two areas active in 2001 were not active in 2002 and two additional sites were selected that year. The number of family areas surveyed each year represented 38% (8/21) of the known active interior (non-shoreline) areas in 2001 and 40% (8/20) of the known active areas in 2002. One family did not initiate cache building until very late in the season (week 47) in 2001 and is not included in the analysis. The number of known active areas was determined by an annual census, which used presence of a food cache as one of the primary criteria in determining beaver occupation. Beavers in every active family area on the Prescott Peninsula build a food cache each year.

Beginning in early September (week 36) and continuing through November (week 48) of 2001 and 2002 each family area was surveyed. Once the initiation of a food cache was observed the length, width and height (both above and below the water line) were measured weekly. The depth of the water where the cache was located was measured at the center of the cache (approximately 2 m from the shore). As the cache grew in size a number of depth measurements were taken at each cache and the mean depth was used to calculate the volume. Woody species composition in the cache was also documented. Woody species composition in the cache is not reported in this paper because the species composition did not influence the study design or general hypothesis being tested and simply reflected the abundance of woody species found in each family area. I report mean minimum daily and weekly air temperatures that were collected at the Harvard Forest, Petersham, MA, USA (Lat. 42.533 N, Lon. 72.190 W, Elev. 340 m). This site is approximately 12 km from the research area with a similar habitat and elevation.

Results

Cache initiation date

The first food cache was observed in week 39 (September 28) in 2001 and week 38 (September 18) in 2002. Five of the eight families initiated their cache by week 41 (October 10) and all caches were initiated by week 44 (the end of October) during both years. A different family initiated the earliest cache each year and each of the six families surveyed both years initiated their cache during a different week (figure 2).

Cache development

In 2001 the mean change in cache volume per week was 10.5 m^3 (range = 5.3-14.6 m^3) for 7 families. In 2002 the mean change in cache volume per week was 11.2 m^3 (range = 4.6-21.3 m^3) for 8 families. Beginning in late October or early November (week 43-44) a general pattern of increased cache building behaviour was observed although this was more pronounced in 2001 than 2002 (figure 3 and figure 4). The change in food cache volume stored by each family was then compared for two temporal periods, October and November, of each year. In 2001 a greater average change in cache volume during November was observed in all seven families, but the difference was only significant in two families, FF and R21 (*Chi-square* with Yates correction = 4.61, df=1, P<0.05 at area FF; *Chi-square* with Yates correction = 6.45, df=1, P<0.025 at area R21). A different pattern was observed in 2002 when only five of the eight families had greater cache volume changes in November than in October. However, only one of these families had a significantly greater mean change in cache volume (*Chi-square* with Yates correction = 7.49, df=1, P<0.01). Three of the families had a greater mean change in volume during October than November and two of these were significantly different. Beavers at area R21 had a significantly larger mean change in volume in October than November (*Chi-square* with Yates correction = 8.58, df=1, P<0.01). This was also true for beavers at area K where the mean volume change was greater in October than November (*Chi-square* with Yates correction = 7.13, df=1, P<0.01). Cache construction began during week 44 in both of these families and the initial volume of each cache was larger than caches began in September or early October. One additional family had a larger mean volume change in October than November but the difference was not significant.

The initial cache volume was dependent on the week of initiation. In general caches initiated early in the autumn were smaller than caches initiated later in autumn. This pattern was

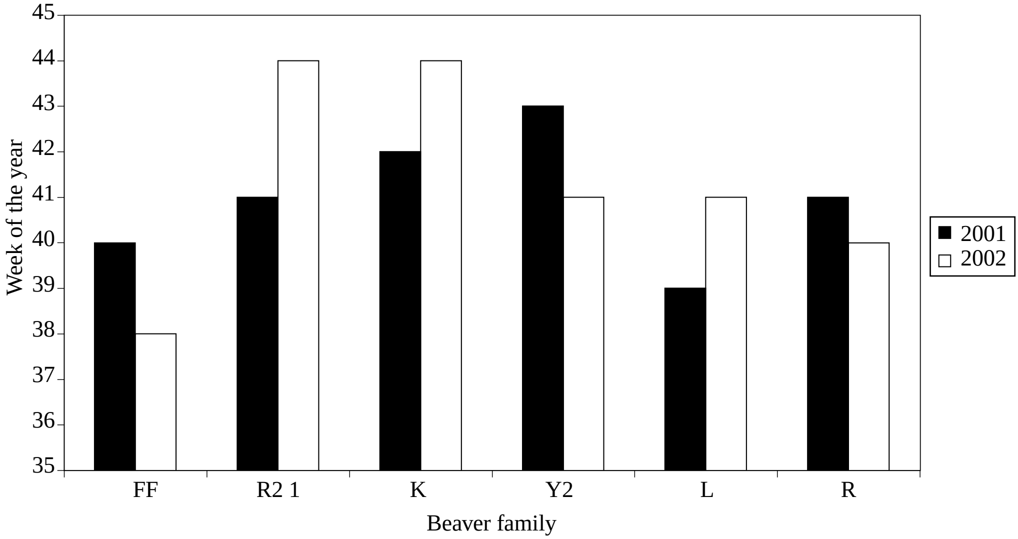

Figure 2. Yearly food cache initiation dates for the six beaver families observed both years. Weeks 38-39 are in September, weeks 40-43 in October and weeks 44-45 in November.

especially pronounced in 2002 when three of the eight families initiated caches during week 44 while the other five families had all initiated caches by week 41. The mean volume of caches initiated early in autumn 2002 was 4.9 m^3 (range 2.3-10.5 m^3) while the mean volume of caches initiated during week 44 was 25.3 m^3 (range 17.3-38.6 m^3) and this difference was significant (*Chi-square* with Yates correction = 12.5, df=1, P<0.01). This pattern is not as pronounced in 2001 since no caches were initiated late in October.

The total volume of all food caches was not significantly different in 2001 and 2002. The total volume in 2001 was 510.4 m^3 and in 2002 it was 576.5 m^3. A similar pattern in total volume change per week was observed each year. October volumes were larger during 2001 while November volumes were larger in 2002. The total change in volume of all caches in October was 202.3 m^3 in 2001 and 254.3 m^3 in 2002. The change in November was 289.9 m^3 in 2001 and 316.8 m^3 in 2002. These data are significantly different from each other in both years (*Chi-square* with Yates correction = 15.23, df=1, P<0.01 in 2001; *Chi-square* = 6.64, df=1, P=0.01 in 2002). The mean final volume of caches in 2001 was 72.9 m^3 (range = 41.6-105.4) and 72.1 m^3 (range = 34.0-153.8 m^3) in 2002.

Water depth at cache

The water depth at the center of each cache was measured multiple times during the autumn. No weekly variation in depth was observed. The mean depth of all caches in 2001 was 1.30 m (range = 1.00-2.05 m) and the mean depth in 2002 was 1.26 m (range = 0.75-1.85). There was no relationship between the water depth and final cache volume.

Air temperature and food caching behaviour

In both years there was a significant inverse correlation between the mean weekly minimum air temperature and the mean weekly change in volume of the food cache per family (r^2=0.47, F=6.2, df=1 and 7, P<0.05 in 2001; r^2=0.53, F=8.0, df=1 and 7, P<0.05 in 2002). The mean weekly minimum temperature was slightly lower in 2001 than in 2002 from weeks 38 to 41 (8.3 °C in 2001 vs. 10.4 °C in 2002) but higher from

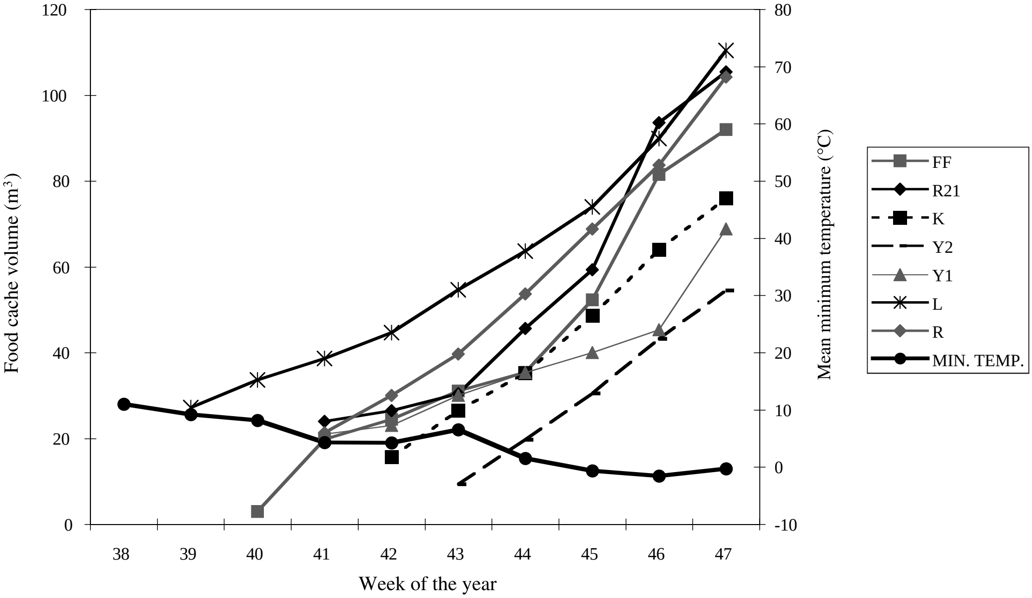

Figure 3. Weekly change in food cache volume for seven beaver families in 2001 and the mean weekly minimum temperature (°C). Weeks 38-39 are in September, weeks 40-43 in October and weeks 44-47 in November. The legend codes refer to the individual beaver families on the annual census routes (for example, FF is one family, R21 is a second family, etc.) and Min. Temp. is the mean weekly minimum temperature (°C).

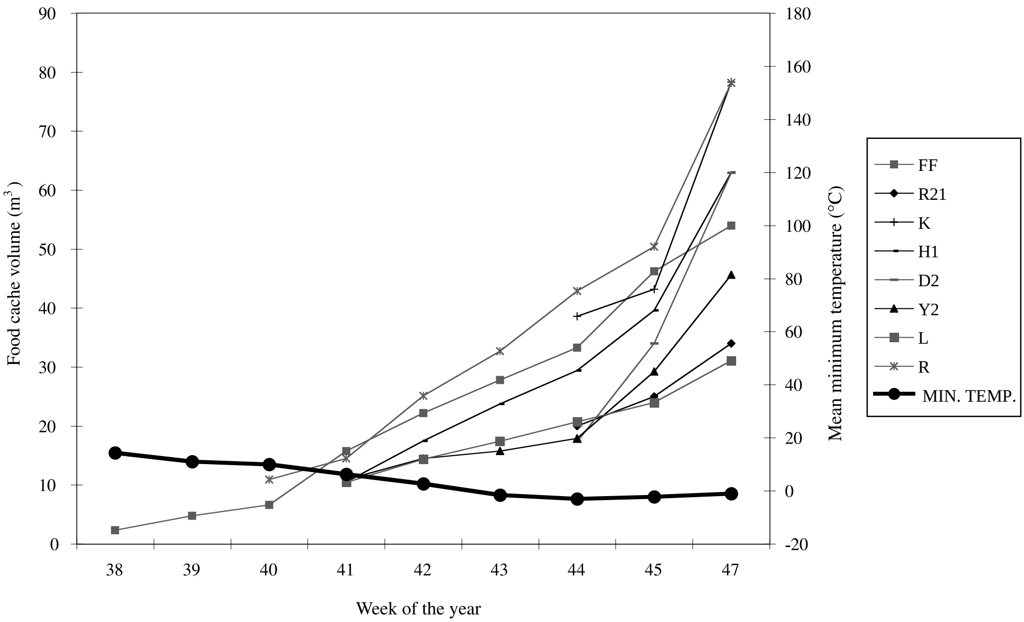

Figure 4. Weekly change in food cache volume for eight beaver families in 2002 and the mean weekly minimum temperature (°C). Weeks 38-39 are in September, weeks 40-43 in October and weeks 44-47 in November. The legend codes refer to the individual beaver families on the annual census routes (for example, FF is one family, R21 is a second family, etc.) and Min. Temp. is the mean weekly minimum temperature (°C).

weeks 42 to 45 (2.9 °C in 2001 vs. -0.9 °C in 2002). In week 46 it was cooler during 2001 (-1.6 °C) than in 2002 (4.1 °C), but then warmer the following week (-0.3 °C in 2001 vs. -1.1 °C in 2002). Although it was slightly warmer during early autumn in 2002, the first food cache was initiated a week earlier than in 2001 (figure 5). However, two caches were initiated during each year from weeks 38-40. The weekly mean minimum temperature during week 41, the week the median number of food caches were initiated (5 of 8 caches were initiated by week 41 each year), was 4.3 °C in 2001 and 6.2 °C in 2002. The first hard frost (minimum air temperature below freezing) occurred during week 41 (3 days with a minimum temperature below freezing) in 2001, but not until week 42 in 2002. In 2001 the weekly mean minimum temperature remained above freezing through week 44 (time when all food caches were initiated) while in 2002 the weekly mean temperature dropped to -1.6 °C during week 43 and -3.0 °C in week 44. Three families initiated their food caches during week 44 in 2002 (figure 5).

There is an inverse relationship between increasing food cache volume and mean minimum air temperature (figures 3 and 4) during both years. Only October of 2002 had a significant correlation between the mean weekly minimum temperature and the mean weekly change in food cache volume per family (r^2=0.68, F=8.62, df=1 and 4, P<0.05). There was no significant correlation for October 2001, November 2001 and November 2002.

Discussion

The cache initiation patterns observed were consistent with data collected on the Prescott Peninsula during 1972-1973. The earliest initiation date in 1972-1973 was week 38, the median date was week 41 and the latest initiation date was week 43 (Hodgdon 1978). These initiation dates are similar with my observations of week 37, week 41 and week 44 for the earliest, median and latest initiation dates. Hodgdon (1978) suggested that peak cache initiation activity was stimulated by the first hard frost. This is also true for 2001 in my study where the median initiation date (week 41) occurred after the first frost. However, in 2002 the first hard frost occurred during week 42 yet 5 of 8 caches were initiated by week 41. In Sweden, caches were first initiated in week 38, week 43 was the median date and week 48 the last date of initiation (Hartman & Axelsson, in press). The climate in the study area in Sweden is similar to that in central Massachusetts with both areas recording mean minimum temperatures below freezing in mid-October (G. Hartman, personal communication) and there is reasonable agreement between initiation dates. However, the variation in initiation dates within the same family group between years and the overall variation in initiation dates within a population suggest a plasticity of cache initiation behaviour. Additionally, I have only examined the mean minimum air temperatures and these are from a weather station approximately 12 km from the research site. In future years I plan to collect air and water temperatures at the family areas being studied and hope to be able to examine the relationship between food caching behaviour and temperature with more precision. Further investigation of the actual environmental cues that may trigger cache construction in both beaver species is necessary.

The only other study to report cache development patterns similar to this study is from a relatively high elevation (2300-2500 m) population in Wyoming (Osmundson & Buskirk 1993). They reported that cache growth rates and final cache sizes did not deviate between years, comparable to my observations in Massachusetts. Cache growth rates in Wyoming were 0.45 m^3 per day or 3.15 m^3 per week (0.45 m^3 x 7 days). No temporal change in cache growth rates was reported. In Massachusetts, the mean weekly growth rates were larger each year (10.5 m^3 and 11.2 m^3) and even the lowest mean changes for a specific family were larger (5.3 m^3 in 2001; 4.6 m^3 in 2002). Cache construction effectively stopped earlier in

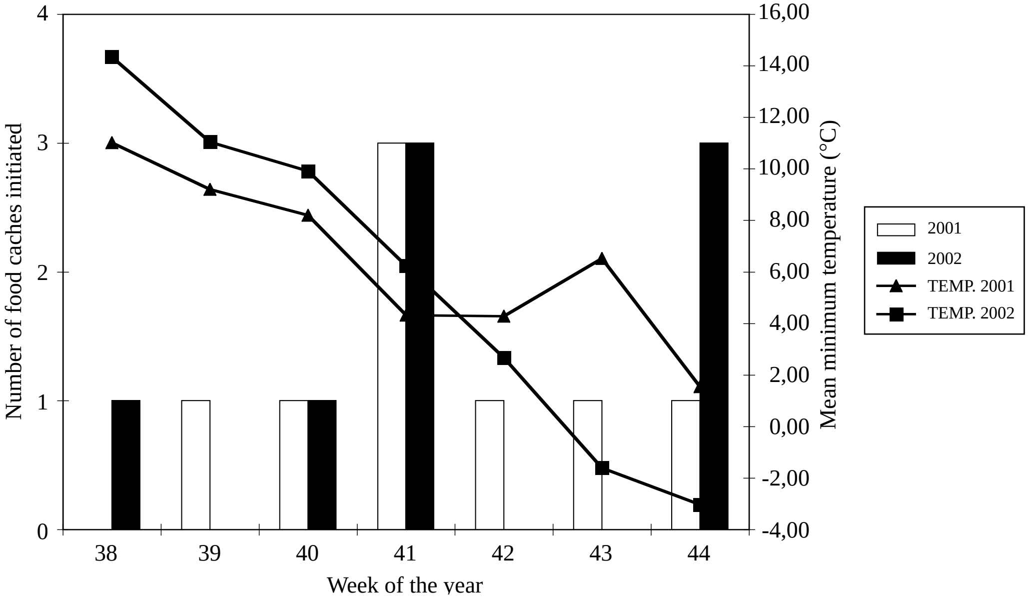

Figure 5. The number of food caches initiated each week and the mean weekly minimum temperature (°C) for 2001 and 2002. Weeks 38-39 are in September, weeks 40-43 in October and week 44 in November. Min. Temp. in the legend is the mean weekly minimum temperature (°C).

Wyoming when freeze up was reported between November 1-11. This is at least 2-3 weeks if not 4-5 weeks earlier than normal freeze up in Massachusetts.

No correlation between family size and cache size was found in Wyoming (Osmundson & Buskirk 1993) although a correlation between cache size and family size had been reported in Montana (Easter-Pilcher 1990). Family size in Massachusetts was estimated to range from 2-6 and no clear pattern was evident between final cache size and family size. However, additional data are required to adequately resolve the relationship between family size and finite cache size. Additionally, age of family members and actual time beaver are dependent on the cache for food may play a role in the cache construction behaviour.

Further investigations into food cache construction behaviour, including field experiments on species selection and nutrient evaluation of the stored food will provide better understanding of this critical aspect of beaver life history. Additionally, since beavers exhibit individual and family variability in many behaviours the observed variability in cache construction behaviour, both within and between populations, may reflect the overall behavioural plasticity that has evolved in both beaver species.

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Samenvatting

Aanleg van voedselvoorraden door de Amerikaanse bever (*Castor canadensis*) in Massachusetts

In de noordelijke delen van Noord-Amerika leggen bevers (*Castor canadensis*) in de herfst voorraden aan. Deze bestaan uit takken van houtachtige gewassen, en dienen als voedselvoorziening voor groepen bevers tijdens de winter. In die tijd is er moeilijk aan voedsel te komen vanwege de afwezigheid van plantengroei en omdat de actieradius van bevers wordt beperkt door sneeuw en ijs. In het westen van Massachusetts werd in de herfst van 2001 en 2002 onderzoek gedaan naar de fysieke omstandigheden van acht verschillende locaties waar voorraden werden aangelegd. De bouw van opslagplaatsen voor voedselvoorraden begon op 28 september in 2001 en op 18 september in 2002, de aanleg van voorraden zelf op 9-10 oktober in beide jaren. Het gemiddelde volume van de voorraden bedroeg 60,4 m^3 in 2001 en 72,1 m^3 in 2002. De verschillen in volume per week bedroegen 8,9 m^3 in 2001 en 9,2 m^3 in 2002. De diepte van het water waar voorraden werden aangelegd lag tussen 1,00 en de 2,05 m (gemiddeld 1,31 m) in 2001 en 0,75-1,85 m (gemiddeld 1,26 m) in 2002. De in dit artikel beschreven observaties kunnen worden gebruikt voor een vergelijking met het gedrag van de Europese bever (*Castor fiber*).

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Adaptation of beavers (*Castor fiber*) to extreme water level fluctuations and ecological implications

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Abstract: We have observed how beavers (*Castor fiber*) cope with water fluctuations in the Millingerwaard, part of the Gelderse Poort, a floodplain system of the river Rhine in the Netherlands. Beavers were introduced here in the mid 1990s. After severe losses in the first years the population grew gradually, up to about 60 animals in 2004. The narrow floodplain causes extreme fluctuations in water levels, normally between 6-7 m on an annual basis. During a series of floods in the 1990s it was observed that the beavers could cope with these fluctuations, constructing special lodges on higher ground within a few days. During the extreme dry summer of 2003 most beaver habitat in the Millingerwaard dried up completely. The beavers constructed burrows in the banks of a sand pit as safe homes to survive the drought. These events show that beavers readily adapt to periods of extreme flooding and drought. Each event stimulates the settlement of beaver territories at new locations. The concentration of beaver activity in periods of extreme drought may heavily influence the landscape. In the Millingerwaard concentrated beaver activity in the summer of 2003 resulted in more open alluvial forests.

Keywords: river dynamics, population growth, habitat, stress, Rhine, Gelderse Poort, Millingerwaard, migration, beaver activity.

Introduction

In large river ecosystems beavers (*Castor fiber*) have to cope with quite severe water level fluctuations. During extreme floods beaver families are forced to leave their permanent homes (lodges and tubes) to avoid drowning and temporarily move to higher and drier locations. Research in the Elbe floodplain in Germany has shown that beavers are able to construct new lodges and other types of refuge in response to rising floods (Nitsche 2001). Although beavers are able to adapt to flooding, these events cause stress and a loss of animals, particularly of the young. During extreme droughts beavers are also forced to leave their permanent homes, in this case to stay close to the water edge, which provides them with food and safety from predators. In this article we describe the impacts of extreme flooding and extreme drought on beaver territories in the floodplains of the Millingerwaard.

Beavers in the Millingerwaard

Between 1994 and 2000, 54 beavers from the Elbe region (Germany) were introduced in the Gelderse Poort area in the eastern part of the Netherlands (figure 1). The area is characterised by the river Rhine and its floodplains (3000 ha) near the Dutch-German border. One of the largest floodplain reserves in the Gelderse Poort area is the Millingerwaard (500 ha), which is largely managed by the State Forestry Service. In recent times the agricultural fields (formed by centuries of clay sedimentation) in this floodplain were transformed into natural habitats as a result of clay extraction. Today a wide variety of habitat types exists in the floodplain: sandy river dunes, alluvial forests, marshland, and newly excavated side channels.

After severe losses (more than 50%) in the years immediately following their reintroduction, the beaver population in the Gelderse Poort has started to gradually increase. The number of adults in spring 2002 was estimated at about 40 (ten families and nine solitary territories; Niewold 2002). In the beginning of 2004 the total number of beavers may reach approximately 60 animals, of which some 20 are present in the Millingerwaard (Teunissen 2004).

In the Millingerwaard floodplain beaver habitat consists of former riverbeds with nymphaeid vegetation, clay and sand pits with pioneer and marshland vegetation, and alluvial forests that mainly consist of *Salix alba*, *Salix viminalis* and *Populus nigra*. Niewold and Müskens (2000) showed that, apart from trees, the beavers in this area prefer to feed on plants such as *Glyceria maxima*, *Nymphoides peltata* and *Senecio paludosus*.

Figure 1. Location of the Gelderse Poort area, i.e. where the river Rhine enters the Netherlands from Germany.

River dynamics and adaptations to extreme water level fluctuations

Human intervention has diminished the size of the lower Rhine's floodplain from an original 15 km to approximately 1 km. This process started in the 13th century, with the construction of the first dikes. The much narrower floodplain and the canalisation and normalisation of the upstream river have led to extreme fluctuations in water levels, whose amplitude reaches almost ten metres. Since the beavers were reintroduced to the Millingerwaard they have already had to deal with extreme flooding (January 1995: +16.6 m above sea level) and an extreme drought, with the lowest discharge in decades (September 2003: +6.9 m above sea level). Normal annual water level fluctuations vary between 6-7 meters.

At times of average water levels (between +9 and +12 m above sea level) the beavers in the Millingerwaard live in lodges on the banks of clay pits and former river beds. During a series of floods in the 1990s it was observed that the beavers coped rather well with sudden and severe inundations. When the regular lodges disappeared under water the beavers quickly constructed special lodges or tubes on higher grounds, preferably within their territories (e.g. at old dikes or raised brick factory terrains). Sometimes these high water lodges were finished within a few days. During next floods those additional lodges were occupied again and often extended.

Extreme high water levels, as experienced in January 1995, were stressful events for beavers because even the highest grounds were flooded. In these circumstances they survived by sitting on top of the 'high water' lodges or by resting on floating wood in the alluvial forests (photo1). Afterwards typical signs of beaver activity were found high up in the trees.

During the extreme dry summer of 2003 (which lasted until flooding in mid-January 2004) most beaver habitat in the Millingerwaard dried up completely (photo 2). Nearly all regular lodges were abandoned and the beavers moved to the few remaining deeper water bodies (sand pits). They constructed burrows in the sandy banks as safe homes to survive the drought. To reach their favourite food (pioneer willow forest) the animals had to pass broad sandy beaches. Tracks in the sand, usually a combination of dragged branches, leg and tail prints, revealed that distances of up to 20 m were crossed. A few beaver families stayed in their lodges near the deep sand pit and daily used a track of more than 100 m to the water. The animals constructed a large network of deep channels to get the last bit of water around their lodges.

Although similar experiences have been reported from the floodplain of the river Elbe in Germany (water level fluctuations up to 6 m; Heidecke 1988), adaptation of beavers to fluctuations of nearly ten metres has not reported before. It re-emphasises the capability of beavers to survive in different habitats and extreme circumstances.

Ecological implications

Although severe flooding and extreme drought can cause major stress for settled beaver families in large river systems, and cause a loss of individuals, these events also have important ecological implications for the population on a larger scale and for the landscape development of the floodplain.

Both flooding and drought stimulate the settlement of new beaver territories within the floodplain, downstream as well as upstream. As suggested by Nitsche (2001) flooding may lead to migration of young beavers to other territories and to the formation of new pairs. Consequently, it affects genetic diversity of populations and thus may improve the viability of beaver populations in the long term.

During the drought in the Millingerwaard we found an extreme concentration of beaver activity around the last remaining water body in the reserve. Over the past ten years hardly any beaver activity was found in this part of the reserve. From autumn onwards, but mainly in winter, the beavers cut most of the willow scrub and wood along the shore of this sand pit. In this way the drought forced the beavers to find food in totally new locations. Because of the concen-

Photo 1. Beaver sitting on floating wood during extreme flooding in January 1995. *Photograph: Johan Bekhuis*.

Photo 2. Dried up beaver pond with lodge and canals in the Millingerwaard (August 2003). *Photograph: Johan Bekhuis.*

tration of beaver activity the landscape of the sand-pit has been heavily influenced. Instead of closed alluvial forest the habitats around the lake are more open as a result of this beaver activity, which is likely to lead to a shift in the species composition of the forests.

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Samenvatting

Aanpassingen van bevers aan extreme wisselingen in de waterstand en de ecologische implicaties daarvan

We observeerden hoe bevers (*Castor fiber*) reageren op veranderingen in het waterpeil in de Millingerwaard. De Millingerwaard is een onderdeel van de Gelderse Poort, een uiterwaar-

densysteem van de Rijn in het oosten van Nederland. In het midden van de jaren ’90 zijn hier bevers uitgezet. Na zware verliezen in de beginjaren, groeide de populatie langzaam, tot ongeveer 60 individuen aan het begin van 2004. De smalle uiterwaarden hebben er toe geleid dat er extreme wisselingen in de waterstand optreden, onder normale omstandigheden 6-7 m op jaarbasis. Tijdens een reeks van overstromingen van de uiterwaarden in de jaren ’90 werd waargenomen dat bevers adequaat reageerden op de wisselingen in de waterstand; zo bouwden ze binnen een paar dagen speciale burchten in hoger gelegen delen van het gebied. Tijdens de extreem droge zomer van 2003 kwam vrijwel al het beverbiotoop in de Millingerwaard volledig droog te liggen. Om deze droogte veilig te kunnen doorkomen bouwden de bevers burchten in de zandige oevers van een zandwinplas. Deze gebeurtenissen tonen aan dat bevers zich gemakkelijk aanpassen aan perioden van extreme overstroming of extreme droogte. Zowel overstroming als droogte stimuleert de vestiging van beverterritoria in nieuwe gebieden. De concentratie van beveractiviteit in perioden van extreme droogte kan een grote invloed hebben op het landschap. In de Millingerwaard resulteerde de geconcentreerde beveractiviteit in de zomer van 2003 tot meer open rivierbegeleidende bossen.

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Monitoring of reintroduced beavers (*Castor fiber*) in Denmark

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Abstract: The European beaver (*Castor fiber*) returned to Denmark in 1999 when 18 beavers were released in Klosterheden State Forest District in the northwestern part of the country. A monitoring programme was initiated to trace the population and distribution of the beavers, beaver-human conflicts, and effects on flora and fauna. The status of flora and fauna in the reintroduction area was systematically investigated prior to the beaver reintroduction. By 2003, beavers inhabited the entire catchment basin in which they were released and had dispersed to a neighbouring river system 25-30 km away. Beaver kits were observed every year and the population was estimated at 51 individuals in 2003. The beavers mainly fed on willow scrubs during the winter season and non-woody plants in the summer. No damage was reported in forests or agricultural production areas but the beavers caused minor problems by flooding an arable field, gardens, meadows, and forest roads and by blocking inlets to a fish farm. Few significant alterations of water flow were recorded but the diversity of the wetland biotopes increased. The only negative effects appeared to be a restriction of spawning migration of sea trout (*Salmo trutta*) by beaver dams in brooks. Other fish species were thought to benefit from the beaver ponds. Ponds enhanced spawning potentials for amphibians and enabled new species of birds to breed in the area. Bats profited by more suitable hunting sites. Occurrence of otters (*Lutra lutra*) increased but no clear relationship with beaver distribution was demonstrated.

Keywords: reintroduction, European beaver, *Castor fiber*, population development, management problems, ecological effects.

Introduction

Beavers (*Castor fiber* L., 1758) became extinct in Denmark more than one thousand years ago. In the late 1990s the Danish Forest and Nature Agency initiated a plan to reintroduce beavers in Denmark to recreate natural dynamics and enhance diversity in wetland ecosystems (Skov- og Naturstyrelsen 1998). The reintroduction of beavers in Denmark resulted in widespread public discussions. Anglers were particularly concerned. The Danish National Environmental Research Institute (NERI) was commissioned to carry out a five-year monitoring programme to follow the development of the beaver population and its influence on flora and fauna (table 1). Four annual progress reports and a preliminary evaluation of the reintroduction have been published (Berthelsen 2000, Berthelsen et al. 2001, Madsen et al. 2001, Berthelsen & Madsen 2002, Berthelsen & Madsen 2003). This paper describes the monitoring programme and its provisional conclusions and makes predictions of likely future developments.

Reintroduction, distribution and population development

Eighteen beavers, originating from the Elbe River in Germany, were released at six sites in Klosterheden State Forest District (KLS) in the north-western part of Denmark in October 1999 (figure 1). The beavers were introduced into upstream parts of the Flynder stream catchment

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Table 1. Parameters surveyed in the monitoring programme for reintroduced beavers.

Parameters	1999	2000	2001	2002	2003
Distribution and population development	x	x	x	x	x
Habitat descriptions	x	x	x	x	x
Food analysis			x	x	
Management problems	x	x	x	x	x
Vegetation in streams and valleys	x				x
Vegetation and abiotic parameters in lakes	x				x
Fish populations	x				x
Fish spawning grounds		x			x
Fish passage at beaver dams			x	x	x
Aquatic invertebrates	x				x
Insects in dead wood		x			x
Breeding birds		x			x
Amphibians		x			x
Bats		x			x
Otters	x	x		x	x

area in the KLS. The KLS consists of coniferous forests, heath lands and wetlands with small artificial lakes. It contains brooks and streams up to 4 m wide. The valleys around the watercourses and lakes are dominated by purple moor grass (*Molinia caerulea*), bog myrtle (*Myrica gale*), and willow scrubs (*Salix* sp.).

The distribution of beavers was determined by regular observations and identification of beaver lodges and core areas. A few weeks after the release, beavers had explored approximately 20 km downstream from the reintroduction areas. Beavers abandoned most release sites within months. Two beavers dispersed to a site approximately 10 km downstream of the reintroduction area and two pairs settled in the immediate vicinity of the reintroduction area. By 2003 beavers occupied most of the Flynder stream catchment basin and had established 13 territories. Signs of beaver activity were observed in a neighbouring catchment basin at a site approximately 25-30 km away from the reintroduction area (figure 1).

Population development was estimated from observations during regular work in the reintroduction area and two annual counts in spring and autumn. Beavers were counted at dawn and dusk in two days at all active lodges and in core areas by several observers primarily to record number of beaver kits. Beaver kits were observed each year. Some young beavers born in 2001 and 2002 were not registered until spring 2003. Seven new kits were registered in the autumn of 2003. One dead kit was found in 2001, one in 2002 and a fully-grown beaver was found dead in 2003. Assuming that all mortalities have been recorded, the population size was estimated to be 51 individuals in autumn 2003 (figure 2). The beavers are restricted to a small catchment basin in which the whole population can still be monitored, although no beavers have been tagged to enable individual identification. Adult mortality rates are low amongst beavers (Nolet & Baveco 1996) and we assume that the annual recruitment was underestimated more than the annual mortality rate. Thus, the population size estimate is assumed to be a conservative one.

Diet of beavers

The beavers' feeding habits were investigated by analyses of 400 excrement samples collected at three study sites in 2001 and 2002 (Borglykke 2002). Content of the excrement was sorted into woody and non-woody plants. The degradation of non-woody plants, which included herbs, grasses, aquatic plants, and deciduous leaves, was too advanced for more detailed analysis. Woody species were identified from different

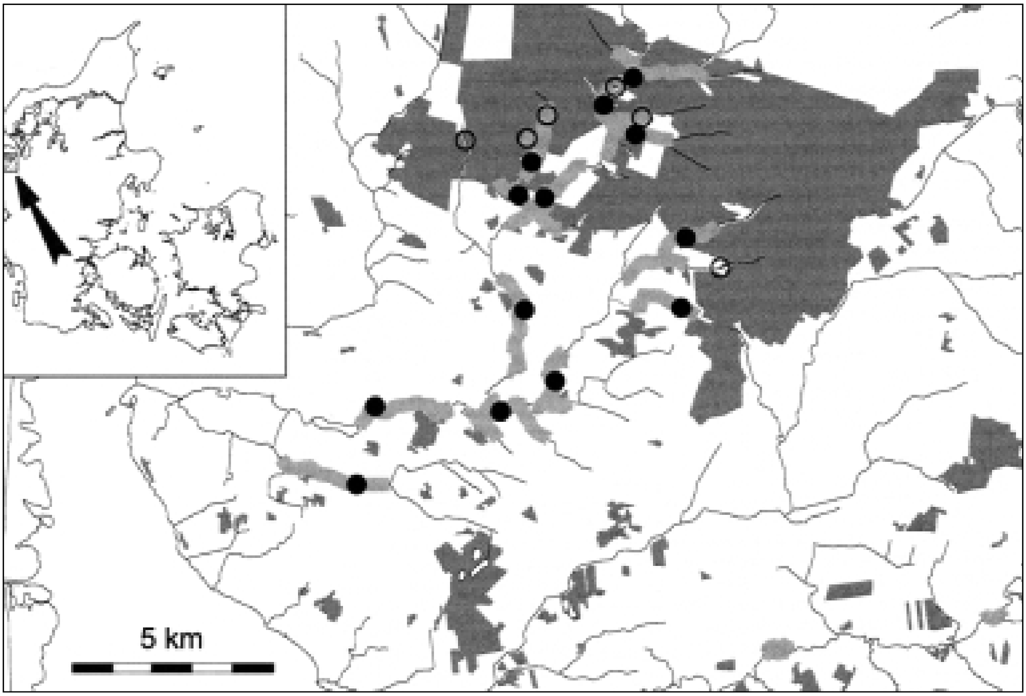


Figure 1. Reintroduction area in the north-western part of Denmark. Circles indicate release sites in 1999. Dots indicate locations of active beaver lodges in 2003. Medium grey areas indicate beaver territories along watercourses (thin black lines). Dark shaded areas indicate forests.

anatomic characteristics, e.g. rays and perforation of vessel elements. The prevalence of different woody plant species was evaluated according to Jacobs (1974). Feeding experiments with captive beavers have shown this method to be reliable (Borglykke 2002).

