

# The feasibility and acceptability of reintroducing the European beaver to England

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# Introduction

Natural England commission a range of reports from external contractors to provide evidence and advice to assist it in delivering its duties. This report was commissioned jointly by Natural England and the People's Trust for Endangered Species. The views in the report are those of the authors and do not necessarily represent those of Natural England.

## Background

The beaver *Castor fiber* is a native species that was hunted to extinction in Britain, probably by the 16th Century. Recently, there has been considerable interest in reintroducing it, both to restore lost biodiversity and because of the contribution it could make to river and wetland management. The European Habitats & Species Directive also requires Member States to consider the reintroduction of extinct native species.

The beaver has been widely reintroduced across Europe and there is a considerable body of evidence arising from these projects.

In 2008 the Scottish Executive issued a licence for a trial reintroduction of beavers to Knapdale, Argyll. These are expected to be released in 2009. In Wales a feasibility study is under way. In England there are captive beavers in large enclosures in five places around the country.

It seems likely that Natural England will receive an application for a licence to release beavers into the wild within the next few years. This would be considered in the context of the International Union for Conservation of Nature's Guidelines for Reintroductions and the reintroductions policy adopted by the conservation agencies in the UK. Specific background information would also be required.

It is important for Natural England:

- to understand the benefits and drawbacks of beaver reintroductions;
- to consider to what extent the beaver may be able to help deliver wider river and wetland restoration objectives; and
- to understand the challenges that the presence of the beaver may bring.

**The purpose of this report is to help Natural England:**

- **As the lead delivery body for the England Biodiversity Strategy** - develop a view on the feasibility and desirability of beaver reintroductions in England and what contribution beavers might make to national habitat restoration targets.
- **As the licensing authority** - prepare itself for making a decision when it receives an application to release beavers into the wild in England.

At the time of publication, Natural England's Board has not considered its position on beaver reintroductions. This report will contribute to that debate.

**Natural England Project Manager** - Tony Mitchell-Jones, Northminster House, Peterborough, PE1 1UA

**Contractor** - Professor John Gurnell (Consortium Leader), School of Biological and Chemical Sciences, Queen Mary, University of London, London E1 4NS

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### Further information

This report can be downloaded from the Natural England website: [www.naturalengland.org.uk](http://www.naturalengland.org.uk). For information on Natural England publications contact the Natural England Enquiry Service on 0845 600 3078 or e-mail [enquiries@naturalengland.org.uk](mailto:enquiries@naturalengland.org.uk).



# The feasibility and acceptability of reintroducing the European beaver to England

Report prepared for:  
Natural England and the People's Trust for Endangered Species

By

J. Gurnell<sup>1</sup>, A.M. Gurnell<sup>2</sup>, D. Demeritt<sup>2</sup>, P.W.W. Lurz<sup>3</sup>, M.D.F. Shirley<sup>3</sup>, S.P. Rushton<sup>3</sup>, C.G. Faulkes<sup>1</sup>, S. Nobert<sup>2</sup> & E.J. Hare<sup>1</sup>

- <sup>1</sup> School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS  
<sup>2</sup> Department of Geography, King's College London, The Strand, London WC2R 2LS  
<sup>3</sup> Centre for Life Sciences Modelling (CLSM), University of Newcastle upon Tyne, Newcastle upon Tyne NE1 7RU



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# Project Details

## Project manager

Dr A J Mitchell-Jones, Evidence Team, Natural England  
J Nelson, Chief Executive, People's Trust for Endangered Species

## Contractor

Dr J Gurnell, School of Biological and Chemical Sciences, Queen Mary University of London, London  
E1 4NS

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# Executive Summary

This review considers the technical feasibility, and ecological and social desirability of reintroducing European beavers *Castor fiber* to England and follows on from the recent decision by the Scottish Parliament to reintroduce beavers into Knapdale, Scotland in 2009. The particular objectives are:

- To review the ecology of beavers with respect to potential benefits of the ecosystem services they may provide and the possible ecological risks of their reintroduction.
- To define criteria for identifying candidate reintroduction sites.
- To identify the most appropriate source populations for potential reintroduction to England.
- To assess stakeholder concerns regarding reintroducing beavers.
- To identify actions and mechanisms that would maximise the benefits and eliminate or control any risks related to reintroductions.
- To make recommendations for further work that would be required to develop and implement a reintroduction programme, if this is considered desirable.

Beavers are large (15 – 38 kg in weight), semi-aquatic rodents that live in rivers, streams, ditches, lakes and wetland areas. At one time they were widespread and common in Europe, but by 1900 they had been lost completely from large parts of their native ranges, including the United Kingdom, as a result of hunting and habitat loss. However, since then they have returned to much of their former range through regulation of hunting, translocations, reintroductions, and natural processes. Now, the United Kingdom is one of the few areas within Europe that does not currently have wild beavers. A similar story can be told about the Canadian beaver *C. canadensis* in North America and, because of the similarities between the two species, we draw on studies on both species in this review.

Beavers live in small family groups consisting of an adult male and female, and one to three young (kits, yearlings or subadults) within a territory that may consist of from 1 to 13 km length of river or lake bank. They are strictly herbivorous; they do not eat fish or any other animals. In spring and summer they eat aquatic and riparian plants, at other times of the year they depend heavily on woody species for food, such as willow *Salix* spp.. They fell trees of up to 10 cm diameter or larger, leaving characteristic feeding signs. In autumn, they transport felled wood to store close to their riverbank burrows or lodges made of cut wood, to provide winter food. Beavers sometimes build dams of tree trunks, branches, twigs, earth, mud and stones in order to raise and stabilise the local water level, providing deeper water to cover lodge entrances, support the transport of food, and extend the position of the water's edge into the riparian zone. They may also dig canals a metre or so wide to extend their waterside foraging zone.

The construction of beaver dams and canals introduces many additional habitats to river reaches, resulting in a substantial increase in habitat diversity, the spatial complexity of the habitat mosaic, and the overall resilience of river and riparian ecosystems to disturbances. Beaver dams introduce steps along the river's long profile, where energy is dissipated. These steps and upstream ponds, coupled with enhanced management of catchment sediment sources, can contribute to a reduction in catchment sediment yields as well as inducing beneficial biogeochemical changes, particularly an increase in carbon, nutrient and fine sediment retention and their incorporation into the riparian zone through beaver meadow development. Larger dams are usually associated with extending marginal wetlands, rather than damming large river widths. In general, the effect of beaver dams and ponds on high river flows is to help to regulate flows and so beneficially reduce flood peak levels downstream. The ability of beavers to build, dams and canals, create ponds and fell trees have resulted in them being called *ecosystem engineers*.

The formation of extensive, heterogeneous wetland habitats as a result of beaver activity increases substantially the number of species of herbaceous plants in the riparian zone, rejuvenates riparian forests, increases the number of tree stems and helps stabilise the banks of water bodies. Overall, the impact of beavers on plant diversity is extremely positive, particularly when viewed from a landscape perspective. Beaver engineering significantly increases the extent of aquatic habitats and their diversity, positively influencing invertebrate abundance, species richness and diversity and so

providing essential food for many other animals, such as birds, fish, mammals, reptiles and amphibians. In fact, the presence of beavers has largely beneficial impacts on these animal groups, resulting in a substantially higher level of biodiversity overall. For example, the effects on amphibians are positive, and bird abundance, production, diversity and species richness is generally much greater at beaver-created wetlands than at non-dammed sites. The effects of beavers on fish and fishing have been a particular point of discussion. The evidence indicates that beaver reintroductions into England are likely to have a positive impact on fish populations, creating foraging habitat and refuge for a wide variety of species, including those that are considered commercially important. Increased growth rates experienced by some fish in beaver pools, along with a tendency for larger species to replace smaller ones in warm water streams, could provide excellent opportunities for anglers. Furthermore, the positive impacts of beaver on fish populations are likely to increase with maturity of beaver ponds. However, it is possible that beaver dams may restrict fish movement, migration, and prohibit recolonisation under certain climatic conditions, and this should be monitored closely if beavers are reintroduced.

There appear to be four broad features that characterise prime beaver habitat: (i) easy access to grasses, forbs and riparian tree species, especially the Salicaceae (e.g. willow and poplar); (ii) low flow water depths, at least near lodge and burrow sites, of  $>0.6$  m; (iii) river channel gradients  $< 0.15$  and preferably  $< 0.06$  and (iv) 'soft' or finer calibre bed and bank materials. The majority of British rivers have relatively low gradients and narrow widths, making them physically suitable for beaver colonisation. However, the presence of bedrock or very coarse sediment banks, relatively shallow water depths, and limited presence of riparian trees (particularly Salicaceae) make some river types less than ideal. The most suitable habitat conditions for beavers are found along the least degraded lowland rivers that have the lowest river gradients, the finest bed and bank sediment with occasionally deep pool habitats, and plentiful riparian tree cover. Not only do these river types provide very good beaver habitat but also their low gradients strongly reduce the likelihood of dam construction. These low gradient river types often have wide flood plains and occupy subdued landscapes that offer a variety of suitable off-river and side stream, as well as main channel habitats for beaver colonisation.

A preliminary GIS analysis of beaver habitat preference across England's rivers indicates a wide range of potential release sites. Candidate release sites would need to be explored more fully in a second phase of GIS modelling that incorporates more focused (e.g. River Habitat Survey) and higher resolution (e.g. air photo and airborne scanner) data. Other considerations for release sites include their proximity to urban or suburban areas, whether they have SAC or SSSI designations, whether beavers are likely to build dams and whether there may be any consequential chance of flooding. A second modelling phase should also incorporate habitat suitability information into a population-based model that would combine habitat requirements with known life history parameters to simulate beaver population establishment and growth. These models would predict the spread of beaver from the point of release; and provide information about potential human-beaver interactions that could be taken into account in the management plan for the site.

A review of the literature and of recent public consultations suggests broad but shallow support from the public at large, and the majority of stakeholders consulted for this project are supportive, at least in principle, of reintroducing European beaver to England. Although detailed research is yet to be carried out, there are strong indications that considerable financial benefits will accrue from ecosystem services provided by beavers such as the removal of pollutants, flood alleviation and erosion control, as well as from tourism and recreation. Indeed, these are the most commonly perceived benefits of reintroducing beaver. Further, costs resulting from damage to trees, ditches, dykes, ponds, roads and flooding of agricultural land as a result of beaver reintroductions are likely to be low, and mitigation costs are small and more than offset by the financial benefits of beavers. Damage control and mitigation, and potential effects on fish are important concerns of stakeholders. Any future reintroduction plans must involve extensive public consultation, backed by clear and trustworthy information about the management and likely environmental impacts of reintroduced beaver.

Beaver management methods are well-established and can be used to control beavers subsequent to reintroductions and to mitigate any detrimental impacts such that there should be minimal risks

associated with reintroducing beaver into the English countryside. However, the legal status of the beaver in England is complex and the possession of wild-bred beavers and their release will require a license from Natural England. Once they become established in the wild, the UK will be obliged to protect the species. *C. fiber galliae* (from the Rhone in France) or *C. fiber albicus* (from the Elbe in Germany) are the geographically closest populations for reintroductions into England and would be most suited for introductions to southern England as they are adapted to lowland habitats.

The evidence gathered in this report clearly shows that it is feasible to reintroduce beavers into England and that many benefits are likely to accrue, not least the potential of beaver to assist with river and floodplain restoration. Moreover, the success of reintroductions elsewhere in Europe has demonstrated the feasibility of putting in place measures to deal with any possible adverse consequences. A second phase of consultation and actions concerning beaver reintroductions to England should focus on education of the wider public about beavers, investigation of specific candidate sites for releasing beavers, drawing up detailed management plans and costings, and, if agreed by all interested parties, releasing beavers within the umbrella of pilot studies. Not only would this be a first step in the possible restoration of a native species, but also such studies would offer an unparalleled opportunity to assess and quantify the benefits that beavers could bring in terms of ecosystem services. This would not only be valuable information with regard to beavers, but would also improve our understanding of the economic, social and ecological value of ecosystem services generally.

This review concludes with a list of actions that need to be taken into account in any plan to reintroduce beavers into England:

1. Education
  - To prepare and disseminate educational material about beavers, their habits, ecosystem services, possible impacts and management, to gain a consensus of approval for a pilot reintroduction programme or programmes;
2. Legal aspects
  - To review legislative mechanisms to protect and manage beaver populations in England, and draw up proposals to amend the legal status of beavers as necessary;
3. Who is responsible?
  - To consider who will be responsible for the release and management of beavers and set up grant-aid schemes to offset any financial costs of management and mitigation;
4. Candidate release sites and consultation
  - To select candidate sites for detailed habitat analysis, population modelling and the production of a human-beaver interaction risk analysis;
  - To carry out a local consultation exercise of local stakeholders, including landowners and the general public, at each candidate site and gain their approval;
  - To determine which site or sites are most suitable for beaver reintroductions and explore the costs and benefits of such a reintroduction;
5. Source of beavers and quarantine
  - To determine the costs, time frame, source of beavers and quarantine holding facilities that will be used for each candidate site and to obtain the necessary licences and permits to carry out the importation, quarantine and release of beavers;
6. Research, monitoring and management
  - To produce detailed guidance on costs, research (including that into ecosystem services), and monitoring to be carried out at each site, and to establish a local management group to oversee and monitor the release;
  - To carry out pre-emptive management at the candidate site(s) (e.g. protect vulnerable trees and crops);
7. Funding and implementation of reintroduction
  - To raise sufficient funds to carry out the reintroduction programme;
  - To import the beavers and place into quarantine with appropriate health checks;
  - To prepare the site(s) for a soft release. After six months of quarantine, release the beavers and start monitoring for a period lasting at least five years;
  - To publicise locally and nationally the presence and conservation importance of the return of beavers to England.

# 1. Introduction

## Summary

- 1.1. Beavers are large (15 – 38 kg in weight), herbivorous, semi-aquatic rodents that live in rivers, streams, ditches, lakes and wetland areas. There are two living species: the European beaver *Castor fiber* and the North American or Canadian beaver *C. canadensis*. In former times, both species were widespread and common in Europe and North America, respectively, but by 1900, they had been lost completely from large parts of their native ranges as a result of hunting and habitat loss. However, since 1900, numbers of both species have recovered through regulation of hunting, translocations, reintroductions, and natural processes. It has been estimated that numbers were as low as 1200 in Europe in 1900, but this had risen to about 250,000 in the early 1990s and about 640,000 by 2003. The United Kingdom is one of the few areas within Europe that formed part of the former range of the European beaver which does not currently have wild beavers, the others being Portugal, Italy and the southern Balkans.
- 1.2. Beavers live in small family groups consisting of an adult male and female, and one to three young (kits, yearlings or subadults) within a territory that may consist of from 1 to 13 km length of river or lake bank (normally 2-4 km). They may live for 7-8 years and the adult pairs can produce 1-3 kits per year. They mark their territories with a secretion, called castoreum, from glands found under the base of their tails. In former times, castoreum was highly sought after by humans because of its medicinal properties and so was a major contributor to the overhunting of beavers.
- 1.3. Beavers are strictly herbivorous, they do not eat fish or any other animals. In spring and summer they mainly eat aquatic and riparian plants, at other times of the year they depend heavily on woody species for food, such as willow *Salix* spp., alder *Alnus glutinosa*, aspen *Populus tremula*, and birch *Betula* spp., particularly those that are found in very close proximity to the water's edge. Using their large, continuously-growing incisors, beavers fell trees of up to 10 cm diameter or larger, leaving characteristic feeding signs. In autumn, they transport cut wood to store close to their burrows or lodges to provide winter food. They may also dig canals a metre or so wide to extend their waterside foraging zone.
- 1.4. The European beaver usually digs burrows in riverbanks in which to nest. However, it cuts wood to build dams if the water is not deep enough to cover the entrance to the burrow. It will also build lodges from wood if burrowing in banks is difficult. Generally, Canadian beavers are much more likely to build dams and lodges than European beavers. The ability of beavers to build, dams and canals, create ponds and fell trees have resulted in them being called *ecosystem engineers*.
- 1.5. Following the recent decision by the Scottish Parliament to reintroduce beavers to Scotland, this report looks at the feasibility of reintroducing beavers to England. Indeed, there has been a great surge of interest in beavers within the last 10 years or so, with a marked increase in the number of publications that have appeared in the scientific literature and the public press. Because of the similarities between the two species, in this review we draw on studies that have been carried out on both European and Canadian beavers.

## Background

- 1.6. Beavers are large (15 – 38 kg in weight), herbivorous, semi-aquatic rodents that belong to the Family Castoridae. There are two species of beaver in the Holarctic ecozone: the European beaver *Castor fiber* and the North American or Canadian beaver, *C. canadensis*. Both occurred widely throughout Europe (Corbet 1978) and North America (Baker & Hill 2003) respectively, but extensive harvesting, especially for food, fur and castoreum<sup>1</sup>, in addition to

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<sup>1</sup> An orange-brown substance, with a strong odour, found in two castor sacs that lie inside the beaver next to the anal glands. Beavers mark their territories with castoreum; humans use it in medicine, and in the perfume industry.

some instances of habitat loss, caused a widespread decline in numbers (Kitchener & Conroy 1997). By 1900, beavers had been lost completely from large parts of their native ranges. For example, in Europe, it has been estimated that numbers were as low as 1200 at this time (Halley & Rossell 2002). Since then, numbers have recovered substantially through regulation of hunting, translocations and reintroductions<sup>2</sup> and natural processes; this recovery is well documented (see Table 1.1, Figure 1.1, Nolet & Rossell 1998, Yalden 1999, Halley & Rossell 2002, Baker & Hill 2003). By 2003, it was estimated that beaver numbers had reached ~693,000 (Halley & Rossell 2002). The Canadian beaver was introduced into Finland in 1935 and 1937 (Lahti & Helminen 1974), where they continue to thrive in the central and eastern parts of the country (e.g. Härkönen 1999a,b). European and Canadian beaver do not inter-breed but are similar in most respects, although Canadian beaver have slightly larger litters and have a greater tendency to build lodges. Canadian beaver have also been introduced into South America, where they have become a pest (Anderson *et al.* 2009), and Kamchatka, Russia (Baker & Hill 2003).

- 1.7. Beavers and wood are natural components of British river systems. Prior to the widespread clearance of woodlands for agriculture, which commenced in the Neolithic period, the British landscape was heavily wooded (Rackham, 1986) and driftwood structures (Gurnell and Petts, 2002; Gurnell *et al.*, 2002), beaver dams and lodges (Coles, 2006) would have been pervasive elements of British river landscapes. In Britain, beavers died out in the 16<sup>th</sup> century, although there is some evidence that they may have survived through to the 18<sup>th</sup> century in northern England (Coles 2006). In the last 10-15 years, there has been a great deal of interest in reintroducing beavers into Britain<sup>3</sup>. Plans to reintroduce beaver into Scotland have been extensively researched for more than 10 years (e.g. Kitchen & Conroy 1997, Gurnell 1998, South *et al.* 2000, Macdonald *et al.*, 2000, Gorman 2007), and are well publicised (e.g. see Vines 2007). The Scottish Wildlife Trust and The Royal Zoological Society of Scotland (see Scottish Beaver Trial website) were recently granted permission by the Scottish Government for a trial reintroduction of European beavers into Scotland (Scottish Government 2008). Within the last few years, there has also been strong interest in reintroducing beavers to Wales (see <http://beaverinfo.org/index.htm>) and England (e.g. Woodroffe 2005, 2006). There have been several semi-captive introductions of beavers into England: to Wildwood, Kent, Ham Fen SSSI Kent (Kent Wildlife Trust); Cotswold Water Park, near South Cerney, Gloucester; and WWT Martin Mere, Lancashire. In 2007, Natural England and the People's Trust for Endangered Species commissioned us to carry out a desktop feasibility study on reintroducing beavers to England. This report concerns the results of the feasibility study.

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<sup>2</sup> IUCN (1998) define "**re-introduction**" as: an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct, and "**translocation**" as the deliberate and mediated movement of wild individuals or populations from one part of their range to another.

<sup>3</sup> Note: Beavers have never been present in Ireland.

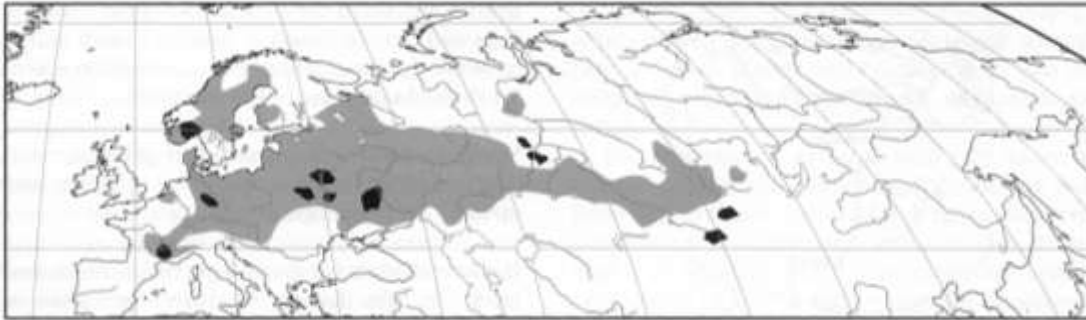
Table 1.1 Reintroductions of beavers throughout Europe (from Halley and Rossell 2002).

Country	Extirpation	Protection	Reintroduction and/or translocation	Present population size
Albania	?	-	-	0
Austria	1869	-	1970-90	>1300
Belarus	remnant	1922	-	24,000
Belgium	1848	-	1998-99	100-130
Bosnia & Herzegovina	?	-	-	
Bulgaria	?	-	2001-2	0
Croatia	1857?	-	1996-98	150
Czech Republic	17th century	-	1991-92, 1996	300
Denmark	c.500 BC	-	1999	18
England	<12th century*	-	(2002, fenced)	6
Estonia	1841	-	1957	10,000
Finland	1868	1868	1935-37, 1995	1500
France	remnant	1909	1959-95	7000-10,000
Germany	remnant	1910	1936-40, 1966-89	8000-10,000
Greece	?	-	-	0
Hungary	1865	-	1980-2000	70
Italy	1541	-	proposed	0
Kazakhstan	?	-	-	1000
Latvia	1830s	-	1927-52, 1975-84	50,000
Lithuania	1938	-	1947-59	32,000- 50,000
Luxembourg	?	-	2000	<10
Macedonia	?	-	-	0
Moldova	19th century	-	-	0
Mongolia & China (Xinjiang)	remnant	-	1959-85	800
Netherlands	1826	-	1988-2000	>150
Norway	remnant	1845	1925-32, 1952-65	>70,000
Poland	1844	1923	1943-49, 1975-86	17,000
Portugal	?	-	-	0
Romania	1824?	-	1998-99	>28
Russia	remnant	1922	1927-33, 1934-41, 1946-64	232,000-300,000
Scotland	16th century	-	proposed	0
Serbia & Montenegro	1903?	-	Spring 2004	20-30
Slovakia	1851	-	1995	>500
Slovenia	?	-	2000	<10
Spain	c. 400AD	-	2003	18
Sweden	1871	1873	1922-39	>100,000
Switzerland	1820	-	1956-77	>350
Ukraine	remnant	1922	-	6000
Wales	12th century	-	-	0

\*but see Coles (2006)/paragraph 1.7.



Figure 1.1 Distribution of European beaver; black - in 1900, grey – recovered distribution in 2002 (from Cole et al. 2007).



## Why reintroduce beavers?

- 1.8. Why reintroduce beavers to Britain? The reasons put forward include (e.g. see Macdonald & Tattersall 1999, Coles 2006):
- Beavers are part of Britain's native fauna;
  - Beavers have been lost entirely by the activity of humans;
  - As a member of the European Community, Britain has a responsibility to carry out studies on the desirability of reintroducing species that have become extinct (Beavers are listed on Annex III of the Bern Convention, and on Annexes II and IV of the EC 'Habitats and Species' Directive in 1992. The Directive aspires to achieve a favourable conservation status of the priority habitats and species listed in its annexes.);
  - Beavers are a 'keystone species'<sup>4</sup>; they are frequently called ecosystem engineers and act as 'natural managers' of riparian, wetland and forest ecosystems;
  - Beavers are inherently interesting to humans and could be a 'flagship' species for raising awareness about nature conservation;
  - Beavers fulfil philosophical and aesthetic ideals associated with returning native species to the wild.

## Literature

- 1.9. Over the last 10 years, many new scientific papers have been published on both Canadian and European beaver. A literature search, based largely on Thompson's Web of Knowledge / Web of Science but with some additions from other sources, identified >755 publications referring to these two species. 179 included some assessment of European beaver, of which 43% were published after 1996 (Figure 1.2.). These sources have been entered into an Endnote bibliographic database and full copies, or at least abstracts, of most of the journal papers and some of the books have been obtained. Also, through web searches, 33 items of grey literature that relate to the European beaver have been identified and included in a separate Endnote bibliographic database.
- 1.10. Whilst the literature on European beavers has grown considerably in recent years, the numbers of publications that refer to the key issues of interest for this review remain relatively limited (e.g. Figure 1.3.), and so this report continues to draw on literature referring to Canadian beavers, to provide additional detail to that available for the European beaver.
- 1.11. There are some excellent books that consider the past and present distributions of beavers, and their biology, including: *The History of British Mammals* by Yalden (1999), *The beaver: natural history of a wetlands engineer* by Müller-Schwarze & Sun (2003) and *Beavers in Britain's Past* by Coles (2006). We do not consider all aspects of the natural history of beavers

<sup>4</sup> A keystone species is one whose loss from a community can have a profound effect on community composition, ecosystem processes and biodiversity.

in this report, but focus on those aspects that we believe are most relevant to their reintroduction in England. Some general characteristics of beavers are summarised in Table 1.2.

Figure 1.2 Number of publications in the stated time periods on both Canadian and European beavers (total publications) and those solely concerning the European beaver.

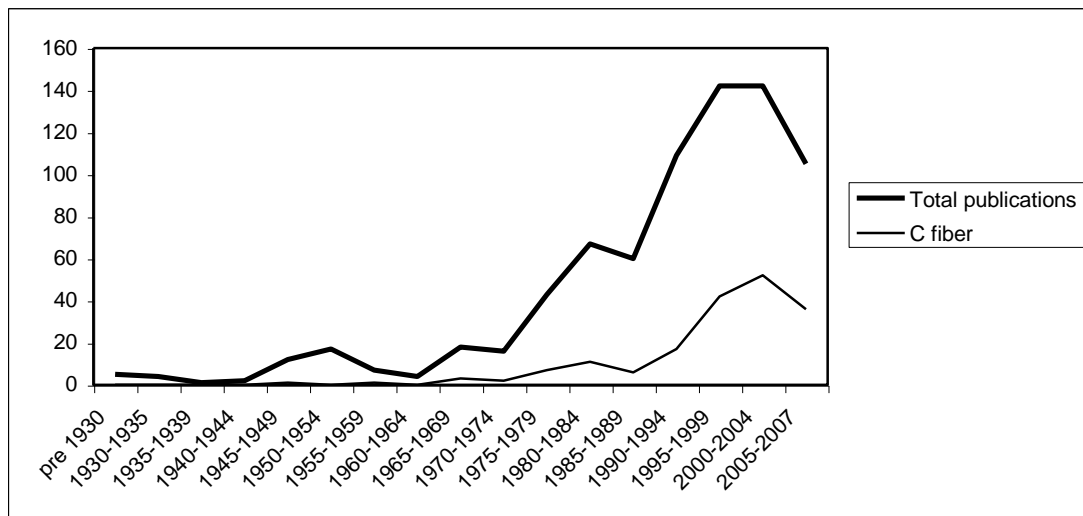
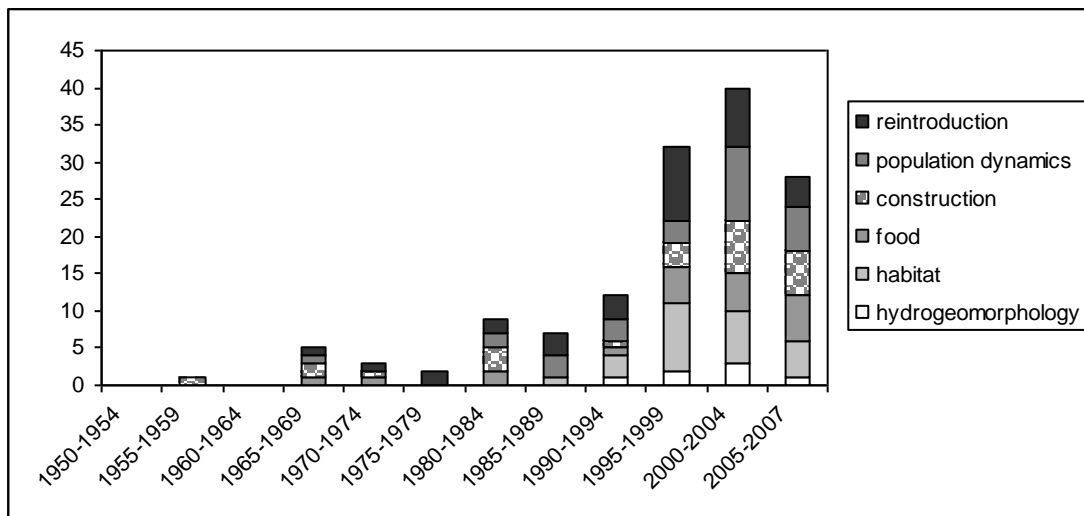


Figure 1.3 Number of publications in the stated time periods which refer to the specific aspects of the ecology of the European beaver, noted in the key.



## Aim and objectives

### Aim

- 1.12. To evaluate the technical feasibility, and ecological and social desirability of reintroducing European Beaver to England.

### Objectives

- 1.13. To review the ecology of beavers with respect to potential benefits of the ecosystem services they may provide and the possible ecological risks of their reintroduction.

- 1.14. To define criteria for identifying candidate reintroduction sites.
- 1.15. To identify the most appropriate source populations for potential reintroduction to England.
- 1.16. To assess stakeholder concerns of reintroducing beavers;
- 1.17. To identify actions and mechanisms that would maximise the benefits and eliminate or control any risks related to reintroductions.
- 1.18. To make recommendations for further work that would be required to develop and implement a reintroduction programme, if this is considered desirable.

## The report

- 1.19. The report is in three parts. Part 1 (Chapters 2 to 4) reviews the behaviour and ecology of beavers with respect the medium- and longer-term, potential costs and benefits of reintroducing beavers into England. Part 2 (Chapters 5 to 11) looks more closely at the short-term considerations including: how to identify candidate release sites, source populations for beaver reintroductions, legal considerations, the concerns and perceptions of stakeholders, and the financial costs and benefits of returning beavers and of their management after release. In the final chapter (Chapter 12) we consider reintroductions of beavers in relation to IUCN guidelines, and summarise the way forward. Each chapter is prefaced by a summary with an overall Executive Summary at the front of the report. The references cited in the report are listed at the end; a more extensive bibliography is available on request.

Table 1.2. Some characteristics of beavers (based on Müller-Schwarze & Sun 2003, Cole *et al.* 2007)

Feature	Description
International status of European beavers	Bern Convention (Convention on the Conservation of European Natural and Wildlife Habitats, Appendix III Conservation on Natural Habitats of Wild Fauna and Flora, Annexes II and IV (not including Swedish and Finnish beaver which are Annex V)
Chromosomes	European beaver 2n = 48, Canadian beaver, 2n = 40
Density	0.2 - 0.6 beaver pairs per sq km
Dispersal	Usually when 1 to 2 years old; maximum distance 170 km, median 25 km
Use of space	Territorial
Social group	Adult pair plus young of year (kits), and possibly young of previous year (yearlings), average number of animals ~4.
Life span and survival	Can live 7-8 years; high mortality when <6 months old and during dispersal.
Breeding system	Obligate monogamy; monoestrous; average litter size European beaver: 1.9-3.1, Canadian beaver: 3.2-4.7; gestation 105 days; suckling 60-90 days; births peak in May/June. Mature at 2 years old, first breed at 3 years old. Young precocious, fully furred and with open eyes at birth.
Dam building	More sophisticated and developed in Canadian beaver than European beaver
Dens or lodges	European beaver prefer lodges or burrows in riverbank with entrance below water level. Lodges may be built out of woody debris, twigs and soil where bank burrows are not possible. Canadian beaver also construct freestanding lodges
Scent-marking	Scent mounds marked with spray from castor glands, or secretions from anal glands by anal dragging - can be much larger in Canadian beavers
Warning sound	Tail slap on surface of water
Activity	Crepuscular and nocturnal, all year
Diet	Herbivores, mainly herbs from spring to summer, and wood bark during autumn and winter - aspen, willow, poplar, alder preferred. Central place foragers with most feeding closest to lodge, and within 20 m of river margin. Digs feeding channels. Caches food under water near den during winter.

# Part 1. The ecology and behaviour of beavers and the effects of beavers on the environment

## 2. Habitat requirements and population densities

### Summary

- 2.1. Initial growth of a newly introduced beaver population may be low as the animals establish themselves in the new habitat. This may then be followed by a period of rapid growth followed by a decline to stabilise at a density lower than the peak level. Thus, densities of beaver populations at particular sites vary as a function of the length of time sites have been occupied. Depending on the landscape, population growth may continue for 25 years or more until all available sites have been occupied. Where there are data available, over half of introductions of beavers in Europe have been successful. Failed introductions have been attributed to: release into unsuitable habitat and too few individuals being released with subsequent poor population growth.
- 2.2. Beavers are able to occupy and/or modify a wide range of water-marginal environments, but in general there appear to be four broad characteristics of prime beaver habitat: (i) easy access to grasses, forbs and riparian tree species, especially the *Salicaceae*; (ii) low flow water depths, at least near lodge and burrow sites, of >0.6m; (iii) river channel gradients < 0.15 and preferably <0.06 and (iv) 'soft' or finer calibre bed and bank materials.
- 2.3. Beavers normally live as a family unit or colony of four or five individuals, consisting of two parental adults, the yearlings born the previous year and the young of the current year. A wide range of colony densities is reported in the literature. European beaver densities range from 0.08 to 0.57 colonies per km river length, or per 2 km river bank. This suggests that a 2 km length of river with suitable habitat should be sufficient to support a colony, where habitat is assessed within 20 m of the water's edge.