Seasonal utilisation of woody and non-woody plants varied (figure 3). Beavers foraged primarily on non-woody plants from June to September (69.6 ± 2.7%) and on woody plants (89.0 ± 2.6%) from November to May. Willow was the most important woody species (90.7 ± 1.6%) and was the only woody species positively selected by beavers. Spatial variations in the diet and utilisation of woody plants reflected differences in availability between study sites. The temporal variations in beavers' utilisation of plant species are governed by seasonal availability, changes in nutrient content and digestibility of the plants (Nolet et al. 1994). Roberts and Arner (1984) have reported similar seasonal variations between woody and non-woody plants in beavers' food habits.

Beaver-human conflicts, impact on biotopes, and production areas

Beavers had considerable impact on areas adjacent to watercourses by the damming of small streams. Dams built on streams less than 2 m wide created wetland areas larger than 1 ha. Ninety-five percent of beaver-cut trees were recorded less than 5 m from water. However, in coniferous stands, a few deciduous trees were collected from more than 25 m away from streams. At eight locations beavers have established lodges and territories on privately owned lands. Beaver activity on private land was concentrated in undisturbed semi-natural bogs and fens.

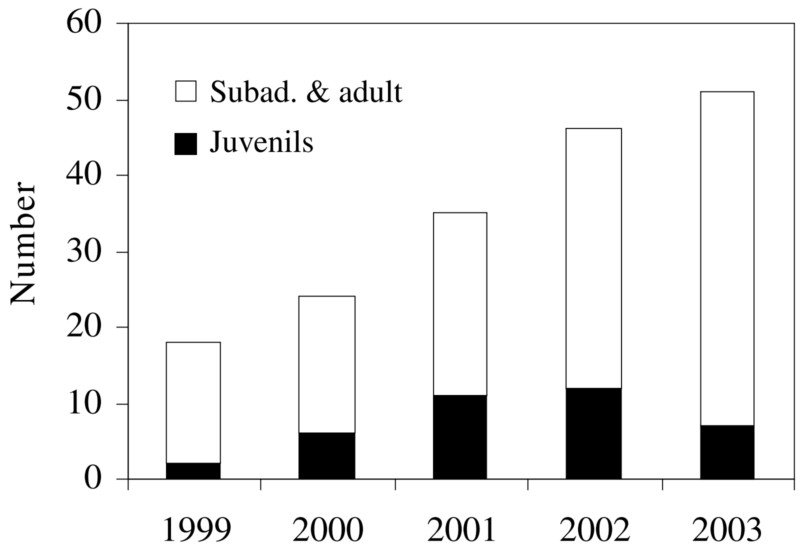


Figure 2. Estimated annual population size of reintroduced beavers in Denmark. Dead kits were found in 2001 and 2002, and a fully-grown beaver was found dead in 2003.

Beavers have not exploited resources in productive areas in forests or farmlands, but minor management problems have been encountered. At two privately owned locations significant numbers of birch (*Betula* sp.) and alder (*Alnus* sp.) were felled and a few trees had to be protected by chicken wire around the stems. Two meadows have been flooded. At one of these sites a pipe was installed in the dam to control the water level. At two other locations, dams in brooks have been repeatedly removed to prevent flooding of an arable field and gardens in a village. Beaver-cut sticks and aquatic plants have blocked the inlet gate on a fish farm at several occasions. Clogged culverts on forest roads have been cleared to prevent flooding at three locations. Despite these minor problems the private landowners have generally responded favourably towards the beavers.

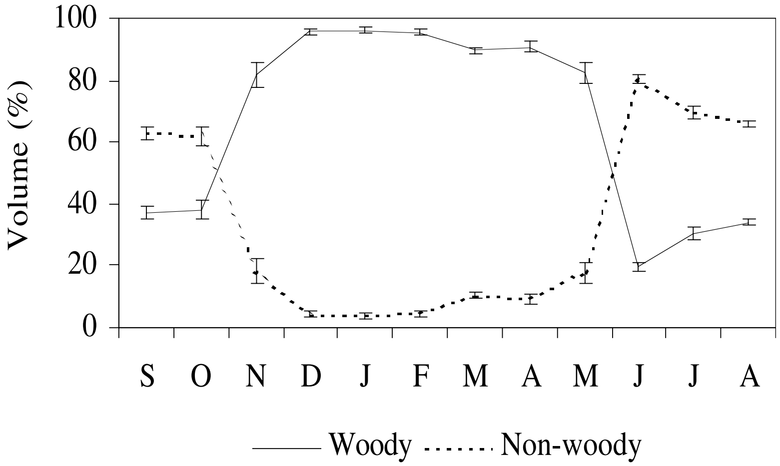
Vegetation, aquatic invertebrates and dead wood insects

Prior to the reintroduction some semi-qualitative baseline studies of the vegetation in selected plots in meadows, streams and lakes, and of aquatic invertebrate fauna in streams were carried out (Miljøstyrelsen 1998). Beaver-cut wood was examined to analyse the insect fauna associated with dead wood. However, detailed assessments of effects of beavers on vegetation and aquatic invertebrates were hampered as the beavers abandoned most release sites and the sites that they did eventually settle, and most heavily alter, were not covered in the pre-reintroduction surveys.

The abundance of willow and bog myrtle scrubs increased in the reintroduction area, although the extra growth was restricted at sites with beaver activity (table 2). No overall change in the abundance of aquatic vegetation in the streams was recorded. The abundance of scrub only decreased very locally at a few sites with heavy beaver activity. At these, previously shaded, sites herbaceous vegetation started to develop and the abundance and diversity of aquatic vegetation increased. The vegetation in new beaver ponds was poorly developed, probably because the sediment consists of detritus, which is a poor substrate for plant growth. Only negligible changes, attributable to natural variations, were recorded in abundance of vegetation in lakes.

Overall, the number of aquatic invertebrate species/taxa increased from 71 in the 1999-survey to 81 in the 2003-survey. The most com-

Figure 3. Seasonal food choice (volume % ± S.E.) of beavers in Denmark.



mon groups in both surveys were dipterans (*Diptera*), caddis flies (*Trichoptera*), and beetles (*Coleoptera*). Species living in running water disappeared at sites where impoundments changed a stream habitat to a pond habitat. Oxygen levels may drop in new beaver ponds and the diversity of invertebrates may decrease (Dgebuadze, unpublished data), although it may be expected to increase again later (Rosell & Pedersen 1999, Collen & Gibson 2001). The effects of the beavers' alterations of stream habitats are limited to small areas and insect species that disappear from these sites are assumed to exist in unaffected streams elsewhere in the reintroduction area. No notable changes in the diversity of dead wood insects in beaver-cut wood were recorded.

Impact on fish populations

The structure of fish communities was determined prior to the reintroduction and again in 2003 by electro-fishing streams (Bohlin et al. 1989). Brown and sea trout (*Salmo trutta*), roach (*Rutilus rutilus*), three-spined stickleback (*Gasterosteus aculeatus*), nine-spined stickleback (*Pungitius pungitius*), brook lamprey (*Lampetra planeri*), and eel (*Anguilla anguilla*) were the most common species recorded in both surveys. A few individual rainbow trout (*Oncorhynchus mykiss*) were registered prior to the beaver release, and a few dace (*Leuciscus leuciscus*) and pike (*Esox lucius*) were registered in the post-introduction survey. Trout was only recorded at substantial densities at two localities in the largest watercourses, where anglers regularly restock trout populations. The observed variations in the fish community structure and population sizes were attributable to natural variations in small populations and restocking.

The substrate of the riverbed was mapped in selected stretches of watercourses in the reintroduction area and the occurrence of spawning areas and spawning activities of trout was evaluated. The stretches of stream most heavily

Table 2. Percentage cover of willow and bog myrtle scrubs and aquatic vegetation at sites with beavers and reference sites along neighbouring streams with no beaver activity.

		1999	2003
Scrubs	Beaver sites (*n*=16)	32	32
	Reference sites (*n*=3)	33	45
Aquatic vegetation	Beaver sites (*n*=18)	46	44
	Reference sites (*n*=3)	42	40

altered by beavers, were surveyed four years after the reintroduction. As in the pre-reintroduction survey, none of the observed gravel banks showed any indication of trout spawning. Beaver dams may increase sedimentation on upstream spawning areas (Collen & Gibson 2001). However, they are not thought to cause a significant reduction in the spawning potential of brown and sea trout in the watercourses in the KLS. Rather, the absence of spawning activities, and natural recruitment of brown and sea trout, were attributed to the poor physical conditions of the watercourses.

Long-persisting beaver dams on streams and brooks were examined regularly to assess whether fish were able to pass the dams, and to assess the possible effects of the damming of the watercourses on various fish populations. Most dams were situated on streams less than 2 m wide. It was considered that eels would be able to pass all the dams and that brown and sea trout would be able to pass dams in the main watercourses during periods of high water flow. Only a few dams had a small pool immediately downstream. The absence of such a feature was considered as a constraint on the spawning migration of sea trout to more upstream stretches. Dams acted as total barriers for roach, sticklebacks and brook lamprey. However, small bypasses, formed around some dams, would enable these small fish to migrate upstream of the dam.

Table 3. Egg clusters from common frog at locations for spawning amphibians. The impoundments at Hestbæk, Flynder Å I, and Risbæk II had created wetlands, which were not available for spawning amphibians in 2000. Depotsøen is located near Risbæk I. Øvre Sø & Nedre Sø, and Døjbæk are located near Risbæk II.

Location	2000	2003
Hestbæk	–	11
Flynder Å I	–	451
Flynder Å II	10	0
Risbæk I	30	400
Depotsøen	164	50
Risbæk II	–	443
Øvre Sø & Nedre Sø	300	100
Døjbæk	4	5
Unnamed lake near Risbæk	225	3

Salmonids may negotiate beaver dams under some conditions and juveniles have been recorded upstream of dams (Collen & Gibson 2001, Halley & Lamberg 2001). Brown trout may eventually profit by small beaver ponds (Collen & Gibson 2001). The dams are not expected to have a negative impact on populations of eel or brook lamprey. Populations of roach and sticklebacks are expected to benefit from the beaver dams when the new ponds eventually develop into productive lake biotopes (Collen & Gibson 2001).

Amphibian surveys

Occurrence of spawning amphibians was determined in the reintroduction area and at active beaver sites in spring in 2000 and 2003. Lakes and ponds were surveyed for amphibians, egg clusters, egg strings and croaking males. Only common frog (*Rana temporaria)*, moor frog (*Rana arvalis*) and common toad (*Bufo bufo*) were recorded in both surveys. Spawning activity of common frog in the artificial lakes decreased (table 3: Depotsøen, Øvre Sø & Nedre Sø, and the unnamed lake near Risbæk II). However, numerous egg clusters from the common frog were found in nearby shallow waters in new wetlands created by the beavers at Risbæk I and Risbæk II. Egg strings of the common toad were only found at one location in 2003. However, the 2003 survey was performed at the beginning of the spawning season for common toads. Several common toads were recorded in beaver ponds and upstream stretches at Hestbæk, Risbæk I, and Risbæk II. The common toad may use the deeper parts of the larger beaver ponds for spawning. Moor frogs were only recorded at one of the release sites in both surveys, a site that the beavers quickly abandoned.

The ponds and wetlands created by beavers were assumed to have increased the numbers of suitable spawning areas for amphibians in the KLS. Flooded meadows with shallow waters and tussocks are a favourable habitat for moor frog. The distribution of moor frog is expected to increase due to the changes induced by beavers.

Breeding bird surveys

The occurrence of breeding birds was surveyed in valleys along watercourses and lakes each spring and during beaver counts. Species composition and numbers of breeding pairs were determined visually and aurally (Enemar 1959).

The development of breeding bird species at locations with beavers differed (table 4), although the number of species tended to increase. A total of 36 breeding species were recorded in 2003. Nine species recorded in low numbers in previous surveys had disappeared, but this was attributed to natural variations in small populations. The species were all breeding in forest or on heath lands (e.g. at Risbæk II). As scrubs along the watercourses became flooded, passerines abandoned the scrubs and started to breed in the nearby forest edges. An overall decline in the breeding population of whitethroat (*Sylvia communis*) was registered. The largest beaver ponds have improved the habitat for kingfisher (*Alcedo atthis*) and water birds, such as water rail (*Rallus aquaticus*). The number of breeding water birds is expected to increase in the future.

Bat surveys

The occurrence of bats was surveyed in the summers of 2000 and 2003, using ultrasound detection (Ahlén & Baagøe 1999). Daubenton's bat (*Myotis daubentonii*) was the only species detected in both surveys. They were detected at more locations in 2003, and there was a higher rate of activity near potential roost sites. Serotine (*Eptesicus serotinus*), pond bat (*Myotis dasycneme*), noctule (*Nyctalus noctula*), and Nathusius' pipistrelle (*Pipistrellus nathusii*) also occurred in the area (Baagøe 2001). The oligotrophic lakes in the forest support small insect biomasses. The low occurrence of bats in the forest and at beaver sites outside the reintroduction area is attributed to a low availability of prey and a shortage of suitable old trees and buildings for day hides and breeding sites. The landscape changes caused by the beavers have not significantly affected the occurrence of bats, but the 2003 survey indicates that larger ponds with open water surfaces have resulted in more suitable hunting grounds for Daubenton's bats.

Otter surveys

Otters leave spraints at conspicuous sites along the waterside to mark their territories and access to resources, e.g. food (Kruuk 1995). The banks and shores of watercourses and lakes were searched for otter spraints to record occurrence of otters (Anonymous 1984) and, in 2003 otter tracks were surveyed at the larger dams to investigate the relationship between beaver activity and otters.

Otter spraints were recorded at, or near, all beaver dams, which may represent conspicuous

Table 4. Number of breeding bird species at seven locations surveyed repeatedly during the monitoring programme. The beavers' alterations of the habitat at Risbæk I had created a large wetland area. Habitats at Møllesøen, Øvre Sø & Nedre Sø, and Døjbæk were relatively unaffected by the occurrence of beavers.

Location	2000	2001	2002	2003
Hestbæk		14	14	11
Møllesøen	22		16	21
Flynder Å II	7		8	12
Risbæk I	11	14	18	19
Risbæk II		13	21	11
Øvre Sø & Nedre Sø	13		13	
Døjbæk			8	9

sites in the stream habitats. During the monitoring period the occurrence of otters increased throughout the whole catchment basin (table 5). The increased site occupancy of otter also occurred on watercourses without beavers. A positive development of the otter population has occurred throughout the country (Elmeros & Madsen, unpublished data). The increased site occupancy of otters in the beaver reintroduction area was less pronounced when the results from national survey stations were compared with earlier national surveys (Madsen et al. 1992, Hammershøj et al. 1996).

Otters occurred in most parts of the Flynder stream catchment basin. Relatively stable food resources are probably found in the artificial lakes but the streams hold only small fish stocks. Otters have large home ranges (Kruuk 1995) and their occurrence in the upstream stretches of the Flynder probably fluctuates. The biomass of fish in new beaver ponds is low (Dgebuadze, unpublished data), but these ponds may eventually supply stable food resources for otters (Collen & Gibson 2001). It is uncertain whether the reintroduction of beavers has had a significant influence on the increased occurrence of otters in this part of Flynder stream catchment basin.

Conclusion

Beavers were reintroduced to recreate natural dynamics and variability in wetland ecosystems. The reintroduction was successful and the beavers are thriving. The population has nearly tripled in four years and beavers now occupy the whole freshwater system in which they were reintroduced. Only minor management problems have been encountered. Few significant changes in biodiversity and occurrences of the various flora and fauna groups were recorded. A longer post-reintroduction survey period would probably show more significant effects on flora and fauna, as beavers have extensively modified wetland biotopes at some locations and, as a result the diversity at various levels of the ecosystem can be expected to increase.

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Table 5. Percentage of positive stations for otters in the beaver monitoring programme. Seven of the stations were also surveyed in the previous national otter surveys (NERI stations) in 1991 and 1996.

	1991	1996	1999	2000	2002
Beaver monitoring stations			43	57	89
NERI stations (*n*=7)	71	86	71	71	100

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Samenvatting

Monitoring van geherintroduceerde bevers (*Castor fiber*) in Denemarken

Na een afwezigheid van meer dan 1000 jaar, vond in 1999 een herintroductie plaats van de bever (*Castor fiber*) in Denemarken. Achttien bevers werden uitgezet in Klosterheden State Forest District, in het noordwesten van het land. Een monitoring-programma werd opgezet om de populatie-ontwikkeling te beschrijven, alsmede de effecten op de flora en fauna, en de eventuele conflicten met menselijke activiteiten. Voorafgaand aan de uitzetting was reeds een uitvoerige studie gemaakt van de flora en fauna in het herintroductiegebied. Bevers bleken het gehele stroomgebied van de rivier waar zij waren uitgezet, te hebben bevolkt. Daarnaast hadden zij zich gevestigd in een naburige rivier, 25-30 km vanaf de plek waar zij waren uitgezet. De populatie groeide jaarlijks. Volgens de meest recente telling in 2003, bestaat de populatie uit 51 dieren.

De bevers eten vooral wilgen en kruidachtige planten die dicht bij het water groeien. Schade door vraat in landbouw- en bosgebieden werd niet gemeld. Kleine problemen ontstonden door ondergelopen akkers, tuinen, graslanden en boswegen, en doordat de inlaten van een viskwekerij werden geblokkeerd. In de relatief korte onderzoeksperiode werden slechts kleine veranderingen in de flora en fauna geconstateerd. Toch nam de algehele biodiversiteit van de natte biotopen in het gebied toe, een effect dat naar verwachting in de komende jaren duidelijker zal worden. Op de forel (*Salmo trutta*) na, zullen alle vissoorten naar verwachting in de toekomst populatiegroei te zien geven. Ook de voortplantingsmogelijkheden voor amfibieën namen toe. Een aantal nieuwe vogelsoorten vestigde zich in het gebied. Vleermuizen profiteerden, doordat nieuwe foerageergebieden werden gecreëerd. Het aantal otters (*Lutra lutra*) steeg, maar een verband met de toename van bevers kon niet worden aangetoond.

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Felling and foraging: results of the first year of beaver (*Castor fiber*) activity in an enclosed Scottish site

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Abstract: A trial reintroduction of the European beaver (*Castor fiber*) to Scotland has been proposed and is awaiting Scottish Executive approval. Currently, no data have been published on the actual effects of beavers on the Scottish landscape, although many authors have predicted potential impacts. Such predictions have been based on the impacts of the beaver in other European countries. The aim of this study is to provide a better predictive capability as to the potential effects on tree felling immediately following beaver reintroduction by using data of beavers in captivity. In 2002, four European beavers were released into two large, semi-natural enclosures – the Willow Carr Site and the Lake Site - in eastern Scotland. This paper represents data from the first year of a three-year monitoring programme to investigate the felling and feeding activities of these beavers. In absolute terms, willow (*Salix* spp.) were the favoured species at both sites, being felled in the greatest numbers, followed by alder (*Alnus* spp.) and birch (*Betula* spp.). In terms of relative abundance, only the selections against birch at both sites, and for willow at the Lake site, were found to be significant. No size-selectivity at the Willow Carr Site was evident, but significantly smaller than average trees of all three genera were felled at the Lake Site. Decreased felling activity was observed with increasing distance from the lodge at the Willow Carr Site, whilst most trees felled at the Lake Site were situated within the shallow margins of the lakes. Approximate felling rates were 0.5 and 0.8 trees per beaver per day, at the Willow Carr Site and Lake Site respectively.

Keywords: *Castor fiber*, beaver diet, reintroduction, Scotland, feeding preferences.

Introduction

The European beaver (*Castor fiber*) was a common sight along British watercourses until the sixteenth century (Conroy & Kitchener 1996), when hunting and habitat loss finally extirpated the species from the United Kingdom (UK), and indeed throughout the majority of their natural range. Following several successful recent re-introductions of the species throughout Europe (Nolet & Rosell 1998), a trial reintroduction of free-ranging beaver from a Norwegian donor population to the Knapdale area of Scotland was proposed by Scottish Natural Heritage (Gaywood 2001). This proposal is currently awaiting Scottish Executive approval. However, a captive population of four adult individuals from natural European stock was established early in 2002 into a semi-natural environment on a privately owned estate in eastern Scotland. These beavers – three females and a single male – were placed in pairs, in two large enclosures. Here, space is presumed non-limiting and the beavers have been left largely free of human disturbance (Ramsay 2002).

The activities of beavers affect the landscape, which in turn affects the flora and fauna that share the habitat with them. The beaver therefore acts as a keystone species (Kitchener 2001). Furthermore, they have also been described as ecosystem engineers due to the direct physical mechanisms used by beavers to modify the ecosystem (Jones et al. 1994). Such physical effects on the environment include damming of streams, wetland creation, and tree felling. The foraging and feeding behaviour of the European beaver are integral aspects to its roles of keystone species and ecosystem engineer. Indeed, due to the ability of beavers to fell mature trees and because foraging is confined to a zone surrounding a central place, beavers have great potential to alter forest ecosystems through herbivory (Johnston & Naiman 1990).

Whilst previous studies have modelled and predicted the extent of such potential ecological effects of reintroducing the European beaver to Scotland (Macdonald & Tattersall 1999, Rushton et al. 2000, South et al. 2000), no studies have been conducted on the actual effects of beaver activity in Scotland. Furthermore, any future reintroduction of beavers to Scotland will be subjected to very close scrutiny in the period immediately following release of the animals. Although many studies have investigated the tree felling activity and woody species food preferences of the beaver in Europe, most have been conducted on well-established beaver colonies (e.g. Simonsen 1973, Lahti & Helminen 1974). The studies of the reintroduced beavers in the Biesbosch area of the Netherlands offer a notable exception (Nolet et al. 1994).

The aim of this study is to provide a predictive capability as to the likely effects of beaver foraging and felling activity immediately following reintroduction into the UK, based on data gathered on captive beavers in Scotland. The preferences for certain woody species, the tree size-selectivity exhibited, and the distances foraged over by beavers in two enclosed sites in Scotland during the first year of colonisation have been investigated here. From these data, approximate tree felling rates have also been derived. This paper represents the first phase of a three-year monitoring programme.

Figure 1. Location of the study area.

Methods and materials

The Bamff estate is located in eastern Scotland near Blairgowrie, approximately 25 miles northeast of Perth (figure 1). Situated in the foothills of the Highlands, the estate comprises 525 ha of hills, forest and farmland, with the highest point rising 425 m above mean sea level. The area receives approximately 1,250 mm of rain annually, with a mean maximum temperature of 11.6°C and mean minimum temperature of 4.7°C (British Atmospheric Data Centre 2003). Snow and short-term ice cover occasionally occur in winter.

The beavers are located in two large enclosures located approximately 0.9 km apart. The first site ("Willow Carr Site") is an area of young willow plantation and meadow of approximately 13 ha, containing two small purpose-built ponds and a network of drainage ditches (photo 1). The predominant tree species are willow (*Salix cinerea*, *Salix aurita* and *Salix caprea*), birch (*Betula pendula* and *Betula pubescens*) and alder (*Alnus glutinosa* and *Alnus incana*). In March 2002, a male and female beaver from Norway were introduced to this site. In late January 2003 the male died and was not replaced.

The second site ("Lake Site") consists of two small artificial lakes linked to each other by a short channel, surrounded by mature conifer

Photo 1. The Willow Carr Site. *Photograph: Kevin Jones*.

plantation comprised predominantly of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and European larch (*Larix decidua*), covering approximately 9 ha. Large areas of willow and birch scrub, bog vegetation and fringing macrophytes, especially yellow flag (*Iris pseudacorus*), are also present at this site (photo 2). Two young female beavers, each approximately 14 months old, were introduced to the Lake Site in July 2002 and have thrived since that date.

In early spring 2003 at the Willow Carr Site twenty 10x10 m random quadrats were used to assess tree species composition. Where possible, deciduous trees were recorded to species although in some cases some deciduous trees were only recorded to genus. The genera of conifers were not recorded. Within the quadrats the girths of all trees were measured at the point of beaver activity (approximately 30 cm up the trunk) or in the case of felled trees immediately below the cut, and the approximate distances from the nearest pond were estimated.

Similarly in spring 2003 tree composition of the Lake Site was assessed by using ten 10 m wide belt transects stretching 50 m from the lake bank into the surrounding woodland. The transects were spaced regularly around the lake margin. Again deciduous trees were recorded to species although in some cases some deciduous trees were only recorded to genus. The genera of conifers were not recorded. Within the transects girths of all trees were measured in the same way as at the Willow Carr Site. The approximate distance from the shore of all trees was also measured.

In addition, at both sites complete surveys of all cut tree girths and genera (both within and outside the random quadrats at the Willow Carr Site c.q. transects at the Lake Site) were conducted in late January 2003. The distance of all felled trees from the water's edge was also

Photo 2. The Lake Site. *Photograph: Nigel Willby*.

measured at the Lake Site during the complete survey.

The preference of beavers for a particular genus was examined by calculating an electivity index (*ln Q*) (after Jacobs 1974) which relates the relative abundance (*ra*) of a genus to the relative use (*ru*) of that genus. The index was calculated using the data collected in the random quadrats at the Willow Carr Site and the belt transects and complete survey of felled trees at the Lake Site. The index used was:

$$ln\ Q = \ln [(ru(1-ra)) / (ra(1-ru))]$$

with a value greater than zero indicating preference for a genus, and a value less than zero indicating selection against the genus (Jacobs 1974). The significance of the *ln Q* of a genus *i* was calculated by the equation:

$$X^2=(ln\ Q)^2 / [1/x_i + 1/(m - x_i) + 1/y_i + 1/(n - y_i)]$$

where x_i is the number of trees of genus *i* felled and y_i is the number of all trees of genus *i* present (i.e. felled and standing). The total number of all felled trees irrespective of species is represented by *m*, whilst *n* is the total number of all trees (felled and standing) present in the sampled area. The X^2 statistic was then compared to a χ^2–distribution with one degree of freedom (Jenkins 1979, Nolet et al. 1994). The data used to calculate the mean values for both available and felled trees at the Willow Carr Site were from the random quadrats. The data used to calculate the mean values for available trees and felled trees at the Lake Site were from the belt transects and the complete survey respectively. The tree size-selectivity data were tested for statistical significance using the Mann-Whitney U-test.

Results

At the Willow Carr Site willow, birch and alder are dominant with only a small number of conifers present (figure 2A). At the Lake Site coniferous woodland dominates with smaller amounts of willow, birch and alder mainly on the lake shoreline and within the lake shallows (figure 2B). These shallows have in part been created by a beaver dam at the lake outlet, which has raised the water level by approximately 0.1 m.

The complete surveys of all felled trees at both sites indicated that 298 trees were felled at the Willow Carr Site, and 320 trees were felled at the Lake Site. Dividing these data by the number of beavers present at each site, and the number of days elapsed between the release of the beavers and the time of the full survey (324 and 205 days at the Willow Carr Site and Lake Site respect-

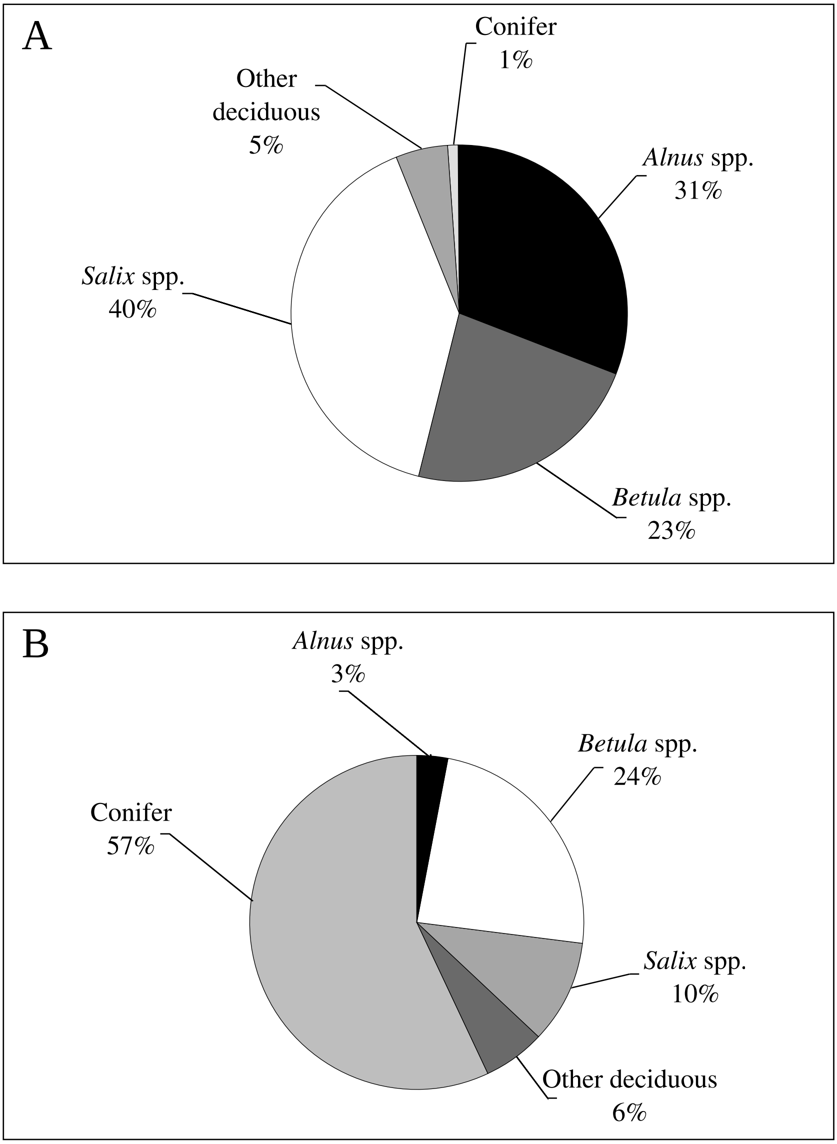

Figure 2. Tree species composition at (A) the Willow Carr Site (n=348), and (B) the Lake Site (n=578).

ively), yields approximate felling rates of 0.5 trees per beaver per day at the Willow Carr Site and 0.8 trees per beaver per day at the Lake Site.

At both sites, only trees of three genera were felled: *Alnus* spp., *Betula* spp. and *Salix* spp., whilst conifers were avoided except for occasional incidences of bark stripping. Of the felled trees only the selections against birch at both sites ($P<0.05$ at the Willow Carr Site and $P<0.001$ at the Lake Site) and for willow at the Lake Site ($P<0.001$) are statistically significant (table 1). Whilst available genera were of broadly similar size classes at both sites, the degree of size-selectivity varied between the sites (table 2). The beavers at the Willow Carr Site showed no preference in tree size for any of the three genera that were felled. At the Lake Site smaller trees were selected than the average size available for all three genera that were felled. At the Willow Carr Site trees at the larger end of the size range (6-12 cm in diameter) made up the majority of the felling, whilst smaller diameter classes of trees (4-10 cm in diameter) were chosen at the Lake Site (figure 3).

The foraging distances at the Willow Carr Site show decreased felling activity with increasing distance from the ponds (figure 4A). At the Lake Site there was an apparent locational preference for trees situated in the shallow margins of the lake itself (figure 4B). Maximum and mean distances from the water's edge travelled by beavers to fell trees were 49 m and 24 m at the Willow Carr Site, and 2 m landward and 10 m into the water at the Lake Site.

Discussion

The European beaver is known to have a very broad diet and Kitchener (2001) documented 80

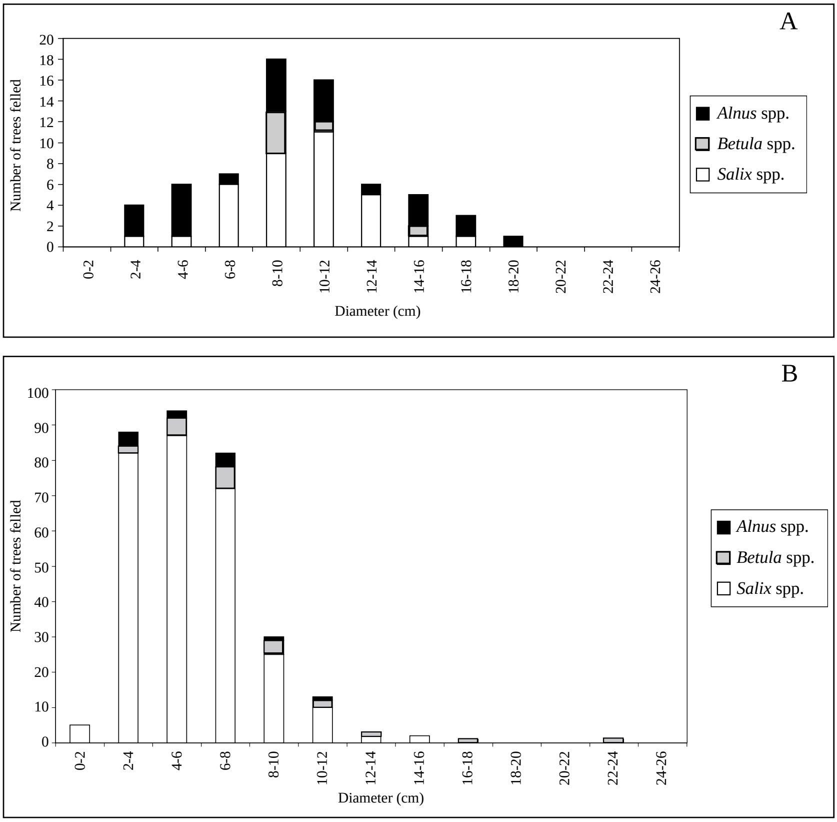

Figure 3. Diameters of felled trees at (A) the Willow Carr Site (n=66), and (B) the Lake Site (n=320).

Table 1. Genus electivity indices (*ln Q*). *** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; NS = not significant ($P>0.05$).

Site	Species	Abundance	Use	% Abundance	% Use	*ln Q*	X^2	*P*
Willow Carr	*Alnus* spp.	107	25	30.7	37.9	0.32	1.29	NS
	Betula spp.	79	6	22.7	9.1	-1.08	5.81	*
	Salix spp.	144	35	41.4	53	0.47	3.04	NS
Lake	*Alnus* spp.	18	12	3.1	3.8	0.19	0.26	NS
	Betula spp.	137	23	23.7	7.2	-1.39	34.21	***
	Salix spp.	60	285	10.4	89.1	4.25	356.89	***

Table 2. Mean available and felled tree sizes at the Willow Carr Site and the Lake Site. *d* = mean diameter (cm); *sd* = standard deviation; *** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; NS = not significant ($P>0.05$).

Site	Species	Available trees			Felled trees			*P*
		n	*d*	*sd*	*n*	*d*	*sd*	
Willow Carr	*Alnus* spp.	107	11	±5	25	10	±5	NS
	Betula spp.	79	10	±4	6	11	±2	NS
	Salix spp.	144	9	±3	35	10	±3	NS
Lake	*Alnus* spp.	18	15	±5	12	6	±3	***
	Betula spp.	137	14	±8	23	9	±5	**
	Salix spp.	60	9	±3	285	6	±2	***

woody species in its diet, although marked preferences for certain genera and species have been recorded (Bryant & Kuropat 1980). European aspen (*Populus tremula*) is widely regarded as the food item favoured above all others when available (Simonsen 1973, Lahti & Helminen 1974, Kitchener 2001). Only a very small number of aspen were present at the Willow Carr Site at Bamff and none at the Lake Site. These trees did not fall into any of the random sampling quadrats. We noted, however, that all of these trees were felled soon after the beavers were introduced to the site, suggesting high species preference despite the low availability.

Willow species are also highly preferred by beavers (Nolet et al. 1994, Lapinski & Stalinski 2001) and data from the Lake Site strongly support this preference, with *Salix* spp. making up 89% of all the felled trees, but only 10% of the trees available. At the Willow Carr Site this positive preference for *Salix* spp. also exists but not significantly so, indicating that either a larger dataset is required to reveal a significant preference or that preference is site or beaver specific. Such differences in preference between individual beavers or beavers from different regions have been observed in other studies (Shelton 1966, cited in Müller-Schwarze & Sun 2003). In absolute terms the data from both sites indicate that willow is felled in the greatest amounts, followed by alder and birch. Furthermore, the significant negative electivity indices for *Betula* spp. at both sites indicate a negative preference for birch by the beavers, even when relative abundance is accounted for.

It is also interesting to note the relatively large amount of alder felled at both sites given the well-documented low preference of beavers for *Alnus* spp. (Nolet et al. 1994). This finding may be due to the role of alder as a construction material rather than as a food item (Pinkowski 1983). It could be reasonable to assume that dam and lodge building activities would be most marked during the first year of colonisation of a new territory, and that the relatively large amounts of alder felled during

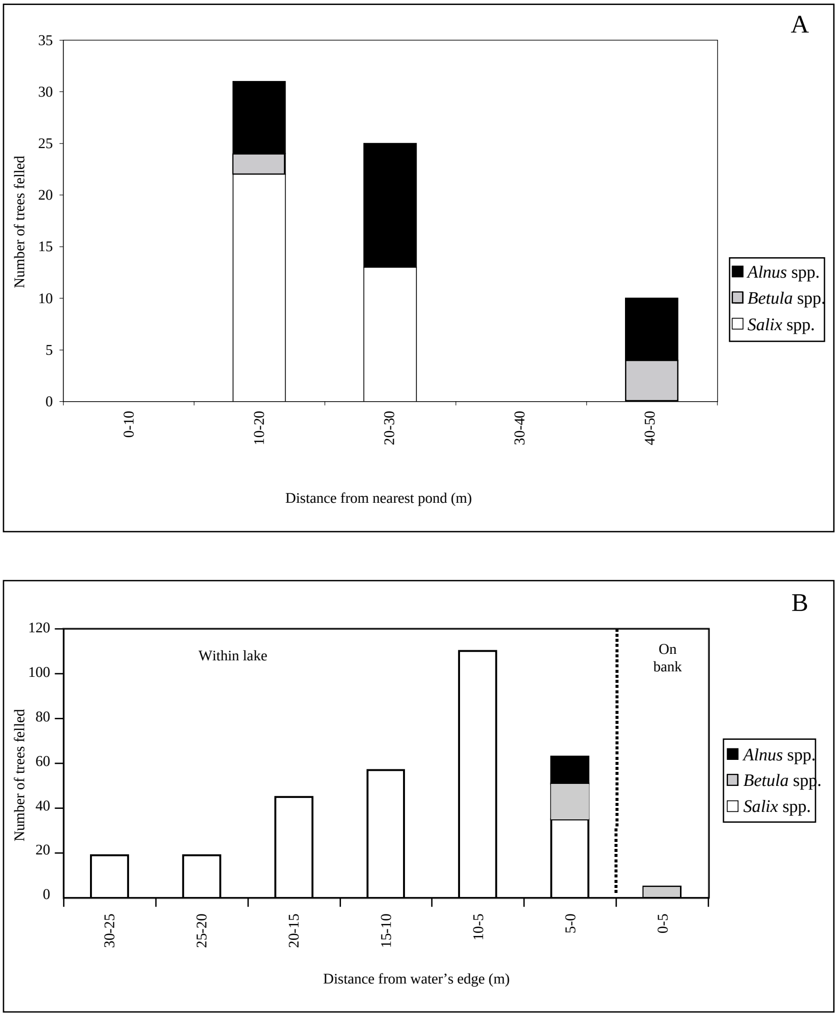

Figure 4. Foraging patterns at (A) the Willow Carr Site (*n*=66), and (B) the Lake Site (*n*=318).

this study could be due to such a construction phase. Small dams have been built at both of the study sites, as well as a relatively large bank lodge at the Lake Site.

Another interesting, but unquantified, aspect of the feeding behaviour of the beavers has been the stripping of small patches of bark from conifers at the Lake Site. Such behaviour has been documented in the European beaver (Simonsen 1973) and the American beaver (*Castor canadensis*; Svendsen 1980), and is thought to be a mechanism by which the nutritional quality of a tree is tested (Jenkins 1980). It is also possible that the ingestion of small amounts of coniferous sap and bark helps to provide a balanced diet (Jenkins 1979).

Beavers are known to select trees by size as well as species, with smaller trees being felled before larger ones (Simonsen 1973, Jenkins 1979). The general trend at the Lake Site supports this pattern of selection, and, in all three genera felled by beaver smaller trees are preferred. At the Willow Carr Site, however, beaver do not exhibit any significant size-selectivity. This lack of distinct size-selectivity could be due to the greater role played by alder in the felling behaviour at this site. If alder is largely being utilised for construction, size may simply be of lesser importance than when felling for food.

Studies have demonstrated that beaver felling largely takes place in the riparian zone, although exact distances travelled to acquire food will vary according to habitat quality (Simonsen 1973, Johnston & Naiman 1990). Our preliminary data support this observation. At the Lake Site the vast majority of felling occurs within the aquatic zone, with no incidence of the beavers browsing further than five metres from the shoreline. At the Willow Carr Site this aquatic supply of woody material is not present and the beavers are forced to browse further from the safety of the small ponds and drainage ditches.

Conclusion

This paper documents the first year (2002-2003) of beaver felling and foraging activity following reintroduction to an enclosed Scottish site. During this period an average of 0.5 trees and 0.8 trees per beaver per day were felled at the Willow Carr Site and Lake Site respectively. Woody species felled included willow, birch and alder with a strong preference for *Salix* spp., a negative preference for *Betula* spp., and complete avoidance of conifer felling. Felling was undertaken for lodge and dam construction as well as feeding activity. Collation of data from the winter of 2003-2004, when construction activities have to date not been apparent, will allow us to determine the relative importance of felling for feeding and building. Although the felling and foraging activities may not be sustained long-term, an understanding of the initial impacts is important for trial reintroduction projects where public scrutiny may be intense. Whilst these results may not be directly transferable to other Scottish sites or other European regions with markedly different environmental conditions, they do however give an indication of the preference for specific woody species and tree sizes, and the possible levels of felling activity by reintroduced beaver.

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Samenvatting

Vellen en foerageren: resultaten van het eerste jaar van activiteiten van bevers (*Castor fiber*) in een omrasterd gebied in Schotland

Een proef-herintroductie van de Europese bever (*Castor fiber*) in Schotland is voorgesteld en wacht op goedkeuring door de Schotse overheid. Op dit moment zijn er geen gegevens gepubliceerd over de effecten van bevers op het Schotse landschap, hoewel veel auteurs potentiële effecten hebben voorspeld. Dergelijke voorspellingen zijn gebaseerd op de effecten van bevers in andere Europese landen. Doel van deze studie is om met gebruik van gegevens van bevers in gevangenschap betere voorspellingen te kunnen doen van het potentiële effect van bevers op het vellen van bomen direct na de herintroductie van de dieren. In 2002 zijn vier Europese bevers uitgezet in twee grote, omheinde, semi-natuurlijke gebieden in het oosten van Schotland: de *Willow Carr Site* en de *Lake Site*. Dit artikel presenteert de gegevens van het eerste jaar van een driejarig monitoringprogramma, dat zich richt op de vel- en foerageer-activiteiten van deze bevers. In absolute zin zijn op beide lokaties wilgen (*Salix* spp.) in de grootste aantallen geveld, gevolgd door els (*Alnus* spp.) en berk (*Betula* spp.). In termen van relatieve dichtheid zijn alleen de negatieve selectie van berk in de Willow Carr Site en de positieve selectie van berk in de Lake Site significant. In de Willow Carr Site is geen voorkeur voor boomgrootte aangetoond. In de Lake Site zijn de gevelde bomen van alle soorten significant kleiner dan gemiddeld. In de Willow Carr Site nam het aantal gevelde bomen af bij toenemende afstand tot de beverburcht, terwijl in de Lake Site de meeste gevelde bomen in de ondiepe randen van de meren groeiden. Per bever zijn per dag gemiddeld 0,5 bomen geveld in de Willow Carr Site, en 0,8 bomen in de Lake Site.

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Beaver (*Castor canadensis*) in heavily browsed environments[1]

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Abstract: Beaver (*Castor canadensis*) populations have declined or failed to recover in heavily browsed environments. I suggest that intense browsing by livestock or ungulates can disrupt beaver-willow (*Salix* spp.) mutualisms that likely evolved under relatively low herbivory in a more predator-rich environment, and that this interaction may explain beaver and willow declines. Field experiments in Rocky Mountain National Park, Colorado, USA, found the interaction of beaver and elk (*Cervus elaphus*) herbivory suppressed compensatory growth in willow. Intense elk browsing of simulated beaver-cut willow produced plants which were small and hedged with a high percentage of dead stems, whereas protected plants were large and highly branched with a low percentage of dead stems. Evaluation of a winter food cache showed beaver had selected woody stems with a lower percentage of leaders browsed by elk. A lack of willow stems suitable as winter beaver food may cause beaver populations to decline, creating a negative feedback mechanism for beaver and willow. In contrast, if browsing by livestock or ungulates can be controlled, and beaver can disperse from a nearby source population, then beaver may build dams in marginal habitat which will benefit willow and cause a positive riparian response that restores proper function to degraded habitat. In a shrub-steppe riparian ecosystem of northwestern Colorado, USA, rest from overgrazing of livestock released herbaceous vegetation initiating restoration of a beaver-willow community. Thus, competition from livestock or ungulates can cause beaver and willow to decline and can prevent their restoration in heavily browsed riparian environments, but beaver and willow populations can recover under proper grazing management.

Keywords: beaver, *Castor canadensis*, *Cervus elaphus*, competition, elk, facilitation, livestock, montane, mutualism, riparian restoration, *Salix,* shrub-steppe, tamarisk, *Tamarix ramosissima*, willow.

Introduction

Seton (1929) estimated the beaver (*Castor canadensis*) population in North America at 60-400 million before European settlement. Despite this legendary abundance most beaver populations were decimated by fur trappers during the 1700s and 1800s, primarily to support the European fashion for felt hats. Growing public concern over declines in beaver and other wildlife led to regulations that controlled harvest through seasons and methods of take, initiating a continent-wide recovery of beaver populations. To supplement natural recovery, beaver were live-trapped and successfully reintroduced into much of their former range during the mid-1900s, a remarkable achievement of early wildlife managers. Beaver now occupy much of their former range in North America and their population is estimated at 6-12 million (Naiman et al. 1988). However, beaver populations have not recovered or have failed to persist in many riparian areas that have become heavily browsed environments since European settlement. Livestock and ungulates congregate in riparian areas that provide water and productive vegetation and lack disturbance from large predators such as gray wolves (*Canis lupus*) (Belsky et al. 1999, Beschta 2003). Also, in 1968 the National Park Service initiated a natural regulation policy for parks in the United States, which restricted pop-

[1] Parts of this review paper were adapted or extracted from Baker & Hill (2003) and Baker et al. (in press).

ulation control and allowed wildlife to self-regulate. Since then elk (*Cervus elaphus*) populations in some parks have increased and large herds forage relatively undisturbed in open riparian meadows and remnant willow (*Salix* spp.) stands, areas that are popular tourist attractions because elk are easy to observe in the short vegetation. Willow is highly palatable and selected for by livestock and ungulates, especially after herbaceous vegetation becomes dormant during late summer (Kay 1994). The distribution and height of willow has dramatically decreased in these heavily browsed environments. However, willow and other woody riparian species may recover if browsing pressure is reduced. For example, cottonwood (*Populus* spp.) and willow increased in height following the introduction of gray wolves into Yellowstone National Park, USA, in 1995-1996 (Ripple & Beschta 2003). This suggests increased predation risk to elk in riparian areas and/or top-down population control may reduce competition for woody riparian vegetation and improve habitat for beaver.

Beaver are a definitive example of both a keystone species and an ecosystem engineer (Baker & Hill 2003). The dam-building, canal-building, and foraging activities of beaver have profound effects on ecosystem structure and function. Beaver dams slow current velocity, increase deposition and retention of sediment and organic matter in the pond, reduce turbidity downstream of the dam, increase the area of soil-water interface, elevate the water table, change the annual stream discharge rate by retaining precipitation runoff during high flows and slowly releasing it during low flows, alter stream gradients by creating a stair-step profile, and increase resistance to disturbance (Gurnell 1998, Naiman et al. 1988). Canals dug by beaver spread impounded water across a larger surface area, thus magnifying the effects of single dams. The foraging activity of beaver alters the species composition, density, growth form, and distribution of woody vegetation. Beaver dams raise the water table by creating a pond and an umbrella-shaped zone of influence that radiates out from the pond, creating a new water table gradient controlled by soil texture and other factors. The soil behind dams can act like a sponge, retaining water during wetter months and slowly releasing it during drier months. In areas of low or irregular precipitation, beaver dams may convert streams from intermittent flow to perennial flow. Changes in the amount, timing, or duration of available water can create a competitive advantage for many species of riparian-wetland plants such as willow, thus increasing their survival and dominance in the landscape. Higher water tables caused by beaver ponds generally kill upland vegetation and promote establishment and growth of wetland vegetation. Sediment deposited behind beaver dams creates an ideal moist soil substrate that can become exposed as water levels in the pond decrease due to dam washouts or other causes. Beaver cuttings also may be an important mechanism of plant establishment for willow (Cottrell 1995). Thus, beaver can benefit the establishment and survival processes of willow and many phreatophytic species.

Willow is important as food and construction material for beaver (Baker & Hill 2003). Willow leaves are high in protein content and are readily eaten during the summer. The bark of willow stems stored in a food cache accessible from under the ice may be the only source of winter food for beaver that live in climates where surface water freezes during winter; thus, the availability of suitable willow stems can limit beaver populations in cold climates (Baker & Cade 1995). Beaver-cutting stimulates vigorous sprouts from below the cut on the same stem or from nearby root suckers. In a study of red willow (*Salix lasiandra*) in Oregon, USA, trees that had a higher percentage of stems cut by beaver responded by producing a higher percentage of regrowth the following season (Kindschy 1985). Cutting by beaver can also stimulate plants to initiate growth earlier in the spring, further increasing stem production (Kindschy 1989). Thus, I suggest that where willow benefit beaver as food and construction material and beaver benefit willow establishment and survival processes, beaver and willow can be considered facultative mutualists.

In this paper I discuss how beaver-willow mutualisms can collapse in heavily browsed environments and how proper grazing practices can restore these mutualisms in degraded riparian ecosystems. As examples I use (1) a montane, beaver-willow community in Rocky Mountain National Park (RMNP), northcentral Colorado, USA, where elk are the dominant herbivore and (2) a shrub-steppe, beaver-willow community (Douglas Creek) on land managed by the Bureau of Land Management (BLM) in northwestern Colorado, USA, where livestock are the dominant herbivore.

Factors limiting beaver in a heavily browsed environment

Beaver were once abundant in RMNP but declined dramatically after 1940. Population estimates in Moraine Park, a riparian valley within RMNP, were 315 in 1939-1940, 102 in 1964, 12 in 1980, and 6 in 1999 (Baker et al., in press). Elk were reintroduced to RMNP in 1913-1914 after nearly being extirpated by the late 1800s. They had increased to 1,200 animals in 1940 when Packard (1947) first noted beaver and elk competition for willow. Control efforts reduced the elk population to 500 until 1968, when a policy of natural regulation precluded control and numbers had increased to 3,000 by the late 1990s (Singer et al. 1998, Lubow et al. 2002). Elk utilization of riparian willow (% leaders browsed) averaged 85% annually in 1968-1992 as the elk population increased to seven times its 1968 level (Zeigenfuss et al. 1999), evidence that willow was a highly preferred forage species. In a comparison of 1937/1946 and 1996 aerial photographs Peinetti et al. (2002) found tall willow (>3 m) cover declined by 54% in Moraine Park and 65% in Horseshoe Park, and that total willow cover declined by 20%. Short willow (<1.5 m) plants have dominated the area for several decades, likely a result of a change in individual plant stature rather than in willow species composition (Peinetti et al. 2001). Thus, beaver and willow populations both declined in heavily browsed environments within RMNP, but the underlying mechanisms have remained elusive.

Because factors other than competition with elk for willow might limit beaver populations, a radio-telemetry study was initiated to determine the importance of mortality, dispersal, or other life history factors in limiting the remaining beaver populations in RMNP. In fall 2001, 39 beaver were live-trapped using Hancock and box traps. The age distribution of beaver was 20 adults, 4 yearlings, and 15 juveniles. The relatively low number of yearlings suggested poor recruitment due to either dispersal outside RMNP or poor survival of juveniles, assuming no differential trapping success. Blood samples were drawn from each beaver via a blind-stick method through the dorsal surface of the tail. All samples tested negative for tularemia and plague, which effectively ruled-out disease as a mortality factor during at least the past five years. As an interesting side benefit, these blood samples were used to develop a 100% accurate genetic method of gender determination in beaver (Williams et al., in press). Beaver were radio-tagged at the capture site using tail-mounted transmitters (Rothmeyer et al. 2002) with activity/mortality switches to indicate movement, rest, or no movement for >6 hours (indicating possible mortality). Unfortunately, this radio attachment method proved to have poor retention time for most individuals, although it was easy to use and radios with intact whip antennas (those not chewed-off by beaver) had a good signal range (B.W. Baker, unpublished data). Radio tracking results showed 1 adult male mortality due to coyote (*Canis latrans*) predation, 1 adult female mortality due to unknown causes, and 1 dispersal of an adult male of about 10 km to a location within the town of Estes Park adjacent to RMNP. Results also showed that beaver used several different bank dens, bank lodges, or pond lodges, including many that would not have been discovered without the aid of radio telemetry; these data suggest that attempting to census beaver by counts of active dens and lodges would be highly problematic.

An investigation of trapping records in RMNP revealed that 218 beaver had been removed during 1941-1949, which suggests trapping was an important cause of initial population declines. A comparison of aerial photographs taken in 1947 and 1964 shows a dramatic reduction in the area inundated by beaver ponds and canals as beaver populations declined in the Moraine Park study site. Loss of beaver-engineered water sources likely caused loss of willow in some areas, which would reduce beaver habitat even further. But why did beaver populations fail to recover after trapping ceased in 1949? Beaver surveys and aerial photographs taken in 1999 revealed only one beaver colony in Moraine Park, and it was located within a 30x46 m study exclosure that had been erected to protect willow from elk browsing. The elk exclosure had become a beaver food plot. Willow plants protected from elk browsing had grown tall and vigorous, whereas most outside plants were short and hedged due to 30 years of intense use by elk. To determine if elk-browsing affected beaver winter food preferences, in November 2001, elk utilization rates (%) were compared on willow, river birch (*Betula fontinalis*) and alder (*Alnus tenuifolia*) stems used in a winter food cache to those stems available in the beaver colony territory, defined as the area containing recent beaver-cut stems. Results showed beaver had selected stems with a lower percentage of leaders browsed by elk, which suggests elk browsing reduced willow suitability to beaver (B.W. Baker, unpublished data). In addition, beaver had placed willow stems at the bottom of the cache and covered them with a cap of alder and birch stems, which suggests they placed the more preferred forage species (willow) at the bottom of the pond to ensure access when the pond surface was frozen in winter. Thus, beaver appear to prefer relatively tall, unbrowsed willow and to select against short, hedged willow, which dominates much of the former beaver habitat in RMNP.

How did the formerly tall (>3 m) willow community become short (<1.5 m) and hedged and how could beaver have influenced this change? Elk can and do break tall willow stems to reach the tender tips of leaders. Although this behaviour has been observed in RMNP, it usually results in broken stems that are >2 m tall and does not appear to be especially common. If beaver cut tall willow, and elk browsing strongly suppressed willow regrowth, then the interaction of beaver cutting and elk browsing could alter the structure and function of the willow community. This hypothesis was tested with a field experiment that compared willow regrowth 3 years after simulated beaver cutting on paired plants with and without intense elk browsing (85% utilization rate). Simulated beaver cutting with intense elk browsing produced willow regrowth that was small in biomass and diameter and short with far fewer but longer shoots and a high percentage of dead biomass (Baker et al., in press). In contrast, simulated beaver cutting without elk browsing produced willow regrowth that was large, tall, and leafy with many more but shorter shoots and a low percentage of dead biomass. Total stem biomass after 3 years of regrowth was 10 times greater on unbrowsed plants than on browsed plants. Unbrowsed plants recovered 84% of their pre-cut biomass after only two growing seasons, whereas browsed plants had recovered only 6%. Thus, the interaction of beaver cutting and elk browsing strongly suppressed compensatory growth in willow.

How does elk browsing differ from beaver cutting and how do these differences affect compensatory growth mechanisms? Elk and other large herbivores browse the tips of leaders, which removes mostly current annual growth (CAG). A large percentage of leaf and woody biomass remains intact, which contributes to the growth of new shoots via photosynthesis. Browsing frequency can be high because shoot regrowth rapidly becomes suitable as forage. Released apical dominance can activate dormant buds below the point of browsing, which increases branching and growth rates (Honkanen & Haukioja 1998). Repeated browsing of new shoots can create hedged plants that may maintain high forage productivity. However, browsing can reduce or eliminate sexual reproduction in willow by maintaining plants in a juvenile growth phase (Kay 1994). In contrast, beaver usually cut entire stems near ground level and at a relatively low frequency, as it takes several years for regrowth to become suitable as food or building material. Willow plants can rapidly recover mature stems so regrowth is more likely to reach sexual maturity and produce seed on plants where stems have been cut by beaver rather than browsed by elk. Regrowth of beaver-cut willow can be strongly suppressed by intense elk browsing, but willow can often tolerate herbivory by either species alone. The ability of willow to compensate for complete removal of aboveground biomass suggests they have a high level of nutrients stored in roots, which can be rapidly shunted from roots to shoots following herbivory (Strauss & Agrawal 1999). However, this mechanism likely reduces root reserves and places plants in a stressed state until new sprouts can recover stem and leaf tissue necessary for photosynthesis, which is a prerequisite of other compensatory growth mechanisms such as increased photosynthetic rate, leaf nitrogen, and growth rate. Also, when beaver cut tall stems they place regrowth under the canopy of surrounding herbaceous vegetation where further herbivory can prevent new stems from escaping competition for light and increasing their growth rates (Raven 1992). Thus, the interaction of beaver and elk herbivory can greatly reduce the effectiveness of compensatory growth mechanisms.

When beaver cut the stems of woody plants they function as an ecological driver by altering future plant-herbivore interactions and placing regrowth within easy reach of herbivores such as elk. When elk browse beaver-cut willow they can drive a tall willow community into an alternative state consisting of short, hedged plants that lack sexual reproduction and will eventually die of old age. If elk browsing decreases the suitability of willow as beaver food by reducing the biomass of twigs and bark on stems and their preference by beaver, then beaver populations will decline where willow limits populations. In these systems, willow that provides adequate biomass of twigs and bark is *necessary* for beaver as a winter food supply, but short or heavily-browsed willow (or no willow) is *sufficient* for elk, as they can subsist on herbaceous forage in areas lacking deep winter snow (Skovlin 1982). Thus, in riparian systems where elk are overabundant they will outcompete and exclude beaver. When beaver populations decline, then wetlands will lose key willow establishment and survival processes and beaver-engineered wetlands will collapse. Carrying capacity for elk can increase in these sites if areas dominated by beaver ponds and canals dry and succession forms a mosaic of mesic and xeric plant communities, a process equivalent to the agricultural practice of wetland drainage to increase livestock forage production. Alternatively, beaver may increase carrying capacity for elk (or livestock) in very dry environments where dams raise the water table and increase productivity enough to overcompensate for surface area lost to beaver ponds. Thus, when beaver cut willow, and intense elk browsing suppresses regrowth, then the interaction of beaver and elk herbivory will create a feedback mechanism that is negative for beaver and willow but positive, or negative, for elk depending on local conditions. Further research is necessary to determine the level of additional herbivory that beaver-willow communities can tolerate before a negative feedback mechanism will disrupt beaver-willow mutualisms that naturally occur in less competitive environments.

Beaver as a riparian restoration tool in shrub-steppe ecosystems

In the previous section I used a case study of intense elk browsing in RMNP to show how overgrazing by ungulates or livestock can interact with beaver cutting to suppress willow regrowth, which can cause the decline or prevent the recovery of beaver-willow communities. In this section I will present a riparian restoration hypothesis that suggests proper grazing management and beaver can initiate recovery of degraded riparian ecosystems.

Beaver were abundant in forested, shrub-steppe, and some hot desert habitats in the western United States until fur trapping had decimated most beaver populations by the late 1800s. From 1875-1892 shrub-steppe riparian areas experienced a period of low frequency but high intensity rainfall events, decreasing stream-side vegetation and increasing channel incision. Ranchers followed trappers in settlement of the west, and immense numbers of sheep and cattle were introduced during the late 1800s. Overgrazing further stripped streambanks of soil-binding vegetation which, lacking active, functional beaver dams, caused stream channels to respond with accelerated erosion and severe downcutting (see Elliott et al. 1999 for a discussion of possible mechanisms to explain observed channel incision). Willow populations declined and were often replaced with tamarisk (*Tamarix ramosissima*), an invasive, exotic riparian shrub. Restoration and revegetation of incised channels with willow or other native species can be expensive, labor-intensive, and often unsuccessful, so natural restoration can be an attractive alternative. The ability of beaver to store water, trap sediment, reduce channel erosion, and enhance establishment and production of willow and other phreatophytes can be used as a proactive management tool to restore degraded riparian habitat if proper grazing management is present.

Reintroduction of beaver into degraded riparian systems has shown promise as a restoration tool, even where willow or other suitable winter food may occur in remnant populations, usually in the upper stream reaches. In 1975, the BLM initiated restoration of the Douglas Creek watershed by resting the grazing allotment from cattle grazing for two years, developing water sources to attract cattle away from the riparian zone, and implementing a rest-rotation grazing system (Baker et al. 1992). The stream channel in the lower reaches of this watershed had incised nearly 20 m since 1882 when livestock were introduced. At the same time BLM prohibited trapping of a remnant beaver population that occurred at the uppermost reaches of the stream, where cattle had not eliminated willow. Improved livestock grazing management permitted the development of an adequate biomass of herbaceous aquatic and riparian vegetation for summer beaver food, which allowed beaver to disperse into marginal downstream habitat. Comparison of photographs taken before (1975) and after (1992) improved livestock and beaver management showed dramatic changes in riparian condition. The following hypothesis suggests a process of beaver-engineered riparian restoration in areas where proper grazing management can be implemented (figure 1).

Implementation of grazing practices that leave adequate herbaceous vegetation to support beaver during the summer and fall, and that permit willow or other winter food supplies to become established and grow to a size suitable for winter beaver food, must be in place before beaver benefits can be realized. Where beaver can disperse to marginal habitat they may subsist on herbaceous vegetation in summer and fall long enough to build dams, ponds, and canals that can initiate a riparian response, although beaver may occur as 'sink populations' if overwinter food is lacking. In some cases, aspen (*Populus tremuloides*), cottonwood, or willow can be provided at beaver reintroduction sites, or where beaver have initiated dam-building on their own, to encourage beaver to remain at the site and to provide them with stronger dam-building material (Apple et al. 1985). Overwinter beaver survival can also be enhanced where surface water freezes and thaws during winter, allowing increased foraging opportunity of herbaceous vegetation. Even relatively short-lived beaver dams can initiate a positive riparian response, which includes a higher water table, increased summer flows, increased silt deposition, and increased riparian width. This response can increase the establishment and survival of riparian woody vegetation suitable as winter beaver food. Adequate winter food stored in a cache can increase the survival and fecundity of beaver that live in climates where ponds or streams freeze in winter, creating a source population that can disperse to additional marginal habitat. Thus, beaver can create a positive feed-

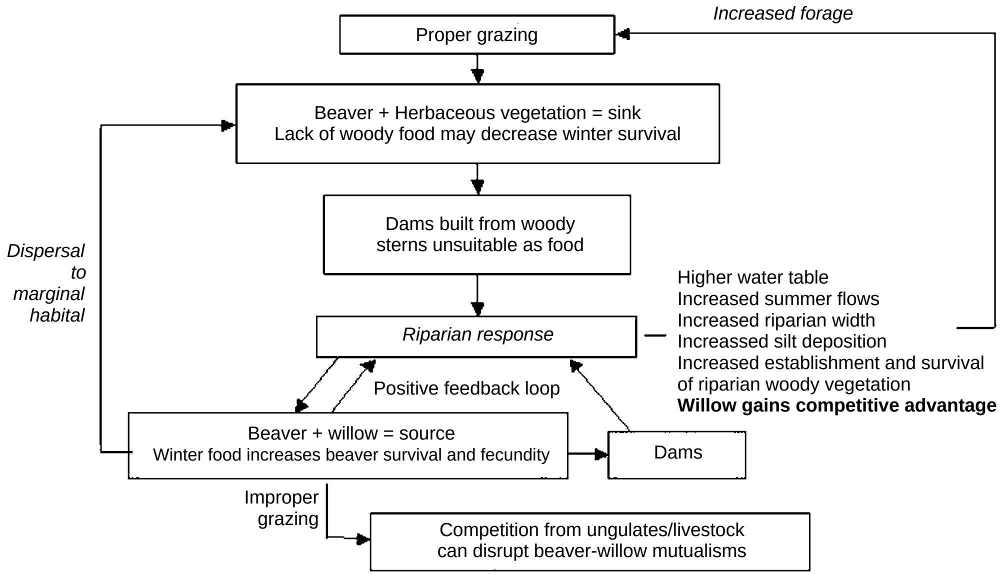

Figure 1. Beaver as a riparian restoration agent in shrub-steppe ecosystems. Modified from Baker & Hill (2003).

back mechanism by temporarily expanding into marginal habitat (naturally or by introduction), creating conditions for the establishment and survival of a winter food supply such as willow, and persisting long enough to raise young that can disperse to new marginal habitat. Increased livestock or ungulate forage in response to greater moisture availability is an additional benefit in many dry environments, which may increase carrying capacity under proper grazing management.

Beaver restoration in western riparian areas may also help control tamarisk, a facultative phreatophyte which tolerates drought and intermittent water tables much better than willow, an obligate phreatophyte. In northwestern Colorado, USA, beaver used tamarisk, big sagebrush (*Artemisia tridentata*), and black greasewood (*Sarcobatus vermiculatus*) as building material for a series of dams that appeared to increase the distribution and abundance of coyote willow (*Salix exigua*) relative to tamarisk (B.W. Baker, unpublished data). A similar response was observed on the Zuni Indian Reservation in New Mexico, USA, following the relocation of 23 beaver to 7 restoration sites (Albert & Trimble 2000). As beaver selectively cut vegetation and impound water behind dams, they alter conditions driving establishment and survival in riparian plant communities. Thus, beaver may create a competitive advantage for willow relative to tamarisk in some riparian systems, although specific mechanisms need further study at different spatial and temporal scales (B.W. Baker, unpublished data).

Conclusions

Where beaver benefit willow and willow benefit beaver, they can be considered mutualists. However, this mutualism can collapse in environments heavily browsed by ungulates or livestock. The interaction of beaver cutting and livestock or ungulate browsing can strongly suppress compensatory growth mechanisms that naturally occur in less competitive environments. More research is needed to determine the threshold of additional utilization that beaver-willow communities can tolerate before ecosystem collapse. Riparian ecosystems that have been overgrazed by livestock or ungulates can be restored if grazing practices are implemented that leave adequate herbaceous and woody vegetation for beaver and where beaver dams initiate a positive riparian response. Competition with other herbivores such as ungulates and livestock should be considered as an important limiting factor in the restoration and management of both species of beaver (*Castor canadensis* and *Castor fiber*).

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Samenvatting

Bevers (*Castor canadensis*) in sterk begraasde milieus

Beverpopulaties (*Castor canadensis*) zijn afgenomen of zijn niet hersteld in sterk begraasde milieus. Ik suggereer dat intensieve begrazing door landbouwhuisdieren of wilde hoefdieren de mutualistische relatie tussen bevers en wilgen (*Salix* spp.) kan verstoren, een relatie die zich waarschijnlijk ontwikkelde in meer predator-rijke milieus met relatief weinig herbivorie, en dat deze verstoorde relatie de afname van bevers en wilgen zou kunnen verklaren. Veldexperimenten in Rocky Mountain National Park, Colorado, VS, toonde aan dat de combinatie van begrazing door bevers en edelherten (*Cervus elaphus*) de hergroei in wilgen onderdrukt. Intensieve begrazing door edelhert van wilgen waar bevervraat was gesimuleerd, resulteerde in kleine, kort afgegraasde planten, met een hoog percentage aan dode stammen, terwijl beschermde planten groot en sterk vertakt waren, met een laag percentage aan dode stammen. De evaluatie van een door bevers aangelegde voedselopslag voor de winter liet zien dat bevers houtige stammen selecteren met een lager percentage door edelherten afgegraasde eindscheuten. Een gebrek aan geschikte wilgenstammen als wintervoedsel voor bevers kan de oorzaak zijn van een afname in beverpopulaties, wat vervolgens weer een negatief effect heeft op wilgen. In tegenstelling hiermee kunnen bevers dammen bouwen in marginaal habitat, mits begrazing door landbouwhuisdieren of wilde hoefdieren beperkt is, en dispersie van bevers mogelijk is vanuit nabijgelegen bronpopulaties. Dit komt de wilgen ten goede en leidt tot herstel van oevervegetaties in aangetaste (overbegraasde) habitats. In door struiken gedomineerde oevervegetaties in noordwest Colorado, VS, initieerde het stopzetten van overbegrazing door landbouwhuisdieren het herstel van een bever-wilgen gemeenschap. Concurrentie van landbouwhuisdieren of wilde hoefdieren kan dus betekenen dat bevers en wilgen afnemen, en kan voorkomen dat sterk begraasde oevervegetaties zich herstellen, maar bever- en wilgenpopulaties kunnen zich herstellen bij een gepast begrazingsbeheer.

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Beaver pond development and its hydrogeomorphic and sedimentary impact on the Jossa floodplain in Germany

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Abstract: This paper presents results of a two-year study showing different beaver (*Castor fiber*) induced hydrogeomorphic changes on the floodplain of the small river Jossa (Spessart Uplands, Germany). Using GIS and aerial photography, different stages of river and floodplain morphology were mapped. In addition, length of water courses, areal extent of ponds and wetlands, sediment depths, volumes and sedimentation rates, as well as erosion rates and amounts of eroded material were calculated with the supplementary aid of precise levelling. The results revealed that beaver dams create large wetlands and greatly increase the area of open water surface by damming-up ponds. Moreover, they enhance the total water flow length by diverting water onto the floodplain, resulting in a multi-channeled drainage network. The new diversion channels induced the erosion of 50 m^3 of overbank fines. By reducing flow velocity within the dammed-up channel and by diverting water onto the floodplain, the dams lead to the deposition of a total amount of 1,890 m^3 of sediments within the beaver ponds and on the inundated floodplain.

Keywords: beaver, channel pattern, GIS, geomorphic factor, sedimentation patterns, sediment fluxes.

Introduction

The manifold alterations of upland streams and floodplain areas by beaver (*Castor* spp.) tree felling or dam building activities are described by many authors. But, the majority of investigations on geomorphic effects of beaver dams have concentrated on the natural landscapes of North-America. However, specific data e.g. relating to sedimentation rates in beaver ponds are still rare (cf. e.g. Butler & Malanson 1995, Meentemeyer & Butler 1999, Naiman et al. 1986).

Publications on the European beaver (*Castor fiber*) concentrate on its ethology and morphology, but little is known about the role of the European beaver as a “geomorphic agent” in the cultivated landscapes of central Europe (cf. Butler 1995, Zahner 1997, Gurnell 1998, Harthun 1998). This lack of knowledge is caused by the human extermination of beavers in most regions of Europe.

In the Spessart Uplands, less than 100 km east of Frankfurt/Main (central Germany), beavers remained extinct from the 17th century until reintroduction of 18 beavers (*Castor fiber albicus*) in 1987/1988. Afterwards, the population size increased to more than 260 individuals in 2003.

Especially in the catchment of the 3rd order river Jossa (figure 1), they showed intensive dam-building activity which led to extensive changes on river and floodplain morphology.

In a two-year study at Jossainsel beaver site, several methods were used to visualise and analyse beaver-induced hydrogeomorphic changes of channel pattern, sediment fluxes and erosion processes on the upland valley floor of the Jossa. The results presented in this paper should make a further useful contribution to draw more attention on the dam-building activity of the European species and its hydrogeo-

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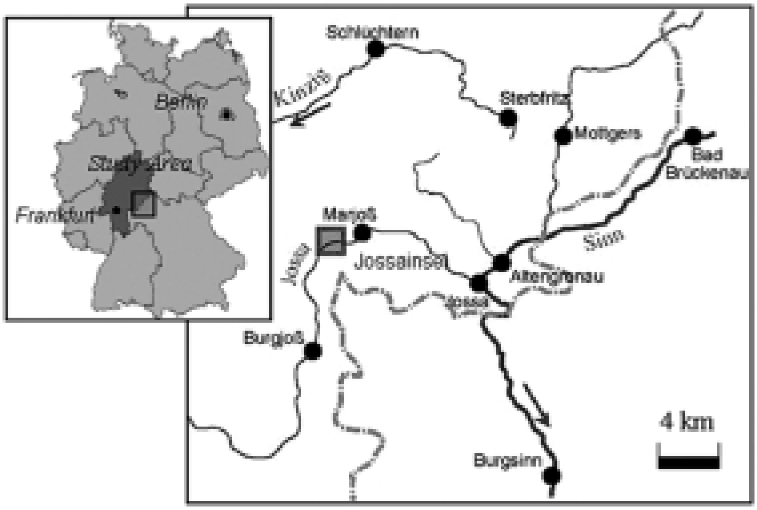


Figure 1. The study area in the Spessart Uplands of Germany. The rectangle shows the study site Jossainsel.

morphic consequences that give beaver great significance as a geomorphic agent.