### Colonisation of new habitat

- 2.4. Although landscapes have changed since the times that beavers were naturally abundant throughout the northern hemisphere, their successful return in the 20<sup>th</sup> century throughout much of their former range demonstrates that rivers and wetlands still contain the necessary habitat and food requirements to support beaver populations, and that their niche has not been pre-empted by any other animal species, such as the successful introductions of the semi-aquatic coypu *Myocastor coypus* and muskrat *Ondatra zibethicus* in Europe. For 87 reintroductions into Europe where population estimates were available 5 years after introduction, 46 (53%) were considered successful (Macdonald *et al.* 1995). Unsuccessful introductions have been mainly attributed to release into unsuitable habitats or the release of too few individuals (Macdonald & Tattersall 1999). Post-introduction mortality is considered in Chapter 7. Beaver can rapidly spread into suitable habitats. Canadian beavers have been estimated to be capable of colonising areas >700 km from their initial nucleus in 46 years (Johnston & Naiman 1990) and, in Tierra del Fuego, where 25 pairs were released in 1946, there are now estimated to be 61,300 individuals (Skewes *et al.* 2006). The densities of beaver populations at particular sites also tend to vary as a function of the length of time sites have been occupied. These time patterns are characterised by initial slow and then rapid growth followed by a rapid decline to stabilise at a density lower than the peak level (e.g. Busher & Lyons 1999).
- 2.5. Like the Canadian beaver, the European beaver exhibits a rapid increase in population during colonisation followed by a decline. Hartmann (1994) found that the rate of population increase turned negative after 34 and 25 years following introduction in two areas of Sweden, whereas in a 25 year study in the Loire Valley, France, Fustec *et al.* (2001) showed that the number of occupied sites had reached a peak and stabilised but a decline has not yet occurred. Observations of European beaver colonisation within Europe indicate highly variable but generally slower colonisation rates than those observed for the Canadian beaver (see Table 2.1.). A direct comparison can be made between European and Canadian beavers in Finland, where both species were introduced early in the 20<sup>th</sup> century. In 1935, 19 European beavers

were introduced from Norway, and in 1937, seven Canadian beavers were introduced from the USA (Lahti & Helminen 1974). By 1990, the former had increased to about 800 individuals whereas the latter had increased to 3300-5200 (MacDonald *et al.* 1995). Canadian beavers have usually been found to dominate or displace European beavers at locations where they have both been introduced (Collen & Gibson 2001, Lahti & Helminen 1974, Ermala *et al.* 1989).

## Habitat requirements

### Water

- 2.6. Proximity to a water body is an essential habitat requirement for beaver. Although beavers are able to modify their habitat (see Chapter 3), the nature of the water body and other habitat properties influence the degree to which beaver might colonise an area and sustain a population. A number of characteristics of water bodies can affect beaver behaviour and population dynamics.
- 2.7. Beavers utilise all types of freshwater body, including lakes, rivers of all sizes, and wetlands. For example, Rebertus (1986) working in Minnesota, found 58% of active Canadian beaver colonies on lakes, 6% on rivers, and 36% on bogs, of which 15% included dams to create open water and 21% used natural open water patches. Bluzma (2003) found in eastern Lithuania that, after a period of colonisation, European beaver colonies were mainly located on dammed swamps, rivulets and ditches (c.50%), followed by peat bogs and ponds (c.30%), and then lakes (c.20%). Dynamic fluvial environments generate a variety of water body types (river channels of varying sizes, cutoffs and floodplain ponds / oxbows), a diversity of bed forms / topography and sediment calibre, and also a range of vegetation patches of different ages, reflecting dynamic colonisation and patch turnover. This mosaic of habitat features within dynamic fluvial environments is highly suitable for beaver colonisation (e.g. Boyce 1983). In such dynamic environments, beaver colonies have been noted to establish particularly frequently around oxbows and other floodplain water bodies adjacent to large river channels (e.g. Townsend & Butler 1996) and along high-sinuosity stretches (Hartman 1996).
- 2.8. The water depth and level regime of the water body is important for beaver, who prefer a stable water surface and relatively deep water to ensure safe underwater access to their burrows, lodges, food sources and caches. Rapid and widely fluctuating water levels, as are found in rivers below hydro-power dams during winter, can have a catastrophic effect on beaver populations (Curry-Lindahl 1967) by both washing away food caches (Martin 1977) and drowning young animals in their lodges and burrows. Thus, Nolet & Rosell (1998) specify a natural flow regime as an important property of prime habitat for beaver. Beier & Barrett (1987) found average water depths in their California study area to be deeper in reaches with active colonies (2.44 m) than in reaches with abandoned colonies (2.13 m); no colonies but signs of past beaver usage (1.85 m); and no signs of beaver usage (0.85 m). In the vicinity of lodges, Dieter & McCabe (1989) found average water depths of 0.76 m, significantly deeper than at a random sample of sites (0.49 m) within the same area. Hartman & Axelsson (2004) found water depth near lodges in their Swedish study to be a good predictor of the co-occurrence of food caches. As a result of the requirement of beavers for deep water, particularly in proximity to lodges and burrows, extremely low river flows can stimulate dam building (Martin 1977), and water surface drawdown in reservoirs can induce enhanced foraging activity because beaver are unable to fully utilise stored food (Smith and Peterson 1991).
- 2.9. The calibre of bed and bank materials is also an important property of beaver habitat. River channels with rocky or bedrock banks and beds are less favoured, whereas 'soft soils' were one of six habitat factors associated with beaver recolonisation of clearcut areas in Oregon (Hacker & Conblentz 1993), and were identified as a factor in beaver habitat selection by Hartman (1996) in Sweden. The bed and bank materials of water bodies are important because they affect the degree to which beaver can construct burrows, lodges, canals and dams. In steep, high energy river channels, dam construction regulates water levels and creates lower-energy, ponded areas where food can be safely cached. However, on steep gradients, dams do not create large ponds, and also steep, high-energy channels tend to have

relatively coarse bed and bank materials. As a result, steep channels are unfavourable for beaver colonisation, explaining why Howard and Larson (1985) found maximum colony densities in Massachusetts associated with gradients of 0.0369 +/- 0.0261; Parker & Ronning (2007) found stretches with beaver had lower slopes (0.015 +/- 0.013) than stretches without beaver (0.028 +/- 0.028) along the Numedalslagen River, Norway; Maringer & Slotta-Bachmayr (2006) defined a maximum slope of 0.15 when locating habitat for European beavers in Austria; and Allen (1983) identified a slope of <0.06 as optimum and >0.15 as unsuitable for Canadian beavers in North America. Also, since floodplains are associated with shallow channel and land surface gradients and low-energy off-river habitats, Atwood (1938) found beavers tended to colonise areas with floodplains over 150 m wide in Michigan. Bank gradient may also be an important water-body characteristic, particularly where the banks are used to construct burrows and lodges. For Canadian beaver, Dieter & McCabe (1989) found that banks were significantly steeper at lodge sites (average 41 degrees) than at a random sample of sites (average 27 degrees).

## Food and foraging

- 2.10. Another crucial habitat factor is food. Beaver diet varies seasonally (Lahti & Helminen 1974, Svendsen 1980, Roberts & Arner 1984), and both Canadian and European beavers consume woody vegetation, grasses, forbs, and aquatic vegetation (Table 2.2.). They depend largely on woody food sources in winter, but can spend up to 90% of feeding time consuming grasses, forbs and aquatic vegetation in summer. Doucet & Fryxell (1993) undertook experimental investigations of the food preferences of Canadian beavers among five plant species. They found the following clear order of preference: aspen *Populus tremuloides*, white water lily *Nymphaea odorata*, raspberry *Rubus idaeus*, speckled alder *Alnus rugosa*, and red maple *Acer rubrum*. Fryxell (2001) also observed that the most productive beaver colonies at Algonquin Park, Ontario, Canada had access to either an abundant supply of emergent aquatic plants or highly nutritious terrestrial vegetation species. An extensive literature illustrates that amongst woody species, Canadian beavers show a strong preference for aspen over all other species, and also preferentially utilise willow, alder, maple and ash species (Allen 1983). Donkor & Fryxell (1999) found that around 15 beaver ponds in Algonquin Park, Ontario, Canada, 80% of the total basal area of woody species cut by beaver were alder *Alnus* spp., white birch *Betula papyrifera*, trembling aspen *Populus tremuloides* and red maple *Acer rubrum*. Barnes & Mallick (2001) subdivided the utilisation of woody species by Canadian beavers in Ontario into five categories: (i) alder *Alnus* spp. - dam construction; (ii) Trembling Aspen *Populus tremuloides* - primary food; (iii) White Birch *Betula papyrifera* and willows *Salix* spp. - secondary foods; (iv) shrubs - occasionally used for food and dam construction; and (v) conifers - occasionally used for dam construction. Beaver prefer smaller woody stems (diameter at breast height, dbh, 2.5-15.2 cm – Allen 1983; 1.5-4.4 cm - Barnes & Mallik 1997), and the size of pieces cut decreases with increasing distance from water (Basey & Jenkins 1995, Jenkins 1980).
- 2.11. European beavers have similar woody species preferences to Canadian beavers. Nolet & Rosell (1998) specified intact riparian woodland as a key habitat requirement for European beaver, and Nolet & Rosell (1994) observed that winter beaver territories included c.3 km of wooded banks. In Finland, European beavers show a clear preference for European aspen *Populus tremula* and birches *Betula pubescens* and *B. verrucosa*, whereas debarking of conifers is rare (Lahti & Helminen 1974). Along the River Loire, France, Fustec *et al.* (2001) found that the main woody species within beaver territories were *Populus nigra* (13.3%), *Salix alba* (11.9%) and *Fraxinus angustifolia* (6.9%), that eight herbaceous species totalled >50.6% cover (*Elymus repens*, *Urtica dioica*, *Aristolochia clematidis*, *Paspalum dilatatum*, *Phalaris arundinacea*, *Carex riparia*, *Hedera helix*, *Carex sepium*) and that common river bank species were *Urtica dioica*, *Berteroa incana*, *Datura stramonium*, *Lamium maculatum*, *Phalaris arundinacea* and *Carex riparia*. In Norway, Haarberg & Rosell (2006) found that beavers fed preferentially on willows *Salix* spp., rowan *Sorbus aucuparia* and birches *Betula* spp., although grey alder *Alnus incana* dominated their diet (order of preference willow > rowan > birch > prunus > alder > conifers), and that foraging intensity declined with increasing distance from the river. In Sweden, European beavers mainly feed on fresh bark, shoots, buds, twigs and leaves of aspen *Populus tremula*, birch *Betula pubescens* and willow species (*Salix caprea*, *S.*

*aurita*, *S. cinerea*, *S. glauca*, *S. lapponum*, *S. pentandra*), as well as roots, stems and leaves of many grasses and flowering plants (Curry-Lindahl 1967). In the willow-dominated Biebosch, The Netherlands, Nolet *et al.* (1994) demonstrated that although willows formed their staple diet, beavers only removed 1.4% of the standing crop and positively selected *Alnus*, *Corylus*, *Fraxinus*, *Populus* and *Prunus* species, which were very uncommon, suggesting an attempt to eat a mixed diet. In Lithuania, Bluzma (2003) evaluated the characteristics of occupied and reoccupied sites for European beaver colonies between 1983 and 2001, noting that reoccupation occurred because food was more favourable. In reoccupied sites, young osier beds and understorey vegetation, which are rich in food resources, replace large trees. Also, swamps, hollows and small valleys often supported reeds, the rhizomes of which form an important part of the beaver diet.

- 2.12. Beavers are central-place foragers<sup>5</sup> with foraging intensity declining with increasing distance from the river and larger food items being favoured at increasing foraging distance (Figure 2.1.; Haarberg & Rosell 2006). The time taken to cut down trees or other plants, the provisioning time or time required to take an item back to the central area, the time spent eating the food and the time spent digesting the food are all important (Haarberg & Rosell 2006). The maximum distance that beavers travel from water to obtain food is thought to be approximately 100 m and beavers commonly browse within 10 m (Howard & Larson 1985, Nolet *et al.* 1994). Donkor and Fryxell (1999, 2000) noted that woody stem cutting by Canadian beavers at Algonquin Park, Ontario, is confined to 60 m from water, with about 60% being concentrated within 10 m. Therefore, the proximity of preferred food to water bodies is extremely important. However, beaver can change proximity by impounding ponds and constructing canals. The resultant change in the position of the water shoreline can extend considerably the access of beaver to food in areas of low relief (see Chapter 3).

### Grouping of habitat features

- 2.13. Several researchers have identified groups of habitat characteristics which best discriminate areas that are likely to be colonised by beaver. For Canadian beavers, Howard & Larson (1985) identified seven variables that were significantly associated with colony site longevity in their Massachusetts study area: watershed size; stream width; stream gradient; soil drainage class; percentage hardwood vegetation within 100 m and 200 m; and percentage abandoned fields within 100 m, suggesting that the best beaver habitat was found in wider, low gradient streams with poor soil drainage and woodland land cover within their sample of relatively narrow streams and small watersheds. Beier & Barrett (1987) analysed 17 physical and vegetation variables that might influence habitat use by Canadian beavers in California and found that three physical variables (stream gradient, stream depth and stream width) discriminated between reaches with: (1) at least one active colony present; (2) at least one abandoned colony; (3) beaver usage but not a colony, and (4) no sign of past/present beaver usage. Low stream gradients were thought to be important because dam and canal building can yield large increases in safe foraging and food transportation areas and these low energy environments reduce the potential for damage to dams, lodges and food caches. Deeper, wider streams offer more cover, more sites for food caches, and a more reliable source of water. Mean values of river channel gradient (s), width (w, in m), depth (d, in m) for the four reach types were: (1) s=0.012, w=8.1, d=2.44; (2) s=0.042, w=5.9, d=2.13; (3) s=0.058, w=4.9, d=1.85; (4) s=0.125, w=1.4, d=0.85.
- 2.14. On the River Sverkestaänin, south central Sweden, Hartman (1996) identified tortuosity of the shoreline and a dominant cover of grasses and forbs as the strongest discriminators of European beaver occupancy (although both may result from, rather than be responsible for, beaver occupancy). Softer soils, a higher cover of deciduous tree species and narrower sections of river were also important, although, since the mean river width was 114 m, these preferred narrower sections were of the order of 40 m wide. There was insufficient variability in river gradient or depth to identify their importance in habitat selection. MacDonald *et al.* (1995)

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<sup>5</sup> A central-place is most commonly a nest to which an animal returns between foraging bouts. With beaver, the central-place is usually the den or lodge, but it could also be the water. Travel time costs are changed because of the need to perform round-trips between the central-place and the foraging patches.



presented criteria for gauging the quality of release sites for the European beaver, suggesting a very broad range in the characteristics of a 'good' site: 2-4 m water depth, 10-100 m river width,  $<0.3 \text{ m s}^{-1}$  flow velocity, bank materials of peat-loam soil, bank height  $>1.5 \text{ m}$ , bank slope  $<60$  degrees, woody species predominantly aspen and willow which are  $<8 \text{ cm}$  diameter, and a good herb cover. In their mapping of prime European beaver habitat in Austria, Maringer & Slotta-Bachmayr (2006) used the following criteria to identify optimal habitat for beaver:  $<0.15$  slope;  $>0.5 \text{ m}$  water depth; human disturbance for less than a few hours during the day; and woodland to provide plentiful summer and winter food within 20 m of the water's edge.

## Density of established beaver populations

- 2.15. Beavers normally live as a family unit or colony, consisting of two parental adults, the yearlings born the previous year and the young of the current year. A beaver colony is 'a group of beavers occupying a pond or stretch of stream, using a common food supply and maintaining a common dam or dams' (Bradt 1938, cited in Hill 1982). Various average colony sizes have been reported, with colonies of European beavers generally being a little smaller than those of Canadian beavers (Table 2.1). The density of colonies within an area varies with the quality of the habitat and the degree to which colonisation has stabilised. From published data (Table 2.3), European beaver colonies appear to be more closely spaced than those of the Canadian beaver. Site reoccupation is frequent as colonisation progresses and vegetation growth and recovery occurs at abandoned sites (Bluzma 2003). As the beaver population and density of colonies in an area increase, new colonies are required to occupy less suitable habitat, and this is often partnered with habitat modification by dam construction (see Chapter 3).

Table 2.1 Colony sizes observed for Canadian and European beavers

Source	Location	Average colony size (individuals)
<b><u>Canadian beaver</u></b>		
Bailey (1954)		
quoting Swank (1949)	West Virginia	5.3
Bergerud & Miller (1977)	Newfoundland	4.2
Brooks <i>et al.</i> (1980)	Massachusetts	8.1
Busher <i>et al.</i> (1983)	Nevada	8.2
	California	4.8
Collen (1995)		
quoting Hodgdon and Hunt (1953)	Maine	4.3
quoting Payne (1982)	Newfoundland	5.3
quoting Novak (1977)	Ontario	7.6
Danilov (1992) and Danilov & Kan'shiev (1983)	NW Russia	3.5
Hill (1982)	North America	2.7 ± 6.2 (recorded averages)
MacDonald & Barrett (1993)	Europe	3 ± 9
McTaggart & Nelson (2003)	Illinois	5.6
Novak (1977)	Ontario	8.0
Rosell & Parker (1995)	Mean from literature	5.2
Skewes <i>et al.</i> (2006)	Chile	5.0
Svendsen (1980)	Ohio	5.9
<b><u>European beaver</u></b>		
Campbell <i>et al.</i> (2005)	Netherlands (Biesbosch, Rhine-Meuse estuary)	1-7 (mean 3) excludes kits
	S. Norway	3–11 (mean 4.5) excludes kits
Curry-Lindahl (1967)	Sweden	
	Angermanland	5.0
	Varmland	3.2
	Jamtland	3.1
Collen (1995)		
quoting Myrberget (1967)	Sweden	4.9
Danilov (1992)	NW Russia	4.2
Danilov & Kan'shiev (1983)		
MacDonald & Barrett (1993)	Europe	5 ± 61
quoting Palionene (1975)	Lithuania	4.0
quoting Golodusko (1975)	Byelorussia	4.4
quoting Tamuch & Tolkarev (1976)	Polesie	3.4
Nolet & Baveco (1996)	Biesbosch, Netherlands	3.1 (>1yr old)
Rosell & Parker (1995)	Mean from literature	3.8
Rosell <i>et al.</i> (2006)	SE Norway (Telemark)	3.7*
Zurowski & Kasperczyk (1986)	Poland	3.7

\* maximum observed for a single colony

Table 2.2. Vegetation characteristics of beaver habitats

Source & location	Property explained	Vegetation
<b>Canadian beaver</b>		
Allen (1983) North America	Habitat suitability index (estimated within 200 m of water's edge)	Preferably within 100 m of water's edge:
		40-60% tree and shrub crown closure, dbh 2.5-15.2 cm
		Willow, aspen, cottonwood and alder are preferred species
Atwood (1938) Michigan, USA	General observations on beaver habitat	Cutting within c. 35 m of water edge.
Barnes & Mallick (2001) Ontario, USA	Riparian tree species	The riparian plants around beaver impoundments were classified into five categories: Alder - dam construction; Trembling Aspen primary food; White Birch ( <i>Betula papyrifera</i> ) and Willows - secondary foods; shrubs - occasionally used for food and dam construction; and conifers - occasionally used for dam construction.
Beier & Barrett (1987) California, USA	Factors important for habitat use by beaver were estimated by analysing the characteristics of four reach types: reaches supporting at least one active colony, reaches with at least one abandoned colony, reaches with signs of past beaver usage, reaches with no signs of past beaver usage.	Vegetation variables added little explanatory power, partly because species abundances bear little resemblance to what was present when a colony was established. Local extinction of quaking aspen and black cottonwood indicates that beaver may have a strong negative impact on these species. Nevertheless, willow showed good vigour despite heavy use.
Curtis & Jensen (2004) New York State, USA	Presence of beaver in road side drainage ditches	Woody vegetation cover > 50%
Dieter & McCabe (1989) South Dakota, USA	Lodge location	Higher vegetation cover at 10 and 15 m horizontal distance and 1 and 2m and overhead above ground surface around lodge than random lodge-free sites.
		Mean cover values: overhead (lodge=41% random=26%); 1 m high at 10 m horizontal distance (lodge=89% random=78%), 2 m at 10 m (lodge=95% random=86%), 1 m at 15 m (lodge=53% random=28%), 2 m at 15 m (lodge=68% random=48%).
Howard & Larson (1985) Massachusetts, USA	Maximum colony density	45 ± 29% hardwood cover
		8 ± 10% abandoned fields within 100 m
Slough & Sadler (1977)	Land capability for beaver	Conserve quaking aspen <i>Populus tremuloides</i> stands
<b>European beaver</b>		
Hartman (1996) Sweden	Habitat selection	High cover of grasses, forbs, deciduous trees
Fustec & Cormier (2007)	Wood for lodge construction	<i>Salicaceae</i> > 4.5 cm diameter
Macdonald <i>et al.</i> (1995) from general literature	Good habitat	Aspen and willow <8 cm diameter, good herb cover
Maringer & Slotta-	Definition of optimal and	Unsuitable - extensive disturbance and food

Source & location	Property explained	Vegetation
Bachmayr (2006) Austria	suboptimal habitat for a GIS application	limited by buildings, infrastructure, rocks and boulders
		Suitable - disturbance during the day, summer food - agriculture, pasture
		Ideal - disturbance less than a few hours during the day, summer and winter food - woodland.
Nolet & Rosell (1994)	Observed winter habitat	3.0 ± 0.4 (SE) km wooded banks within winter territory (7.9 ± 0.9 km)
Nolet & Rosell (1998)	Prime habitat	Riparian (willow) woodland.
Fustec & Cormier (2007)	Wood for lodge construction	<i>Salicaceae</i> > 4.5 cm diameter

Table 2.3. Colony densities observed for Canadian and European beavers (densities are expressed either in km of river (i.e. both banks) or per unit area in km<sup>2</sup>)

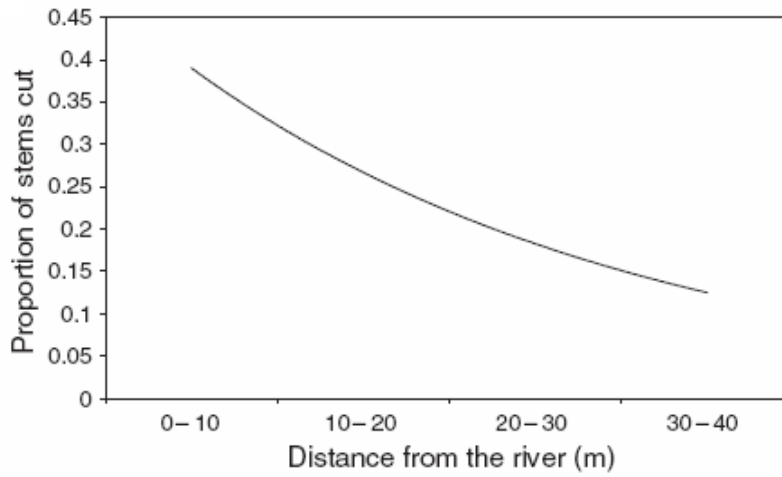
Source	Location	Density
<b>Canadian beaver</b>		
Baker & Hill (2003)	general	0 to 4.6/km <sup>2</sup> (range)
quoting Hill (1976)	Alabama	1.9/km (maximum)
quoting Hill (1982)	Alberta	0.4/km (maximum)
quoting Novak (1987)	New York and Utah	1.2/km (maximum)
Boyce (1983)	Alaska	0.63/km
		(mean nearest neighbour)
Beier and Barrett (1987)	Truckee R., CA	0.74/km
		(sites <2% slope)
Bergerud and Miller (1977)	Newfoundland	2.6/km <sup>2</sup>
Broschart et al. (1989)	Minnesota	1.55/km
Busher (1987)	California	1.3-1.7/'habitable'km
DeStefano et al. (2006)	Massachusetts	0.70/km <sup>2</sup>
Howard and Larson (1985)	Massachusetts	0.83/km
quoting Collins (1976)	Wyoming	0.9/km
quoting Nordstrom (1972)	New Brunswick	1.25/km
Johnston and Naiman (1987)	Minnesota	1.0/km <sup>2</sup>
Larson and Gunson (1983)	Canada (21 areas)	0.11-1.07/km <sup>2</sup> §
Lizarralde (1993)	Tierra del Fuego	0.2±5.8/km
Lizarralde et al.(2004)	Tierra del Fuego	average 0.7/km <sup>2</sup> , in most suitable habitat 5.6/km <sup>2</sup>
McCall et al. (1996)	Maine	0.32/km <sup>2</sup> (no trapping)
Robel and Fox (1993)	Kansas	0.08±1.4/km (rivers)
		0.0±0.25/km (reservoirs)
Robel et al. (1993)	Kansas	0.39/km
quoting Nordstrom (1972)	New Brunswick	1.11/km*
quoting Brooks (1977)	Massachusetts	0.77/km
Skewes et al. (2006)	Chile	1.03/km (range 0.15-1.91)

Source	Location	Density
<b>European beaver</b>		
Bluzma (2003)	Eastern Lithuania	1.9/km <sup>2</sup>
Campbell et al. (2005)	Netherlands (Biesbosch, Rhine- Meuse estuary)	0.08/km*
	SE Norway (Telemark)	0.25/km*
Fustec et al (2001)	Loire River, France	0.117/km (inversely proportional to willow grove length)
Hartman (1996)	Sweden (R. Sverkestaan)	1.0/km
Hartman (1994)	Sweden Varmland and Vasternorrland	0.25/km <sup>2</sup> (modelled peak density)
Herr and Rosell (2004)	SE Norway (Telemark)	0.51/km (average males)*
		0.57/km (average females)*
MacDonald et al. (1995)		
quoting Heidecke (1984)	Peene Valley (Germany)	0.26/km
Nolet and Rosell (1994)	Norway	0.13/km
Nolet and Baveco (1996)	Biesbosch, Netherlands	0.33/km
Parker and Ronning (2007)	Numedalslagen River, Norway	0.32/km <sup>2</sup>
Pupininkas (1999)	Eastern Lithuania	0.23/km <sup>2</sup>
Robel et al. (1993)		
quoting Semyonoff (1951)	Archangel Province, Russia	1.67/km (average)¥
Sidorovich et al. (1996)	Belarus-Poland	0.29/km (average)
		0.0-0.5/km (range)
Zurowski and Kasperczyk (1986)	Poland	0.15/km <sup>2</sup>

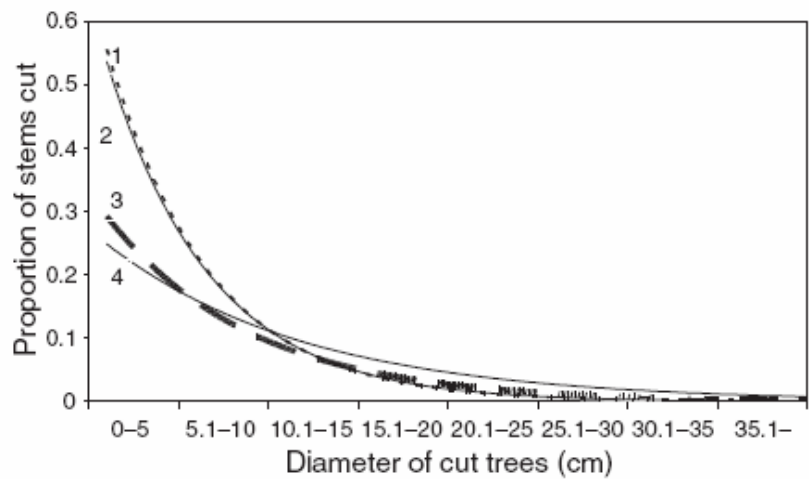
\* from estimated mean territory sizes; § varying impact of trapping, ¥ no species stated but assume *C. fiber*

Figure 2.1. (a) Proportion of stems cut by European beavers in relation to distance from the water's edge at seven territories in Telemark, Norway in 2001; (b) diameter selection - four distance categories measured from the edge of the river (1=0–10 m, 2=10–20 m,

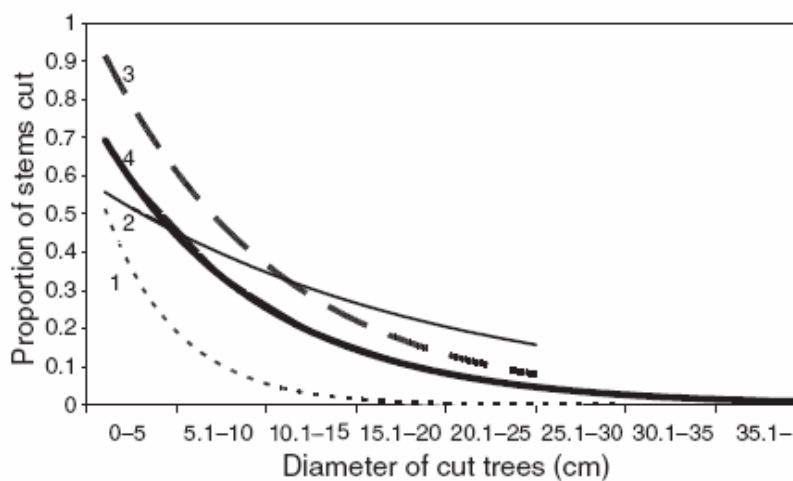
(a)



(b)



(c)



# 3. Beavers dams, hydrogeomorphological ecosystem effects and British rivers

## Summary

- 3.1. Beaver dams and dens - Beavers build dams of tree trunks, branches, twigs, earth, mud and stones to raise and stabilise the local water level, providing deeper water to cover lodge entrances, supporting the transport of food, and extending the position of the water's edge into the riparian zone. Wood piece sizes used in such structures are typically <2 m in length. Larger dams are usually associated with spreading water into the riparian zone, and thus extending marginal wetlands, rather than damming large river widths. Beavers often excavate canals to allow more extensive access to the riparian zone. The number and size of dams varies widely between beaver colonies, and the surface area and volume of water in beaver ponds reflect flow and water level variability, the length of occupancy, local topography, substrate quality, and the availability of food. European beavers are believed to build dams less frequently and also build relatively smaller structures than Canadian beavers. They use four types of den or shelter: natural holes in banks; burrows they excavate in banks; bank lodges, where wood and mud are used to conceal a burrow entrance; and true lodges, built from piles of logs and mud. Bank lodges are most common in European beavers and, in contrast to Canadian beavers, true lodges are relatively rare. The entrance to the lodge or burrow is underwater. Cut wood is cached underwater near the den for consumption during the winter when other foods are scarce.
- 3.2. Broad environmental effects - Beaver dams can be thought of as an extension of the range of wood structures that occur widely in natural or lightly managed river systems. All such structures are natural components of river systems and are dynamic in their position, size and water-retention ability, forming important components of the river habitat mosaic. The construction of beaver dams and ponds introduces many additional habitats to river reaches (ponds; complex stream-riparian aquifer flow paths leading to zones of different water table and soil moisture levels including wetlands; browsed openings within riparian woodland; areas of differing tree density and canopy height), resulting in a substantial increase in habitat diversity, the spatial complexity of the habitat mosaic, and the overall resilience of river and riparian ecosystems to disturbances. Beneficial biogeochemical changes are also induced, particularly an increase in carbon, nutrient and fine sediment retention and their gradual incorporation into the riparian zone through beaver meadow development.
- 3.3. Hydrogeomorphological effects of dams and ponds - The construction of beaver dams provides water stores (ponds) which can sustain low river flows, seepage to the riparian zone, and areas of stored water within the channel network far longer during dry periods than would occur in river channels without beaver dams. Some catastrophic failures of large dams constructed by Canadian beaver have been reported from North America. These have yielded significant floods in some cases, but water from such major dam failures has also been observed to be rapidly absorbed by beaver meadows and ponds downstream. Moreover, the relatively small wood piece sizes associated with beaver dams can be readily trapped within the riparian zone and so are unlikely to generate a significant blockage hazard downstream. In general the effect of beaver dams and ponds on high river flows, and the most likely effect of those constructed by European beavers, is to help to regulate flows and so beneficially reduce flood peak levels downstream.
- 3.4. Beaver dams introduce steps along the river's long profile where energy is dissipated and, as a result, both sediment and organic matter are deposited within beaver ponds. This important retention of sediment and organic matter, coupled with management of sediment sources, has the potential to lead to a reduction in catchment yields as well as an increase in the incorporation of sediment and organic matter into the riparian zone (beaver meadows). Sorting of mineral sediment particles occurs within the ponds, with coarser sediments deposited in pond heads and finer sediments within the main pond body. Within free flowing river sections between ponds, flushing of finer sediment and sorting of coarser bed sediment

may also occur, which may be highly beneficial for fish spawning areas. The storage, decomposition and processing of organic matter and sediment within the beaver ponds may also improve water quality and turbidity downstream. These highly beneficial effects of beaver construction on sediment and organic matter retention (e.g. see chapter 11) have provided a rationale for beaver reintroduction into degraded, incising river systems within the USA.