Methods

To visualise and analyse these beaver-induced alterations, different stages of channel pattern and floodplain morphology (1998-2001) were mapped on the basis of large-scale aerial photographs. Using Geographic Information System (GIS) length of water courses as well as the areal extent of ponds and wetlands were calculated. The additional integration of precise levelling by electronic tacheometry allowed the construction of a digital elevation model (DEM) of the study site. This DEM enabled not only the calculation of pond volumes but also the volume of eroded material by digitising the limits of the area where erosion had occurred, and determination of the former surface elevation level.

The combination of both GIS and DEM allowed the construction of precise large-scale digital maps of the study site. On this basis, sediment depths were mapped in the field by probing with a special measuring rod that was pushed into the sediment as far as it could reach, typically contacting the pond bottom or former soil surface by transition to coarser or more compacted substrates. All field data were added to the GIS and were used to produce a classified map of sediment depth. To calculate the total sediment volume, the sediment depths of each class were averaged and multiplied with the corresponding sedimentation areas. The annual sedimentation rates were calculated by dividing average sediment depth per area by age (in years) of beaver ponds.

Results

The reach of the study site is characterised by a wide, low gradient valley floor. The stream is split up into the main channel Jossa and a lateral channel Jossagraben, which divide and then rejoin after 1 km.

From the year 2000 to 2001 four beaver dams (bp00/1, 00/2, 00/3 and bp01/1) blocked water flow within the Jossagraben impounding four durable beaver ponds in the northeastern part of the study site (figure 2). The amount of impounded water within these ponds fluctuated from 902 m^3 in summer 2000 to 1,708 m^3 in winter 2000/2001 (table 1). Pond drainage led to the development of two back swamps on the floodplain, which stored additional 808 m^3 of water in summer and 1,894 m^3 in winter. The open water surface of all these ponds fluctuated from 5,335 m^2 in summer to 10,059 m^2 in winter. The largest beaver pond was bp00/1 with an area of 2,555 m^2 in winter. However, its value is still surpassed by the area of the beaver induced back swamp (bsw 1 = 4,191 m^2), that could also be called a “secondary beaver pond” in cause of its beaver induced origin.

In autumn 2001 two new dams were built up in the lateral channel Jossagraben (figure 2: map B), leading to large wetlands and the maximum size of the affected area (total submerged area: over 43,700 m^2, corresponding to more than 20% of the study site). The dams increased the total area covered by beaver ponds and back swamps to 11,855 m^2 (table 1). Additionally, these dams enhanced the total water flow length of the affected channel Jossagraben by approximately 140% from 1 km to more than 2.4 km by diverting water onto the floodplain. As a result of this process a multi-channeled (anastomosing) drainage network consisting of numerous interconnected ephemerally, intermittently and perennially occupied channels developed (figure 2).

Most of these channels follow relict drainage ditches or beaver trails. They were deepened by the effects of flowing water and rarely by beaver digging activity. Where pond drainage was concentrated on a few relatively stable channels, linear downcutting and headcut erosion led to the development of one single dominant channel. The total amount of eroded material by these erosion processes was 50 m^3 within three years, corresponding to a total erosion rate of 17 m^3/yr. At least 21 m^3 were due to deep headcut erosion at the mouth of the main diversion channel into the Jossa.

However, the amount of eroded material was surpassed by the effect of beaver dams on sediment storage. An increased fluvial and lacustrine deposition of organic matter, sands and silts led to sediment depths up to 107 cm (average 37 cm) within beaver ponds and up to 38 cm (average 14 cm) on the floodplain (figure 3). This beaver induced sedimentation occurred within an area of 10,740 m^2, leading to a total amount of

Table 1. Selection of the measured values of pond areas, volumes and sediment storage at the Jossainsel study site.

	pond area 2000-2001		max. area (m^2)*	pond volume 2000-2001		pond age (yrs)	sediment storage 2001		
	min. (summer) (m^2)	max. (winter) (m^2)		min. (summer) (m^3)	max. (winter) (m^3)		volume (m^3)	average depth (cm)	rate (cm/yr)
beaver ponds									
bp00/1	1775	2555	2555	460	952	2	516	22.7	11.3
bp00/2	386	754	745	67	287	3	243	32.6	10.9
bp00/3	435	682	428	318	380	2.5	147	24.8	9.9
bp01/1	78	78	78	57	89				
bp01/2			552						
bp01/3			1551						
total beaver ponds	2674	4069	5879	902	1708		905	25.1	10.7
drainage network									
back swamps									
bsw 1	2324	4191	4191	800	1284	3	173	11.6	3.9
bsw 2	337	1599	1507	8	610	3	33	12.4	4.1
bsw x		200	278						
wetlands							779		
total drainage network	2661	5990	5976	808	1894	3	985	14.0	4.7
total	5335	10059	11855	1710	3602		1890	17.6	5.9

* autumn 2001

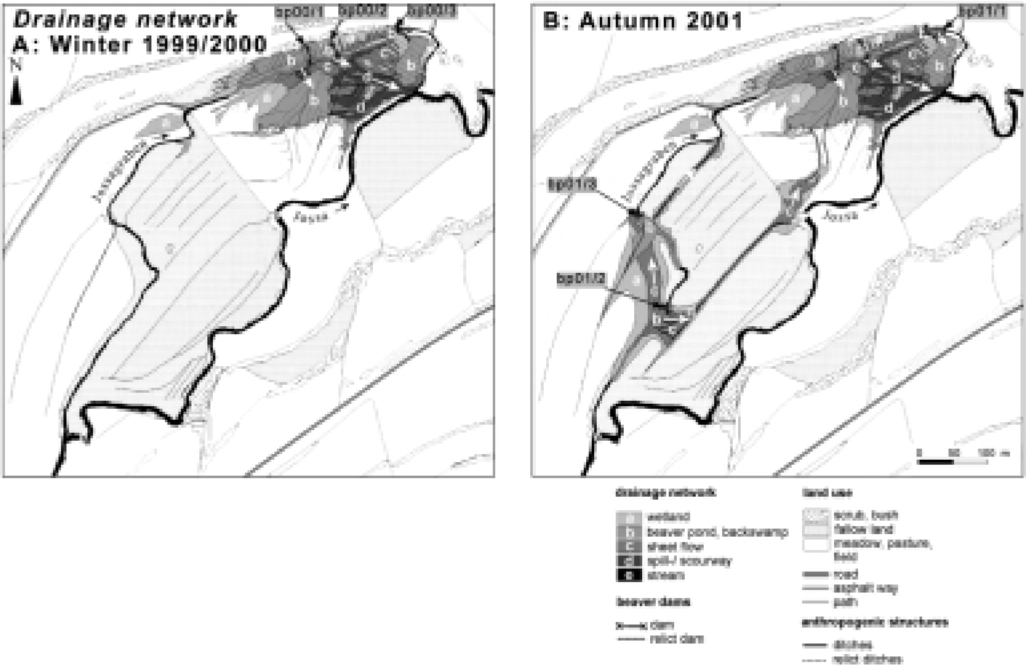


Figure 2. Maps A and B show the formation of a multi-channeled drainage network at the Jossainsel study site from 2000 until 2001. Grey colours distinguish between different stillwater areas, black represent water courses.

1,890 m^3 of sediments. Considering a colonisation period of three years this resulted in a sedimentation rate of approximately 6 cm/yr.

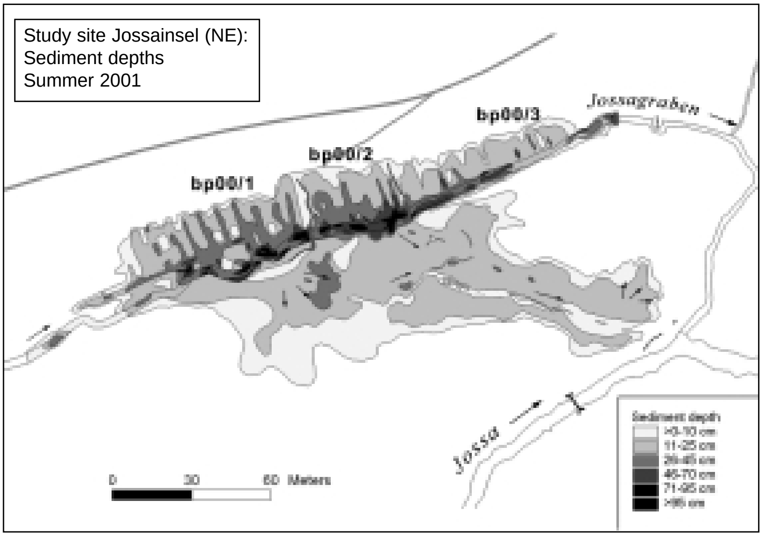
The values of sediment storage within the beaver ponds tend to decrease along the main flow paths. The highest sediment volume occurred in the upper younger pond bp00/1 and the lowest in bp00/3 (table 1), illustrating a downstream reduction of sedimentation in a pond sequence. However, only about 49% of these sediments were deposited within the beaver ponds. The other 51% were caused by permanent overbank flow, leading to accumulation of extended fine, organic rich drainage network deposits on the inundated floodplain (figure 3). This indicates that the multi-channeled drainage network was an important depositional environment.

Discussion

The results illustrate the dynamic character of floodplain sites affected by beavers and show that beavers are important geomorphic agents that alter floodplain morphology in many ways (cf. Naiman et al. 1986, Naiman et al. 1988, Hammerson 1994, Gurnell 1998). However, it is necessary to note that the scale of beaver-induced geomorphic changes depends on the conditions for dam construction, especially river size and hydraulic characteristics e.g. the limitation of dam-building to low order rivers (e.g. Naiman et al. 1988, Gurnell 1998).

As first obvious consequence of beaver dams the areal extent of water surfaces and waterlogged areas increased and a complex multi-channeled drainage network developed on wide low gradient valley floors and enhanced the total water flow length. Many other general descriptions or maps of beaver sites in the literature reveal similar conditions (e.g. Townsend 1953, Retzer et al. 1956, Naiman et al. 1988, Zahner 1997, Gurnell 1998, Harthun 1998). The values of the calculated pond areas are comparable to many others e.g. cited by Naiman et al. (1986), Devito & Dillon (1993) and Harthun (1998). But there are no data in literature

Figure 3. Map of the north-eastern part of the Jossainsel study site showing the distribution of sediment depths within the beaver ponds and the adjacent multiple drainage network.



corresponding to the phenomenon of beaver induced back swamps. At Jossainsel such a "secondary beaver pond" exceeded the maximum size of the largest beaver pond in the Spessart Uplands (over 4,000 m^2) cited by Harthun (1998).

Moreover, erosion of soils and deposition of sediments occurred within the impounded stream (beaver pond) as well as on the floodplain (drainage network). Whereas quantitative investigations into beaver induced erosion processes are lacking, apart from some reports about the effects of catastrophic dam failures (e.g. Butler & Malanson 1995), a few studies concentrate on sedimentation processes in beaver ponds.

Some authors provide estimates for sedimentation rates from 0.6 to >2.5 cm per year (Mills 1913, Ives 1942, Devito & Dillon 1993). Others mention the deposition of several cubic meters of sediments behind a dam by a single flood event (Coleman & Dahm 1990) or calculate a deposition of 35-6,500 m^3 of sediments within an area of 100-14,650 m^2 (Naiman et al. 1986).

The values estimated from the Jossainsel (table 1) are comparable to the average sediment depths (21.8-86.0 cm), sediment volumes (9.4-1,290 m^3) and sedimentation rates (3.6-27.9 cm/yr) of the younger ponds in Glacier National Park (USA) mentioned by Butler & Malanson (1995) and Meentemeyer & Butler (1999).

In contrast to Butler & Malanson (1995), our results reveal that downstream reduction of sedimentation in a pond sequence seems to dominate the influence of pond age. The highest sediment volume and sedimentation rate at Jossainsel occurred at the youngest but upper pond bp00/1 and not in the oldest pond bp00/2.

While previous sedimentary research at beaver sites has focused on sediments within beaver ponds, our results also reveal the importance of drainage network deposits at beaver sites on wide spread valley floors.

If we assume a European beaver population of more than 60 million individuals in the early Holocene (Czech & Schwab 2001) and their extinction no earlier than the 17th century in most regions of central Europe, these data provide further rationale for attributing beaver activities a high significance as a factor of holocene floodplain development along low order rivers in central Europe.

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Samenvatting

De ontwikkeling van bevervijvers en het effect van hydro-geomorfologische en sedimentatieprocessen op de overstromingsvlakte van de Jossa in Duitsland

Deze bijdrage beschrijft de resultaten van een twee jaar durende studie naar de door bevers (*Castor* spp.) veroorzaakte hydro-geomorfologische veranderingen van in riviertje de Jossa (Spessart, Duitsland). Met behulp van het Geografisch Informatie Systeem en luchtfotografie werden de verschillende stadia van de rivier en de overstromingsvlakte morfologisch gekarteerd. Ook de lengte van de waterlopen, de ruimtelijke uitbreiding van vijvers en wetlands, de sedimentatie-diepte, -volume en sedimentatie-snelheid werden berekend. De erosiesnelheid en de hoeveelheid geërodeerd materiaal werd bepaald met behulp van precieze niveauvergelijkingen. De resultaten laten zien dat beverdammen grote wetlands creëren en in sterke mate de oppervlakte open water vergroten door het verder verhogen van dammen bij bevervijvers. Verder verhogen bevers de lengte van de totale waterstroom door het omleiden van water over de overstromingsvlakte, hetgeen resulteert in een wijdvertakt drainage-netwerk. De nieuwe omleidingskanalen veroorzaken de erosie van 50 m^3 van fijn, lemig fluviaal sediment. Door de reductie van de stroomsnelheid binnen het door dammen ontstane kanaal en door omleiding van water over de overstromingsvlakte, veroorzaakten de beverdammen een depositie van in totaal 1890 m^3 sediment in de bevervijvers en op de overstroomde vlakte.

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Is it possible to use beaver building activity to reduce lake sedimentation?

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Abstract: Erosion processes and lake sedimentation are among the major environmental problems in Tatarstan Republic. Ploughed soils from the agricultural lands are easily washed away from the fields during flooding, and carried through rivers and relief depressions to lakes and bogs, which then fill with the sediment. Raifa Lake is an example of such lake degradation. Due to erosion from agricultural lands upstream from the lake its length has decreased from 6 to 1.3 km since 1650, its maximum depth has decreased from 36 to 19 m, and its area has decreased from 150 to 32 ha. The possibility of "harnessing" beavers (*Castor fiber*) to stop sedimentation by building dams is of great interest. We hoped that dams constructed by beavers would reduce the volume of solid particles that flow into Raifa Lake. With this objective in mind, we reintroduced 21 beavers between 1996 and 2000 on the Sumka River, which runs through Raifa Lake. Investigation was done during the annual flooding periods of 1999-2001 when 115 water samples were taken. The main factor that affects sedimentation is the volume of water that can be stopped by beaver ponds. During the flooding period of 2001, 4,250 tons of solid particles were stopped by three beaver dams in the settlement on Sumka River amounting to a cumulative area of 5.2 ha. Sediment mass per litre of water decreased by 53% (from 0.49 to 0.26 g/l) after water had passed the cascade of three dams.

Keywords: beaver, *Castor fiber*, Volga-Kama Nature Preserve, water quality, sedimentation, reintroduction, dams, building activity.

Introduction

Today the role of the beaver (*Castor fiber*) as a hunting-trade species has largely disappeared, at least in the Tatarstan Republic, and emphasis is now placed on researching its landscape-creation role in planning the restoration of riparian zones disturbed by humans. Landscapes in the Tatarstan Republic are influenced by intensive economic activity, such as agriculture (cereals, grain crops, root crops and fodder crops), oil production and cattle grazing. In particular, there is a high anthropogenic pressure on the hydrological system because of the development of erosive processes that cause sedimentation in lakes and bogs.

Detailed research of this problem was carried out in the Raifa portion of Volga-Kama National Nature Preserve (VKNNP). No human settlements were present, and the watershed was covered by forest until 1660, when a monastery was built on the bank of Raifa Lake. Settlements appeared and the forest was cleared for agricultural lands. A reduction in the percentage of land covered by forest and irrational agricultural practices (ploughing up slopes and territories near rivers) have resulted in intensive soil erosion on land upstream of the preserve. Sediment that is washed away from fields during spring flooding enters the Sumka River and is carried to lakes and bogs of the preserve, which has decreased their area. For example, the area of Raifa Lake has decreased from 150 ha to 32 ha during the last 400 years. Without in the introduction of less erosive agricultural techniques in the Sumka River basin, some lakes will disappear or turn to bogs (Taisin 1969, Taisin 1996).

We have attacked the problem on two fronts. One involves the re-establishment of beavers, whose dams may catch sediment and lengthen the life of lakes and bogs. Beaver dams affect sedimentation through (1) reducing sediment loads per cubic metre, and (2) stopping big volumes of water thereby causing a reduction in the absolute amount of sediment carried downstream. Later water evaporates and soaks into the ground and sediment accumulates on the bottom of the pond. The last of the beavers in the Tatarstan Republic were killed in 1802. Beginning in 1949, beavers were reintroduced to many parts of the region and now number about 3,000. But only 16% of the republic is forested and the island of forest in which the preserve is located would take a long time to recolonise, if it happened at all, without human intervention. So, our first step was to reintroduce beavers to the preserve (Gorshkov et al. 1999, Gorshkov et al. 2002). A second and longer-term front on which to solve the erosion problem is to find the sources of sediment and implement less erosive agricultural practices in those areas. Our long-term tactic is to work directly on sediment sources, as beaver ponds will only hold a finite quantity of sediment.

Study area

The Raifa part (5,921 ha) of the VKNNP is located 800 km east of Moscow and 600 km west of the Ural Mountains near the city of Kazan, Tatarstan Republic, Russian Federation. Much of the VKNNP forest is 250-300 years old. Western and eastern sections of the preserve are bordered by forests; the northern and southern sections border agricultural lands (figure 1).

The Sumka River (length 37.5 km) and its main tributary, the Ser-Bulak River (length 11.5 km; figure 1), are connected to ten lakes. The Sumka River watershed contains 46% forest in a patch distribution. The upper part of the Sumka River is agricultural land which causes intensive

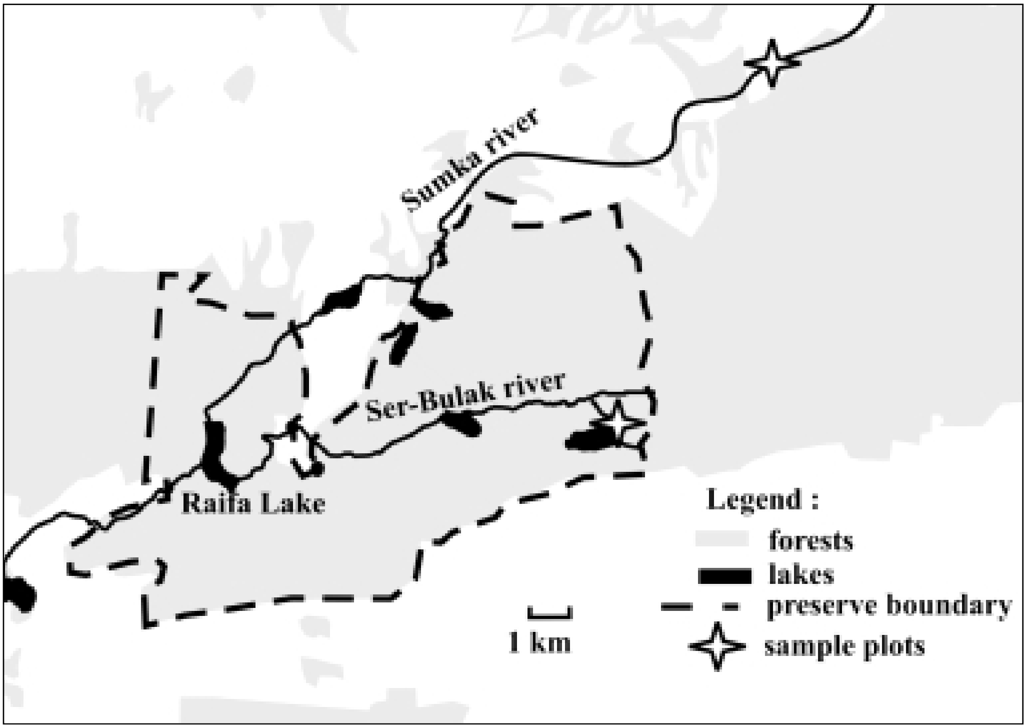

Figure 1. Map of Raifa, part of Volga-Kama National Nature Preserve.

erosion. The watershed of the Ser-Bulak River is almost completely covered by forest. Both rivers flow intermittently, with 80% of the annual runoff in April (Unkovskaia et al. 2002).

Methods and materials

Beavers were relocated from tributaries of the Vyatka River to the Raifa portion of the VKNNP. Animals were released in 1996, 1997, 1999, and 2000, and numbered 6, 7, 3 and 5 individuals, respectively. To study the role of beaver dams in sediment retention, we took water samples during the spring floods of 1999-2001. To perform the investigation we chose two beaver settlements: A and B. Site A, with three dams, was located in the upper part of the Sumka River, in the preserve's buffer zone. Plot A1 was a control plot upstream of all the ponds (figure 2). Plot A2 was in the upper pond and A3 was in the middle pond 50 metres below the upper dam. Plot A4 was downstream from the whole cascade of dams. Site B was located at a beaver settlement in the Ser-Bulak River, which contained plots B1, B2, and B3, respectively above, in and below a single beaver pond (figure 2). Settlements were active throughout the study and the location of the dams did not change.

If the depth was less than 50 cm we took a water sample at half the depth. If the depth was more than 50 cm we took a water sample 20 cm from the bottom and 20 cm from the surface of the river. Water samples were filtered to determine the mass of sediment per litre. We calculated water flow using water velocity and area of wetted cross-section, which were measured using standard methods (Potapova 1975, Luchsheva 1983). Using the amount of sediment per litre and water flow rates, we calculated the amount of sediment that passed through the stream projection in a time period. The difference between total amounts of sediment that passed through plots A1 and A4 during spring flood was the amount of sediment that was retained by beaver dams during flooding.

Using these methods, 115 water samples were collected on the Sumka River and 48 on the Ser-Bulak River. Water samples were taken around midday at each plot (time of sampling was recorded to within a minute accuracy), once every 2-4 days depending on the intensity of flooding.

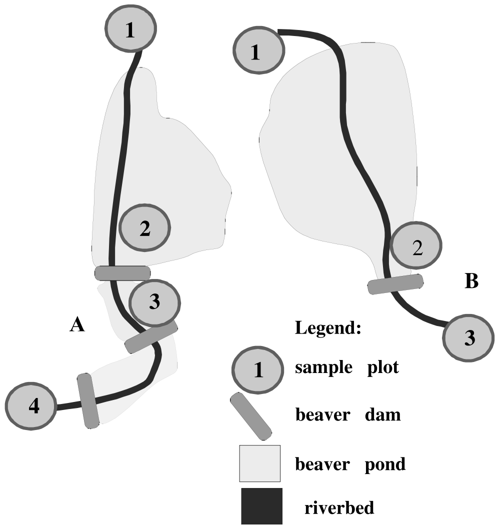

Figure 2. Scheme of hydrometric plots on an observation site on the Sumka River (A) and the Ser-Bulak River (B).

Results

Beavers built 26 dams during the seven years they occupied the Raifa portion of VKNNP and its buffer zone. Dam height varied from 0.3 to 1.6 m, and maximum length was 8 m. The total area of active beaver ponds in the Raifa portion of the preserve was about 14 ha, and 0.54 ha on average (table 1).

The Sumka River within site A (figure 1) was 1-2 m wide during mean flow rates of a year and about 6-8 m during the flooding period. The depth varied from 0.15-0.20 up to 1 m. During the spring flooding of 2001 the total sediment mass at site A reached 4,600 tons (figure 3). The dams decreased the amount of sediment in a litre of water (there was 53% less (reduced from 0.49 to 0.26 g/l) below the cascade of ponds) and also

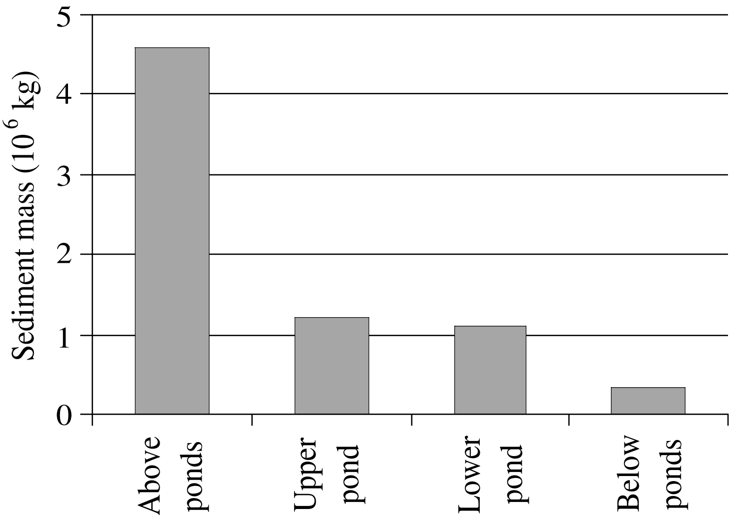

Figure 3. Sediment mass characteristics at hydrometric plots above, in and below beaver ponds on the Sumka River during a spring flooding of 2001.

stopped water that contained sediment. The difference of the parameters of plots A1 and A4 (figure 3) shows that during the flooding period the system of three dams retained about 4,250 tons of sediment. The greatest volume of sediment was filtrated by beaver ponds during the peak of flooding in April 16-18, 2001 (figure 4).

The Ser-Bulak River at site B (figure 2) has a mean width of 0.5 m during low water and about 2 m during flooding. The depth varies from 0.05 to 1 m. During the spring flooding of 2001 the total sediment mass at site B on the Ser-Bulak reached 26.9 tons (figure 5). Because of low mass of sediment per litre (about 0.025 g/l), the weight of sediment retained by a pond (20.6 tons) is only one-hundredth of the amount

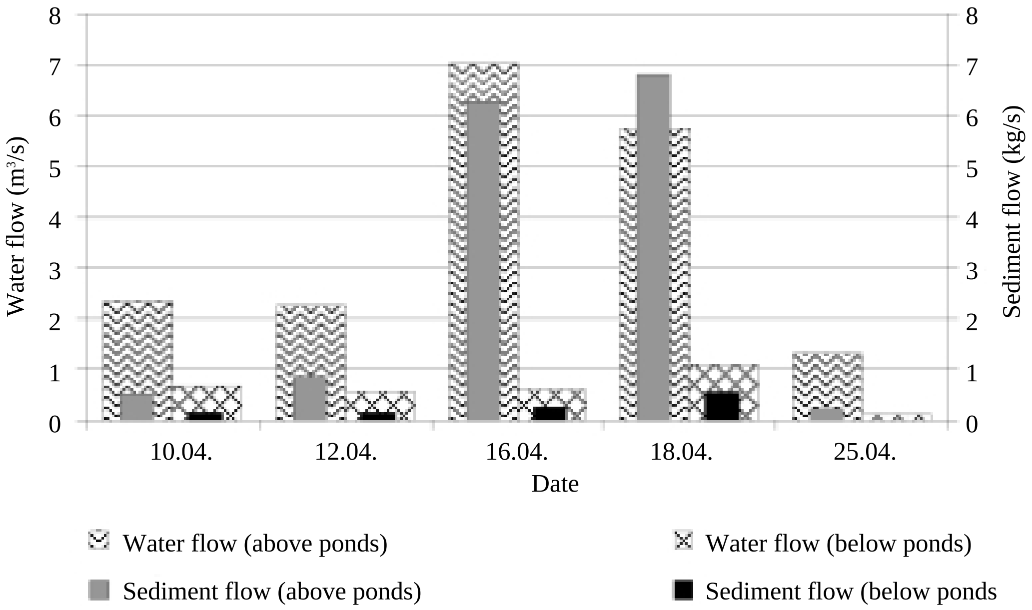

Figure 4. Dynamics of water and sediment flow rate of plots above and below beaver ponds on the Sumka River during a spring flooding of 2001.

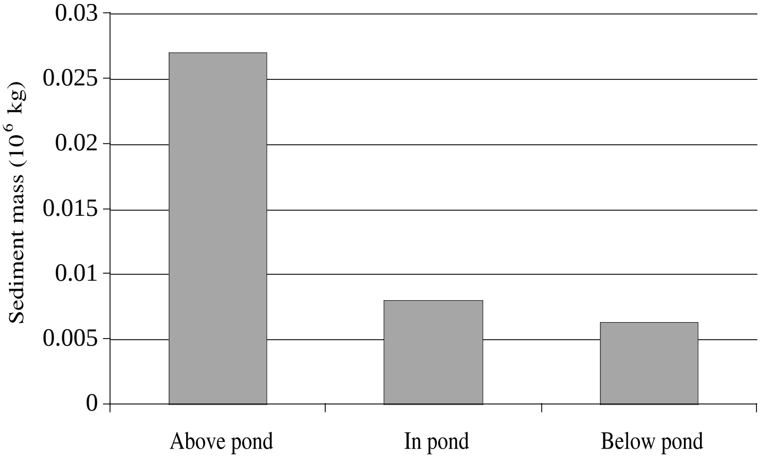

Figure 5. Sediment mass characteristics at hydrometric plots above, in and below a beaver pond on the Ser-Bulak River during a spring flooding in 2001.

retained by a pond on the Sumka River. There was no significant difference in the mass of sediment per litre of water in the samples from plots B1 and B3, and all the sediment was retained due to the slowing of much of the water. The beaver pond on the Ser-Bulak River was 6.8 ha. There was a gradual increase of the water and sediment mass, which reached a maximum by April 23, 2001, the date of peak flooding (figure 6).

Discussion

The amount of the sediment stopped by beaver dams depends on the width of a dam, geological conditions and stream velocity (Bruzuski & Kulczycka 1999). According to the data of Naiman et al. (1986, 1988), an amount of between 1,000 and 6,500 m^3 of sediment accumulated per beaver pond in one year, and according to the data from Czech & Prior (2001), an amount of between 1,000 m^3 up to 10,000 m^3 of sediment accumulated. Brayton (1984), mentions that the daily sediment mass on Current Creek (Wyoming, USA) was reduced from 33 to 4 tons.

In total, at site A on the Sumka River during the flooding period, 4,250 tons of sediment was retained (4,700 m^3). The thickness of the sediment layer that was accumulated in the pond on the Sumka River (area 5.21 ha) during the flooding period of 2001 was about 9 cm. With time, sediment of up to two metres in depth can accumulate (Rasmussen 1940, Call 1966).

A large amount of sediment was stopped during the peak of flooding, when big volumes of water were filtrated by beaver ponds. The mass of sediment per litre of water after it had passed through all dams at the peak of flooding had been reduced by 55%. That is comparable with the data received by Parker (1986). In his research the water sample below beaver dams had 50-75% less sediment. Before and after the peak of a flooding, when the level of water was low, the mass of sediment per litre was reduced by only 8%. The percentage of the sediment that was stopped by dams is highly correlated with the level of water (r=0,94).

Unlike the Sumka River, the watershed of the Ser-Bulak River is covered by forest. It is also the reason for low mass of sediment in a litre of water during flooding. And as a consequence, the mass of retained sediment is hundreds of times less than on the Sumka River.

There was no significant difference in mass of sediment per litre of water between hydrometric plots on the Ser-Bulak River. All sediment was retained because the large volume of water with sediment was stopped by a dam.

Because of the increased number of beavers in the preserve, some of them were forced to move

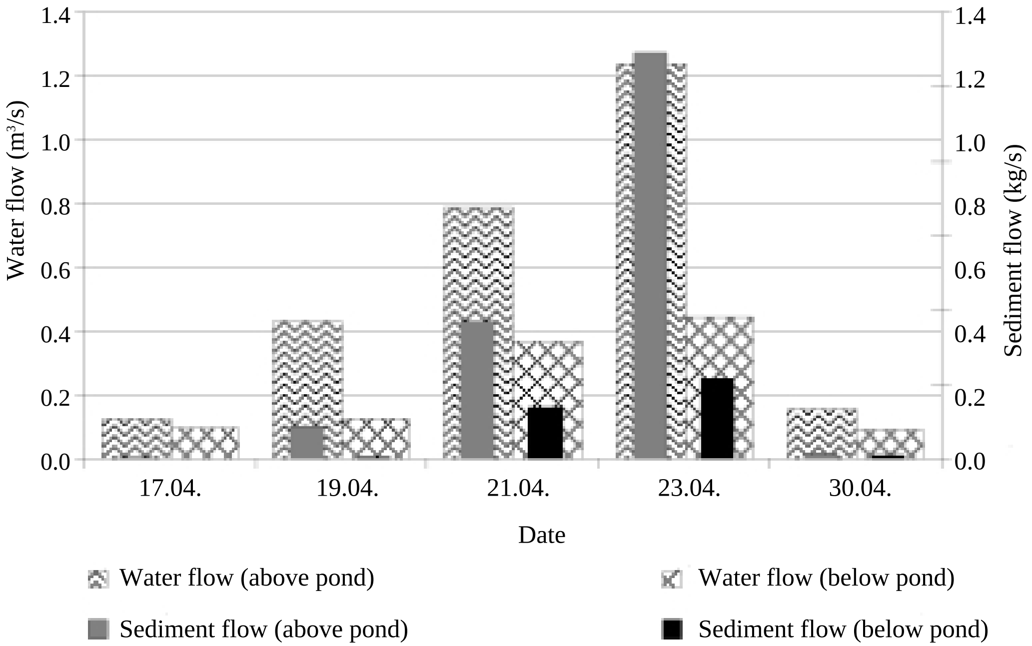

Figure 6. Dynamics of water and sediment flow rate of plots above and below beaver pond on the Ser-Bulak River during a spring flooding in 2001.

to suboptimal conditions where dam building was a necessity to survive. That is why the dams in the preserve were only constructed in the last few years (table 1). Since beavers have been present in the preserve the average amount of dams per settlement has increased from 0 (1996) to 3.3 (2002). As the number of beavers increases in the future, their building activity in the preserve will be more intensive for several reasons. First of all, beavers have constructed dams in those places where there was an opportunity to maximize the area of a pond (table 1). Secondly, the hydrological consequences of beavers are inversely proportional to river discharge (Legeyda 1992). This is the reason that the majority of beaver settlements with dams are in the upper part of the rivers. Stable water flow during the year with the low water discharge gives beavers an opportunity to adjust the level of water according to their needs. Secondly, the area of the flooded pond depends not so much on the size of a dam, but on the local relief (Legeyda 1992). Therefore, the average size of beaver ponds in Raifa portion of VKNNP is small (0.54 ha). The floodplain landscape only allows beavers to make big ponds in a few places. In the majority of cases, after construction of a dam there is only a small increase of width and depth of a pond. In different conditions the area of beaver ponds varied by 0.47 ha in one study

Table 1. Numbers of beaver dams and the size of beaver ponds on rivers of Raifa portion of the preserve and its buffer zone. From the time of reintroduction (1996) till 2002 all the beaver settlements with dams were active.

	1996	1997	1998	1999	2000	2001	2002	Total
Area of new ponds (ha)	0	6.9	3.1	1.8	1.6	0.3	0.4	14.1
Average size of a pond (ha)	0	2.3	1.03	0.9	0.8	0.05	0.04	0.54
Number of new constructed dams	0	3	3	2	2	6	10	26
Average number of dams per settlement	0	0.5	1	1.3	1.4	2.3	3.3	3.3

(Sinitsin 1994), ranged from 0.08 up to 15 ha, making an average of 3.3 ±0.57 ha in a second study (Zavyalov 1999), and ranged from 0.5 up to 10 ha in a third study (Czech & Prior 2001).

Most of the dams (20) were constructed on the Sumka River, which is the main supplier of the sediment entering Raifa Lake. As the beaver population increases, some of their numbers should move close to Raifa Lake, which should lead to a greater reduction in sediment volumes filling the lake.