- 3.5. Landscape scale hydrogeomorphological effects - Beaver construction varies in location and intensity along the river continuum as the main river channel widens and reduces its gradient. Steep headwaters may not support beavers, but as slopes gradually decrease, beavers may regulate river levels through dam construction on relatively narrow channels within the headwaters and middle reaches. As the main channel and floodplains widen towards the lower reaches, beaver construction moves from the main channel into side channels and ponds within the riparian – floodplain zone. Wherever beaver construction occurs, a more complex local channel network develops, which can better accommodate high flows. In areas of very low relief beaver construction can encourage the development of multi-thread low energy channel. The overall result of beaver construction is an increase in both aquatic and riparian habitat diversity and an increase in channel stability.
- 3.6. Beavers and British rivers - The majority of British rivers have relatively low gradients and narrow widths, making them physically suitable for beaver colonisation. However, the presence of bedrock or very coarse sediment banks, relatively shallow water depths, and limited presence of riparian trees (particularly *Salicaceae*) make some river types less than ideal. The most suitable habitat conditions for European beavers are found along the least degraded lowland rivers that have the lowest river gradients, the finest bed and bank sediment with occasionally deep pool habitats, and plentiful riparian tree cover (i.e. River Types I, II and III, Table 3.3). Not only do these river types provide very good beaver habitat but their low gradients strongly reduce the likelihood of dam construction. These low gradient river types often have wide flood plains and occupy subdued landscapes that offer a variety of suitable off-river and side stream, lotic and lentic<sup>6</sup>, as well as main channel habitats for beaver colonization.

## Building dams and dens

- 3.7. Dam building activities of Canadian beavers in unexploited situations can influence as much as 40% of the total length of 2nd to 5th-order streams (Naiman *et al.* 1986). However, the impact of European beaver dams is usually more restricted, and they appear to construct dams less frequently than Canadian beavers. For example, in northwest Russia, Danilov (1995, cited in Collen & Gibson 2001) found that whilst 66% of Canadian beaver colonies built dams, only 45% of European beaver colonies did so. Both species cut wood to construct dams, lodges and food caches. The construction of dams raises and stabilises the local water level, providing deeper water to cover lodge entrances and support food transport, and extending the position of the water's edge into the riparian zone. Beavers often excavate canals to allow more extensive access to the riparian zone (Müller-Schwarze & Sun 2003).
- 3.8. Beaver dams consist of tree trunks, branches, twigs, earth, mud and sometimes stones. They are constructed to create beaver ponds, which maintain access to lodges and burrows below water level and extend food foraging areas. Several dams may be built by the same colony to achieve this (Richard 1983, Baker & Hill 2003). The size and number of dams, and the surface area and volume of water in ponds reflect flow / water level variability, length of occupancy, local topography, substrate calibre, and available food / vegetation (Baker & Hill 2003). Whilst early descriptions of dams built by Canadian beavers in relatively undisturbed situations in North America (e.g. Morgan 1868, Dugmore 1914, Warren 1927) indicate occasional very large structures, several hundred metres long and several metres high, most dams were less than 1.5 m high (Dugmore 1914, Townsend 1953). Butler (1995) suggests typical dam sizes of 15-70 m long and 1-2 m wide for Canadian beavers with widely varying heights. Butler does not specify whether the longer dams are constructed to span channels of that width, but it is more likely that they extend across the floodplain to control over-bank water levels. Baker & Hill (2003) comment that as water spreads from dams within the main river channel, beaver

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<sup>6</sup> Lotic- flowing water systems (rivers & streams); lentic – still water systems (lakes, ponds & swamps)



often build small dams on the floodplain to contain and spread water. Thus dams help to extend riparian wetlands as well as stabilising water levels within beaver ponds.

- 3.9. The sound of running water is believed to be an important stimulus for dam building by both species (e.g. Hodgdon & Lancia 1983, Richard 1983), although Zurowski (1992) concluded that this was of secondary importance to the stimulus of improving safety and access to food at particular sites. European beavers are also believed to construct smaller structures than Canadian beavers. For example, beaver dams in Sweden are usually less than 15 m in length and 1 m in height (Curry-Lindahl 1967), and are built in shallow waters less than 10 m wide (Hartman 1994). In Poland, Zurowski & Kasperczyk (1986) found that only 50 of a total of 257 beaver sites in the Suwalki Lakeland had dams, and Zurowski (1992) found that only 17 out of 62 beaver colonies in the Masurian and Brodnica Lakelands had dams. The dams were generally small and located on small rivers or drainage ditches, as were those studied in France by Coles (2006), where the maximum flowing channel width dammed was 16 m. Coles (2006) provides detailed maps and photographs of the dams that were studied in Brittany, demonstrating their predominantly small height (maximum c.1.5 m) and lateral extent, in addition to their complex spatial distribution. Whilst most dams were quite small, they were also numerous at some of the study sites (Table 3.1.).
- 3.10. The planform of dams also varies widely, but upstream-orientated arc-forms (with convex of arc upstream) are common, particularly for the largest structures. Small within-channel dams can be progressively extended into long channel-floodplain dams (Richard 1967), producing large shallow ponds on floodplains where the width of dammed channel may be quite small.
- 3.11. Baker & Hill (2003) describe the structure of dams built by Canadian beavers as follows, “Branches in the bulk of the dam may be anchored and intertwined perpendicular or parallel to the flow of water; however, material on the downstream side is usually placed with the cut end pushed into the stream bottom or bank and the branched end pointing upstream to support and stabilize the dam”. Richard (1955) described a similar structure for dams constructed by European beavers on the River Tave, France. Dams were up to 8-10 m in length and were constructed of wood pieces, typically 1-2 m long, and sometimes stones, which were then sealed with mud on the upstream face. The wood pieces were aligned across the river, parallel to the banks or near vertical. The near-vertical pieces and those parallel to the bank formed the key pieces of the structure, which were then filled out upstream with transverse pieces. Three basic types of structure were found: (1) built around a fallen or inclined tree to give support to the structure; (2) based upon vertical key pieces of wood driven into the stream bed; and (3) counterbalanced by wooden props which support the downstream face of the dam against upstream water pressure (types 2 and 3 are combined in the largest dams). Once a dam and pond are constructed in a low-gradient area, the zone of floodplain accessible to beaver can be further extended by constructing canals, which are used as route-ways to access food and transport timber to the beaver pond.

Table 3.1. Reported densities of beaver dams

Source	Location	Density
<b>Canadian beaver</b>		
Butler & Malanson (1995)		
quoting McComb <i>et al.</i> (1990)	Eastern Oregon	0.14/km
Leidholt-Bruner <i>et al.</i> (1992)	Coastal Oregon	1.1/km
		1.2/km
Naiman <i>et al.</i> (1986; 1988)	Quebec	10.6/km (average)
		8.6 ± 10.6/km (range)
	Minnesota	2.5/km (average)
		2.0 ± 2.9/km (range)
Woo & Waddington (1990)	North Ontario	14.3/km (average)
		5 ± 19/km (range)

Source	Location	Density
<b>European beaver</b>		
Pupininkas (1999)	East Lithuania	4.8 and 12.7 dams per colony, respectively, on lakes and rivers, and 0.23 colonies per km <sup>2</sup>
Parker & Ronning (2007)	Numedalslagen River, Norway	0.07-0.11/km
Coles (2006)	Keriou, Brittany, France	7.1/km
	St Roman, Drome, France*	24.7/km
	Bes River, Drome, France*	33.0/km

\* dams built mainly on small streams and backwaters / side channels

- 3.12. In addition to dams, beavers construct shelters or dens. Erome (1984), working on the River Rhone, France, found that natural holes in the bank are often used and that European beavers also excavate burrows where the bank is sufficiently high and the bank material is appropriate. Elsewhere, intermediate structures between burrows and free-standing lodges, called bank lodges, use wood to conceal the burrow entrance, or to increase soil cohesiveness, effective bank height or effective soil depth. The nest chamber is typically 0.3-0.7 m above the upper edge of the burrow entrance, defining the upper limit to desirable water-level fluctuations, and nest chambers are typically 0.4-0.5 m in height. Thus, bank heights of 1.5-2.0 m above the burrow entrance or 1-1.5 m above normal water level are needed for burrow construction. Elsewhere, the addition of wood to create bank lodges achieves the required height. Erome (1984), Pupininkas (1999) and Danilov (1995, cited in Collen & Gibson 2001) found true lodge (free-standing) construction by European beavers to be relatively rare. For example, Pupininkas (1999) found only semi-lodges on lakes in east Lithuania, whereas the proportion of lodges to semi-lodges to burrows on rivers and streams was 1 : 11.9 : 2.3 respectively. Danilov (1995, cited in Collen & Gibson 2001) found that in northwest Russia, 75% Canadian beaver colonies but only 34% European beaver colonies had lodges, whereas 64% European beaver colonies and only 25% Canadian beaver colonies had bank burrows. Individual colonies often have secondary lodges, semi-lodges or burrows, which may be occupied when the water level is low, near the main lodge, or when the beavers suffer disturbance.
- 3.13. Cut wood is often accumulated under water for consumption in winter when food is scarce. These stores or caches can be very large where the winter is long and the water surface freezes. The caches are usually located close to the lodge or burrow, sometimes being anchored to a dam or to the river or lake bed (Curry-Lindahl 1967).

## Environmental conditions encouraging dam construction

- 3.14. The presence / absence and density of beaver dams vary widely (Table 3.1.), depending upon the number of beaver colonies and the degree to which environmental conditions encourage dam building. Dams may be maintained in the same location for long periods. Alternatively, they may become abandoned and fall into decay, or may pass through cycles of re-occupation. All the literature found to explore this theme, focused on Canadian beaver rather than European beaver.
- 3.15. Beier & Barrett (1987) found that abandoned sites in their California study area fell into two groups. Sites in the first group were physically similar to sites with active colonies, but with relatively low food availability. These may be reoccupied when the vegetation recovers and then dam building and maintenance may recommence. The second group comprised sites that were more similar to uncolonised sites (i.e. steep stream gradients and narrow stream widths), and were probably only occupied for a short period of time prior to abandonment. Barnes & Mallick (1997) differentiated between active sites, abandoned sites and sites with no

dams in their Ontario study area. Sites with no dams had significantly larger watersheds (mean = 6247 ha), larger channel cross-sectional areas (mean = 14.2 m<sup>2</sup>) and lower channel gradients (mean = 0.005), but all sites had low gradients with mean gradients for active and abandoned dam sites being 0.011 and 0.006, respectively. These results are similar to Naiman *et al.* (1986), who noted that most dams were built on 1st to 4th-order streams in their Quebec, Canada, study area. Barnes & Mallick (1997) also found that the density of small (1.5-4.4 cm diameter) woody stems at the active and abandoned sites was significantly greater than at sites with no dams. Finally, McComb *et al.* (1990, cited in Collen 1995) found that reaches with dams were shallower, had a lower gradient, a greater tree canopy cover and gentler bank slopes than reaches without dams, and that dams were not built at sites with a rock substrate.

## Environmental effects

3.16. The construction of beaver dams and ponds introduces many additional habitats to river reaches. They modify local hydrology, geomorphology and chemistry, and thus influence the ecology of affected areas. Additional habitats created by beaver construction include: (1) browsed riparian zones, which when influenced by beaver dams, have a raised water table and additional areas of waterlogged and wet but free draining soils; (2) extensive anaerobic sediments beneath beaver pond beds and, in some case, (3) floating mats of peat and vegetation at pond margins (Johnston and Naiman, 1987). With particular reference to the replacement of a section of stream by a beaver pond, Hammerson (1994) identified many environmental changes, outlined as follows:

3.17. Hydrological changes include:

- increased storage of precipitation, reduced flow velocities and reduced variability in the river's discharge regime;
- an enormous increase in water surface area, particularly in low relief environments;
- increased water depth;
- an increase in the level of the local water table.

Biogeochemical changes include:

- a great increase in the amount and availability of organic carbon, nitrogen and other nutrients in the channel;
- an increase in carbon turnover time;
- an increase in nitrogen fixation by sediment microbes;
- amelioration of stream acidity; increased trapping of sediment and a decrease in turbidity downstream;
- an increase in aerobic respiration as a result of increased water-surface area;
- a substantial shift to anaerobic biogeochemical cycles in sediments beneath ponds;
- an increase in the amount of organic matter suitable for methane-producing microorganisms and increased carbon output by methanogenesis;
- reduced oxygen levels in the water in spring and early summer due to decomposition of the augmented organic matter.

Ecological changes include:

- an increase in the extent of open canopy in wooded areas;
- loss of species dependent on riparian trees as habitat;
- more favourable conditions for riparian tree and wetland plant growth;
- creation of conditions favourable to species dependent upon ponds, pond edges and/or dead wood;
- both enhancement and degradation of conditions for fish, depending on the species;
- replacement of running-water invertebrate taxa by pond taxa, an increase in the absolute importance of collectors and predators and a decrease in the relative importance of shredders and scrapers in impounded sites;
- a several-fold increase in the mass of insects emerging from the water surface per unit stream length;
- increased plankton productivity;
- increased ecosystem resistance to perturbation.

- 3.18. To this list we would add the effects of beavers on amphibians, reptiles and mammals. We explore hydrological, geomorphological and chemical effects in the following section , and effects on plants and animals in Chapter 4.

## Hydrology, geomorphology and chemistry

- 3.19. Hering *et al.* (2001) compared reaches containing wood jams and beaver dams with free-flowing reaches in Central Europe, demonstrating large contrasts in the hydrology and geomorphology of these two types of dammed reach in comparison with free flowing reaches (Table 3.2). In essence, beaver dams are an extension of the range of wood structures that occur in natural or lightly managed river systems (e.g. Gurnell *et al.*, 2002). These contrasts between reaches with and without wood structures reflect the fact that wood jams pond back water and that beaver ponds form particularly important and very effective hydrological and sediment stores.
- 3.20. The quantity of water stored in a beaver pond depends on down-valley slope, cross-valley profile and dam dimensions (Johnston & Naiman 1987). Thus, beaver dams located on constricted, steep, upland streams pond back rather small volumes and areas of water, with little lateral extension of the water margin and limited opportunities for canal construction. As a result, beaver dams are rarely constructed on steep gradient streams. Beaver tend to construct dams on lower gradient, floodplain reaches where construction allows spatially extensive, complex pond and canal systems, which regulate the river's discharge regime. Flows in downstream channels are controlled by overtopping of dams when ponds are full, and by seepage through or under dams when water levels fall below the dam crest. However, Devito & Dillon (1993) found that well-maintained dams are remarkably watertight, with negligible outflow once the water drops more than 5 cm below the dam crest.
- 3.21. Water levels in beaver ponds reflect the balance between river flow, precipitation and groundwater seepage into the pond versus river flow and groundwater seepage out of the pond and surface evaporation. As a result, water levels vary seasonally and during flood events. Hydraulic gradients between pond surfaces, downstream water levels and riparian water table levels give rise to significant surface water-groundwater interactions, including downstream flows beneath beaver dams (White 1990); correlated fluctuations in pond and riparian water table levels (Lowry 1993) that are larger than those adjacent to unponded sections of river; and enhanced recharge of the riparian aquifer adjacent to ponds in comparison with free-flowing reaches.
- 3.22. As a result of the sizeable water storage in large beaver ponds, failure of major beaver dams can result in flooding (Butler & Malanson 2005), although the effects of dam failure is often attenuated by beaver-constructed ponds and meadows downstream. For example, Hillman (1998) reported the sudden release of 7500 m<sup>3</sup> of water from a beaver dam failure into a creek in Alberta. The flood wave had a peak flow 3.5 times larger than the maximum discharge recorded over 23 years, destroyed five hydrometric stations, and scoured and deposited large quantities of sediment. However, this large peak flow was reduced to 6% of its estimated upstream magnitude by flood attenuation through a 90-ha wetland containing a small lake and several beaver ponds. Thus, the aggregate effect of beaver constructions on river flow regimes can be very substantial. They increase the time of rise and decrease the magnitude of the flood flows. They also sustain low river flows, seepage to the riparian zone, and areas of water storage within the channel network far longer during dry periods than would occur in river channels without beaver dams.
- 3.23. Significant water storage and low flow velocities within beaver ponds induce deposition of large quantities of mineral and organic sediment (Butler & Malanson 1995). Naiman *et al.* (1994) combined observations from several study sites in Minnesota to evaluate the long-term biogeochemical characteristics of boreal forest drainage networks as a result of hydrological modification and sediment retention by Canadian beaver ponds. They showed that anaerobic conditions caused by saturation of soil greatly alters biogeochemical pathways, leading to the accumulation of large quantities of organic matter from surrounding vegetation in both ponds and wet meadows. This leads to preferential, long-term retention of chemical elements associated with organic matter in these deposited organic horizons, rather than their export downstream or return to the atmosphere. Since large ponds can persist for decades, sediment

trapping can also lead to a transformation of the fluvial environment to include extensive wetlands and ultimately the development of organically rich, gently sloping, beaver meadows (Ruedemann & Schoonmaker 1938). Butler & Malanson (2005) note that published sedimentation rates within beaver ponds in the United States range from  $<1 \text{ cm yr}^{-1}$  to almost  $40 \text{ cm yr}^{-1}$ . This led Butler and Malanson to estimate that the total sediment storage in the ponds of the unexploited beaver population prior to European settlement was between 7.5 and 125 billion  $\text{m}^3$  (based on  $500 \text{ m}^3$  of sediment per pond), and that current sediment storage is 1.9 to 3.9 billion  $\text{m}^3$ . Butler & Malanson (2005) also observe that when dams fail, vegetation colonisation is very rapid forming beaver meadows where most sediment is retained.