Conclusions

Beaver ponds are able to retain a significant mass of sediment (4,250 tons). The mass of the sediment retained by beaver dams depends on the volume of water that was filtrated and stopped by dams. The greatest amount of sediment is retained during the peak of flooding when the biggest volumes of water are filtrated by beaver ponds. During this time the decrease of sediment mass per litre due to beaver ponds can reach more than 50% in a river with high sediment content.

Building activity of beavers becomes more intensive as the beaver numbers increase in a preserve. At first beavers constructed dams in those places where there was an opportunity to maximise the area of a pond. That is the reason why the average size of the pond decreases while average number of dams per settlement increases with the growth of a beaver population. As the beaver pond areas increase, the volumes of sediment filling the lake will decrease.

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Samenvatting

Is het mogelijk om bouwactiviteiten van bevers te gebruiken om sedimentatie in een meer te verminderen?

Erosie en sedimentatie in meren behoren tot de grote milieuproblemen in de Republiek Tatarstan. De omgeploegde gronden in het agrarisch gebied worden tijdens overstromingen gemakkelijk weggespoeld van de velden en via rivieren en laaggelegen gedeelten afgevoerd naar meertjes en moerassen, die zich vervolgens vullen met het sediment. De Sumka Rivier, met zijn grootste zijrivier de Ser-Bulak, stroomt door het Raifa Meer en vormt een voorbeeld van zo'n erosie- en sedimentatieproces. Sinds 1650 verkortte erosie door agrarisch gebruik van land bovenstrooms van het meer de lengte van het meer van 6 tot 1,3 km, de maximale diepte verminderde van 36 tot 19 m, en het oppervlak kromp van 150 tot 32 ha. De mogelijkheid om bevers te gebruiken om sedimentering te stoppen door het bouwen van dammen is een interessante optie. Gehoopt werd dat beverdammen het volume van vaste deeltjes die het Raifa Meer instromen zou beperken.
Met dit doel werden tussen 1996 en 2000 21 bevers uitgezet in de Sumka Rivier, die door het Raifa Meer stroomt. Gedurende de jaarlijkse overstromingen van 1999-2001 werd op twee plaatsen onderzoek uitgevoerd: aan de rivier Sumka en zijn zijrivier de Ser-Bulak, waarbij in totaal 115 respectievelijk 48 watermonsters werden genomen. De hoofdfactor die de sedimentatie beïnvloedt is het volume water dat door de bevervijvers gestopt kan worden. Tijdens de overstromingsperiode van 2001 werd 4.250 ton aan vaste deeltjes gestopt door drie beverdammen bij de bevervijvers van de Sumka Rivier, die bij elkaar een oppervlak hadden van 5,21 ha. De sediment-massa per liter water verminderde met 53% (van 0,49 tot 0,26 g/l) nadat het water de cascade van drie dammen passeerde.

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On morphology and genetics of a successfully restored beaver population in Lithuania

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Abstract: At least six centres of spread of reintroduced or naturally immigrated animals have influenced the formation of the present beaver (*Castor fiber*) population in Lithuania. Phenetic (non-metrics of skull) and genetic (allozyme electrophoresis) analyses show that beaver subpopulations of different origin have preserved their specificity even in conditions of dense population, 30-40 years since the first releases and arrivals. This specificity might be the result of the founder effect in small geographically and temporally isolated groups of reintroduced beavers. Conversely, subpopulations from the supposed zone of intensive hybridisation were found to be very phenetically similar. Metric parameters of the skull varied slightly among subpopulations, showing the higher metric differentiation between reintroduced beavers and natural immigrants. However, beaver skulls from Lithuania were found to be significantly larger than those from the basic maternal population in the Gomel region (Belarus) and of similar size when compared with the skulls from the Voronezh population (Russia). Our investigations show the complicated morphological and genetic structure of a hybrid beaver population and its considerable morphological changes in comparison with the maternal populations.

Keywords: Castor fiber, hybrid population, non-metric parameters, metric parameters, allozymes, morphological relationship, biochemical relationship, morphological differentiation, Lithuania.

Introduction

During the last centuries the European beaver (*Castor fiber*) has survived a drastic decline in population numbers which has gone as far as extinction in many regions of the continent. Small and isolated relict populations became the only materials available to restore the former species range. The most intensive work on beaver reintroduction was carried out in the middle of the 20th century (Lavrov 1981, Macdonald et al. 1995, Halley & Rosell 2002).

Nowadays the process of restoration of the European beaver populations in a number of European countries still continues. Reintroduced beavers have usually extended their range even to neighbouring countries (e.g. Nitsche & Pachinger 2000), thus showing the undoubted success of reintroduction as well as the high vitality of reintroduced populations. The general development pattern of many reintroduced beaver populations is relatively rapid increase in both the population number and range of expansion (e.g. Hartman 1994, Balodis 1990).

The question is why the reintroduced beaver populations are so viable, even when exploited relatively heavily. In this context we should remember that many aboriginal beaver populations were very vulnerable and became extinct in former centuries. On the other hand, it is important to know what the prospects for the restored populations are. Is vitality or welfare of a population reflected on the morphological and genetic levels? Comparative investigations show distinct morphological differences between newly restored mixed and autochthonous but small beaver populations (Saveljev & Milishnikov 2002). Also, some daughter beaver populations demonstrate significant morpho-physiological changes when reintroduced into different ecological conditions compared with those of the maternal populations (Solovjov 1991).

The beaver population in Lithuania is one of the populations that was very successfully restored during the second half of the 20th century. It shows patterns of intensive development such as rapid expansion throughout the country, fast increasing in population number, high current densities in environments with very different habitat structures (Ulevičius 1997, Ulevičius 1999, Ulevičius 2001). A brief history of this population could be described as follows: start of formation of the population in the 1940s, rapid expansion and colonisation throughout the country over approximately 40 years (13-14 generations), high current population numbers despite comparatively high exploitation since the 1970s.

We started by investigating non-metrical characteristics of the skulls of Lithuanian beavers in the context of the origin of different local populations usually inhabiting separate river basins (Ulevičius 1992, Ulevičius 1993, Ulevičius 1994, Ulevičius 1997). Later results of morphological investigations were tested using biochemical markers (Paulauskas & Ulevičius 2001). Recent metrical investigations on beaver skulls were carried out with respect to both the differentiation of a restored population and its relationship with the maternal populations. The aim of the present publication is to summarise the results obtained by three different methods within the context of origin and morphological and genetic differentiation of a hybrid population.

Material and methods

Lithuania is situated on the southeast coast of the Baltic Sea (21°00'–27°00' E and 54°00'–56°30' N). The total area is 65,200 km^2. The entire territory is covered by river basins of the Baltic Sea tributaries. The mean density of the hydrographical network is nearly 1 km/km^2. There are about 3,000 lakes in Lithuania. Mean density of human population is 52.4 inhabitants/km^2. The course of restoration of the beaver population was reconstructed by studying the archival and unpublished documents as well as local publications and personal communications. Special attention was paid to the year when beavers appeared in a certain district for the first time.

The autochthonous beavers in Lithuania became probably extinct somewhere in the 1920s-1930s (Mickus 1988). In the 1940s, beavers

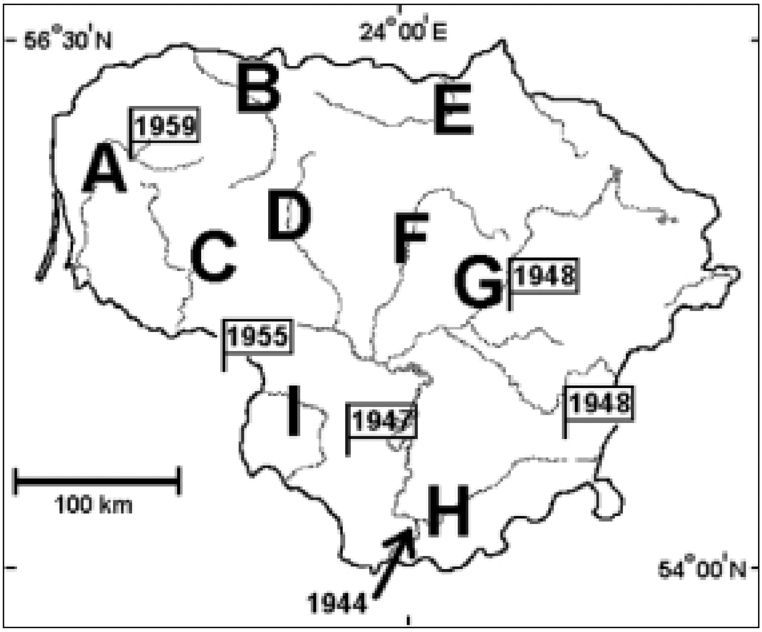

Figure 1. Location and year of beaver reintroductions in Lithuania (designated by flags), and location of samples (designated by capital letters, as in table 1). The black arrow designates spread of natural immigrants from Belarus, the upper reaches of the Neman (Nemunas) river basin.

appeared again in the country as a result of natural immigration and later as a consequence of intensive reintroduction. The genetic pool of the present beaver population in Lithuania has at least potentially been influenced by genetic material of a very different origin. Most reintroduced beavers originated from the Dnepr basin (Belarus). Also, beavers from Voronezh (Russia) may have had a significant genetic influence on some local populations in the southern part (possible gene immigration from Poland) as well as in northern Lithuania (possible gene immigration from Latvia). Phased release of relatively small groups of animals was the characteristic pattern of the reintroduction process. Thus, the genetic structure of such groups was rather strongly influenced by the founder effect, and possibly there were significant genetic differences between groups of animals even from the same maternal population but released at different times.

At least five geographically and temporally isolated reintroduction centres and one centre of natural immigration have influenced the formation of the current beaver population in Lithuania (figure 1). Beaver expansion was very quick and by the end of 1960s beavers were distributed throughout the country. This success was usually explained by favourable ecological conditions (Mickus 1988).

Morphological studies (non-metric and metric parameters) were based on a beaver skull collection sampled in 1986-1988, i.e. when large numbers of beavers were already inhabiting the entire country. Skulls were gathered from hunters during the hunting seasons. Hunters were asked to indicate detailed locality as well as sex and skin colour of a hunted beaver. After rough cleaning, the skulls were boiled for approximately two hours for final cleaning.

For non-metric analysis, 463 beaver skulls from nine local beaver populations were used (figure 1, table 1). These local populations inhabit different river basins: catchment areas of the 2-3 order tributaries of the Baltic Sea. The non-metrical (phenotypic) relationship was studied by analysing the frequencies of 63 variants (phens) of 19 non-metric traits (figure 2, table 2). Primarily, 40 non-metric traits of beaver skull were distinguished. Of them, twelve were rejected as being dependent on age and sex. Nine traits did not work (no significant differences among samples) at this level of intraspecific structural differentiation (Ulevičius 1993). Non-metrical distances were evaluated using the population similarity/dissimilarity measure for polymorphic characters (Zhivotovsky 1979). This method is based on estimating both the similarity index (*r*) and the identity criterion (*I*) (see Appendix).

For metrical analysis, a total of 103 beaver skulls were taken from five local populations of different origin (figure 1, table 1). Skulls with a closed basal foramen of premolar and molar teeth

Table 1. Samples (number of individuals) of beaver skulls for non-metrical and metrical analyses (sampled in 1986-1988) and liver for biochemical analysis (sampled in 1999-2002) from different river basins of Lithuania.

Sample code*	River basin	Skulls studied non-metrically	Skulls studied metrically	Liver studied biochemically
A	Minija	61	34	15
B	Venta	44	–	–
C	Jūra	79	–	–
D	Dubysa	52	16	2
E	Mūša	35	–	–
F	Nevėžis	48	–	–
G	Šventoji	60	23	35
H	Merkys	32	13	10
I	Šešupė	52	17	16
Total		463	103	78

* As in figure 1.

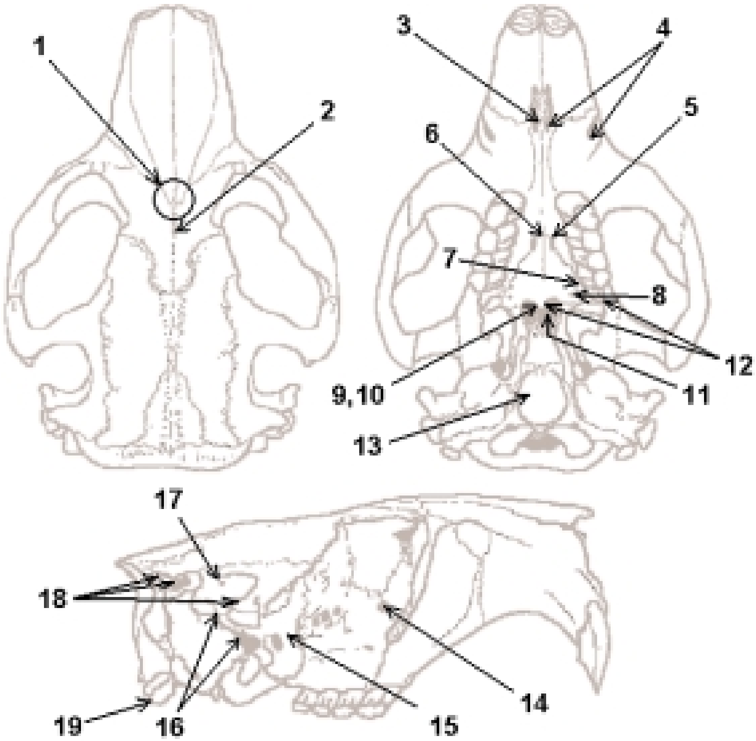

Figure 2. Location of non-metric parameters on beaver skull. Numeration as in table 2.

were analysed. In European beavers the basal foramen usually closes at four years of age (Safonov 1966). Thus, skulls of adult beavers (four years and older; 4+) were measured. For comparison with maternal populations, already published results of metrical investigations were taken from a monograph (Lavrov 1981): 1. Maternal population from Belarus (Sozh, Berezina), *n*=18, adultus. 2. Maternal population from Voronezh, *n*=52, senex (nine years old and older; 9+). 3. Maternal population from Voronezh, *n*=84, adultus (3-8 year old; 3+). Fifteen metrical characters of beaver cranium described by Lavrov (1981) were used for this study (figure 3, table 3). The accuracy of the measurements is within 0.1 mm. The significance of differences between two means in two-sample comparisons for every metrical parameter was evaluated using a *t*-test.

In four river basins containing subpopulations of different origin, livers from hunted beavers (a total of 78 individuals) were sampled for the biochemical (genetic) investigation in 1999-2002 (figure 1, table 1). After each trapping, livers were frozen at -20 ºC until preparation. Liver tissue homogenate was used for the electrophoresis of allozymes. For detailed descriptions see Paulauskas & Ulevičius 2001. The biochemical (genetic) relationship between samples was evaluated using 15 loci of four enzyme systems: malate dehydrogenase, malic enzyme, glucose-6-phosphate dehydrogenase and esterase, and two loci of non-enzymatic proteins. According to Rogers (1972), genetic distances express the biochemical differentiation among subpopulations.

Results and discussion

Phenetic and biochemical (genetic) structure of the restored beaver population

On the basis of non-metric analysis of skull samples studied local beaver populations were

Table 2. Description of the non-metric parameters of beaver skull.

Number	Parameter	Number of alternative variants	Character of variability
1	Frontal part of nasal bones	5	Shape
2	Frontal suture	2	Presence/absence
3	Process of the maxillary bone between incisive foramens	4	Shape
4	Incisive foramens with respect to infraorbital foramens	3	Position
5	Major palatal foramens	2	Number
6	Palato-maxillar suture between the major palatal foramens	2	Configuration
7	M^3 with respect to palatine bone	2	Presence/absence of contact
8	Additional foramen to the hind maxillary foramen	4	Size and position
9	Choan spine	4	General shape
10	Apex of the choan spine	5	Shape
11	Spheno-palatal suture inside the choan cavity	2	Configuration
12	Choan spine with respect to alveolar process	3	Position
13	Fissure on occipital hole	2	Presence/absence
14	Spheno-palatal foramen	4	Size and position
15	Lateral wall of the pterygoid canal	2	Presence/absence
16	Fissura ptero-tympanicum with respect to spheno-squamosal suture	3	Position
17	Temporal foramen	8	Number
18	Auricular tube with respect to auricular and zygomatic processes	3	Position
19	Occipital condyle with respect to the jugular process	3	Position
Total		63	

classified into two groups. Each group (A, E, H, and I; see table 1) could be described as a phenetically specific subpopulation. Each of them originated from different centres of spread. Each sample from these subpopulations showed highly significant phenetic distance from the other samples when compared with a complex of non-metric parameters (table 5).

Samples from the second group (B, C, D, F, and G; see table 1) showed far less phenetic specificity when compared to each other. No significant phenetic distances were found when a complex of non-metric parameters was used among samples of the second group (except between F and G; table 5).

These findings suggest a hypothesis about the presence of a zone of intensive hybridisation of the expanded beaver populations in the centre of Lithuania (samples C, D and F). There were no releases of reintroduced beavers in this part of the country. Most likely, the expanded beaver populations here originated from at least three centres of spread: Kaliningrad region (1955), Kertuša (Šventoji basin) and Krempa (1948), and natural immigrants from southern Lithuania (1944) (figure 1, table 4). On the other hand, high phenetic specificity of subpopulations of different origin suggests strong influence of the founder effect in small groups of reintroduced beavers and the ability to preserve this specifi-

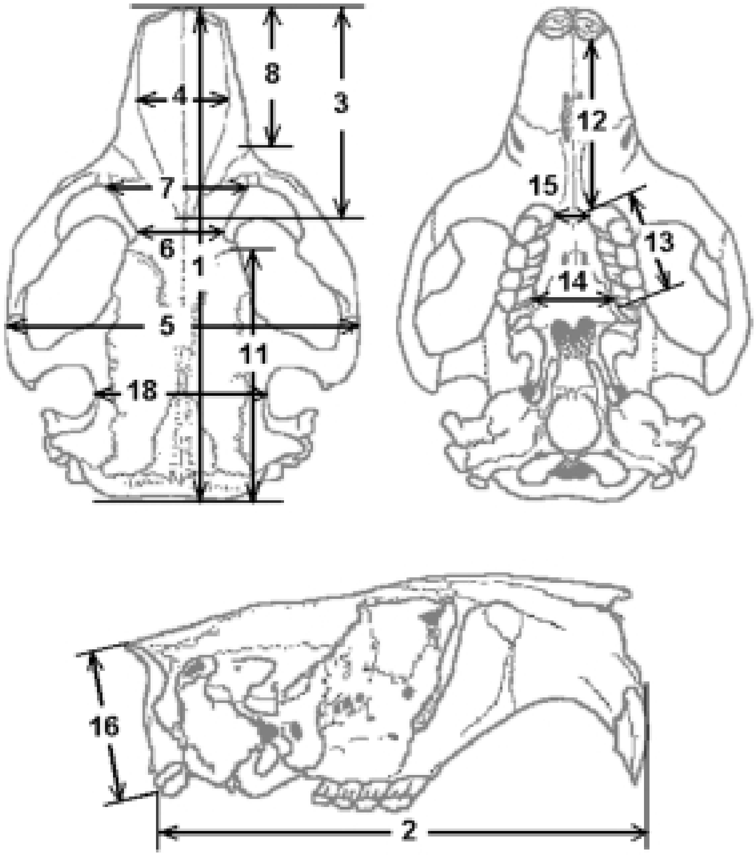

Figure 3. Metric parameters of beaver skull. Numeration of parameters as in table 3 by Lavrov 1981.

city even in conditions of high population density.

Analysis of beaver groups of different origin using biochemical markers displayed a principally similar relationship pattern among samples (figure 4a). The greatest biochemical distances were found between natural immigrants in the southern part of the country (Merkys basin (H)) and the most recently reintroduced subpopulation in north-western Lithuania (Minija basin (A)). However, biochemical clustering of samples was somewhat different than that using non-metric distances (figure 4b). Beavers from the Šventoji (G) and Minija (A) subpopulations are in one biochemical cluster whereas phenetically they differ significantly. Outstanding biochemical specificity of the Dubysa beavers (D) might be biased by the small and not representative sample (*n*=2). Observed inadequacy between non-metric and biochemical distances might be caused by a sampling bias, because the biochemical samples were much more restricted geographically than the craniological ones. Another possible explanation of this inadequacy could be the difference in sensitivity of biochemical and non-metric markers for finding differences among local populations. As was mentioned above, the non-metric parameters that showed no significant differences among samples were excluded from further analysis on the assumption that these parameters were not sensitive enough to expose differences among local populations. This was not done for the biochemical markers. Thus, it is possible that the last ones were less sensitive for detecting differences among local populations. The phenomenon of non-metric parameters of uneven scale has been widely discussed by representatives of popula-

Table 3. Metric parameters of beaver skull (used by Lavrov 1981).

Number	Number used by Lavrov 1981	Parameter	Notes
1	1	Total length of cranium	
2	2	Condylo-basal length	
3	3	Length of nasal bones	
4	4	Maximum width of nasal bones	
5	5	Maximum width of the cranium	Zygomatic width
6	6	Minimum interorbital width	
7	7	Frontal width	Between proximal points of the lacrimal bones
8	8	Length of the nasal part of the cranium	
9	11	Length of the hinder part of the cranium	From the postorbital process to extreme point of the occipital crest
10	12	Length of the upper diastema	
11	13	Alveolar length	Between the foremost point of the Pm alveolus and hinder point of the M^3 alveolus
12	14	Fore palatal width	Shortest distance between Pm alveolus
13	15	Hind palatal width	By centres of the M^3 teeth
14	16	Occipital height of the cranium	From the ground point of the bend between occipital condyles to upper point of the occipital crest
15	18	Temporal width of the cranium	

tion phenetics (see Jablokov & Larina 1985 for review).

Nevertheless, the question of which markers (morphological or biochemical) better reflect the real genetic relationship between the beaver subpopulations remains open. Our present investigation shows that the non-metric relationship fits better the data on origin of different subpopulations. In some other rodents it has been found that genetic variation, as measured by variation in allozymes, explains up to 50-80% of the heterogeneity among populations in levels of cranial (osteometric) variation (Soule & Zegers 1996). However, more detailed biochemical investigations are needed to be able to make well-founded conclusions concerning beavers.

Metric differentiation of skull samples

Metric comparison of the skull samples from five beaver subpopulations of Lithuania uncovered quite a regular and explainable (in context of origin) picture of the metric relationship among the subpopulations. Again, as in the case of non-metric and biochemical analyses, the greatest metric specificity was found in the Merkys basin subpopulation (sample H) originating from early natural immigrants from the upper reaches of the Nemunas basin. This sample differed significantly from other samples for four to six metric parameters of the skull (table 6). Other samples also showed significant metric differences. However, the number of parameters for which these differences were sig-

Table 4. Reintroduction and natural immigration of beavers in Lithuania and the neighbouring countries.

Origin	Year of reintroduction /immigration	Locality of release	Samples that could be most influenced	Number of released animals	Reference
Norway	1927	Irbe basin, Latvia	B	4	Balodis 1990
Natural immigration from a population in Grodno region, Belarus	Early 1940s	Merkys basin, Southern Lithuania	H	?	
Voronezh, Russia	1947	Žuvintas Strict Nature Reserve, Lithuania	I	8	
	1949	Osowiec, Northern Poland	I	6	Macdonald et al. 1995
	1952	Venta basin, Latvia	B	6	Balodis 1990
Dnepr basin, Sozh/ Berezina river system, Gomel region, Belarus	1948	Šventoji basin, Kertuša river, Lithuania	G	25	
	1948	Krempa river, Lithuania	?	15	
	1955	Šešupé- basin, Sovietsk district, Kaliningrad region, Russia	I	30	Beljakov et al. 1980
	1959	Minija basin, Lithuania	A	30	

nificant, appeared to be slightly or considerably less than in the case of sample H. No significant differences for any metric parameter were found between samples D and G. These two samples showed no significant phenetic differences either, suggesting a comparatively closer genetic relationship to each other than to the rest of the studied samples.

Unexpected results were obtained when skulls from Lithuanian beaver population were compared with skulls from two maternal populations: Dnepr basin (local basins of Sozh and Berezina) in Belarus, and from Voronezh region in Russia. From these populations were derived from almost all reintroduced beavers to Lithuania and the neighbouring countries (table 4). The biggest number of Lithuanian reintroduced beavers originated from the Dnepr basin (Belarus). Therefore, it is to be expected that all genetically determined characteristics of Lithuanian beavers would be closely related to those of Sozh and Berezina beavers. However, the skulls of Lithuanian beavers appeared to be significantly larger than the Belarussian ones, for 11 parameters out of 15. These differences were especially expressed in such general measurements as the total and condylo-basal length as well as maximum width of the cranium. For example, the average total length of the cranium of Lithuanian beavers exceeded the Belarussian one in 10 mm (table 7).

In terms of their size, the skulls of Lithuanian

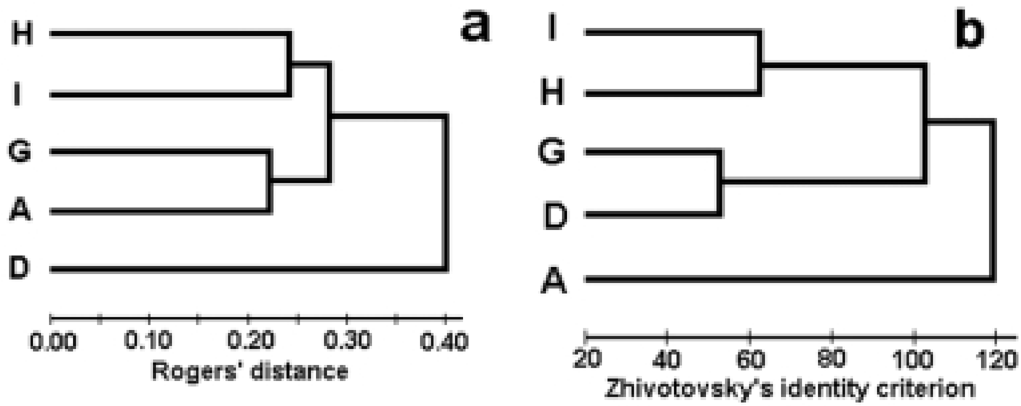

Figure 4. Genetic (biochemical) (a) and phenotypical (non-metric) (b) relationship among studied beaver subpopulations in Lithuania. Dendrograms were constructed using the UPGMA method. Codes of samples as in table 1 and figure 1.

beavers were found to be very close to beavers from Voronezh region. For seven parameters they were smaller than the Voronezh senex. However, when compared with the Voronezh adultus, the skulls of Lithuanian beavers were significantly larger for the majority of the parameters (table 7). Beavers from Voronezh are considered to be the largest among the other geographic forms of *Castor fiber* after beavers from the Elbe basin, Germany. On the contrary, beavers from Belarus were described as comparatively small among other geographical populations (Safonov 1966, Lavrov 1981).

Results of the metrical analysis could be somewhat biased by a possibly uneven age structure of the samples compared. Lavrov's adultus is defined as a 3-8 year-old (3+) (Lavrov 1981). Thus, a certain proportion of 3+ beavers could be present in the samples described by Lavrov (1981). As was mentioned before, we analysed only skulls with already closed basal foramen of premolar and molar teeth that is usually characteristic for the 4+ beavers (Safonov 1966). We also have not distinguished the senex age group (9+) (as Lavrov did) because in an intensively exploited beaver population such animals are expected to be rare. Anyway, big differences in average meanings of a number of parameters suggest that the age bias in this case is not of primary importance.

Why have Lithuanian beavers become so large? This cannot be explained by the founder effect because the majority of Lithuanian reintroduced beavers originated from the

Table 5. Non-metric distances (Zhivotovsky's identity criterion, I) for a complex of 19 non-metric parameters of skull among nine beaver subpopulations in Lithuania. Asterisks indicate the significance level: *= P<0.05, **= P<0.01, ***= P<0.001; ns = not significant.

Samples	A	B	C	D	E	F	G	H
B	125.5***							
C	107.0***	71.8**						
D	84.0***	52.2 ns	28.3 ns					
E	93.3***	75.3**	85.4***	65.9*				
F	105.7***	63.3*	77.8**	53.8 ns	73.9**			
G	91.3***	59.0 ns	76.3**	46.4 ns	72.5**	66.6*		
H	159.6***	109.6***	113.6***	90.4***	112.4***	83.2***	133.6***	
I	135.4***	110.0***	84.0***	62.2*	84.5***	82.0***	112.3***	65.5*

Table 6. Metric parameters of skull in which statistically significant differences were found among five beaver subpopulations in Lithuania. Figures indicate codes of metric parameters as in table 3 and figure 3 (numeration by Lavrov 1981); asterisks indicate the level of significance: *= P<0.05, **= P<0.01, ***= P<0.001.

Samples	D (*n*=16)	G (*n*=23)	H (*n*=13)	I (*n*=17)
A (*n*=34)	16*, 18***	18*	5***, 7*, 11*, 16**, 18***	14**, 15*, 16*, 18***
D		-	5**, 7**, 11**, 18**	14**, 15**
G			3**, 5**, 7*, 11**, 18***	2*, 3**, 6**, 14***, 15***
H				5**, 6**, 7*, 14*, 15***, 18***

Belarussian population(s) where "small beavers" live. The intersubpopulational hybridisation could result in a heterosis effect, at least in the supposed zone of intensive hybridisation. However, our findings at all three levels of analysis (non-metric, biochemical and metric) indicate certain (perhaps genetic) specificity of the studied subpopulations, suggesting that even in conditions of dense population the gene flow among the local populations could be minimal. Another cause of morphological changes in Lithuanian beavers could also be the exploitation effect. High levels of exploitation might promote higher levels of gene flow inside a subpopulation by incorporating the population reserve into the breeding process. In general, the mechanism could be described as follows: the more genotypes breed, the higher the proportion of the genetic pool of a subpopulation that can be realised in a separate individual. Mate replacement by immigrated beavers is a usual pattern in pair formation when one of partners is lost (Kudriashov 1975, Svendsen 1989). High loss of a beaver mate in a family can be expected when beavers are hunted using traps, because traps are usually set near the main lodge (personal communications with many Lithuanian hunters).We suggest that both processes (inter- and intra-subpopulational hybridisation) could bring about distinct morphological changes.

Another interpretation might be related to certain morpho-physiological adaptations of the reintroduced populations to their new environments. A reintroduced northern population living in conditions of eastern taiga and originating from Voronezh (zone of broadleaf forest) showed distinct morpho-physiological changes within approximately four decades after the first releases (Solovjov 1991). Significant morphological differentiation at a population level (among southern and northern populations) was found in the muskrat (*Ondatra zibethicus*) cranium originating from a genetically homogeneous group of animals (Vasil'ev et al. 1999). However, in the case of Lithuanian beavers this interpretation seems to be less acceptable because environmental conditions in daughter and maternal populations differ only slightly, thus the influence of genetic processes on morphological changes is expected to be more important.

Conclusions

The current beaver population in Lithuania has originated from at least three genetically different maternal populations. The majority of reintroduced beavers were from the Dnepr basin, Belarus. Five geographically and temporally isolated reintroduction centres, where the number of the released animals varies from 8 to 30, and one centre of natural immigrants have influenced the formation of the current beaver population in Lithuania.

Phenetic (non-metrics of skull) and genetic (allozyme e-phoresis) analyses showed that beaver subpopulations of different origin (from different maternal populations and different centres of spread) have preserved their specificity even in conditions of dense population. This specificity might be caused by the founder effect in small geographically and temporarily isolated groups of reintroduced beavers. On the contrary, subpopulations from the supposed zone of intensive hybridisation of reintroduced beavers and

Table 7. Differences in metric parameters of skull between Lithuanian beavers (*n*=103) and maternal populations from the Dnepr basin (Belarus) and Voronezh region (Russia). + = skulls of Lithuanian beavers that are larger; - = skulls of Lithuanian beavers that are smaller.

Parameter*	Dnepr basin (adultus, *n*=18), by Lavrov 1981		Voronezh region (senex, *n*=52), by Lavrov 1981		Voronezh region (adultus, *n*=84), by Lavrov 1981	
	Difference between two means (mm)	*P*	Difference between two means (mm)	*P*	Difference between two means (mm)	*P*
1	+10.0	0.0000	0	ns	+4.5	0.0000
2	+8.6	0.0000	-0.9	ns	+3.2	0.0000
3	+3.2	0.0000	-0.9	0.0259	+1.5	0.0000
4	+0.9	ns	+0.1	ns	+0.7	ns
5	+5.6	0.0000	-1.3	0.0084	+1.8	0.0001
6	+1.1	0.0031	+0.1	ns	+0.6	0.0019
7	+1.2	0.0197	-0.2	ns	+1.7	0.0000
8	-1.3	0.0051	-2.8	0.0000	-1.7	0.0000
11	+0.6	ns	-4.6	0.0000	-3.0	0.0000
12	+2.0	0.0002	-0.6	ns	+1.3	0.0000
13	+0.9	0.0008	-1.6	0.0000	-0.5	ns
14	+3.1	0.0000	+3.2	0.0000	+2.8	0.0000
15	+1.5	0.0000	+1.6	0.0000	+1.6	0.0000
16	+1.2	0.0002	-0.7	0.0013	+0.4	ns
18	+0.7	ns	-2.0	0.0000	-1.0	0.0002

* Numeration used by Lavrov 1981 as in table 3 and figure 3.

natural immigrants were found to be very phenetically similar.

Metric differentiation of the skull was found to be considerable when some subpopulations of reintroduced beavers were compared with a subpopulation of natural immigrants. Thus, essentially the same pattern of relationship among subpopulations was found for both the phenetic and genetic analyses.

The most unexpected finding was that skulls of Lithuanian beavers were found to be significantly larger than those of beavers from the basic maternal population from the Dnepr basin, Belarus. According to skull size, Lithuanian beavers are much closer to beavers from the Voronezh region, Russia. The latter are considered to be the largest among other geographical forms/subspecies of *Castor fiber* (except for *Castor fiber albicus*).

Our investigations on morphology and genetics of a successfully restored hybrid population of European beaver in Lithuania show the quite complicated morphological and genetic structure of this population, which seems to be strongly related to the different origins of separate subpopulations. Significant changes at morphologic level might be one of the possible expressions of the potential survival advantage of hybrid populations.

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Samenvatting

Over de morfologie en genetica van een succesvol herstelde beverpopulatie in Litouwen

Tenminste zes verspreidingscentra van uitgezette of langs natuurlijke weg geïmmigreerde dieren hebben de opbouw van de huidige beverpopulatie in Litouwen beïnvloed. Fenotypische

(niet-metrische schedelkenmerken) en genetische (allozyme electrophorese) analyses laten zien dat deelpopulaties van bevers van verschillende herkomst hun specifieke kenmerken behouden, ook in omstandigheden van grote populatiedichtheid, zelfs na 30 tot 40 jaar sinds de eerste uitzettingen en natuurlijke immigraties. Deze specifieke kenmerken kunnen het resultaat zijn van het zogenoemde *founder effect* in geografisch kleine en tijdelijk geïsoleerde groepen uitgezette dieren. Overigens, deelpopulaties van de veronderstelde zone van intensieve hybridisatie vertoonden uitwendig veel overeenkomst. Metrische schedelkenmerken varieerden in geringe mate tussen de deelpopulaties en vertonen een hoge differentiatie tussen uitgezette dieren en door natuurlijke immigratie verschenen dieren. Echter, beverschedels uit Litouwen bleken significant groter te zijn dan die van de oorspronkelijke populatie in de regio Gomel in Wit-Rusland. Onze onderzoekingen laten een gecompliceerde morfologische en genetische opbouw zien van de hybride beverpopulatie en aanzienlijke morfologische veranderingen in vergelijking met de oorspronkelijke populatie.