Table 3.2. Differences in hydrological and morphological properties of reaches affected by wood jams or beaver dams in comparison with free-flowing reaches in Central Europe mountain streams (based on Hering *et al.* 2001).

Property	Reaches with wood jams	Reaches with beaver dams
Mean water depth	0	++
Water depth variability	+	+
Mean stream width	+	++
Stream width variability	+	++
Presence of hyporheic zone	0	-
Variability of hyporheic zone	0	?
Presence of standing water bodies	0	++
Presence of secondary channels and multi-thread sections	+	+
Presence of temporary water bodies	+	+
Shoreline length	+	++
Average water temperature	0	+
Water temperature variability	0	++
Average flow velocity	-	--
Flow velocity variability	+	++
Lotic zones	-	++
Lentic zones	+	++
Habitat diversity (10 m scale)	+	++
Short-lived habitats	+	++
Sediment retention	+	++
Nutrient retention	+	++
Litoral zones	0	+

In comparison with free flowing reaches, -- = considerably less, - = less, 0 = no difference, + = more, ++ = considerably more, ? = not known.

- 3.24. Recent incision (erosional downcutting) of stream and river beds in North America has been partly attributed to the removal of beaver (Parker *et al.* 1985). Butler (2006, p451) states that “*widespread removal of North American beavers via trapping for fur led to increased stream incision, attendant changes from relatively clear-flowing to sediment-laden streams, and pronounced changes in the riparian environments of North American stream systems that are still being experienced in the 21st Century*”. However, Butler & Malanson (1995) note that the provenance of the sediment is unclear and that it is important to distinguish between the accumulation of fluvially-transported sediment and sediment introduced into ponds by beaver activity such as the excavation of canals and burrows. Nevertheless, the great effectiveness with which beaver ponds trap sediment has resulted in the deliberate introduction of beaver to inhibit sediment transfer, stabilise stream banks, reverse channel incision and restore riparian

habitat in some areas of North America (e.g., Ruedemann & Schoonmaker 1938; Farrar 1971; Apple 1982; Brayton 1984; Johnson 1984; Bergstrom 1985, Pollock *et al.* 2007).

- 3.25. Since discharge and sediment transport regimes are the primary controls on the form and dynamics of river systems, beaver construction has far-reaching impacts on the geomorphology of the fluvial system. Beaver dams represent very important structural elements within river channels. They impede flows of water and sediment, producing steps in the river's long profile, diversions of water, and varied patterns of flow velocity and shear stresses that regulate the scour and deposition of sediment. The presence of beaver dams increases variability in channel width and depth, bed sediment calibre, and in-channel morphological features. Where the beaver dams extend across the floodplain, diffuse seepage may lead to the development of floodplain wetlands, and concentrated flow may excavate additional stream channels. Woo & Waddington (1990) noted that in Ontario, although most water draining from beaver ponds re-enters the river a short distance below the dam, in some cases new channels are created which flow when the pond is full, and in time may become sufficiently incised to form part of the permanent drainage network. Townsend (1953) found that beaver dam building in the relatively flat landscape of an area of Montana caused extensive changes to the drainage network, with many distributary channels being created by overflows from ponds, and Cooper *et al.* (2006) describe a characteristic sequence of river channel change through cutoff-development induced by beaver dam construction. Map evidence suggests similar complexity at the European study sites discussed by Coles (2006).

## Beavers and the river continuum

- 3.26. Due to the varying potential for beavers to engineer their aquatic and riparian environment as river channels vary in slope, width and depth, and as side channels and floodplain ponds vary in their extent and availability, it is possible to conceptualise differential impacts of beavers on river landscapes along the river continuum (e.g. Naiman *et al.* 1986, 1988). Naiman *et al.* (1986) specifically considered the implications of beaver activity for the River Continuum Concept (RCC; Vannote *et al.*, 1980), which views river systems as longitudinally interconnected channels where hydrological, geomorphological and biological processes operate along a continuum. The concept does not fully allow for interruptions to the continuum such as ponds and lakes or for major lateral interactions between the river and its floodplain, which characterise the impact of beaver particularly on small streams. This led Naiman *et al.* (1986) to suggest the RCC needed modification to incorporate beaver activities. Naiman *et al.* (1988) outlined how beaver impacted differentially downstream along North American rivers prior to European settlement. "*Where beaver were present in small streams (i.e., approximate orders 1-4) there were numerous reaches with open canopy, large accumulations of detritus and nutrients, expanded wetted areas (including riparian zones), and substantial shifts to anaerobic biogeochemical cycles.... In middle-order streams (i.e., orders 5-8), beaver-cut wood from upstream and the immediate riparian zone augmented local allochthonous<sup>7</sup> inputs. Debris accumulations resulted in massive storage of sediment and detritus in the main channel, often forming small islands. In large rivers (i.e., orders greater than 9) beaver utilized floodplains and backwaters, where they constructed dams and canals and cut large amounts of wood. Although these activities diversified stream habitat in the short term, centuries of sediment deposition behind beaver dams may have reduced floodplain complexity.... The effects of this activity, which can still be seen in the terrestrial vegetation of meadowlands centuries after the extirpation of beaver ...is testimony to their widescale influence on the landscape of North America*".
- 3.27. This description illustrates how the river-network impacts of beaver construction moved from the main channel into side channels and flood plain ponds as rivers widened downstream, and also how the lateral impacts of damming were increasingly restricted as river channels and streams steepened and floodplains disappeared towards headwater areas. Although morphological evidence for the historical impacts of European beaver on British rivers is poorly preserved, the impacts of re-introduced populations across Europe suggest that similar landscape scale effects may have occurred. The relatively low gradients, narrow widths and

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<sup>7</sup> Allochthonous refers to deposits and rocks found in a place other than where they and their constituents were formed; the opposite is autochthonous.

low stream orders of the majority of British streams, suggest that much of the landscape would have been affected in a manner similar to that suggested for middle-order (intermediate slope and width) streams in North America.

## Beavers and British river types

- 3.28. The past and potential future impact of European beavers on the British landscape is likely to vary greatly between river types. Holmes *et al.* (1999) proposed a hierarchical classification of British river types based largely on their physical characteristics and macrophyte communities. From the analysis of data from over 1500 sites, four broad groups of river (A, B, C, D) were separated into 10 types (I to X) and 38 subtypes. Table 3.3 provides a simplified description of the ten river types as a context for considering likely differences in their suitability for supporting beaver populations. These descriptions can be compared with the broad characteristics of suitable beaver habitat identified in Chapter 2 (i) easy access to grasses, forbs and riparian tree species, especially the *Salicaceae*; (ii) where streams are small and shallow, larger, deeper channels are preferentially selected by beaver, whereas in areas of wide channels, the narrower locations are selected, suggesting a preference for channel widths of the order of 8-40 m and water depths, at least near lodge and burrow sites, of >0.6m; (iii) river channel gradients < 0.15 but preferably <0.06 and (iv) 'soft' or finer calibre bed and bank materials
- 3.29. Virtually all British rivers are less than 40 m wide, but types V, VIII and X were found to be relatively shallower than the other types within the sample of reaches analysed by Holmes *et al.* (1999). In relation to vegetation criteria, riparian trees are widespread along river types I to VIII, and aquatic and wetland vegetation is abundant and diverse along river types I to VI (groups A and B) and particularly types I to III (group A excluding impoverished lowland rivers). This suggests that most British river types are of suitable channel dimensions and provide suitable vegetation to support populations of European beavers, but that the most suitable habitat conditions are found along the lowland rivers in group A. Since group A rivers also have the lowest river gradients and finest bed and bank materials of the ten river types, they appear to offer the best habitat for the European beaver. Their low gradients and occasionally deep pool habitats also reduce the likelihood of dam construction. These low gradient river types often have wide flood plains and occupy subdued landscapes, offering a variety of suitable habitats for colonisation, including off-river and side stream, lotic and lentic, as well as main channel beaver habitats.

Table 3.3. Characteristics of British rivers types (developed from Holmes *et al.* 1999 and Mainstone, unpublished)

Community Type	Gradient and energy	Bed rock and bed material	Flow types and bedforms	River channel form	Typical aquatic and wetland plants (found in >75% sites)
Type 1 Lowland low gradient	Generally low gradient (mean 0.001, max 0.007) but discharge very variable	Developed on fine, calcareous (chalk and clay) sedimentary rocks, yielding fine bed material with occasional accumulations of coarser (gravel-pebble) material in riffles	Glide dominated	Sinuuous to meandering channels with alternating eroding and depositional banks and some fine bar deposits on channel margins	Aquatic: <i>Apium nodiflorum</i> , <i>Glyceria maxima</i> , <i>Nuphar lutea</i> , <i>Potamogeton pectinatus</i> , <i>Rorippa nasturtium-aquaticum</i> , <i>Sagittaria sagittifolia</i> , <i>Sparganium emersum</i> , <i>Sparganium erectum</i> , <i>Veronica beccabunga</i> Wetland: <i>Carex riparia</i> , <i>Lycopus europaeus</i> , <i>Iris pseudacorus</i> , <i>Eupatorium cannabinum</i> , <i>Epilobium hirsutum</i> , <i>Phalaris arundacea</i> , <i>Mentha aquatica</i> . Riparian trees: <i>Salicaceae</i> common
Type II Lowland clay-dominated	Low gradient (mean 0.001, max 0.004), generally low energy but with 'flashy' flow regime	Developed predominantly on calcareous clay-dominated sedimentary rocks (with some soft sandstone and limestone but not chalk), yielding fine bed material with occasional accumulations of coarser (gravel-pebble) material in riffles	Glide dominated with occasional riffles and pools	Sinuuous to meandering channels with bank profiles varying in sympathy. Channels tend to have low width to depth ratios because of cohesive nature of bank material, with some fine bar deposits, particularly along channel margins	Aquatic: <i>Cladophora glomerata</i> , <i>Sparganium erectum</i> Wetland: <i>Epilobium hirsutum</i> , <i>Myosotis scorpioides</i> , <i>Phalaris arundacea</i> Riparian trees: <i>Salicaceae</i> common
Type III Chalk and other base-rich rivers with stable flows	Low gradient (mean 0.001, max 0.008); subdued, baseflow-dominated, flow regime gives	Developed mainly on chalk. Bed material dominated by gravel with extensive patches of finer (sand-silt-med) sediment	Glide dominated with occasional riffles and pools	Sinuuous, sometimes multi-thread channels with stable banks and often with relatively high width to depth ratios	Aquatic: <i>Apium nodiflorum</i> , <i>Callitriche obtusangula</i> , <i>Glyceria maxima</i> , <i>Ranunculus penicillatus</i> , <i>Rorippa nasturtium-aquaticum</i> , <i>Sparganium erectum</i> , <i>Veronica anagallis-aquatica</i> , <i>Veronica beccabunga</i> Wetland: <i>Carex acutiformis</i> , <i>Epilobium hirsutum</i> , <i>Filipendula ulmaria</i> , <i>Iris pseudacorus</i> , <i>Mentha aquatica</i> , <i>Myosotis scorpioides</i> , <i>Phalaris arundacea</i> , <i>Scrophularia auriculata</i> Riparian trees: <i>Salicaceae</i> common



Community Type	Gradient and energy	Bed rock and bed material	Flow types and bedforms	River channel form	Typical aquatic and wetland plants (found in >75% sites)
Type IV Impoverished lowland rivers	Low gradient (mean 0.002, max 0.050); generally low energy but flashiness of flow regime increased by human impacts, particularly imposition of artificial drainage and impervious surfaces.	Developed on varied limestone, sandstones and shale giving mixed, relatively fine, mixed (pebble and finer) bed material but with significant human-modification of channel form and reinforcement	Glide and runs with riffles and occasional pools	Generally narrower than other river types, probably indicating bed incision	Aquatic: <i>Sparganium erectum</i> , <i>Veronica beccabunga</i> . Wetland: <i>Epilobium hirsutum</i> , <i>Myosotis scorpioides</i> , <i>Phalaris arundacea</i> Riparian trees: <i>Salicaceae</i> common Mean number of species less than 75% of other river types in group A.
Type V Sandstone, mudstone and hard limestone rivers of England and Wales	Intermediate, occasionally steep slope (mean 0.002, max 0.150) and energy, some with relatively flashy flow regimes	Gravel-pebble-cobble calibre bed material with occasional large calibre material (e.g. boulders) and bed rock exposures	Glides and runs between riffle-pools	Sinuuous, active channels with exposed mid-, point- and marginal gravel bars at low flows, some marginal finer sediment deposits, actively eroding and depositing river banks.	Aquatic: <i>Rorippa nasturtium-aquaticum</i> and specialist mosses ( <i>Rhynchostegium riparoides</i> ) and lichens ( <i>Verrucaria</i> spp.) Wetland: <i>Mentha aquatica</i> , <i>Phalaris arundacea</i> Riparian trees: <i>Salicaceae</i> are widespread.
Type VI Sandstone, mudstone and hard limestone rivers of Scotland and northern England	Intermediate slope (mean 0.001, max 0.017) and energy, some with flashy flow regimes	Gravel-pebble-cobble calibre bed material with occasional large calibre material (e.g. boulders) and bed rock exposures	Glides and runs with some riffle-pools	Sinuuous, active channels with exposed mid-, point- and marginal gravel bars at low flows, some marginal finer sediment deposits, actively eroding and depositing river banks.	Aquatic: <i>Cladophora glomerata</i> , <i>Fontinalis antipyretica</i> , <i>Sparganium erectum</i> and specialist mosses ( <i>Rhynchostegium riparoides</i> ) and lichens ( <i>Verrucaria</i> spp.) Wetland: <i>Mentha aquatica</i> , <i>Myosotis scorpioides</i> , <i>Phalaris arundacea</i> Riparian trees: <i>Salicaceae</i> are widespread.
Type VII Mesotrophic rivers dominated by gravels, pebbles and cobbles	Steep (mean 0.003, max 0.030), high energy with flashy flow regimes	Underlain by resistant rocks such as hard sandstone and limestone and also shales, supporting predominantly cobble-pebble-gravel bed material with occasional	Fast flowing with predominantly riffle- and step-pools and some bedrock exposure	Sinuuous and dynamic with extensive eroding banks, mid, point and lateral gravel and cobble bars and large width to depth ratios	Wetland: <i>Juncus effusus</i> , <i>Glyceria fluitans</i> , <i>Phalaris arundacea</i> Riparian trees: <i>Salicaceae</i> are widespread.

Community Type	Gradient and energy	Bed rock and bed material	Flow types and bedforms	River channel form	Typical aquatic and wetland plants (found in >75% sites)
		boulders and bedrock exposures			
Type VIII Oligo- mesotrophic rivers	Steep (mean 0.003, max 0.075) high energy with flashy flow regimes	Underlain by resistant rocks such as hard sandstone and limestone and also shales, supporting predominantly boulder-cobble-pebble bed material with significant bedrock exposures	Fast flowing with riffle- and step-pools, and rapids with fast-flowing threads between exposed bedforms, boulders and bedrock exposures	Sinuuous and dynamic with extensive eroding banks, exposed coarse bars and large width to depth ratios	Aquatic: Filamentous green algae, <i>Fontinalis antipyretica</i> and specialist mosses ( <i>Rhynchostegium riparoides</i> ) and lichens ( <i>Verrucaria</i> spp.) Wetland: <i>Filipendula ulmaria</i> , <i>Juncus acutiflorus</i> Riparian trees: <i>Salicaceae</i> are widespread.
Type IX Oligotrophic, low-altitude rivers	High slope (mean 0.003, max 0.150) and energy.	Very mixed bed material with a significant coarse component	Fast flowing with a mixture of riffle-pools, step pools and rapids	Sinuuous, coarse often eroding banks	Wetland: <i>Juncus acutiflorus</i> , <i>Juncus effusus</i> .
Type X Ultra- oligotrophic rivers	High slope (mean 0.008, max 0.150) and energy with flashy flow regimes	Boulder-cobble-pebble and bedrock dominated	Fast flowing with step-pools, rapids, cascades	Coarse, frequently eroding banks, relatively large width to depth ratio	Aquatic: <i>Juncus acutiflorus</i> Wetland: <i>Juncus effusus</i>

# 4. The effects of beavers on plants and animals

## Summary

4.1. The effects of beavers on British plants and animals can be summarized as follows:

### Plants

4.2. Beaver dam construction can lead to the formation of extensive, heterogeneous wetland habitats, increasing substantially the number of species of herbaceous plants in the riparian zone. Beavers feed preferentially on a small number of deciduous woody species and other woody species increase in dominance relative to the preferred food species. Shoot development occurs from the stumps of browsed and felled trees. These rejuvenate riparian forests, increase the number of tree stems and help to stabilise the banks of water bodies. Overall, the impact of beavers on plant diversity seems to be extremely positive, particularly when it is placed in a landscape perspective.