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Appendix

Similarity index and criterion of identity

The similarity index, which is the measure of phenetical similarity between two samples, and might be interpreted as frequency of joint morphs (phens, variants of non-metric trait) in both of these samples, has been defined as:

$$r = \sqrt{p_1q_1} + \sqrt{p_2q_2} + ... + \sqrt{p_mq_m},$$

where p_1, p_2, …, p_m are the frequencies of the m phens in the variability of the p-non-metric parameter for the first sample ($p_i<1$), and q_1, q_2, …, q_m are the frequencies of the same m phens in the variability of the q-non-metric parameter for the second sample ($q_i<1$). If the samples are compared by k non-metric parameters, then r is calculated as:

$$r = (r_1+r_2+…+r_k)/k.$$

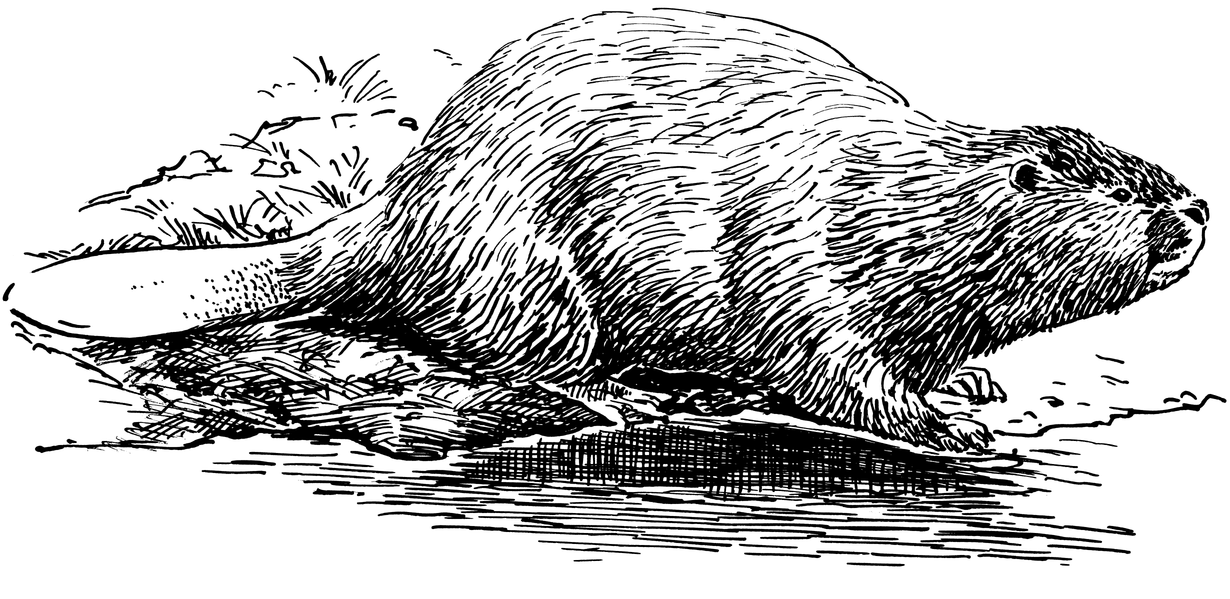
The identity criterion, as a tool for evaluating of significance of phenetic distances, has been defined as follows:

$$I = 8n_1n_2(1\text{-}r\text{-}(p_0+q_0)/4)/n_1+n_2,$$

where n_1 and n_2 are the sizes of the samples compared; p_0 is sum of frequencies of phens that are presented in the first sample but not in the second one, accordingly q_0 is sum of frequencies of phens that are presented in the second sample but not presented in the first one. The identity criterion I is distributed as the well-known Chi-square criterion with the degrees of freedom df = m-1. By involving k non-metric parameters for the pairwise comparison of samples, I has been defined as:

$$I = I_1+I_2+…+I_k,$$

with the degrees of freedom calculated as:
$df = m_1+m_2+…+m_k\text{-}k$.



The use and potential of flow devices in beaver management

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Abstract: After being nearly exterminated during the fur trade European beavers (*Castor fiber*) and American beavers (*Castor canadensis*) have been recovering and gradually re-flooding their long-vacant habitats in recent decades. This development has led to a growing conflict with humans. Flow devices are discussed as an alternative to beaver removal in controlling beaver-human conflicts. Flow devices control damming behaviour and therefore water levels. If well designed and well built they are a long lasting, low-maintenance method of preventing unwanted flooding. Furthermore, by negating the need to remove beavers from an area, flow devices allow for the possibility of other, non-threatening wetlands developing nearby. Consequently, flow devices represent an opportunity to preserve and restore wetlands.

Keywords: Castor fiber, Castor canadensis, flow device, wetland, beaver-human conflict.

Introduction

As European beavers (*Castor fiber*) and American beavers (*Castor canadensis*) continue to recover from the fur trade they are re-occupying a massive historical range (much of Eurasia and North America) that is now widely dominated by humans. Range expansion, particularly in Eurasia, can be expected to be dramatic in the next few decades (Halley & Rosell 2001). Given this pattern, beaver-human conflicts such as flooding of agricultural land or roads are likely to increase (Czech & Lisle 2003).

Conflicts are typically solved by removing beavers by trapping or shooting. Because of the tendency and ability of beavers to disperse around the landscape seeking new habitats, this is often a short-term solution, particularly if regional beaver populations are healthy and the local habitat is attractive. Therefore, an effective removal strategy has to be perpetual and cover a relatively large area surrounding conflict points (Lisle 2001). Ultimately, this can be expensive.

The installation of so-called flow devices represents an alternative strategy to diminish beaver-human conflicts. By controlling damming behaviour, flow devices allow for the presence of beavers while simultaneously protecting human properties for long periods of time. This has ecological and economic benefits. In this paper flow devices are discussed as an alternative for resolving beaver-human conflicts.

Flow devices

Flow devices control damming behaviour and water levels by making favorable damming sites less desirable, reducing damming stimuli (the sound and feel of running water and visual cues), and essentially sneaking water away from beavers. There are basically two categories of conflict sites: “regular” beaver dams not attached to human structures, and narrow outlets (e.g., road culverts) in manmade barriers. Pipes are almost always used in flow devices in beaver dams. The upstream ends of pipes and outlets both have to be protected with some sort of filter that is usually made with fencing material. Filters exclude beavers and damming debris while dispersing inflowing water over a broad area so it is difficult to detect. Following are two examples of how flow

Photo 1. Castor Master™ pipe systems use a Round Fence™ (RF) for a filter. Many types and sizes of pipes can be used; this one is of polyvinylchloride and measures 0.2 x 4 m. Because the pipe is placed level it has a silencing elbow to prevent the sound of running water from escaping and attracting beavers. This RF is small (diameter: 1.2 m) and lightweight so it has a rock on top of it to help counter liquid-displacement forces acting on the pipe. The pipe is also weighted down where it ends in the dam and covered with branches so beavers cannot access it. This is a relatively small system to match a small stream. *Photograph: Skip Lisle.*

devices and filter design vary according to site type.

The Castor Master™ is a pipe system that is used with a filter called the Round Fence™ (Lisle 2001; photos 1 and 2). Because beavers are conditioned to look for dam leaks *in* dams, pipes should extend into the impoundment until the intake is well separated from the dam. Unlike outlet filters, these filters are not attached directly to the dam or embankment. Therefore, they are relatively small, consistent in shape (upright cylinders), self-supporting, and, because they are used below or near the water surface, capped.

By contrast, culverts end at the edge of the embankment and are typically protected with more traditional fences with frames (at least posts) and no "roofs." A framed fence built "in place" allows for optimum design flexibility, which is important because the topography of every outlet is different. Furthermore, one can build a larger fence in this manner, which is often required for security because of the absence of dam-filter separation. For even more security pipe systems can be added to fence systems at outlets. Beaver Deceivers™ are rugged, wood-frame fences that are molded to match individual sites (Lisle 1999, Lisle 2001; photo 3). It should be noted that fences on culverts should not be allowed to become ecological barriers. Mesh size should be large enough to allow aquatic animals smaller than beavers to pass through. Especially when culverts are underneath busy roads or roads with steep embankments, special "doors" or openings in the fences also may be necessary to allow passage of beavers and large turtles (photo 4).

There have been few studies done on the effectiveness of high-quality flow devices. However, at 277 sites where flow devices were in place for an average of two years problems were solved to the satisfaction of the customer without the need for trapping over 90% of the time (Callahan 2003). In another study (Lisle 1999, and Lisle, unpublished data) maintenance was largely eliminated at 20 sites where clogged culverts and flooded roads had previously been a routine occurrence. This is a seven year record despite the near-constant presence of nearby, untrapped beaver colonies.

Discussion

The beaver-human conflict has become a widespread phenomenon in North America. To date, however, flow devices have not been widely used. Beaver removal has been emphasized over all other management techniques. Four reasons can be identified for the slow acceptance of flow devices: 1. *Legal status and perception of beavers:* Beavers are typically classified simply as "furbearers" and often managed as pests. In most US states harvests are limited only by trapper effort, which is largely determined by pelt prices (Hammerson 1994). There is usually no restriction on the number of beavers that can be taken and seasons are rarely less than several months long. 2. *Concerns about the scale of the problem:* The general perception of wildlife managers may be that the scale of the problem is too large to address by the use of flow devices only. However, beavers focus their damming efforts in small, low-gradient streams (Lizarralde 1993, Lisle 2001). Within these areas, which may only represent 1-2% of the landscape, conflicts are frequently limited to "flash points" like road culverts (Lisle 1994). For example, despite high beaver populations,

Photo 2. A Castor Master™ with a submerged polyethylene pipe 0.3 x 12 m. If pipes are placed so there is little difference between the water level above and below beaver dams, fish can easily swim through. *Photograph: David Wilkins.*

Photo 3. At narrow sites Beaver Deceivers™ should create a salient down the middle of the stream that allows beavers to swim by the front of the fence. If the fence blocks the channel, the front is likely to become a beaver dam. Crescent-shaped models like this one (perimeter: 11 m) work well at sites where the stream enters the outlet at an angle. *Photograph: Skip Lisle.*

relatively dense road networks, and fairly flat terrain, there were only 18 conflict points on 52,610 ha in Maine (Lisle 2001). It is also possible that a class of private contractors will develop to take over this work, which has historically been the responsibility of government agencies with insufficient resources to do it themselves. 3. *Limited and apparently bad experience with flow devices:* In certain occasions flow devices have been used, but the construction has been of a low quality and they have failed, reinforcing the original belief in the necessity of lethal control (Langlois & Decker 1997). 4. *Public opinion:* People may opt for a removal strategy simply because of a lack of knowledge and understanding of the key role beaver play in ecosystems (Muller-Schwarze & Sun 2003). Human intolerance of beavers, reinforced by a centuries-old predator and pest-control mentality, is often compounded by the belief that the presence of beavers will invariably lead to economic loss. Furthermore, the re-birth of ancient beaver-created wetlands, or flowages, is frequently greeted with the shocked sense that the land was "never like that before".

On the positive front, society is beginning to recognize that healthy aquatic ecosystems have significant monetary value (Costanza et al. 1997, Hey & Philippi 1999). For example, the US government instituted a "no net loss" programme that has attempted, with mixed results, to arrest the steady, longstanding loss of wetlands by building manmade replacements (cf. National Research Council 2001). There is great potential to recruit beavers in this effort. If a small fraction of wetland mitigation money or other funds now used for extirpation programmes could be diverted to landowners or municipalities to help protect properties non-lethally, and keep beavers in place, it could result

Photo 4. A 30 cm polyethylene T-joint in the front of this Beaver Deceiver™ keeps beavers and large turtles out of traffic by allowing them to travel through the fence and therefore the road culvert. The 90° angle prohibits beavers from transferring woody damming material inside. *Photograph: Skip Lisle.*

in a phenomenal increase in natural, high-value and low-cost wetlands. This type of monetary incentive would also encourage businesses to specialize in non-lethal strategies for controlling beaver damage. Furthermore, by protecting properties in a long-term manner flow devices can greatly decrease maintenance costs (Lisle 1999).

Conclusion

Well-built flow devices are an effective way to control beaver-related flooding. Success is greatly enhanced when designs are site-specific and when the builder has a good understanding of beavers and flow devices. Depending on the site, some monitoring is required to guarantee functionality. To increase the use of flow devices a change in the legal status of beavers is needed to reflect their status as a keystone species. The public image of beavers also needs to be improved through education. If beaver removal policies are replaced by non-lethal strategies, property defense and maintenance expenses could be reduced while simultaneously restoring a wealth of age-old wetlands.

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Samenvatting

Het gebruik en de potenties van stroomapparaten bij het beheer van bevers

Nadat de Europese en de Amerikaanse bevers (*Castor fiber* en *Castor canadensis*) door de pelsjacht vrijwel waren uitgeroeid, herstellen de beide soorten zich nu en hebben in de afgelopen decennia hun lange tijd leeg gebleven niche opnieuw bezet. Deze ontwikkeling leidt tot steeds meer conflicten met de mens. We bespreken het gebruik van zogenoemde 'stroomapparaten', een alternatief voor het verwijderen van bevers van plaatsen waar ze problemen voor mensen veroorzaken. Stroomapparaten houden het bouwen van dammen door bevers onder controle en daarmee ook de waterstanden. Als ze op juiste wijze worden ontworpen en geïnstalleerd vormen deze voorzieningen een duurzame en weinig onderhoud vergende aanpak ter voorkoming van ongewenste overstromingen. Het grootste voordeel is dat bevers niet uit het gebied hoeven te worden verwijderd. Hierdoor ontstaat de mogelijkheid om meer wetlands tot ontwikkeling te laten komen zonder dat dit gevaren met zich meebrengt. Dit betekent dat stroomapparaten een mogelijkheid bieden voor het herstel van wetlands.

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Managing conflicts with beaver in the United States: an animal welfare perspective

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Abstract: As had happened earlier in Europe, the American beaver (*Castor canadensis*) was almost completely extirpated from its historic range because of human exploitation. Anywhere from 50 to 400 million beaver may have occurred throughout North America prior to the arrival of Europeans. Today, the population in the United States has recovered from unknown historic lows to a point where conflicts with humans have notably increased. The standard approach to resolving human-beaver conflicts has been to kill beaver and destroy their structures. From both an environmental as well as animal welfare perspective this approach is regarded as short-sighted. This paper addresses the issue of humane and environmentally responsible beaver conflict management, and identifies alternatives that control the problems beaver cause without necessitating their removal. It also addresses the benefits created by the presence of beaver in even highly urbanized ecosystems and details the strategy of one animal protection organization, the *Humane Society of the United States*, to educate the public about the beneficial role these animals can play.

Keywords: beaver, animal welfare, conflicts, Humane Society of the United States.

Introduction

As happened earlier in most of Europe, the American beaver (*Castor canadensis*) was nearly extirpated throughout its historic range to meet the commercial demands of the fur trade (Müller-Schwarze & Sun 2003). Beaver trapping reached such an extraordinary peak in 1700 that three quarters of the skins that had been collected in Montreal that year were burned in order to make the remaining portion worth exporting (Martin 1892). By 1800 the market had begun to play out and by the 1830s beaver were gone or becoming rare throughout their former range, with the fur trade moving on to other, more profitable sources (Ray 1987). The overexploitation of the beaver mirrored other environmental tragedies, such as the destruction of the passenger pigeon (*Ectopistes migratorius*) and near destruction of the bison (*Bison bison*), that accompanied the European colonization of the New World. The removal of beaver went beyond just the destruction of the animals, it destroyed the unique and timeless wetlands landscape they had created as well (Naiman et al. 1988).

The estimate of beaver numbers in North America prior to the arrival of Europeans has been set variously at somewhere between 50 to 90 million (Müller-Schwarze & Sun 2003) and 60 to 400 million (Seton 1929). While these can at best be educated guesses, it is certain that beaver were formerly numerous, and that wherever they occurred it is almost certain they impounded a majority of first through third order (and even some larger) streams (Naiman et al. 1988). Among the few who saw and wrote about early beaver landscapes was Morgan (1868). The Marquette and Ontonagon Railroad had blazed a trail through the wilderness near Lake Superior in the early 1800s to exploit the then recently discovered abundant iron deposits, and Morgan followed it into unaltered lands where beaver could still be found. He described in detail a countryside dotted with beaver impoundments, ranging from ponds of less than a quarter to those more than sixty acres in extent, held in place by dams ranging from fifty to five hundred feet long. Beaver lodges, canals and meadows added additional elements to the beaver-influenced landscape, making unique ecological contributions of their own. On a continental scale, the activities of beaver undoubtedly influenced the ecological landscape of North America in ways we are only beginning to appreciate (Naiman et al. 1988, Hey & Philippi 1995, Müller-Schwarze & Sun 2003).

The current estimate for the beaver population of North America is set at no fewer than six million animals (Kwon 1997), although this figure is at best only an educated guess. The return of the species can be attributed to various protections afforded under game animal laws, direct efforts by state wildlife agencies to repatriate the animals, and the adaptability of beaver themselves. The former range into which beavers are now returning is almost wholly occupied by humans, and consists largely of floodplains along which there is always a struggle to maintain a foothold that natural events threaten to undermine. Inevitably, the return of the beaver has led to conflicts with humans, of which three general sorts can be said to occur: (1) beaver destroy trees that humans place value on, (2) they impound waters that can flood economically valuable land, structures or roads, and (3) they are associated, albeit to an undetermined extent, with potential threats to human health and safety. These concerns lead to the designation of "nuisance" beaver and the controversy surrounding whether killing or removal is either needed or warranted as the preferred management approach.

Statement of problem

Population control via the harvest of "surplus" beaver by licensed fur takers is advocated and promoted by all federal, state and provincial wildlife agencies in North America, and usually argued as the most sensible and economic way to deal with human-beaver conflicts (e.g. Novak 1987). For many North Americans, trapping is a time honored enterprise regarded as part of a noble tradition that has evolved from livelihood and avocation to, most recently, a public service activity helping to "control" population growth in animals that might cause economic damage to human interests. This viewpoint has been challenged by animal protection interests who oppose the trapping of wild animals for recreational purposes, take issue with the humaneness of trapping technologies, and question the presumption that indiscriminate population reduction can remediate human-wildlife conflicts.

The clash of differing viewpoints often takes shape within a vacuum of needed information concerning the wildlife population at issue. It may also lead to political action outside the usual ambit of wildlife management policy-making and debates that rage in the press, not the scientific journals. One current illustration of this involves beaver management in the state of Massachusetts. There, a 1996 ballot initiative took place in which the Humane Society of the United States (HSUS), the Massachusetts Society of the Prevention of Cruelty to Animals (MSPCA), and the Massachusetts Audubon Society joined in support of a proposition to ban body gripping traps (leg hold traps had been banned some years earlier). More than 60% of the public voted for this ban, with an urban majority playing a clear role in the vote's passage. The state wildlife agency vigorously opposed the trap ban and argued that the beaver population would grow exponentially without trapping control (Talbot 1998). Figures published by the state demonstrated how beaver populations could grow from two individuals to more than 600 over a decade (Jackson & Decker 1993), but failed to explain that such increases were modeled on populations into which no mortality was ever introduced. With the debate centered in the press almost exclusively on the issue of population, animal interests led by the MSPCA sought to change focus to the actual issue of controlling beaver damage. They began to work directly with local communities to facilitate installation of flow devices, such as beaver deceivers, that prevented damage and left beaver colonies intact (Lisle 2001). This was in an effort to shift the focus away from what they felt were alarmist population projections to one in which the public understood that there were solutions to conflicts with beaver that did not involve killing and removing the animals.

The record of population changes reported by the state of Massachusetts do show growth, although the estimated increase from 18,000 in 1995 to nearly 60,000 in 2000 (Talbot 1998, Higgins 2000) seems based entirely on general approximations. No peer-reviewed estimate of population status and trends has emerged from the maelstrom of contention over beaver populations in Massachusetts, and even if it had it would not address the issue of conflicts unless it could differentiate between beaver occupancy of sites where no problems exist as opposed to sites where they do. The oft-made claim that denying the take of beaver with body-gripping traps during the recreational trapping season has allowed exponential growth to occur is, as well, argued more in principle than in fact. The one inescapable fact that does seem to emerge from the long period of debate is that far more effort and energy have been devoted to the defense of ideological ground than the physical ground on which conflicts have been occurring. Missing from the debate has been the simple explication of why all parties should be concerned about the control of beaver populations.

Beyond the debate

Concern for the welfare of beaver should be accepted as a central component of contemporary management practices because beaver are sentient beings deserving of moral consideration. At least three issues can be identified from an animal protection perspective as crucial to a discussion of this concern.

Are methods of control humane? By current standards many of the means commonly used to control "problem" beaver cause unnecessary suffering and are inhumane. While "humaneness" may mean different things to different people, there is increasing recognition in both professional and lay circles that suffering and distress can be empirically defined and measured (e.g. Mench 1993). Standards for humane death (euthanasia) as defined by organizations such as the American Veterinary Medical Association (AVMA) are one example. By criteria acknowledged by the veterinary community, then, practices such as drowning and bludgeoning have been recognized as inhumane (Ludders et al. 1999, AVMA 2001). Kill traps, deemed acceptable for "small, free-ranging mammals" (AVMA 2001), are not endorsed for animals as large as beaver, and reviews of test data on them support the general conclusion that they cannot ensure a humane death for beaver (IAFWA 1997). Gunshot, under certain conditions, and permitted injected agents are among the few techniques that could be called humane in killing beaver, if used carefully and correctly. Inhumane killing practices employed in beaver management should be discontinued, or banned.

Is control necessary? While animal welfare and protection interests traditionally have focused on the individual animal, the need to look at populations (and even ecological communities) and the ethical concerns surrounding their management are increasingly being recognized (Eggleston et al. 2003). A typical current argument for population control is that human-altered landscapes have created such provident habitat for some wildlife species that populations must be culled or reduced in order to mitigate the problems they cause for humans, for the environment, and even for themselves (Rutberg 1997, Kenyon et al. 1999). The *prima facie* assumption that a linear relationship exists between the abundance of an animal species and the economic and other damage it causes has been challenged and found lacking (Hone 1996), even though at face value this notion has an apparent logic. It would now be a good time to begin to examine other "apparent logics" in wildlife management, such as the widely held belief that only regulated trapping by fur harvesters will control beaver populations (e.g. Langlois 1994).

Today, most "control" of problem-causing beaver is almost certainly accomplished by lethal means, but no accurate estimate of the extent of this can be given since few states keep records or track the taking of nuisance beaver. The U.S. Department of Agriculture's Wildlife Services, the only federal wildlife damage control agency, reported killing 29,312 beaver in 34 different states in 2001, the only centrally reported figures available for the taking of "nuisance" beaver. The numbers taken ranged from 1 to 5,410 animals, with a mean of 862 and a standard deviation of 1,511 (USDA 2002). Such variability suggests that either beaver problems are varying enormously from state to state or that beaver control programmes are not being administered in anything approaching a well-grounded and systematic set of operational practices. Even where body counts are published, nothing seems to be known of the consequences of management actions, how much nonlethal control has been attempted, or the timing or extent of recurrence of problems at sites where control occurred. In short, no agency or group seems able to unify biological and ecological information with administrative information to produce a consistent and meaningful overview of beaver management.

Would alternatives provide greater benefits? The environmental benefits that might result from beaver presence and activity are fairly well known, if not fully appreciated. Substantial lists of ecological "services" ranging from water storage to increased resistance to ecosystem perturbation (Naiman et al. 1988, Hammerson 1994, Kwon 1997) testify to the potential role beaver and the wetlands they create and maintain might play in promoting ecosystem health. Further, some researchers now argue that were beaver allowed to reclaim all or even just some of the floodplains that delineate their usable habitat, they might do so to the general benefit of humans. Hey & Philippi (1995) have analyzed flood events in the Upper Mississippi River Basin with an eye toward the role beaver impoundments might have played in the past in mitigating flood events. Their analysis shows in principle that the effect could have been significant. Estimating the original storage capacity of beaver ponds at 11% of the watershed and wetlands at 10%, they calculate that the 26 million acres of wetlands lost since colonization could have easily accommodated the 111 million acre-feet of water that passed through St. Louis in 1993, creating many millions of dollars in damage.

Donald Hey (personal comunication) has also estimated the potential for retiring agricultural land from production, the same lands that were drained in the 1800s, and allowing them to serve as mitigation "banks", principally to capture, store and process nitrogen generated by agricultural activities. The potential benefits could be considerable, given the staggering environmental problems facing the Mississippi River drainage that arise from agriculture (Turner & Rabalais 2003). It is obvious for advantages such as this to even be considered, a broad, multi-disciplinary, multi-jurisdictional systems management concept has to be put into play. Attempting to do so within the context of traditional beaver management policies would be unwieldy at best, and perhaps impossible.

Discussion

A combined humane and environmental perspective represents the most realistic and practical basis from which to approach the future of beaver management. Education should play a significant role in such an approach. Since 1997, the HSUS, working with various partners, has sponsored a national programme of educational workshops that emphasize the integration of information on beaver biology and ecology with the contemporary and practical aspects of non-lethal ways to solve human-beaver conflicts. A total of eight workshops in seven different states have begun, albeit slowly, the process of promoting better public awareness about alternatives. The HSUS can not, and should not, be the only group organizing such events.

The key to future human-beaver interactions will not reside in the advocates who call for change without attempting to understand what that change would mean nor the traditional interests that resist change without admitting that it is already upon them. The future of beaver management will lie in new perspectives generated from a better understanding of these animals, their populations, their communities, and the ecosystems of which they are a key part. Animal welfare interests cannot expect or demand that every human-beaver conflict be resolved by nonlethal means, only that they be resolved humanely. They might expect, or demand, that the full benefit of having beaver present at any individual site be weighed before control is authorized; that the time it might take for a site to be reoccupied given weight in management recommendations to avoid recurring cycles of control; and that the most contemporary and effective means of nonlethal conflict resolution be employed before lethal control is authorized. On their side of the debate, animal interests should be more open to discussing the "ecocentric" aspects of management (Eggleston et al. 2003) and aware of the complex interplay between species, their ecological associates, and what could be called their welfare state. On the opposing side, almost exactly the same could be said, adding as well that it is important for traditional wildlife managers to acknowledge the importance of giving beaver moral consideration for and of themselves.

Conclusions

A considerable agenda remains to be addressed on the possible future of beaver management, especially as this relates to our urban and suburban environments. We must have a better understanding of the relationship between population management and resolution of human-beaver conflicts in order to devise optimal strategies. We must devise ways to keep humans out of flood plains to maximize the environmental benefits of these ecologically critical areas. We must approach beaver as an issue involving environmental management as much as one of animal management. To do so can lead to environments that benefit humans as well as beaver, and the myriad of other living things that comprise their community associates.

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Samenvatting

Het oplossen van problemen met bevers in de Verenigde Staten: gezien vanuit het oogpunt van dierenwelzijn

Zoals eerder al gebeurde in Europa, was ook de Amerikaanse bever (*Castor canadensis*) bijna geheel uitgeroeid in het gebied waar deze soort in historische tijden voorkwam. Vóór de komst van de kolonisten uit Europa leefde er een groot aantal bevers in Noord-Amerika, ergens tussen de 50 en 400 miljoen individuen. De beverpopulatie in de Verenigde Staten heeft zich na een historisch dieptepunt - de precieze aantallen zijn onbekend - hersteld tot een niveau waarbij de conflicten met mensen aanzienlijk zijn toegenomen. De standaardaanpak voor het oplossen van deze conflicten was en is nog steeds het doden van bevers en het vernietigen van hun bouwsels. Bezien vanuit het oogpunt van het milieu en dierenwelzijn is dit een kortzichtige benadering. Dit artikel gaat in op de mogelijkheden voor een milieuvriendelijk beverbeheer waarbij ook rekening gehouden wordt met het welzijn van bevers. Alternatieve methoden voor het oplossen van problemen bij het beheer van bevers worden voorgesteld; alternatieven die niet noodzakelijkerwijs neerkomen op het verwijderen van bevers. Ook worden de voordelen aangegeven van de aanwezigheid van bevers, zelfs in ecosystemen die sterk zijn verstedelijkt. Het artikel beschrijft de strategie die één van de organisaties voor de bescherming van dieren, de *Humane Society of the United States*, hanteert om het grote publiek op de hoogte te brengen van de nuttige rol die bevers in ecosystemen kunnen spelen.

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Beaver management in Norway: a model for continental Europe?

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Abstract: While Norway has been managing beaver (*Castor fiber*) for more than 150 years, most central European countries have little experience and none are presently harvesting beaver, despite rapidly growing populations and conflicts. Here we present the Norwegian beaver management model as an example. The main goals are to enhance biodiversity, produce a harvestable surplus, and reduce beaver-human conflicts. Beaver management should maximize recreational opportunities and allow landowners to profit from the beaver resource, e.g. through the lease of beaver hunting. Harvest quotas are determined by municipal game boards and divided among landowners according to the amount of beaver habitat they own. Few landowners hunt beaver themselves. Most beaver are shot by hunters with center-fire rifles during spring for recreation and the meat provided. No compensation is paid for beaver damage. Landowners who experience damage by beaver can receive permission to remove dams, lodges and nuisance individuals. Few non-lethal methods of damage control are presently employed. Though problems exist, the success of Norwegian beaver management lies in (1) increasing understanding of the species' ecological role, (2) the gradual status transformation from nuisance to valuable game animal, and (3) the ease with which nuisance animals can be dealt with. Presently, beaver management incurs few costs to the public while beaver hunting is increasing in popularity, along with income to landowners.

Keywords: beaver, *Castor canadensis*, *Castor fiber*, hunting, trapping, Norway, population control, wildlife management.

Introduction

The European beaver (*Castor fiber*) was extirpated from most of its former range in Europe and Asia between 1000-1870 (Halley & Rosell 2002). Following numerous reintroductions and natural dispersion during the 20th century, many countries in Europe and Asia now have viable and expanding beaver populations. Population status and management experience, however, vary considerably between nations. Whereas many countries in northern Europe and northern Asia have been managing beaver for decades, most central European countries have had far less experience. Currently, little detailed information regarding beaver management in Europe is available (but see: Balodis et al. 1999, Härkönen 1999, and Hartman 1999).

As human-wildlife associations go our relationship with the beaver is rather unique. Because of their importance for clothing, food, and castoreum for medicine, both the European and American beaver (*Castor canadensis*) were nearly hunted and trapped to extinction (Martin 1978, Todd & Boggess 1987, Nolet & Rosell 1998). With the advent of modern ecosystem management we now recognize the beaver's importance as a keystone riparian species (Naiman et al. 1986, Novak 1987, Naiman et al. 1988, Collen & Gibson 2001). However, its return to landscapes now highly modified by man for agriculture, forestry and housing has led to considerable conflict (Müller-Schwarze & Sun 2003). While many landowners and managers prefer the use of traditional lethal methods such as kill-trapping or hunting to control nuisance individuals and limit population size, others more concerned with animal welfare and wetland management would prefer to see all exploitation cease and nuisance animals controlled non-lethally. Needless-to-say, modern beaver management is highly controversial.

Norway is one of the few countries in Eurasia where beaver were not extirpated (Nolet & Rosell 1998). From its initial total protection in 1845 to the present spans 157 years of management experience. Our goal here is to (1) review the ecological, cultural, social and economic roots of Norwegian beaver management, (2) describe present key elements of Norwegian beaver management, and (3) discuss strengths and weaknesses of beaver management practices in hopes that this experience might benefit }those countries presently developing beaver management strategies.

Organization of wildlife management in Norway

The hierarchy of governmental wildlife management in Norway includes from top to bottom the Department of Environment, the Directorate for Nature Management, the county conservation commissions and the municipal game boards, or their equivalent, found in each of the 434 townships of the country. The private sector includes landowners and non-governmental organizations (NGO's). The top 3 governmental levels determine national policy, create and enforce laws, initiate applied research and distribute information. The main responsibility for practical beaver management, however, resides with the municipal game boards in close cooperation with landowners. NGO's are primarily concerned with the development of beaver management policy.

Beaver habitat and population development in Norway

Most of Norway is mountainous with a high density of streams and lakes. Approximately 48% lies below tree line and is potential beaver habitat, comprised of 37% forest, 4% cultivated, 6% bog/wetland, and 1% urban landscapes. Collet (1897) stated that beaver were common throughout most of Norway around mid-18th century and almost extirpated 100 years later. A small remnant population survived in the southeast. Many of the best habitats in southeast and central Norway have since been repopulated and the beaver's range is presently expanding both west and north (Rosell & Parker 1995). Present national population size is believed to be about 70,000 animals. The autumn density of occupied colonies in well-established populations in southeast Norway has been shown to be about 0.25 colony per km^2 (Parker et al. 2002a, Bergan 2003), which seems to be typical for populations near ecological carrying capacity in south and mid-Scandinavia (Hartman 1994). Mature boreal forests in Norway contain about 15% broadleaf species dominated by birch (*Betula pubescens*) with lesser amounts of primarily aspen (*Populus tremula*), willow (*Salix* spp.), rowan (*Sorbus aucuparia*) and grey alder (*Alnus incana*). Early successional stage forests typically contain more broadleaves and are preferred by beaver to older stands (Parker et al. 2001a).

Goals of the Wildlife Act

According to the Wildlife Act of 1981 (Lov om viltet, 1981) and its accompanying bylaw for beaver (Forskrift om forvaltning av hjortevilt og bever, 2002), the main goal of beaver management is to maintain populations at levels sufficient to enhance biodiversity, produce a harvestable surplus, and reduce beaver-human conflicts. In addition, beaver management should optimize recreational opportunities for the public and economic opportunities for landowners, e.g. through the lease of beaver hunting.

Norwegian beaver management is better understood in light of two basic fundaments of Norwegian wildlife management. (1) All wildlife is publicly owned, and therefore wildlife management should seek to maximize public enjoyment and utilization of wildlife resources. (2) The hunting privilege, however, belongs to the landowner. Once government officials have determined when, where and how much game can be harvested, landowners can either harvest their proportion of the quota themselves or lease the hunting rights to others (albeit temporarily). In the later case, the wildlife resource becomes a source of income to landowners while providing hunting opportunities for others.

Some basic elements of Norwegian beaver management

The bulk of Norwegian beaver legislation deals with when and where beaver can be harvested, the organizing of landowners into practical hunting units, how hunting quotas are determined and distributed among landowners, and how beaver damage is to be dealt with.

Establishment and distribution of harvest quotas

The municipal game boards decide when beaver hunting and trapping shall begin in a township based on their impression of population development and levels of damage. A census of occupied lodges is sometimes conducted, though more often a rough estimate is made from various information sources including e.g. landowners and hunters. Based on this information, a harvest quota for the entire township is then established. In order to distribute this quota among landowners, the area of beaver habitat or the length of stream and lake shoreline used by beaver in the township is first calculated. The minimum area required for landowners to receive one beaver permit is determined by dividing the total area of beaver habitat by the harvest quota. Alternatively, a minimum shoreline length is determined by dividing the total beaver-used shoreline length by the harvest quota. Municipal game boards can choose between the two alternatives, though the minimum shore length method has been found to be more accurate at predicting colony density on a smaller scale (Steifetten & Uren 1997). Landowners, either alone or in groups, then establish beaver management units that must be approved by the municipal game board. As Norwegian forest properties average small, most beaver management units usually consist of mergers of many landowners.

Each beaver management unit within the township is then allotted its portion of the total quota based on the relative amount of beaver habitat or beaver shoreline within respective units. Management units not meeting the required minimum area or minimum shoreline length receive no quota, which serves to motivate landowners to merge into larger units. Once beaver management units are approved, they automatically receive their quota from the game board each year. Township quotas may vary annually with changes in population size or management objectives. At the end of each hunting season, units are required to report the number of beaver harvested that year.

Harvest methods

The traditional harvest method for beaver worldwide is trapping (Baker & Dwyer 1987, Novak 1987). Shooting is illegal in much of North America where beaver have traditionally been managed primarily as a furbearer, and until just recently in most of the former Soviet Union as well (D. Gorshkov, personal communication). Beaver trapping was prohibited in Norway in 1932 seemingly to stimulate population growth, though hunting with firearms during autumn was still allowed. Forty years later in 1972, with beaver populations rapidly expanding and the quick-killing Conibear trap now available, trapping was again allowed (Parker & Rosell 2001). In the interim, however, beaver hunting with firearms had become entrenched as the main harvest form for this species. Hunting in spring, when shooting is most effective, was first allowed in 1981. Presently an estimated 80-90% of all beaver harvested in Norway are shot then. Most beaver harvested in Sweden and Finland are also shot in spring (Hartman 1999). Thus, with the exception of Norway, Sweden and Finland, trapping is the prime harvest method for beaver worldwide.

As harvest forms, hunting and trapping have quite different attributes with respect to beaver. Trapping is usually more time efficient than hunting and is more readily practiced at any time of year, particularly below the ice during midwinter when pelts are prime. In addition, trapping does not leave bullet holes in the pelt. Trapping is also quieter and less conspicuous than shooting in populated areas. Hunting, however, is more species selective than trapping, e.g. underwater beaver sets with Conibear traps are known to take non-target species such as the otter (*Lutra lutra*), that presently is a threatened species in much of Europe (Hartman 1999). Selectively harvesting beaver by size may also be possible by hunting (Parker et al. 2001b). Additionally, hunters far outnumber trappers, and hunting is more publicly acceptable than trapping. Therefore beaver hunting should provide recreational opportunities to far more individuals than trapping.

Because beaver are primarily nocturnal, hunting at northern latitudes is most effective during spring when nights are short and winter-weary beaver increase their activity outside the lodge during daylight hours (Parker & Rosell 2001). Hunting at other times of the hunting season when nights are longer is far less effective. Thus in Norway, most beaver are shot during the last 2-3 weeks of the hunting season in late April and early May, despite the fact that the season opens on 1 October (Parker & Rosell 2001, Parker et al. 2002a.) Spring beaver hunting is also popular because few other species can be hunted then.

Two valid criticisms of beaver shooting are that projectiles puncture the pelt, thereby reducing pelt quality, and that wounded beaver may escape to deep water and be lost. H. Parker, J. Danielsen and F. Rosell (unpublished data), however, found that pelt damage from shooting can be considerably reduced through the proper selection of caliber and projectile and that the incidence of wounding can be kept to a minimum. A goal of beaver management in Norway is to create recreational opportunities for the general public. As most beaver hunters are not landowners (Parker et al. 2002a), this goal has in part been realized.

Resource use and economic value

Though studies are lacking, the prime motivation for hunting beaver in Norway appears to be for recreation and the meat provided. This contrasts with North America (Todd & Boggess 1987) and the former Soviet Union (Ozolins & Baumanis 2001, Ulevičius 2001, Y. Gorshkov, personal communication) where the main motivation for beaver trapping is income from the sale of pelts, though the recreation provided is also important for many. An exception is the importance of spring-shot beaver as food for indigenous Americans in parts of northern Canada (Todd & Boggess 1987). As beaver have a wide distribution in the Nordic countries, beaver hunting is potentially available to many. Beaver hunting is also comparatively inexpensive which makes it a popular game species among younger hunters. Indeed, many landowners offer free hunting in an attempt to control damage.

Wild game can be legally sold in Norway. Beaver meat is prized by many and increasing in popularity as witnessed by the increasing number of butcher shops selling beaver meat, restaurants with beaver periodically on their menus, and cookbooks containing beaver recipes (Rosell & Pedersen 1999). Hunters currently can sell dressed and skinned beaver carcasses for about 50 Norwegian crowns/kg, comparable to about 6.0 Euro or 6.5 American dollars/kg (B. Hovde, personal communication). Shops and restaurants, however, often are unable to obtain beaver in desired quantities as most hunters eat the meat themselves.

As most beaver are shot in late spring when pelt quality is poor, their potential commercial value is low (Obbard 1987). In addition, few hunters are skilled in pelt handling, and holes in the pelt from shooting can reduce pelt value (Hall & Obbard 1987). Nevertheless many hunters have their pelts dressed for private use. At present the only fur auction in Norway (Oslo

Fur Auction) does not buy beaver pelts from Norwegian hunters and trappers because both the volume and quality are low (C. Fjeld, personal communication). Though income from the lease of beaver hunting is minor compared to hunting leases of e.g. red deer (*Cervus elaphus*) and moose (*Alces alces*), it is increasing (Parker et al. 2001a). Landowners who sell package hunts that include lodging, and in some cases guiding, seem to be profiting most.

Beaver provide income from non-consumptive recreation as well. Guided evening canoe "safaris" to observe beaver and other wildlife are becoming a popular form for eco-tourism (Rosell & Pedersen 1999). In our experience, both spring hunting and subsequent summer safaris may be conducted along the same stretches of shoreline.

Beaver damage management

Initially, all beaver dams and lodges are protected by law. In cases where beaver cause "considerable" damage to property, crops, fruit trees or forest, landowners can apply to their municipal game board for permission to remove dams and lodges, and to trap or shoot damage individuals outside the normal hunting season. Local game boards decide what constitutes considerable damage. Dead animals either become the property of the municipal game board or are given to the landowner and subtracted from his hunting quota.

Once permission has been granted, the landowners themselves are responsible for removing dams, lodges and nuisance beaver from their own property. However, local trappers or hunters often are willing to remove nuisance animals free of charge in exchange for the carcass. Trapping is usually more efficient than shooting for removing nuisance beaver in acute situations (Hammerson 1994). No governmental or private compensation for damage caused by beaver is payed to landowners. Thus the cost of beaver management to government agencies in Norway is negligible.

A major goal of Norwegian beaver management has been to transform the status of beaver from nuisance animal to valuable game species. This goal can partly be accomplished by concentrating the hunting effort to nuisance colonies and by limiting population density in general through trapping and hunting. Landowners, however, must first be motivated to cooperate on creating beaver management units large enough to receive a harvest quota. Beaver hunting can then be leased to hunters, thus providing income to landowners that will partly or wholly compensate for damage experienced (Parker et al. 2001a). Ironically, many interested hunters are unable to obtain beaver hunting because landowners are not well enough organized to receive quotas.

Damage from flooding and tree-felling in Norway (Parker et al. 2001a) is minor compared to that experienced in parts of North America (Arner & Dubose 1982, Wigley & Garner 1987) and Finland (Härkönen 1999). This is primarily because dams built in mountainous landscapes usually result in small impoundments and because birch, the dominating species felled by beaver in Norway, has limited commercial value. Thus the negative economic effects of beaver damage in Norway may be easier to compensate for through the lease of hunting rights than would be possible in countries experiencing more extensive damage.

The relative economic loss that beaver inflict on forest owners is also dependant upon property size. Parker et al. (2001a) demonstrated that in typical Norwegian landscapes, large forest owners, in the long run, would lose only about 0.1% of their conifer production from flooding by beaver. For a forester, this is a negligible loss compared to the combined losses from e.g. insect damage, windfall, moose grazing, and fungus. Owners of small forest properties, however, may occasionally by chance experience considerable beaver damage. In Norway, forest properties are relatively small averaging only 47 ha for those >2.5 ha (Nedkvitne et al. 1990). Thus Norwegian wildlife managers must deal with relatively many complaints from small landowners. Beaver activity occurring in agricultural, urban and suburban landscapes can be particularly damaging and solutions to conflicts controversial (De Almeida 1987, Conover 2002). In Norway the total incidence of nuisance beaver in these landscapes is minor as only a small proportion of the country is farmed (4%) or residential (1%).

Aside from the removal of dams and lodges in acute cases of flooding and the use of protective sheathing around tree trunks to prevent felling, non-lethal methods to alleviate or prevent beaver damage are seldom employed in Norway. In many instances however, non-lethal control methods, in the long run, might provide less costly solutions for landowners than lethal methods. For instance, where road flooding is a problem and wetland maintanence desirable, the installation of a flow control device may prove more cost effective in the long run than the continual removal of nuisance individuals (Lisle 2001).

Does beaver hunting limit population density?

Although there may be no direct one-to-one relationship between an increasing wildlife population and the severity of a specific wildlife problem, human-wildlife conflicts usually tend to increase with increasing population density (Conover 2002). An implicit goal of Norwegian beaver management is damage reduction through population limitation. But does mortality from beaver hunting add to or merely compensate for natural mortality? Though precise data are lacking, our experience suggests that present mortality rates from hunting and trapping in most Norwegian townships are insufficient to significantly reduce beaver density. The national beaver harvest for the years 2000–2003 averaged 3100 ± 507 (standard deviation) individuals (T. Rundtom, personal communication). Assuming a population size of 70,000 gives an annual harvest of 4-5%, which would predictably have only a minor effect on population growth and density (Parker et al. 2002b). The present main deterrent to damage therefore appears to be site-specific control of nuisance individuals.

There is however, evidence that spring hunting can effectively reduce population density. Parker et al. (2002b) shot 22-26% of the estimated spring population of beaver in late April and early May on 242 km^2 and experienced a 47% fall in the number of occupied colonies after only three years. One reason for this dramatic decline was the apparent susceptibility of adults, and particularly pregnant females, to being shot first in colonies. Following several years of little or no hunting, the population is rebounding quickly (H. Parker & F. Rosell, unpublished data). In southwest Finland, hunting has apparently slowed the expected rate of increase of both North American and European beaver over many years (Ermala 1997, Ermala 2001, Lathi 1997). In Sweden, however, the take-off from spring hunting seems to have had no additive effect on natural mortality (Hartman 1999).

In general, lethal methods are usually more effective at suppressing populations if conducted after they have passed through a mortality bottleneck, that being late winter or early spring in the north (Conover 2002). Spring hunting, because it occurs late and tends to select for adults (Ermala 1997, Lahti 1997, Parker et al. 2002b) has particular potential for controlling population density at more northerly latitudes.

Can beaver be satisfactorily managed without lethal control?

Harvesting has been, and still is, a cornerstone of beaver management in most countries, states and provinces with extensive beaver populations. Present exceptions are France, Germany and Poland with estimated populations of 10,000-20,000 animals each (Halley & Rosell 2002) and the American states of Colorado where beaver trapping was recently prohibited (Manfredo et al. 1997) and Massachusetts where beaver trapping is highly restricted (Deblinger et al. 1999, Siemer et al. 2003). Increasingly, wildlife management institutions, both governmental and NGO's, are seeking new, non-lethal methods to limit beaver damage in order to maximize the species' positive ecological contribution to riparian and wetland habitats and to achieve animal rights and welfare goals (Conover 2002). Non-lethal methods presently used in beaver management or undergoing development include e.g. live capture and relocation, water level control, chemical repellants and protective sheathing to inhibit tree felling, habitat alteration, and fertility control (Hammerson 1994). Though non-lethal control methods do not involve killing animals directly, they may cause suffering and are often expensive (Conover 2002). The acceptability of lethal control by the public tends to increase with an increase in beaver-related problems (Siemer et al. 2003). It remains to be seen whether beaver can be adequately managed on large temporal and spatial scales using only non-lethal control methods.

Problems facing Norwegian beaver management

In our experience there are two major and closely related problems facing Norwegian beaver management. The first involves a willingness to accept the beaver as a legitimate member of the ecosystem, a process termed reconciliation-ecology (Busher & Dzieciolowski 1999). If we are to coexist with the beaver and increase our tolerance level we must first learn to appreciate its role as a keystone species, particularly in habitats highly modified by humans. The greater value beaver have for us, the more damage will be tolerated. Increased tolerance will likely develop with increased knowledge through more education at all age levels, from primary school to adult education (Nielsen & Knuth 2001). An example of the later is the course recently offered to Norwegian forest owners by the Norwegian Federation of Foresters on ways to increase biodiversity in managed forests, including the beaver's role (Aanderaa et al. 1996). A management problem that could be lessened through more education is the common practice among landowners of illegally removing the dams and lodges of nuisance beaver without permission. In our experience many landowners are not aware that permission, in fact, is necessary, suggesting that better information to the public would reduce this practice.

Another way to increase acceptance for beaver is through increased economic returns to landowners. Presently, though interest in beaver hunting and profits from hunting lease are gradually increasing (Parker et al. 2001a), many landowners are still reluctant to organize beaver management units. The result is that too few quotas are issued and many beaver must therefore be removed as nuisance animals, often outside the normal hunting season. Beaver management is reduced to damage control and few get to hunt. Harvests are small, populations and conflicts increase, and management goals go unattained. Thus the beaver's value for landowners is a key driving force behind effective beaver management in Norway (Parker et al. 2001a).

The other major problem involves recent resistance among animal welfare advocates, and hunters alike, to hunting in late spring when many adult females are shot in the late stages of pregnancy (Parker et al. 2001b, Parker & Rosell 2001). In Norway, the hunting of all wildlife is prohibited during the breeding season after females have given birth. This prompted Solheim (1991) and Frafjord (1991) to question whether mothers were being shot from new-born beaver young in late April and early May. Experience from both Norway (Parker & Rosell 2001) and Sweden (Mörner 1990) however has shown that post-parturition females are not shot within the normal hunting season. Parker & Rosell (2001) demonstrated that this was primarily because few births occur before hunting stops in early May. In addition, females are seldom seen outside the lodge during the first 1-2 weeks following parturition (F. Rosell, personal observation). As spring hunting is most effective during the last 2-3 weeks of the season, it seems likely that this practice will continue in the near future.

Is the Norwegian model likely to be adopted in central Europe?

The control of nuisance individuals and the exploitation of populations through trapping and hunting long have been essential aspects of beaver management in Norway and many other countries. In contrast, no country in central Europe is presently harvesting beaver as part of their management strategy, despite large and rapidly expanding populations.

There appears to be several reasons for this. First, the traditions associated with exploiting beaver gradually disappeared as populations disappeared over the past millennium. For the past 400-500 years most beaver pelts used in central Europe have been imported from North America (Shieff & Baker 1987). Though hunting is still widespread in Europe, fur trapping is not and has even been banned in some central European countries (J. Sieber, personal communication). This is despite the fact that Europeans are still major producers and consumers of fur garments (Shieff & Baker 1987). The hunting of beaver with firearms, as presently performed in the Nordic countries, has never been practiced in central Europe. Neither is beaver eaten by central Europeans. Thus, with the exception of damage control, no reason for harvesting beaver exists here any longer.

In addition, the prime impetuous for reintroducing beaver to Europe has been the restoration of native fauna and improvement of riparian habitats and not the reintroduction of a harvestable game species or furbearer (Nolet & Rosell 1998). Beaver are also perceived by many to possess human-like qualities including e.g. strong family bonds, industriousness and intelligence, and therefore should be protected. Even among central European hunters there seems to be little interest in establishing the beaver as a game species. One reason for this is the practice in many countries, e.g. Poland, Germany, Austria and Switzerland whereby hunters must compensate landowners for the damage done by the game species they hunt. Beaver apparently are not considered to be worth the expense this might entail. Neither is there any particular trophy associated with beaver. In short, most Europeans, hunters and non-hunters alike, at the moment see little reason why beaver should be harvested.

Presently, most nuisance animals throughout much of central Europe are being live-trapped and relocated to establish new populations when non-lethal methods of control prove impractical (Schwab & Schmidbauer 2001, Halley & Rosell 2002). Eventually, as habitats become saturated with beaver, this practice will become a less suitable solution and nuisance colonies will have to be dealt with in other ways. Alternatives to hunting or trapping might be the increased use of non-lethal methods of control, along with increased damage compensation. It is also conceivable that professional trappers using either live-traps and euthanasia, or quick-killing, body-gripping traps could be employed to regulate population density and remove nuisance individuals. Sale of the pelt and meat might constitute part of the trappers pay. Indeed, a system analogous to the registered trapline system practiced in Canada might be desirable. Regardless of the management solutions eventually employed, it is difficult to envision large-scale beaver management in central Europe without some use of lethal control. Though hunters are highly conservative and new traditions take time to develop, recreational hunting could eventually constitute a major portion of that control, and at little governmental cost.

Conclusions

The Norwegian experience suggests that successful beaver management must incorporate certain elements. First, landowners and other stakeholders experiencing conflicts with beaver must be provided with a quick and efficient means of solving the problem. If not, public tolerance for beaver may decrease and support for beaver and beaver management will likely suffer (Bishop et al. 1992). It is also important that all stakeholders be allowed to participate in the development of local beaver management plans.

Secondly, beaver must increasingly be perceived as a valuable resource; as income for landowners, game for hunters, and as a fascinating keystone species for everyone. Finally, beaver are here to stay and we must learn to live with them. Increased knowledge of their ecological importance and recreational value should lead to increased tolerance.

For those countries contemplating the use of hunting and trapping to remove nuisance animals and exploit populations we would suggest that managers, long before populations and conflicts peak, begin planning on how hunting and trapping should be organized to realize management goals. For those countries where hunting and trapping are not management alternatives, serious thought should be given early on to other methods of controlling populations and individuals. The need to limit conflicts will inevitably occur where humans and beaver coexist.

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Samenvatting

Beverbeheer in Noorwegen: een aanpak die ook elders in Europa kan worden gevolgd?

Terwijl men in Noorwegen al meer dan 150 jaar ervaring heeft met het beheer van bevers, is daarmee in de meeste landen in Midden-Europa nog nauwelijks ervaring opgedaan. Ondanks de snel groeiende populaties en toenemende conflicten worden er in deze landen geen bevers geoogst. Als een voorbeeld voor de wijze waarop in de toekomst met bevers zou kunnen worden omgegaan, presenteren wij hier de wijze waarop bevers worden beheerd in Noorwegen. De belangrijkste doelen van dit beheer zijn het vergroten van de biodiversiteit, het produceren van een oogstbaar surplus en het terugdringen van conflicten tussen de mens en bevers. Het beverbeheer zou zich moeten richten op het maximaliseren van de recreatiemogelijkheden en zou het landeigenaren mogelijk moeten maken te profiteren van de bever als inkomstenbron, namelijk door de verkoop van jachtrechten. De gemeenten bepalen het aantal dieren dat jaarlijks geschoten mag worden, waarbij de toewijzing aan de landeigenaren gebeurt op basis van de hoeveelheid beverbiotoop die zij bezitten. Het aantal landeigenaren dat zelf jaagt is overigens gering. De meeste bevers worden in de lente geschoten door jagers, als vorm van recreatie en voor het vlees. Schade veroorzaakt door bevers wordt niet financieel vergoed. Landeigenaren die substantiële schade ondervinden kunnen een vergunning krijgen voor het verwijderen van dammen, burchten en dieren die schade veroorzaken. De inzet van niet-dodelijke bestrijdingsmethoden is beperkt. Alhoewel er nog problemen zijn, is het beverbeheer in Noorwegen succesvol gebleken, omdat (1) er meer kennis

beschikbaar komt over de ecologische rol van de soort, (2) er sprake is van een langzame verandering in de beleving; van een plaagdier naar een waardevolle soort voor de jacht, en (3) deze aanpak van plaagdieren zo eenvoudig is. Op dit moment kost het beverbeheer de overheid nauwelijks geld; tegelijkertijd wordt de beverjacht steeds populairder en neemt het inkomen van de landeigenaren toe.

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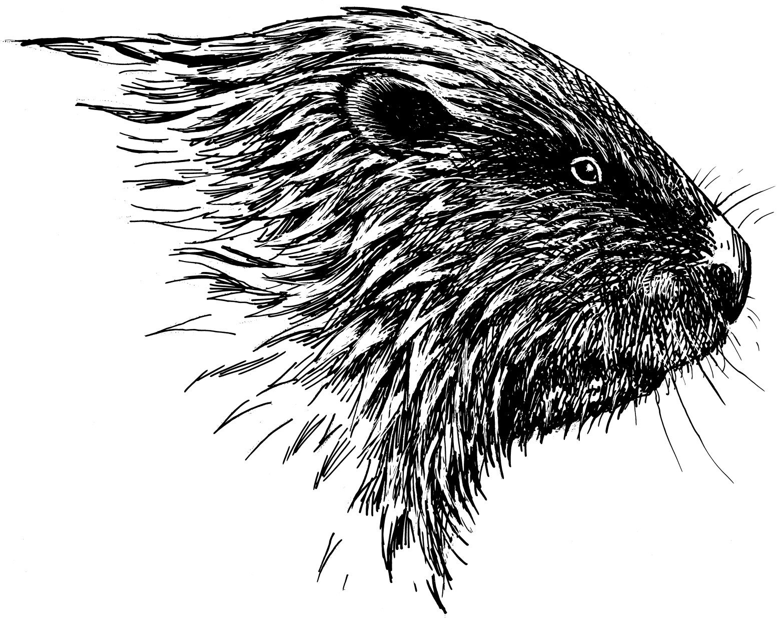

Fire and beaver in the boreal forest-grassland transition of western Canada – A case study from Elk Island National Park, Canada

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Abstract: Prescribed fire is used as a management tool in many areas throughout the world to restore vegetation communities, reduce fuel loading, and enhance wildlife habitats. However, the effect of prescribed fire on many wildlife species has not been well studied, especially on beavers (*Castor canadensis*). The purpose of our study was to examine whether prescribed fire influences beaver lodge occupancy in the aspen and mixed-wood habitats of Elk Island National Park, Alberta, Canada. In particular, we examined whether lodges in burned habitats experience lower occupancy levels than lodges in unburned habitats, whether the frequency of burns influences lodge abandonment, and whether the distance to suitable habitat potentially accessible from those lodges abandoned following a burn, influence beaver lodge occupancy. Since 1979, over 51% of Elk Island National Park (196 km^2) has been burned with the goal of restoring prairie plant communities. We found that fire negatively affected beaver lodge occupancy, an effect compounded with frequent burns. Though prescribed fire is considered an important landscape restoration process, the frequency of prescribed burning should be mitigated to ensure that flooding by beavers can continue as a key process that maintains wetlands on the landscape.

Keywords: Castor canadensis, beaver, fire, drought, ungulates, Elk Island National Park, Alberta, Canada.

Introduction

In Canada, there are several pressing issues in ecology, but one of the most controversial is the use of prescribed fire. Despite the major ecological role that beavers (*Castor canadensis*) play on the landscape (Naiman et al. 1988, Johnston & Naiman 1990), studies that specifically examine how fire affects beaver populations are lacking. Elk Island National Park (EINP) (figure 1) provides an ideal setting for such a study. Beaver numbers have been documented there since the early 1960s, there has been an active prescribed fire programme in the park since 1979, and being completely fenced, it has some of the highest year-round ungulate densities in the world. Over 340 lodges in the park are in areas exposed to prescribed fire, while approximately 800 lodges are in unburned areas. Six species of large ungulates roam freely in both burned and unburned habitats where they feed on riparian vegetation adjacent to beaver ponds.

Since 1979 over 51% of the park has been burned; in some areas as many as eight times. The most recent burn was in 2002. Beaver populations are regularly surveyed and the park has been divided into 20 beaver units to facilitate these surveys. The park is located in the Aspen Parkland Natural Subregion (Achuff 1994) and is dominated by trembling aspen (*Populus tremuloides*). These stands typically have a diverse understory in which beaked hazel (*Corylus cornuta*) is prevalent. The topography is morainal and consists of numerous small lakes and ponds within a hummocky landscape. Major rivers and streams are uncommon. The Aspen Parkland is the transition zone between the boreal forests to the north and the prairie grasslands to the south. EINP, located in the Beaver Hills of east-central Alberta, provides one of the few remaining protected areas between these two dramatically different ecosystems.

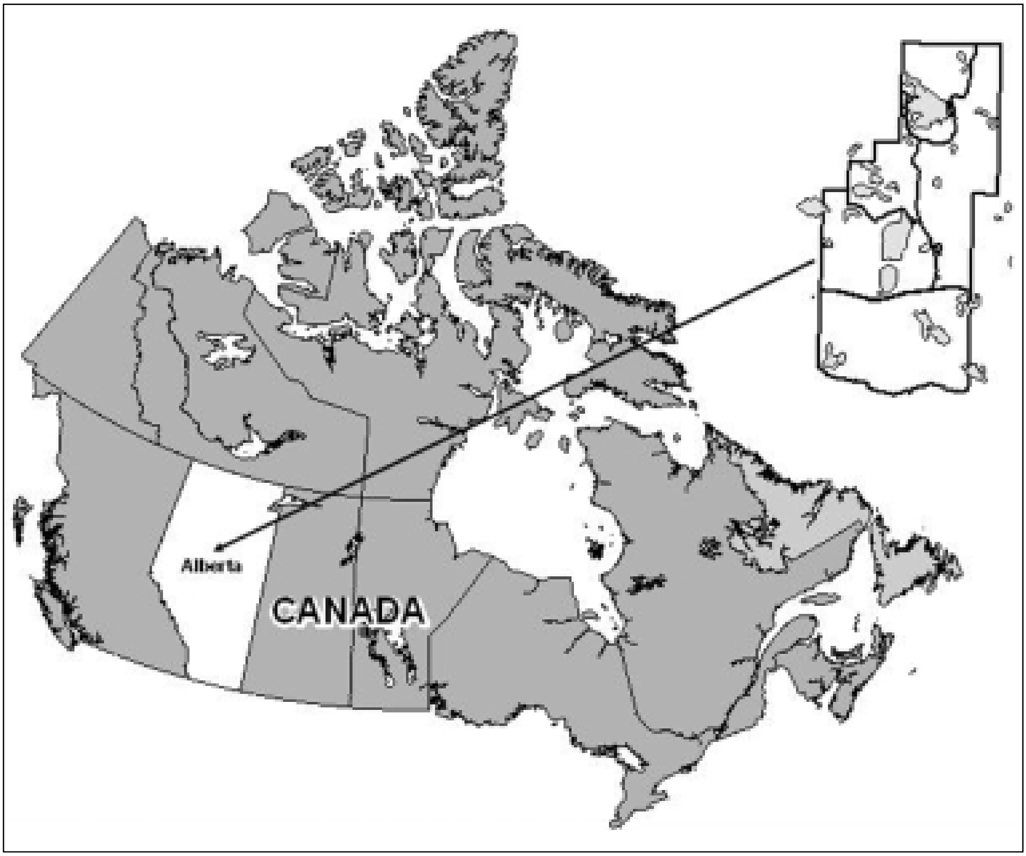

Figure 1. Location of Elk Island National Park in east-central Alberta, Canada.

Prescribed fire has been used in North America since pre-colonial times. Aboriginal people used fire as a game management tool and early settlers used it for land clearing (Lewis 1982, Murphy 1985). However, with increased settlement and dependence on forest resources, fire suppression became the primary focus throughout much of the 20th century (Woodley 1993). And now, after decades of fire suppression activities, fire is often used by land managers inside and outside of protected areas to regenerate early seral stages of vegetation, enhance wildlife habitat, and reduce fuel loads (Woodley 1993). But the question is: does it accomplish these goals given all the variables in today's ecosystems? Specifically, we addressed whether fire enhances wildlife habitat for beavers. We investigated whether fires decrease beaver lodge occupancy and if the distance between active and abandoned lodges increases under a burning regime. We also addressed whether the cumulative impacts of drought (plus fire) and high levels of ungulate herbivory cause an additive loss of active beaver lodges. Some studies have found that the use of prescribed fire does not always achieve expected results (White et al. 1998). In areas with high densities of ungulates, woody plant species, such as those preferred by beavers, fail to regenerate following a burn (Campbell et al. 1994, Bailey & Whitham 2002). The combination of repeated burning and climatic conditions (e.g. drought) are known to reduce the ability of woody plants to recover from fire (Elliot et al. 1999, Roques et al. 2001). Given the presence of all these conditions (prescribed fire, high densities of ungulates, repeated burning, and a recent drought) in EINP, we predicted that (1) beaver lodge occupancy would be lower in burned areas, (2) repeated burning would result in the long-term abandonment of previously active beaver lodges, and (3) burning during drought conditions would intensify the effects of prescribed fire on beaver lodge occupancy. Further, we predicted that if there was an increase in the abandonment of beaver lodges in burned areas, the distances separating active and abandoned lodges would be greater than in areas that had never been burned. Fires in EINP often consume or damage most woody vegetation that would otherwise be available as forage. Consequently, burned areas would experience a delay in the re-colonization of abandoned lodge sites.

Lodge occupancy in burned and unburned areas

EINP currently has 1,172 beaver lodges, of which 152 were active during the aerial survey in the fall of 2002 (Hood et al., in review). To facilitate our analysis only the occupancy data from 1989-2003 were used and all lodges that were never active during this time period were removed from the dataset. Of the total number of lodges analyzed for this study, 346 were in burned areas and 799 were in unburned areas. As expected, the proportion of active lodges in burned areas was significantly lower than the proportion of active lodges in unburned areas. In addition, when we compared the year immediately prior to a burn to the year immediately following a burn we had almost identical results (Hood et al., in review). When we examined the entire ten-year period following a burn, there was no predictable reoccupation of lodges despite the fact that various authors indicate that beavers should benefit from the regeneration of woody species after a burn (Bird 1961, Kellyhouse 1979, Lewis 1982, Naiman et al. 1988, Fryxell 2001). Although there was an increase in occupancy two years after a burn, it was not sustained. This finding indicates that food resources were still available to beavers two years after a burn, however, it was evident that the subsequent declines in the occupancy rate were likely driven by something else than just fire.

Fire and ungulate herbivory

At 196 km^2, EINP has extremely high year-round ungulate densities with 13 ungulates/km^2 (Hood & Bayley, unpublished data). There are five ungulate species in the park: Manitoba elk (*Cervus elaphus manitobensis*), moose (*Alces alces*), plains bison (*Bison bison bison*), wood bison (*Bison bison athabascae*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*). Apart from coyote (*Canis latrans*), the park lacks any large resident species of predators. Park officials periodically cull elk and bison from the park to reduce ungulate densities.

Studies that have examined ungulate use of burned areas indicate that many ungulate species are drawn to these areas (Vinton et al. 1993, Bailey & Whitham 2002). Use can increase to the point where overgrazing by ungulates in burned areas inhibits the regeneration of woody plants (Bork et al. 1997, Campbell et al. 1994, White et al. 1998, Bailey & Whitham 2002, Hessl & Graumlich 2002). In their study on the effects of fire and herbivory on vegetation in EINP, Bork et al. (1997) found that fire-tolerant species such as beaked hazel and wild raspberry (*Rubes ideaus*) were significantly shorter and more hedged than those same species outside the park. They also found that the use of fire in the park failed to increase smaller size classes of woody species. We too found that shrubby vegetation inside the park, such as beaked hazel, was significantly shorter than the same species immediately outside the park (Hood et al., in review). Although one of the beaver's preferred forage species, serviceberry (*Amelancier alnifolia*), is considered a fire-tolerant species (Noste & Bushey 1987), mature forms of this plant were rarely present inside the park (Bork et al. 1997, Hood & Bayley, unpublished data). The interaction of fire and herbivory is a commonly cited mechanism of the historic maintenance of the grassland ecosystems of the Great Plains of North America (Bird 1961, Vinton et al. 1993, Campbell et al. 1994). Even now, fire, in combination with cattle grazing, is often used as a means to remove woody species for the creation of agricultural pasturelands (Anderson & Bailey 1979, Bailey et al. 1990). The combined effect of fire and intense ungulate herbivory is likely having similar effects on woody vegetation in EINP.

Fire frequency

When we examined the effects of fire frequency on beaver lodge occupancy in the park, we found a clear trend in lodge abandonment. Lodge occupancy increased slightly after one burn (from 25% to 26%), which could be a reflection of the increase in lodge occupancy during the second year post-burn, but is just as likely due to natural variation. After two burns, however, occupancy decreased dramatically (from 26% to 16%) and after three or more burns, occupancy dropped to zero (Hood et al., in review). Beavers are a cyclic animal, abandoning areas when food supplies are exhausted and moving on to new areas (Ives 1942). They also exhibit density-dependent reproduction and beaver colonies regulate themselves once reaching carrying capacity (Paine 1984, Schulte 1998). It could be that the occupancy patterns we observed in response to fire were part of a normal cycle for the area. An examination of the trend in beaver populations since 1963 revealed that the population does have natural fluctuations. However, when the lodges in burned areas were analyzed separately from the lodges in unburned areas, only the lodges in burned areas showed a dramatic decrease in occupancy.

Suitable habitat in burned areas

Of the 121 fires in the park since 1979, 95% of prescribed fires in EINP were lit in the spring, which can result in fires that burn right up to wetland edges. Some lodges in the park have been completely consumed by prescribed fires. Beavers are then forced to either disperse to more suitable habitat or rebuild. To capture some indication of the typical distance to the nearest potential (previously occupied) habitats for dispersing juveniles from active lodges, we measured the distance from all abandoned lodges to the nearest active lodge in both burned and unburned habitats for each year since 1989.

The average distance to the nearest active lodge in burned areas was significantly higher than that in unburned areas (Hood et al., in review), indicating that suitable habitat was less accessible in burned areas. The higher risk of predation associated with these long distances that beavers would have to travel to find new lodge locations or reconstruction materials may have translated to a higher mortality of beavers in these areas, contributing to the lower occupancy we observed immediately after fires. In addition, re-colonization of abandoned areas might take a long time due to the larger distances between active lodges and abandoned lodges in burned areas.

Cumulative disturbances

In our analysis, we also found a particularly large increase in distances between abandoned and active lodges during the years 1999-2003 (Hood et al., in review). Two events that might have influenced this trend are a record-breaking drought from 1999-2002 (most severe in 2002), and extensive burning in three of the beaver units in the year 2000.

Both the drought and high levels of ungulate herbivory allowed us to address cumulative disturbances to beaver habitats in burned areas. We compared the beaver units that were extensively burned in 2000 to units that had never been exposed to prescribed fire. In the four units that had never been burned, the distance between abandoned and active lodges actually decreased (except in one unit where there was a slight increase). In the three units that had been extensively burned during the drought, the distances between abandoned and active lodges did the opposite and actually increased significantly. It is possible that unburned areas provide habitats that endure drought, while habitats in burned areas were less likely to maintain adequate water and forage. Morgan (1991) noted in her beaver habitat assessments that beavers in EINP did not browse on charred or singed wood. To find appropriate forage, beavers would be forced to either disperse or increase their foraging distances in burned areas.

Although we know that factors like topography, predation, disease, and population densities will always affect how beavers move across the landscape (Johnston & Naiman 1990), the combined effects of fire and drought appear to be possible factors influencing the dispersal of beavers to alternate habitat in this case. Our results suggest that fire alone can have some effect on access for beavers to suitable habitats, but when occurring during drought, the combination appears to be too much for wetland habitats (and beavers) to accommodate.

Conclusions

Through our study, we found that fire does not always enhance beaver habitat as has been assumed in the scant literature available. Single burns without drought did not appear to affect lodge occupancy. Repeated burning in beaver habitats caused the most dramatic effects on beaver persistence in established ponds and resulted in the long-term abandonment of lodges after three or more burns. It is also possible that in areas of multiple burns, the inter-fire period is too short for adequate recovery of woody plant species and results in grassland habitats being dominant. As a result, multiple burns in beaver habitat had the most negative effect on long-term lodge occupancy. We also found that the mean distance between abandoned lodges and active lodges increased significantly in burned areas. The cumulative impacts of fire and drought appear to intensify the effect: mean distances increased dramatically in burned areas even though they decreased in unburned beaver units. Combining multiple perturbations such as drought and extensive burning appears to cause more disruption to wetland habitat than beavers can tolerate. The combined effects of ungulate herbivory and fire also appears to result in less suitable beaver habitat, largely by depressing shrub growth.

In many areas, beavers play a pivotal role in the dominant ecological processes. The appropriate use of fire in both natural areas and agricultural environments can help ensure that beaver habitats remain viable, so their populations can continue to contribute to the creation and maintenance of wetland ecosystems.

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Samenvatting

Branden en bevers in de boreale overganszone bos-grasland van west Canada – Een case-studie in Elk Island National Park, Canada

Gecontroleerd branden wordt wereldwijd gebruikt in het natuurbeheer met het doel bepaalde vegetatietypen terug te brengen, de kans op oncontroleerbare branden te verkleinen en habitats te verbeteren. Het exacte effect van branden op veel diersoorten, waaronder de bever (*Castor canadensis*), is echter weinig bestudeerd. Het doel van onze studie is te onderzoeken of branden de bezetting van beverburchten beïnvloedt in de populierenbossen en gemengde bossen van Elk Island National Park, Alberta, Canada. We onderzochten met name of de bezettingsgraad van de burchten in gebrande delen lager is dan die in ongebrande delen, of de frequentie van branden het verlaten van burchten beïnvloedt en of de afstand tot het dichtstbijzijnde geschikte habitat de bezettingsgraad van burchten beïn-

vloedt. Sinds 1979 is meer dan 51% van Elk Island National Park (196 km^2) gebrand om de prairie-plantengemeenschappen terug te brengen. We ontdekten dat vuur de bezetting van beverburchten negatief kan beïnvloeden: hoewel één keer branden geen effect op de burchtbezetting heeft, brengt drie of meer jaren achtereen branden de proportie bewoonde burchten omlaag. Afstanden tussen bezette burchten waren hoger in gebrande dan in ongebrande gebieden. Dit duidt erop dat in de gebrande gebieden minder geschikt habitat aanwezig is. Deze afstanden tussen burchten en geschikte gebieden wijst er tevens op dat in gebrande gebieden de burchten minder snel geherkoloniseerd worden, en zou kunnen resulteren in een hogere mortaliteit onder de bevers na een brand. Bij brand tijdens een droogte nam deze afstand nog sterker toe: gecombineerde verstoringen lijken dus een ongewenst effect te geven. Alhoewel het gecontroleerd branden beschouwd wordt als een belangrijk landschapsherstellend proces, dient de frequentie van branden aangepast te worden om te verzekeren dat overstromingen door bevers kunnen blijven plaatsvinden als een sleutelproces voor het behoud van wetlands in het landschap.