### Invertebrates

4.3. Beaver impoundment significantly changes local invertebrate fauna but the impacts are predominantly positive; increasing invertebrate abundance, species richness and diversity. Although beaver ponds favour lentic species, lengths of side channel induced by these structures and lengths of main channel between them provide extensive habitats for lotic species. As a result, the overall increase in aquatic habitats of all types is likely to support a high diversity of macroinvertebrate groups. Invertebrates are an essential food source for a vast amount of other fauna, thus beaver-created wetlands are likely to provide additional foraging habitat for numerous species of birds, fish, mammals, reptiles and amphibians. Possible negative impacts of beaver impoundments include potential harm to endangered freshwater pearl mussels. Beaver reintroduction schemes should obviously take into account conservation efforts towards this protected species, and there may be a need to ensure that some critical river sections are protected against impoundment to avoid impacts on such rare and threatened lotic species.

### Fish

4.4. The presence of beavers has largely beneficial impacts on fish populations but there are some potentially detrimental impacts. Interactions are highly complex and dependent on many variables including fish species, fish size and age class, seasonality, climatic conditions, dam characteristics and the natural hydrology of sites. Overall, beaver reintroduction is likely to have a positive impact on fish populations creating foraging habitat and refuge for a wide variety of species including those that are considered commercially important. Increased growth rates experienced by some fish in beaver pools, along with a tendency for larger species to replace smaller ones in warm water streams, could provide excellent opportunities for anglers. Nevertheless, beaver dams may restrict fish movement, migration, and prohibit recolonisation under certain climatic conditions, or cause unfavourable shifts in community structure. Many of these problems could initially be avoided by siting reintroduced beaver populations in areas where flow to adjacent water bodies is unlikely to significantly decrease, preventing the likelihood of prohibiting fish passage. Furthermore, the positive impacts of beaver on fish populations are likely to increase with maturity of beaver ponds. Monitoring of fish populations following beaver reintroduction is essential and may prove useful in placating local fisheries and landowners if positive impacts on commercially important species can be demonstrated.

## **Amphibians**

- 4.5. The reintroduction of beaver to England is likely to have a positive impact on native British amphibians by increasing suitable breeding habitat, although in certain parts of the country this could also benefit non-native species such as the American Bullfrog.

## **Reptiles**

- 4.6. British reptiles are terrestrial and will not be particularly affected by the reintroduction of beavers, although grass snakes favour damp areas and are good swimmers so they could benefit from beaver impoundments.

## **Birds**

- 4.7. Beaver ponds provide suitable nesting, foraging, breeding and roosting habitat for multitude of avian species. Bird abundance, production, diversity and species richness is generally much greater at beaver-created wetlands than at non-impounded (non-dammed) sites and very few species decrease in abundance with the presence of beaver. Beaver reintroduction in England is likely to benefit species from the majority of avian families and could provide additional foraging habitat for conservation priority species, such as the osprey.

## **Mammals**

- 4.8. Beaver impoundments attract a large number of mammals, and could provide food and shelter for many native British species, including semi-aquatic mammals such as water voles, otters, and water shrews. Any negative impacts on mammalian fauna are most likely to be an indirect result of beaver activity, via creation of ideal habitat for introduced pest species, such as American mink.
- 4.9. The net result of the presence of beaver is likely to be positive with a substantially higher level of biodiversity.

## **Introduction**

- 4.10. Beaver construction has far-reaching effects on the ecological as well as the hydrogeomorphological characteristics of streams, reflecting the new and modified hydrological, hydraulic and sediment habitats created by beaver engineering. In addition beaver foraging has widespread direct effects on plant species and animal communities.

## **Plants**

- 4.11. A study by DeGraaf & Yamasaki (2003) noted the importance of Canadian beaver in forest disturbance and regeneration in the north-eastern United States, where beavers remain one of only two major natural disturbances (the second is wind) following marked declines in the impacts of fire, flooding and Native American agriculture. Wright *et al.* (2002) noted that ecosystem engineering by beavers in the central Adirondacks, New York, USA, leads to the formation of extensive, heterogeneous wetland habitats, increasing the number of species of herbaceous plants in the riparian zone by over 33%. This landscape-scale increase in species richness reflects the presence of species that require at least one beaver-engineered habitat at some stage in their life cycle. In a further study, Wright *et al.* (2003) attempted to separate the influences on high species richness in beaver wetlands between landscape-scale dispersal factors and local scale hydrological factors. They found little evidence of significant dispersal limitation. Variability in water table depth and years since beaver abandonment appeared to be the main, essentially local, controls on species richness. This suggests that local beaver engineering and browsing/population pressures are the main influences on plant community composition and structure and thus species richness and diversity at local to landscape scales.
- 4.12. The food preferences of beaver were reviewed in Chapter 2.2. Selective browsing on vegetation inevitably impacts on the extent and age structure of certain species (e.g. O'Connell *et al.* 2008) as well as having broader impacts on plant community structure. Donkor & Fryxell (1999, 2000) working in Ontario, Canada, noted that, because beavers feed preferentially on a small number of deciduous woody species, other woody species, especially

conifers, increase in dominance relative to deciduous species. However, the canopy gaps that had been created by beaver activity facilitate the regeneration of stems of both preferred and non-preferred species. Donkor and Fryxell found that plant species richness and stem and basal area diversity peaked at intermediate distances of about 25 m from beaver ponds and that pronounced soil moisture gradients around the ponds supported notable patterns in plant diversity, which changed following beaver pond abandonment as a result of recruitment patterns of preferred and non-preferred species.

- 4.13. Several studies have focused on the fate of specific beaver-browsed species. For example, Kindschy (1985) compared the growth performance of red willows *Salix lasiandra* that were affected and unaffected by beaver browsing in Oregon and found that those used by beaver were able to maintain high growth rates and increased their basal diameter at a similar rate to unused trees. Even prolonged heavy utilization by beaver did not appear to be responsible for deterioration or loss of this species. King *et al.* (1998) assessed beaver damage on bald cypress *Taxodium distichum* in a wetland system on the Texas-Louisiana border and concluded that despite intensive use of the species by beavers, tree recruitment was not heavily affected and so herbivore damage appeared to be having a minimal effect on the forest. Parker *et al.* (2007) working in Georgia, investigated beaver herbivory of aquatic plants, demonstrating that it reduced aquatic plant biomass by 60%, plant litter by 75%, and significantly affected plant species composition. A preferred plant, lizard's tail *Saururus cernuus*, was reduced to less than 5% of plant biomass in beaver grazed areas whilst being greater than 50% of plant biomass in beaver exclusions. Beaver herbivory also had the beneficial effect of reducing the abundance of an invasive aquatic plant (*Myriophyllum aquaticum*) by almost 90%. In relation to herbivory by *C. fiber*, Fustec *et al.* (2001) noted that shoot development was stimulated from the stumps of browsed and felled trees, which rejuvenated riparian forests, increased the number of tree stems and helped to stabilize the banks of water bodies. Fustec *et al.* suggested that this woody plant morphogenesis may have consequences for the helophyte communities used as food or habitat by other aquatic species.

## Animals

- 4.14. A recent review by Rosell *et al.* (2005) gives a detailed assessment of the impacts of beaver on aquatic and terrestrial invertebrates; fish; amphibians; reptiles; birds; semi-aquatic and terrestrial mammals. As a result, here we provide a brief, updated summary of the effects of beaver on fauna rather than attempting to develop a detailed review from the broader literature. We also mention potential effects on British species where appropriate.

## Invertebrates

- 4.15. Beaver are known to have a significant impact on aquatic invertebrate community structure through direct (impoundment) and indirect (changes in water chemistry, temperature and vegetative growth) modifications of the surrounding habitat (Margolis *et al.* 2001). Creation of ponds from riffle or glide habitat will generally promote a shift from lotic species to lentic species (Rosell *et al.* 2005). However, dams themselves provide good habitat for species that require fast-flowing water and therefore may be crucial in maintaining populations of lotic species, in low-gradient, slow-moving streams (Clifford *et al.* 1993).
- 4.16. In relation to aquatic and water marginal fauna, Rolauffs *et al.* (2001) summarise the impacts of both accumulations of large wood and the construction of beaver dams on macroinvertebrates in Central European mountain streams in comparison with free-flowing sections (Table 4.1.). This illustrates an overall increase in macroinvertebrate numbers and species richness in response to beaver construction, with only a few macroinvertebrate groups showing a negative impact. Median emergence density of invertebrates was significantly higher on the dams than in the beaver pools or free-flowing streams respectively.
- 4.17. Many authors have recorded an overall increase in invertebrate abundance in beaver impoundments compared to un-impounded water bodies (France 1997, Longcore *et al.* 2006, Nummi & Hahlota 2008). However in some cases, increased abundance may be linked to decreased species richness and decreased diversity (e.g. Smith *et al.* 1991). Anderson &

Rosemond (2007) examined the impact of North American beaver on aquatic macroinvertebrate community structure, outside of its native range in southern Chile. These authors found that, although overall invertebrate abundance, biomass and secondary productivity were greatly increased in beaver ponds, species richness and diversity were significantly decreased. Only half of the functional feeding groups existing in unimpacted sites were present in beaver ponds, yet macroinvertebrate predators increased in diversity and biomass. This shift in community structure was attributed to increased retention of organic matter, which provided an increase in food availability in an otherwise nutrient poor system. Nevertheless, it is notable that whilst sites downstream of beaver impoundments suffered some alterations to their community structure, macroinvertebrate assemblages were generally more similar to those at natural forested sites than those in beaver ponds.

- 4.18. Loss of diversity was not experienced amongst beaver impoundments in the Swedish streams studied by Sjöberg (1999 in Müller-Schwarze & Sun 2003). Comparable slow-flowing water bodies housed species from 18 different invertebrate families, whilst beaver ponds contained invertebrates from 24 families. Longcore *et al.* (2006) compared invertebrate community composition between three beaver pools and seven deep, glacial type wetland areas in southeastern Maine. Beaver ponds were found to have significantly increased invertebrate abundance at the Class, Order and Family levels. This significantly affected pond usage preference by birds (see Chapter 4.2.2.5). Further evidence for an increase in biodiversity comes from Harthun (in Bräuer 2006) who found that the number of dragonfly species (Odonata) rose from 3 to 17 within 10 years of reintroducing beavers to the Spesshart Mountains in Germany. The number of snails and mussels species (Gastropoda and Bivalvia) doubled and the average number of caddis flies *Trichoptera* species increased from 3.5 to 16.5.
- 4.19. Wallace *et al.* (1995) recorded a dramatic shift in the community structure of aquatic invertebrates when logs were experimentally added to three cobble riffle sites in North Carolina. Changes in stream depth, velocity and silting rates affected the abundance and biomass of most functional groups; filterers and scrapers decreased whilst collectors and predators increased. The total shredder biomass was unaffected but biomass of different Orders of shredder changed (trichopterans and dipterans increased but plecopteran shredders decreased). Other authors have also reported a general switch in the dominant feeding groups from filterers and shredders to predators and collectors following beaver impoundment (McDowell & Naiman 1986, Smith *et al.* 1991, Clifford *et al.* 1993).
- 4.20. Butts (2001) looked at the occurrence of anthropophilic mosquitoes near three beaver ponds in New York State, over a thirty-year period. Although only one site had been sampled prior to impoundment by beaver, the research indicated that beaver presence may help to reduce the occurrence of permanent water mosquitoes because none of the beaver ponds supported substantial populations of these species. Previously, the sampled site has contained large populations of *Aedes stimulans* and *Aedes punctor* as well as lesser numbers of other typical Northern *Aedes* species.
- 4.21. In the U.S., beaver dams present a significant threat to the conservation of the Louisiana pearlshell mussel *Margaritifera hembeli* (Rosell *et al.* 2005). Like other members of this genus, the mussel requires clean, fast-flowing water and is likely to be killed by the changing flow and siltation caused by beaver dam construction. Freshwater mussel larvae, known as glochida, are obligate parasites of fish. Therefore, it has been suggested that erection of dams may interrupt the life-cycle of mussels by forming obstructive barriers to their migrating hosts.
- 4.22. There are three species of freshwater mussel of particular conservation concern in the UK. The depressed river mussel *Pseudanodonta complanata* and the freshwater pea mussel *Pisidium tenuilineatum* reside in slow-flowing lowland rivers and canals, whereas the freshwater pearl mussel *Margaritifera margaritifera* requires clean, fast-flowing water like its North American relative. Depressed river mussels are considered seriously threatened throughout their range in Europe and the UK currently supports one of the healthiest populations. Pea mussels appear as 'rare' on the GB Red List (UK Biodiversity Action Plan). Whilst it is difficult to accurately predict the impact that beaver habitat modification may have on these two species, it is postulated that an increase in lentic habitat may be beneficial. Conversely, the potential effects of beaver on freshwater pearl mussels are likely to be

analogous to that experienced by the Louisiana pearlshell mussel. *M. margaritifera* is listed as Endangered on the IUCN Invertebrate Red List (IUCN 1996). It is protected under Schedule 5 of the UK Wildlife and Countryside Act (1981), and is also listed on annexes II and V of the EU Habitats Directive and Appendix III of the Bern Convention. Present data indicate that there is only one functional population of this species existing in England (Cosgrove *et al.* 2000) and therefore beaver reintroduction is unlikely to further contribute to current population decline. Nevertheless, some critical river sections may require protection against impoundment to avoid impacts on such rare and threatened lotic species.

- 4.23. Beavers alter woodland structure by preferentially selecting and felling specific tree species. Consequentially, they may have an indirect impact on some terrestrial invertebrate communities. McNeel (1964) found that white pine weevils *Pissodes strobe* were able to colonise and attack white pine trees *Pinus strobes* that had previously been protected by shading, following beaver felling of surrounding aspen trees. Beaver cutting of cottonwood produces high levels of phenolic glycosides in the regrowth. Leaf beetles *Chrysomela confluens* are attracted to these chemicals, which enhance their development (Martinsen *et al.* 1998). Terrestrial invertebrates that lay their eggs in decaying wood can also benefit from beaver activity. Fruit flies, *Drosophila viridis*, are only able to utilise rotting bark of specific tree species and the abundance of these trees at beaver sites has been linked to increased fly populations (Spieth 1979). In England, an abundance of decaying wood is likely to benefit species such as the European stag beetle *Lucanus cervas*, which has slow-developing larvae that live in tree stumps and felled wood. This species is listed on Annex II of the EC Habitats Directive and is included in the UK Biodiversity Action Plan.

Table 4.1. Differences in macroinvertebrate community composition between reaches affected by wood jams or beaver dams in comparison with free-flowing reaches in Central Europe mountain streams (based on Hering *et al.* 2001).

Property	Reaches with wood jams	Reaches with beaver dams
Species number	+	++
Macroinvertebrate density	+	+
Grazers	0/+	-/0
Filter feeders (active)	0	+
Filter feeders (passive)	+	+
Collectors	0	+
Shredders	0/+	0/+
Predators	0/+	+
Xylophagous species	+	+
Lotic species	0	+
Lentic species	0	+
Litoral preferring species	0	+
Xylal preferring species	+	+
Lithal preferring species	+	+
Akal preferring species	0	-
Psammal/Pelal preferring species	0	+
Phytral preferring species	0	+
Mollusca	0	+
Amphipoda	+	0
Ephemeroptera	0	+
Odonata	0	+

Plecoptera	0	-/0
Trichoptera	0/+	-/+
Diptera	0/+	+
Pisces	0/+	+

In comparison with free flowing reaches, - = less, 0 = no difference, + = more, ++ = considerably more.