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Planning, coordination and realization of Northern European beaver management, based on the experience of 50 years of beaver restoration in Russia, Finland, and Scandinavia

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Abstract: By 1900 the beaver (*Castor fiber*) had disappeared from many parts of Northern Europe. Beaver population restoration started during the 1930s, and mass releasings of animals took place after the 1950s. The extinction and reintroduction of the beaver can thus be seen as a giant field experiment in landscape ecology and ecological engineering. A general evaluation of this experiment, however, has not been made yet. It is argued here that two main natural causes of beaver population fluctuations should be studied: 1. The carrying capacity of the environment, where food resources at northern sites are expected to be exhausted within some years. 2. Control from predators, which has led to the evolution of the beavers' complicated constructing behaviour. A cost–benefit analysis of beaver reintroduction, which could result in management policies, needs to be made.

Keywords: beaver, *Castor fiber*, *Castor canadensis*, reintroduction, restoration, carrying capacity, predation refuge, ecological engineering, landscape modification.

Introduction

Until the 19th century, beavers (*Castor fiber*) occurred in large areas of Northern Europe, from the west coast of Norway to the Ural Mountains. By 1900 the species was extinct in large parts of its former range of distribution, as a result of hunting and habitat change. It was, however, still present in a few areas of central Russia, Belarus and Ukraine, as well as in small areas of Norway, Germany and France. Since the restoration of beaver populations in north-eastern Europe started, researchers have reported on the status of the newly established populations (Segal' & Orlova 1961, Lavrov 1965, Zharkov 1969, Zaripov & Yushina 1973, D'yakov 1975, Danilov 1992, Hartman 1994, Baskin 1998). In Russia the first small numbers of beavers were caught in the central parts of the country and released in northern areas already in the years 1936-1938, although most animals were released after the 1950s (Pavlov et al. 1973). After 30 years of reintroduction, beavers had occupied all suitable habitats. Nowadays we observe the highest beaver densities in small forest streams where they are able to transform the environment according to their needs. Events in human society have also been favourable for the beaver. Since the market for beaver fur has declined, hunters have lost interest in trapping more beavers.

In Finland and Russian Karelia the American beaver (*Castor canadensis*) was released, in addition to the European beaver, resulting in established populations (Lahti & Helminen 1974). American beavers are now distributed in areas close to those occupied by European beavers. The two species inhabit the same streams and lakes of Karelia and Finland (Danilov & Kan'shiev 1983, Danilov et al. 1999,

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Fyodorov 2003). From the modern point of view the introduction of American beaver in Europe was a mistake that contradicts principles of conservation of fauna diversity (Sjöberg & Hokkanen 1996, Nummi 2001). The question is whether or not this introduction threatens the existence of the aboriginal European beaver populations.

The beaver is a keystone species and its activities have important consequences for the landscape (Naiman et al. 1988, Johnston 1994, Jones et al. 1994). The extinction and reintroduction of the beaver can thus be seen as a giant field experiment in landscape ecology and ecological engineering. A general review of this experiment has, however, not been made. The dynamics of the beaver population have not been analysed, nor have the beavers' ecological niche, the limiting factors, or the carrying capacity of the environment been sufficiently studied. There is a significant gap also in the knowledge of landscape changes during the last 50 years as a result of the return of the beavers.

The experiment has been replicated in areas of widely differing ecological, climatic and edaphic characteristics. Seven teams of researchers (four teams from Russia, along with Finnish, Norwegian and Swedish teams) intend to use this diversity in reintroduction areas for a study (see: http://www.szooek.slu.se/eng/projekt/projekt.cfm?ID=104). The research is being conducted in flowing and standing reservoirs, in streams and large rivers, in very shallow and quite deep waters, and in natural as well as artificial water reservoirs. The little-known swamp populations of the beaver, inhabiting floating peat islands, will also be studied. The teams will work in areas dominated by forests, as well as in the Republic of Tatarstan where 70% of the area is occupied by arable land. In Tatarstan most beaver settlements are situated in rivers straightened by humans, where the animals browse sparse willow shrubs growing along the water edge. Furthermore, in the Scandinavian countries and Finland, beavers have existed in an environment without large predators (Rosell et al. 1996), while these have been present in large parts of Russia. The aim of the researchers working under different environmental conditions is to find general as well as specific answers to a number of questions.

Questions and hypotheses

There are some questions that should be addressed in an evaluation of the beaver "experiment" as described above: 1. How does the beaver change the landscape conditions, species composition and biomass in aquatic and riparian environments in different relief and soil conditions of different vegetation zones? 2. How important is predation in determining the engineering activities of beavers? What is the current role of predators, e.g. wolf (*Canis lupus*), brown bear (*Ursus arctos*), lynx (*Lynx lynx*), and other species? 3. What influence does the beaver have on vegetation in poor northern conditions, and how long does it take for beavers to return to places previously deserted by them? 4. What different kinds of beaver-human conflicts occur? 5. How do new conditions created by beavers correspond to pristine conditions? Introducing beavers as a method of restoring primeval landscapes is practised more and more often, and it needs to be developed more.

A number of hypotheses can be made based on ecological theory and results of previous studies on interactions of European and American beavers with their environment: 1. Population densities of beavers should be higher in more productive areas, i.e. warmer and more humid regions. Turnover time of beaver settlements should also be longer in more productive areas. 2. Locations of beaver settlements are strongly determined by relief. It is possible to predict positions of the localities using map information and parameters that are necessary for beaver survival (D'yakov 1975, Dezhkin et al. 1986). 3. Successions of all kinds of biotic communities should differ significantly in areas with beavers compared to areas where the species is absent, and they should follow different paths in time (Naiman et al. 1988). These changes are expected to last long after beavers have deserted areas, and these effects should be more pronounced in harsh than in more productive areas. 4. Biodiversity of all biotic communities is expected to increase as a consequence of the beavers' activities. Species adapted to wetland conditions are expected to benefit from the effects of beavers on the landscape (cf. Medin & Clary 1990). 5. The effects on beaver populations of the presence of wolves is expected to be significant, as a result of the risk of predation and changes in beaver behaviour (Basey & Jenkins 1995). 6. Differences in construction activity of the two beaver species depend on environmental conditions more than on innate species differences (Danilov et al. 1999, Fyodorov 2003). Also a competitive advantage of the respective species is expected to vary with environmental conditions.

Proposed research fields

An estimate of the large-scale results of the reintroduction of beavers in Northern Europe
A general review should be made of beaver population densities, geographic distribution and habitat occupation after 50 years of reintroductions and restoration of populations. A comparative study should be made along east-west and north-south gradients. Data on beaver populations advancing in Northern Europe should be compiled. Mapping of fresh waters occupied by beavers in the second half of the 20th century should be done.

The starting conditions of the different beaver restoration projects varied. The population growth depended on many factors, e.g. abundance of fresh water, number of released animals, number of years since the first group of animals was released, and predator density. A comparison of beaver status of 32 populations in Eastern Europe in 1972 demonstrated that the beaver densities in northern areas had been growing much more slowly than in central areas. However, a comparison of the same populations in 2000 showed that beaver densities in the areas south of 57°N had, on average, doubled only, while numbers of populations northwards from 57°N had increased by seven times (figure 1).

Predators and beaver construction activities
To our knowledge there are no studies emphasizing that predators were the stimulus for the evolution of a specific protective behaviour of the beaver. We suggest that predators are the most important factor determining that beavers can only survive if they have a water refuge. In the areas of on-going investigations, the wolf, the brown bear and the lynx are the main beaver predators. Predation is most obvious in March-April, when beavers are forced to come out of their ice hole to find food. In spring about 20% of wolf excrements contain beaver hairs. The vulnerability of beavers in winter is supported by an anecdotal observation. Once in spring we found an unsuspecting beaver browsing an aspen (*Populus tremula*) and were able to be ahead of it near its ice hole. We observed the desperate attempts of the beaver to push off the human from the hole as the only refuge (L. Baskin, personal observation).

According to Dezhkin et al. (1986), the minimum size of a water reservoir for the survival of at least one animal is 1 m by 10 m and 1-1.5 m deep. We observed, however, that one animal survived for a month in a pond 2 by 2 m and 0.5 m deep. The principal question here is what the minimum depth is of waters where beavers can survive. We studied the depth of streams where beaver presence was obvious, e.g. there were fresh exits at shores or fresh browsing marks. The depth in these places fluctuated between 15 and 150 cm. However, in 90% of the occasions it was 35 cm or more (L. Baskin, unpublished data).

Another limiting factor is the distance to safe feeding. In southern boreal forests, 90% of the browsed trees are found not further than 13 m from a water refuge (L. Baskin, unpublished data). Only 1% of the browsed trees were more than 20 m removed from a water refuge. The maximum was 26 m, not taking into account the trees browsed during spring flood. The hypothesis that a significant part of landscape modifica-

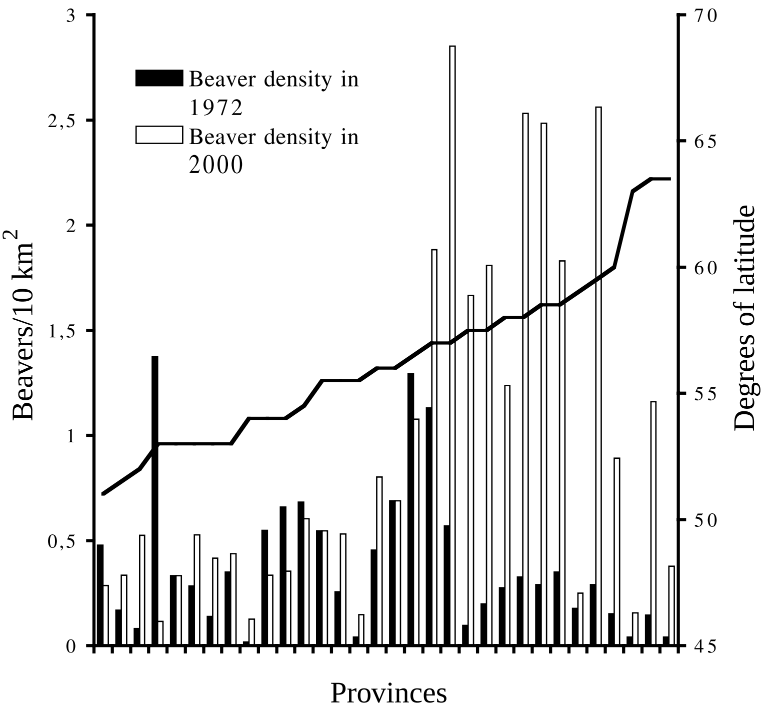

Figure 1. Beaver numbers since their reintroduction in 32 provinces, listed from south to north, of European Russia in 1972 and in 2000.

tion activities by beavers are an anti-predator strategy needs to be tested and developed. We need to know the exact parameters of water refuges. The risk of predation also needs to be estimated more correctly.

Testing models for predicting beaver population density and the time of existence of settlements

Thirty-eight species of trees and shrubs were found to be used by beavers. However, only twelve of these are found in all areas of northern Russia (Makarov & Tkachenko 1957, Solov'ev & Tyurnina 1971, D'yakov 1975). In southern boreal forest from 1977-2003, 43% of the 4,900 browsed trees were aspen, 30% were birch (*Betula* spp.), 11% were alder (*Alnus* spp.), 8% were willow (*Salix* spp.), 6% were lime tree (*Tilia* spp.), and additional trees included cherry tree (*Padus racemosa*), mountain ash (*Sorbus aucuparia*), buckthorn (*Frangula alnus*) and currant (*Ribes pubescens*) (L. Baskin, unpublished data).

The number of years required for beavers to exhaust the carrying capacity of northern habitats is an important problem. In a river that has been under investigation since 1977 the proportion of aspen among browsed trees was 88% in 1977, but only 27% in 2003 (L. Baskin, unpublished data). After the depletion of local food resources, the next stage of environmental exploitation was to build a dam to elevate the water level and thus have access to food resources situated at higher elevations. In 1977, along 22 km of the river, we observed nine large dams, but in 2003 only one. The beavers left the river and settled in small tributaries. Along the main river, strips of meadow stretched out along the water and only willows and birches were able to occupy those sites in the short term, while aspen needed more years for re-growth. Re-settling of beavers in these sites, which have been used in the past, now takes place in essentially worse conditions. We need to describe this cycle of exhaustion and recovery under different conditions.

Mapping of environmental variables, including the impact of humans and food availability, should be made. Models need to be developed for assessing beaver population density and duration of settlements. This can be done using GIS to take into account characteristics of landscape and climate. Already collected data sets should be compared to newly collected data upon which to base more reliable models and predictions.

Predicting landscape changes after reintroduction of beavers in various vegetation zones

Where there is a flood plain, building a dam leads to the creation of a pond. Then the beavers can safely reach feeding places situated further away from the main stream. Also after spring flood beavers dig canals to transport stumps of wood and tree branches.

The first beaver meadows occurred 20 years after the first reintroduction of beavers (L. Baskin, unpublished data). Nowadays, after 50 years of beaver restoration in Northern Europe, the meadows stretch along most of the rivers and streams where beaver settlements have existed and where beavers have elevated water levels by dam constructions. It is an interesting task to determine the areas of beaver meadows and their dependence on topographic conditions and forest type. A helpful tool would be a model to predict the appearance of beaver meadows. The next step would then be to validate these predictions in the field. The width of beaver meadows depend on the elevation of flood plains. In lowlands, beavers can flood much larger areas. We will use maps to predict which sites are more suitable for the creation of beaver ponds, and which will later develop into beaver meadows. By using large-scale topographic maps it should be possible to find sites where beavers can create water refuges. With maps (scale 1:10,000), and assuming 0.5 m as a minimum acceptable depth of a beaver refuge, we can point out sections of streams where dams of different height (e.g. 0.5, 1, 1.5, or 2 m) will keep a sufficient water level. Dam influence reaches 200 m and more upstream. This value may fluctuate depending on the depth and width of the stream. A simple example from a drainage system is presented in figure 2.

Studying the role of beavers in aquatic and riparian communities, and determining the role of predators as a factor limiting beaver populations

The effects of beaver reintroductions on biodiversity, community composition and biomass (vegetation, vertebrates, and invertebrates) in aquatic and riparian environments should be estimated. The following studies need to be done: 1. Changes of bank vegetation resulting from beaver grazing and other activities. 2. Vegetation, plankton, benthos and fish communities in habitats with and without beaver (cf. McDowell & Naiman 1986). 3. Land vertebrates in habitats with and without beavers, especially beaver-predator relationships (cf. Potvin et al. 1992, Rosell et al. 1996). 4. Breeding success of ducks in habitats with and without beavers, and the role of invertebrates in this (cf. Nummi 1992). As a result, beaver ponds, irrigated meadows, and water canals create an environment with new conditions favourable for other animals including moose (*Alces alces*), rodents, and various species of birds.

Identifying long-term consequences of the introduction of the American beaver in Northern Europe

The importance of interactions between beaver species (*Castor fiber* and *Castor canadensis*) when co-occurring should be assessed, and predictions should be made of their long-term consequences. It should be studied what species currently is the strongest competitor where they coexist. Maps of European and American beaver settlements should be prepared, data should be collected for comparison of habitats and characteristics, and dynamics of numbers and distribution of American and European beavers during the last 50 years should be estimated.

Production of a cost–benefit analysis of beaver reintroduction, to be used in management policies

In the past centuries, the beaver has been important to humans mainly for its fur. Nowadays there is no longer a good market for beaver skins

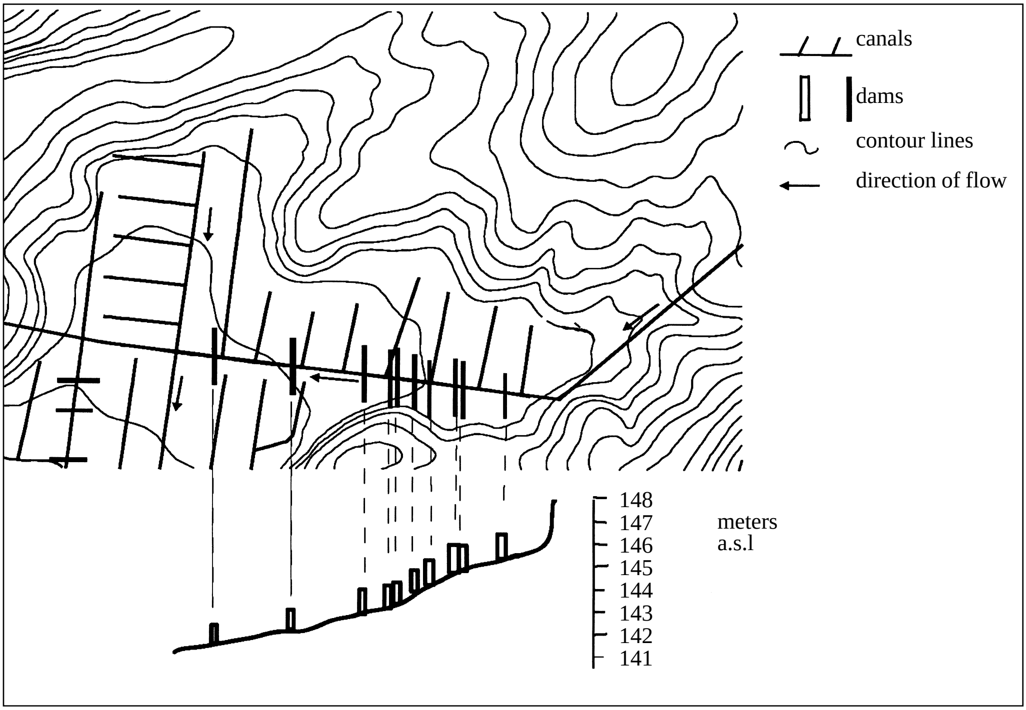

Figure 2. An example of a system of beaver dams from a drainage system in the Kostroma Province, Manturovo District, Russia (58.2654 °N, 44.4538 °E). The upper part shows a view from above and the lower part of the picture shows a profile.

and a decline of beaver harvest is observed. As a consequence the necessity for special measures to protect the species has disappeared. The browsing activity of the beaver is of limited importance to humans since the species generally uses trees and shrubs of little value. Dam construction is the most harmful beaver activity, since significant areas of forest, hay fields and roads can be flooded (Fyodorov 2003). Drainage systems can be partly paralysed by beaver dams. However, in our studies we found that after some period the beavers abandon the drainage canals after having exhausted the food resources within a 20 m distance from the canals (L. Baskin, unpublished data). Some damage may remain, however, as old dams may survive for over ten years. Water flow may wash out one of the shores in passing beside the dam. Beaver burrows may also destroy canal banks.

The landscape modification role of the beaver is positive in areas where agriculture, straightening of streams and drying up of swamps have led to loss of biodiversity and natural communities. Human activities have simplified the aquatic environment (straight canals instead of naturally winding streams, more or less dead waters instead of complicated ecosystems of water plants and animals). The importance of the role of the beaver for restoration of an environment disturbed by humans has been confirmed (Balodis 1990, Gorshkov et al. 1999), but it is still unknown whether the new conditions created by beavers correspond to pristine conditions. An introduction of beavers as a method of restoration of primeval landscapes is more commonly practised, and it needs to be further developed.

Conclusion

Large-scale field experiments investigating the extinction and restoration of beaver populations should be a valuable tool for understanding processes in landscape ecology. To reach this aim teams working in different parts of Northern Europe have been involved. These teams use different methods and approaches. Coordination of their activities, directions and methods is necessary. Preference will be given to long-term data on populations and landscape changes.

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Samenvatting

Planning, coördinatie en realisatie van een beheersplan voor de bever in Noord-Europa, gebaseerd op 50 jaar ervaring met herstel van beverpopulaties in Rusland, Finland en Scandinavië

Rond 1900 was de bever uit grote delen van Noord-Europa verdwenen. De eerste bescheiden herintroducties in Rusland vonden plaats in de jaren ’30, maar pas vanaf de jaren ’50 werd de bever op grotere schaal in Noord-Europa uitgezet. Naast de Europese bever (*Castor fiber*), ging het in delen van het gebied ook om de Amerikaanse bever (*Castor canadensis*).

De geslaagde poging om de bijna uitgestorven bever weer terug te brengen in Noord-Europa, kan worden gezien als een enorm veldexperiment. Een gedegen evaluatie van dit experiment, is echter niet voorhanden. Bovendien wordt het enorme potentieel aan onderzoeksmogelijkheden onvoldoende benut. Dit artikel presenteert plannen voor samenwerking tussen onderzoekers uit Noorwegen, Zweden, Finland en Rusland. Er worden vragen geformuleerd, uitmondend in een aantal belangrijke onderzoeksvelden. Argumenten hiervoor komen uit de literatuur, en worden deels ook ondersteund door eigen waarnemingen. Speciale aandacht moet uitgaan naar twee onderwerpen: 1. de draagkracht van noordelijke biotopen voor de bever, en 2. de invloed van predatoren op het gedrag en de ecologie van bevers. Daarnaast zouden de herintroducties onderworpen moeten worden aan een kosten-batenanalyse. De resultaten van het onderzoek kunnen worden toegepast in de ontwikkeling van toekomstig beleid voor en het beheer van beverpopulaties.

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Book Reviews

Beavers (1)

The beaver: natural history of a wetlands engineer. D. Müller-Schwarze & L. Sun 2003. Cornell University Press, Ithaca, New York, USA. 190 pp. ISBN 08-0144-098-X. Prize: € 30,–.

Following a literary tradition that began with Lewis Henry Morgan's 1868 classic, *The American Beaver and His Work*, Dietland Müller-Schwarze and Lixing Sun have maintained the high standard of natural history reporting on this species in their 2003 publication, *The Beaver: Natural History of a Wetlands Engineer*. Müller-Schwarze, a professor at the State University of New York at Syracuse and his former graduate student Sun, who now teaches at Central Washington University, have given us a comprehensive overview of our contemporary biological as well as sociological understanding of these fascinating animals. While the authors draw primarily on information on the American beaver (*Castor canadensis*), numerous references to the European beaver (*Castor fiber*) dot the work as well. The disparity, if it can be called that, seems simply due to the greater availability of information on the North American species, especially with respect to ecological relationships. This is hardly surprising, considering that efforts to repatriate European beaver are still very much underway, while beaver in North America have been reestablished through much of their former range for at least several decades.

Given the enormous role human intervention has played with these animals, any account of the natural history of beaver has to be approached from a sociological as much as biological perspective. Müller-Schwarze and Sun have done a masterful job of capturing this in portraying the complex interplay that exists between these factors. The concise and compact 200 pages of information is divided into five parts with twenty-one chapters. The authors move from considering the beaver as a biological organism in evolutionary context through a logical progression that addresses behaviour, social organization, and finally ecology, to end with chapters that detail both historic and contemporary relationships between beaver and people. Each section is succinctly written with excellent references and an economy of presentation that capitalizes upon known facts without excessive diversion into many of the inviting side streams associated with research on these animals.

The facts are often fascinating. We learn, for example, about many of the distinctive biological adaptations of beaver that so effectively allow these animals to succeed in their specialized evolutionary niche as a keystone species. Most people may already know that the beaver's tail is used as a multi-purpose tool that can sound alarm, help balance the animal on land and propel it in water (but not, as the cartoons often show, to transport building materials). How well known is it, however, that the tail also allows for a sophisticated adjustment in heat exchange through a countercurrent arrangement of blood vessels that permits heat loss of up to 25% in summer but less than 2% in winter?

From behaviour to populations, these chapters nicely tie the preceding information to its consequences with respect to abundance and distribution of beaver across landscapes. From there, we are introduced to information on the ecology of beaver, establishing what is coming increasingly to be recognized as the vital role these animals play in establishing and maintaining wetland ecosystems. It soon becomes hard to imagine what the American and Eurasian landscapes were like before humans destroyed beaver populations and eliminated the wetlands they had created. The suggestion inherent in the descriptions provided by Müller-Schwarze and Sun is that our image of a pre-settlement North America, in which vast contiguous forests or vast contiguous prairies comprised the primeval landscape, needs to be seriously questioned and revised to take into account the ubiquitous presence of beaver.

Beaver were crucial in allowing Europeans to gain a foothold in the New World, and Müller-Schwarze and Sun go so far as to claim that no other wild animal has had such a profound influence on the human history of North America. The search for beaver literally drove exploration of the continent and the earliest settlements were often organized around the trade in their skins. Beaver pelts became the coin of the realm in early America, exported by the hundreds of thousands annually to satisfy the demand for the latest European fashion, mostly in the hat trade. Moreover, the rich wetlands beaver had colonized for centuries yielded some of the best agricultural land possible once drained and seeded. Greatly overexploited, the beaver offered the fledging nations of Canada and the United States an opportunity to practice ecological reason by recognizing that the resources of the continent were not inexhaustible. Neither took to this lesson and populations were decimated. Slow to recover, the re-emergent populations of today again offer humans the opportunity to work in cooperation with natural forces, an offer that we may finally be ready to accept, if only in part.

This opportunity leads us to the concluding chapters, which deal with conservation and proactive management. With our contemporary understanding of beaver biology and ecological requirements, Müller-Schwarze and Sun make an argument for management that occurs proactively, before crisis situations arise and the need to impose blunt and forceful solutions seems mandated. The steps necessary in such an approach range from building on higher ground to providing alternatives in the form of food and wetlands where beaver will not harm human interests. Briefly chronicled are the available technologies (deceivers, levelers and stoppers) that enable humans to out-engineer beaver and prevent adverse consequences from damming. The approach embraced is both comprehensive as well as visionary. Sadly, it seems as yet little acknowledged or practiced in North America by traditional wildlife management interests.

If any disappointment awaits the reader of this work it is that the authors do not digress from their focus on what we know about beaver to speculate more about some of the fascinating questions awaiting research. For scholars in-

Photograph: Rollin Verlinden.

terested in evolutionary biology, comparisons of the two species could open a hundred new areas of research and the propinquity of their being sympatric in many parts of Eurasia at this time almost demands critical examination. More attention could be focused as well on the potential environmental services beaver might provide. Research in this area is nascent, with only a few pathfinders willing to challenge the orthodox view of flood control to speculate that beaver-restored wetlands might actually do more service in this area than the enormous multi-billion dollar construction projects we so avidly pursue.

Müller-Schwarze and Sun have introduced in an economy of fact and theory much of what we need to recognize as valuable about beaver and their contemporary relationship to humans. What they cannot provide is the wisdom or the will to use the information we now have to maximize the benefits we derive from our association with these animals while minimizing our conflicts and seeking their resolution in environmentally sound, lasting and humane solutions.

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Beavers (2)

The European beaver in a New Millennium. Proceedings of 2nd European Beaver Symposium, 27-30 September 2000, Bialowieza, Poland. A. Czech & G. Schwab (eds.) 2003. Carpathian Heritage Society and Publishing House "Green Brigades", Kraków, Poland. 196 p. ISBN 83-87331-29-5.

Interest in beavers has grown rapidly over the last few years. Whereas there were 60 participants at the second international beaver symposium in Poland in 2000, the third symposium held recently in Arnhem in the Netherlands was attended by over 100 people. The increase in interest is certainly linked to the growth in population numbers of the largest European rodent. While at the beginning of the 1900s there were only 1000 animals left in five isolated population groups, Halley & Rosell (see this publication) estimate the current total to be almost 600,000 beavers. The beavers are a success story of protection and reintroduction. Thousands of beavers have been translocated in nearly all European countries, with the exception of the British Isles, the southern Balkan countries, Italy and the Iberian peninsula. In central Europe especially, 'problem beavers' from areas such as Bavaria are moved to other countries such as Belgium with no reference to the provenance of these animals. Nevertheless the beaver is still on the IUCN red list as a threatened species. It is also an Annex II and Annex IV species for the EU Habitat Directive, because of the fragmented small populations occurring in large parts of the area in which the beaver was originally found.

A problem with the publication of unedited presentations and reports from symposia is the variation in subject and quality, and this publication is no exception here. In addition to a number of in-depth articles, the book also includes short summaries and presentations: twenty presentations on monitoring and management, seven on the effects of the presence of beavers, which are regarded as boosting the dynamics in wetland areas, and six presentations on the biology and ecology of the species. The contributions indicate that much descriptive research is taking place, but there is an absence of experimental research. Countries such as Denmark are keen to show how well they are dealing with monitoring and information provision, perhaps in anticipation of the problems that are likely to arise as a result of successful reintroduction programmes. A number of presentations discuss solutions to problems that have arisen. These vary from culling (Scandinavia) to the implementation of measures to reduce damage and nuisance. The beaver populations are still young but seem to be expanding rapidly, although much of the data are based on apparently optimistic estimates that do not make use of trackable animals (fitted with transmitters, earmarked). As populations become more dense, especially in Fenno-Scandinavia and a number of eastern European countries, there is a growing amount of information on the enormous effects that beavers can have on the landscape. In Poland, for example, thousands of hectares of new wetlands are being created as a result of beavers' dam building activities. Many other species have benefited from these activities, including amphibians, other semi-aquatic mammals such as the otter, and various plant and fish species. But according to Norwegian research, dam building also creates problems for migratory fish species, which encounter difficulties reaching their spawning areas. Nitsche's description of beavers' anticipation of high water levels along the Elbe echoes the behaviour of beavers in the area of the large rivers in the Netherlands, although the use of heavy trees as places of refuge from high water are not mentioned. Denmark has followed the example of Scotland in using GIS to estimate vegetation units and landscape cover in the calculation of the potential beaver carrying capacity of areas. Unfortunately there is no good validation of these models.

The lengthy final summary on biology, ecology, behaviour and management of beavers by the German beaver expert Schneider unfortunately does not help to clarify matters. The extensive article contains a number of statements that are not of general value or are already outdated, and in a number of cases the author appears to contradict himself. For instance, he states: 'where there is sufficient natural food available, beavers are unlikely to go for agricultural crops' (this is known not to be the case) and 'genetic impoverishment is still threatening the populations as a result of past bottlenecks and translocations'. This statement is contradicted by the calculation that, at the current growth rate of the German beaver population (10%), the distribution area in Western Europe of one hundred years ago will be occupied again within the next fifty years. The proposition that genetic research is urgently needed would seem valid. In anticipation of this research, Schneider indicates that there is no need for widespread reintroductions, but that local population groups need to be joined to each other by adding animals from the surrounding genetically different populations. Schneider also suggests that genetic research is more important than current research aimed at gathering knowledge on beaver activities and economic damage. According to Schneider the beaver issue in its entirety (including increasing fragmentation of populations by traffic routes, management of populations and informing the public) will be of such great importance to the conservation of the beaver that national efforts alone will not be sufficient. Rather, these will have to be coordinated by the European Beaver Society, and a 'studbook' in which all translocations are recorded will be necessary. I wonder, however, whether readers of the Proceedings, including Schneider's somewhat subjective contribution, will all reach the same conclusions. The publication is carefully put together and is a snapshot of the development, research and management of the beaver population in Europe. Many of the subjects in the book were also discussed during the Beaver Symposium held in Arnhem, the Netherlands, in October 2003. A number of the presentations from the last symposium are printed in this edition of Lutra, which may be of influence in the decision whether or not to acquire the Proceedings of the previous symposium reviewed here.

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Preview

Are they "listening in the dark"? – Behaviour of beavers in their lodge

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From February 1997 to October 1998, covering all seasons, Donald R. Griffin (Concord Field Station, Harvard University), author of *Listening in the Dark* (1958), video-recorded behaviour of a beaver (*Castor canadensis*) family inside their lodge at Mink Pond in Harvard University's Estabrook Woods, near Concord, Massachusetts, USA. His purpose was to play back sounds such as whines of beaver kits or coyote howls and study the responses of beavers to these sounds while in the darkness of their lodge. Very few visual recordings of in-lodge behaviour of beavers exist (e.g. Patenaude 1982).

Shortly before his death in November 2003, Dr. Griffin sent us his videotapes for behaviour analysis. We have screened about 60 hours of video and are digitising the footage. This short communication is meant to be a preview, with a larger publication to follow. Even though filmed for another purpose, the videotapes document many details of behaviour inside the lodge, and reveal some behaviour never reported before.

Scent communication: Reflecting our research interest (Müller-Schwarze & Sun 2003), we

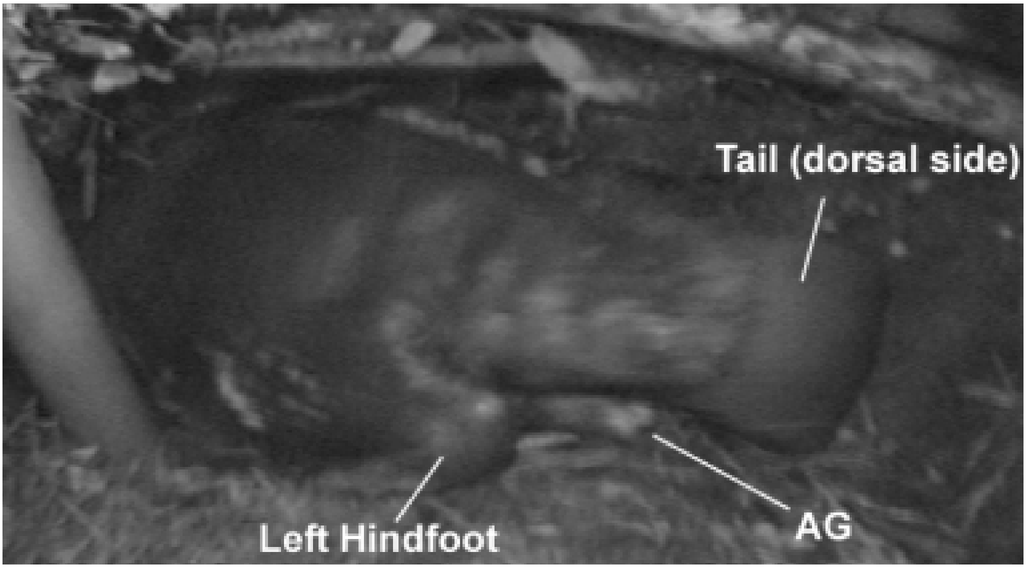

Photo 1. Adult beaver extrudes anal glands when leaving the lodge's resting platform. It drags the gland tips over the substrate before diving into the plunge hole. This may be a form of scent marking. AG: anal glands. *Photograph: taken from videotapes made by D.R. Griffin.*

Photo 2. Pilfering: muskrat gathers up twigs from beavers' resting platform and carries it away via the plunge hole, presumably as bedding material (and possibly food) for its own nest. In the background a pipe for a microphone to record beaver vocalizations. *Photograph: taken from videotapes made by D.R. Griffin.*

searched the footage for sequences that suggest chemical communication, such as use of scent glands, or sniffing in social contexts, preceded and/or followed by specific behaviours. Perhaps most significantly, we saw in a number of episodes that inside the lodge, adult beavers extrude their anal glands and drag them over the substrate when leaving the sleeping platform and diving into the plunge hole to travel to the outside (photo 1). To our knowledge, this has never been described before. An adult beaver protrudes the pair of anal glands and brushes them over the sticks and duff that form the slope between platform and plunge hole. In some scenes, a kit left behind can be seen sniffing the area just so "marked".

Play behaviour: In their lodge, beaver kits, an estimated eight weeks old, engaged in sequences of rapidly changing patterns of behaviour. Within one minute, a kit "builds" with a stick, feeds, grooms mutually with another kit, rolls over on its back, and picks up a stick and starts feeding. Such disjointed behaviour is one hallmark of "play" behaviour. The fact that it occurred when all other needs had been met is another. The kits enjoyed the safety of the lodge, had had hours of rest, and had been chewing on sticks.

Adult-kit interactions: On more than one occasion we have observed an adult beaver pushing a kit repeatedly under the water surface in the plunge hole. The kit's extensive splashing and loud whines suggest that it is strongly resisting the adult's efforts to being submerged. The adult uses its head and front feet to submerge the kit. These sequences always end with the kit being released without being dragged outside the lodge.

Mutual grooming: In the lodge, beavers groom themselves and each other extensively. We are analysing social aspects of grooming behaviour, based on behavioural sequences surrounding allogrooming and mutual grooming. In the films, the specialized second toe ("Putzklaue") of the hindfoot is clearly visible as it moves through the fur.

Tooth grinding: While sleeping or dozing, beavers quite frequently grind their teeth. Described as "tooth sharpening" (Wilsson 1971), this behaviour may have a social function.

Other animals visit the living chamber of the beaver lodge. Some, such as muskrats (*Ondatra zibethicus*) (photo 2), deer mice (*Peromyscus* spp.), southern red-backed voles (*Clethrionomys gapperi*), and shrews, forage and/or pilfer nesting material. Insects such as moths, hymenopterans, and mosquitoes flew in the chamber repeatedly. They may have ended up in the lodge incidentally.

A more extensive description and quantitative analysis of the behaviour of beavers inside their lodge, based on these videotapes, will appear elsewhere.

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Photograph: Dick Klees.

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