## Fish

- 4.24. Rosell *et al.* (2005) review in detail the literature on the impacts of beaver activity on fish. Table 4.2 provides a brief outline of the main impacts and summarises the effects on individual species.
- 4.25. Habitat modification and changes in aquatic invertebrate fauna, which are associated with beaver presence, can have significant impacts on fish populations. North American studies reported increased body size in brown trout *Salmo trutta* and other salmonids inhabiting beaver ponds (Murphy *et al.* 1989, Hagglund & Sjoberg 1999), presumably a result of increase in food availability. Sigourney *et al.* (2006) found that two-year old Atlantic salmon *Salmo salar* inhabiting beaver ponds experienced increased growth rates and faster maturation of males than salmon found upstream or downstream of the pond. Beaver pond fish also maintained condition, over the course of the summer, better than conspecifics.
- 4.26. Environmental changes induced by beaver activity have been shown to positively impact on the abundance of some species whilst decreasing the abundance of others (see Table 4.2.). Mitchell & Cunjak (2007) found that community composition upstream of dams previously impenetrable to Atlantic salmon *Salmo salar* changed when dams were made semipermeable to this otherwise dominant species. For a variety of piscine species, beaver ponds can provide important seasonal habitat, refuge from low-flow conditions, and act as a source for recolonisation for adjacent streams (Rosell *et al.* 2005). Schlosser (1995) showed that North American beaver ponds could act as a reproductive “source” population for species such as creek chub *Semotilus atromaculatus*, which then disperse into adjacent streams (acting as “sink” populations) under high density conditions. Beaver ponds have been shown to provide important habitat for adult salmonids during winter months (Cunjak 1996) and provide refuge during periods of drought (Duncan 1984). Conversely, small, shallow beaver pools can actually reduce suitable habitat and result in impoverished fish communities containing individuals of smaller body size than those of adjacent lake assemblages (Keast & Fox 1990). Some authors suggest that a general community shift from lotic to lentic piscine species, following beaver colonisation, could benefit anglers because in warmer water bodies there may be a tendency for smaller species such as cyprinids to become replaced by larger bodied fish, such as centrarchids<sup>8</sup> and esocids<sup>9</sup> (Collen & Gibson 2001).
- 4.27. Beaver dams affect silt content of the surrounding waters by reducing flow rates. Lower flow rates are generally associated with lower silt loads thus generally benefiting commercially important species such as salmonids, which require clean gravel for spawning. However silt deposition can increase both within beaver ponds (Rasmussen 1941) and downstream of dams (Knudsen 1962). Thus beaver activity can have both positive and negative impacts on the reproductive success of these species. Silt accumulation resulting from beaver dams was partially responsible for the decline of golden trout *Salmo irideus* in the Californian Sierras (Müller-Schwarze & Sun 2003).
- 4.28. For trout to reproduce successfully, water temperatures must remain above a lower critical threshold, but not significantly exceed optimal spawning temperature. Thus, increases in water temperature associated with beaver pools may increase or decrease trout reproductive success (Rasmussen 1941, Huey & Wolfrum 1956, Cook 1940, Adams 1949, Avery 1983). At ponds where temperatures have exceeded optimal salmonid preferred temperatures, trout

<sup>8</sup> Small carnivorous freshwater percid fishes of North America

<sup>9</sup> Fish of the pike family Esocidae



may become displaced by other species such as *cyprinids*, *catostomids*, *percids* or *centrarchids* (Collen & Gibson 2001). Dams may contribute to anoxic conditions in beaver ponds, particularly if ponds ice over during the winter months, and this has been linked to local extinctions of brook trout *Salvelinus fontinalis* in the Boreal Shield lakes of Canada (Bertolo *et al.*, 2008). However, there is much less risk of this occurring in the more temperate British climate.

- 4.29. Research on North American beaver suggests dams may present obstacles to movement, migration and colonisation of streams by some species (see Table 4.2.). Migration is particularly important for anadromous salmonids. Dams are most likely to become obstructive when flow levels are low, therefore autumn migrating species are more likely to encounter passage difficulties than those that migrate in spring (Rosell *et al.* 2005). Other important factors that influence the likelihood of successful passage are characteristics and maintenance state of individual dams, as well as size and species of fish. In England, reintroduced beaver populations would be best sited in areas where flow to adjacent water bodies is unlikely to significantly decrease, in order to reduce the likelihood of beaver dams prohibiting fish passage. Longer term strategies to ameliorate the potential negative impacts of beaver dams on fish migration could include the complete removal of problem dams or management to increase the permeability of dams to important species.
- 4.30. In Europe, the largest area for potential conflict to arise between fisheries and conservation organisations is if beaver are perceived to affect productivity of commercially valuable fish species. However, in a detailed study on a major Norwegian catchment, salmon and sea trout reproduction was largely unaffected by beaver presence (Parker & Ronning 2007). Furthermore, nine of 14 landowners in the area were very positive about having beaver together with salmon and sea trout. The authors concluded from this study that the presence of beaver on similar catchments is likely to have only an insignificant negative impact on the reproduction of sea trout and salmon. Nevertheless, it has been reported that fish, and notably brown trout, were trapped and died in a beaver pond in a drought year in Estonia and dams appeared to prevent the upstream colonization of fish the following year (Tambets *et al.* 2005).
- 4.31. It is important that beaver reintroduction schemes include a monitoring programme to assess the impact of beaver habitat modification on local fish populations because the impacts on individual species may be difficult to predict *a priori*. Current evidence suggests that beaver reintroduction may have many positive effects on commercially valuable fish species and thus monitoring programmes may help to alleviate the concerns of fisheries and landowners about the perceived negative impacts of beaver. Conversely, any detrimental impacts on fish populations may be reversible through dam management or removal.

Table 4.2. The effects of beaver activity on fish species

Species	Change in abundance?	Migration/movements affected by dams?	Obstacle to colonisation ?	Increased body size in beaver ponds?	Seasonal refuge?	References
Atlantic salmon <i>Salmo salar</i>			Potentially			Cunjac & Therrien 1998
Brook char <i>Salvelinus fontinalis</i>	-	Potentially		Yes		Cook 1940, Rupp 1955, Rutherford 1955, Balon & Chadwick 1979
Brook sticklebacks <i>Culaea inconstans</i>	+					France 1997
Brown trout <i>Salmo trutta</i>	-	Potentially		Yes		Cook 1940, Rupp 1955, Hagglund & Sjöberg 1999
Coho <i>Oncorhynchus kisutch</i>			Potentially	Yes	Winter & Summer	Murphy <i>et al.</i> 1989, Nickelson <i>et al.</i> 1992, Leidholt-Bruner <i>et al.</i> 1992
Creek chub <i>Semotilus atromaculatus</i>					Spring	Schlosser 1998
Cutthroat trout <i>Oncorhynchus clarki</i>		Rarely				Grasse 1951, Rasmussen 1941
Dusky shiner <i>Notropis cummingsae</i>	0					Rohde & Arndt 1991
Fathead minnows <i>Pimephales promelas</i>	+					France 1997
Finescale dace <i>Phoxinus neogaeus</i>	+					France 1997
Minnow <i>Phoxinus phoxinus</i>					Spring	Hagglund & Sjöberg 1999
Mudminnows <i>Umbra limi</i>	+					Knudsen 1962
Ninespine stickleback <i>Pungititius pungititius</i>	+					Rupp 1955
Northern redbelly dace <i>Phoxinus eos</i>	+					France 1997
Pike <i>Esox lucius</i>	+	Potentially				Knudsen 1962
Pinewoods darter <i>Etheostoma mariae</i>	-					Rohde & Arndt 1991
Rainbow trout <i>Oncorhynchus mykiss</i>		Rarely				Grasse 1951, Rasmussen 1941, Gard 1961
Sandhills chub <i>Semotilus lumbee</i>	-					Rohde & Arndt 1991
Slimy sculpins <i>Cottus cognatus</i>	+					France 1997
Sockeye salmon <i>Oncorhynchus nerka</i>			Potentially	Yes	Summer	Murphy <i>et al.</i> 1989
White suckers <i>Catostomus commersoni</i>	+					France 1997
Yellow perch <i>Perca flavescens</i>	+					Balon & Chadwick 1979

+ = increase, - = decrease, 0 = no change

## Amphibians

- 4.32. Several North American studies have investigated the impact of beaver on amphibian abundance and assemblages. Overall, species richness, species diversity and total amphibian abundance tend to remain unaffected by the presence of beaver (Metts *et al.* 2001, Russell *et al.* 1999, Suzuki and McComb 2004). However, individual species abundance can vary between beaver occupied and unoccupied sites. Metts *et al.* (2001) found an increase in the capture rates of anurans (frogs and toads) at beaver impoundments and lower capture rates of salamander (Table 4.3, including reptiles, see Chapter 4.2.2.4). The presence or absence of certain species at beaver ponds (including reptiles; see below) was attributed to individual species preference for lentic or lotic habitat, cover provided by stream or pond margins and the presence/absence of predatory fish. Russell *et al.* (1999) also recorded a preference of anuran species for beaver occupied sites, noting that several species were either solely or predominantly captured at beaver pools.
- 4.33. Beaver habitat modification results in ponds with shallow shorelines, which provide ideal habitat for breeding anurans and newts (Cunningham *et al.* 2006, France 1997). Studies in Alberta, Canada suggest that the presence of beaver increased breeding habitat for wood frogs *Rana sylvatica*, boreal chorus frogs *Pseudacris maculate* and western toads *Bufo boreas* (Stevens *et al.* 2007). Calling anuran males were only found at beaver impounded streams and trapping results indicated that juvenile recruitment was higher for these species in beaver inhabited areas.
- 4.34. Suitable breeding habitat for anurans is likely to increase as beaver ponds mature. Stevens *et al.* (2006) compared old (>25 years) and newly (<10 years) established beaver ponds and found that density of calling male wood frogs was positively related to pond age. Larval survival rates were not significantly different between age classes of pond. However, larval development and growth rates were enhanced in the older ponds. Older ponds were characterised by reduced riparian canopy, increased abundance of submerged vegetation, elevated water temperatures and higher concentrations of dissolved oxygen, making conditions favourable for larval development. Canopy cover was probably the primary factor that influenced pond selection by breeding males.
- 4.35. Skelly & Freidenburg (2000) demonstrated additional effects of beaver presence on amphibian larval development. Wood frog larvae from beaver ponds evolved higher critical thermal maxima than conspecifics from shaded wetlands. As a result, hatching rates of beaver pond larvae were reduced when placed in a shaded garden setting. The rapid (<36 years) evolutionary divergence between the two populations was presumed to be a response to the increased average temperatures characteristic of beaver ponds. These authors recorded a 2 °C increase in mean water temperature and a 15 °C increase in maximal water temperature in beaver ponds compared to shaded wetland areas.
- 4.36. There are seven species of amphibian native to the UK; three species of newt (*Triturus* sp.), common and natterjack toad (*Bufo* sp.), pool frog *Pelophylax lessonae* and common frog *Rana temporaria*. Two are listed as endangered – natterjack *Bufo calamita* and great crested newt *Triturus cristatus*. Following reintroduction schemes, localised populations of pool frog now exist in several sites in Norfolk and the species is now listed on schedule 2 of the Conservation (Natural Habitats &c) Regulations 1994. One non-native species of newt and seven non-native anurans have become established in localised populations but are not currently a serious threat. Two species pose significant problems to native fauna American bullfrog *Rana catesbeiana* and Italian crested newt *Triturus carnifex*. Current evidence indicates that the reintroduction of beaver to England is likely to have positive impact on native British amphibians, primarily by increasing suitable breeding habitat, although in certain parts of the country this could also benefit non-native, problematic species such as the American bullfrog.

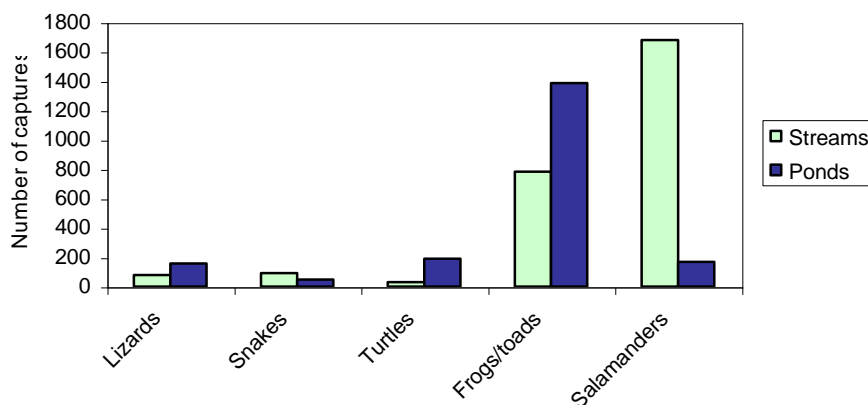
## Reptiles

- 4.37. North American studies of herpetological fauna have shown that reptile diversity, abundance and species richness tend to differ between beaver-active and non-active sites. Metts *et al.*

(2001) found increased species diversity at beaver ponds in South Carolina, compared to unimpounded sites. Beaver occupied sites had a higher abundance of turtles and lizards. The details of their results are that three lizards, one snake and three turtles were significantly more abundant at beaver ponds whereas two snakes were significantly more abundant along the banks of unimpounded streams (Figure 4.1.). Metts *et al.* (2001) indicated that the greater abundance and diversity of reptiles at beaver ponds was probably related to the association of many species of lizards and snakes with early successional habitats. Over time, as beavers consume trees near the water for dam construction and foraging, they move farther away from the edge of permanent water. This increases, through time, the amount of early successional habitat adjacent to beaver ponds. Russell *et al.* (1999) found that reptile abundance and richness were significantly greater at old than new beaver ponds. Exceptions from Metts *et al.*'s (2001) study were two small species of woodland snake that preferred moist and/or cool microclimates.

- 4.38. There are three species of snake (smooth snake *Coronella austriaca*, grass snake *Natrix natrix*, adder *Vipera berus*) and three species of lizard (sand lizard *Lacerta agilis*, common lizard *L vivipara*, slow worm *Anguis fragilis*) native to the UK: two are endangered, the smooth snake and the sand lizard. All are terrestrial and thus unlikely to be dramatically affected one way or the other by reintroduction of beaver, although grass snakes are very good swimmers and feed mainly on toads, frogs, newts and small fish, so they could benefit from beaver impoundments. North American red-eared terrapins *Trachemys scripta* have been introduced to the wild in some areas and cause minor conservational problems by preying on native wildlife. However, their distribution is highly localised (animals are generally released by irresponsible pet owners into ponds and lakes within close proximity to urban areas), and their current inability to reproduce in cold British waters stop them from becoming a serious threat.

Figure 4.1. Number of individuals of herpetofaunal taxa captured from unimpounded streams and beaver ponds in the Clemson University Experimental Forest, South Carolina Piedmont, 1998-1999 (from Metts *et al.* 2001).



## Birds

- 4.39. The presence of beavers has been shown to impact on water birds and other avian species in a number of ways. Here we outline the consequences of beaver habitat modification on major bird groups, whilst demonstrable effects on individual species are summarised in Table 4.3.
- 4.40. Beaver habitat modification can significantly increase the abundance of invertebrates, amphibians and fish (see previous sections). This will inevitably enhance foraging opportunities for insectivorous, omnivorous and piscivorous birds. Grover & Baldassarre (1995) studied avian species richness at 70 wetland sites in New York State. These authors found significantly more species present at beaver active sites than at comparably-sized inactive or potential sites. Medin (1990) reported higher density, biomass, species richness and diversity amongst birds visiting beaver versus non beaver ponds. Brown *et al.* (1996) concluded that the shallow, warm, vegetation rich waters surrounding beaver pools provide

excellent foraging habitats for ducks, which are able to take advantage of an abundant supply of invertebrates, seeds and plant matter. However, successful duck habitats generally had a pond surface area greater than 1000 m<sup>2</sup>.

- 4.41. Longcore *et al.* (2006) compared avian usage of beaver-created wetlands and glacial wetlands. Of the 21 species recorded, 13 used beaver ponds significantly more than glacial habitats, four species preferentially used glacial habitats and four species showed no significant usage preference for either habitat. When species were pooled into functional foraging groups, beaver-created wetlands were used significantly more than glacial habitats by both the two omnivorous and the two insectivorous groups. This was almost certainly due to the increased abundance of invertebrates present in the beaver impounded areas. Piscivores were the only foraging group that collectively showed no significant preference for either habitat. Individually, only some piscivorous species showed significant preference for either glacial wetland or beaver-created habitat and this was probably related to water pH, water transparency and species fishing method. Species feeding in the littoral zone and 'surface plungers', such as herons, osprey and kingfishers, are less affected by decreases in water transparency than 'pursuit divers' such as loons and mergansers.
- 4.42. Beaver ponds provide ideal habitat for brood rearing waterfowl (Table 4.4, Renouf 1972; Nummi & Poysa 1997; McKinstry *et al.* 2001; Longcore *et al.* 2006). Increased invertebrate abundance provides essential nutrients for breeding birds and their broods. Some duck species (e.g. wood duck *Aix sponsa*) switch from a diet of predominantly plant matter to an invertebrate dominated intake during egg laying and egg production (Hartke & Hepp 2004). Thus, beaver ponds can prove particularly important in otherwise resource limited habitats (Nummi *et al.* 2005). Furthermore, beaver-mediated modification of shoreline vegetation provides nesting and roosting habitat, brood refuge from predators as well as foraging opportunities (Nummi & Hahtola 2008).
- 4.43. In a twelve-year study in Finland, the presence of beavers in boreal ponds resulted in increased brood density and lower brood mortality in teal *Anas crecca*. This was linked to increased invertebrate abundance in beaver ponds and also modification of habitat by decreasing shore depth. Shallower shores were more favourable to ducklings because they provide easy access in and out of ponds, shallow benthic foraging areas and protection from mammalian and avian predators (by providing foraging areas not immediately adjacent to shoreline) (Nummi & Hahtola 2008). In the North American wetlands studied by Longcore *et al.* (2006), brood abundance was higher on beaver ponds than glacial wetland for 9/10 species. Only American goldeneye *Bucephala clangula americana* preferred to raise broods in glacial habitat. Renouf (1972) found that beaver-active ponds contained an average of 1.85 broods ha<sup>-1</sup> whereas inactive ponds contained 0.27 broods ha<sup>-1</sup>. However, in some cases positive effects on brood success may be short-lived. Nummi (1984 in Rossell *et al.* 2005) found that brood production of ducks declined in beaver ponds greater than five years of age, corresponding with a decrease in invertebrate abundance.
- 4.44. Beavers create and continually "manage" riparian habitat and the resulting early-successional vegetation is considered beneficial to many species of passerine (Longcore *et al.* 2007). DeGraaf & Yamasaki (2003) point out that many "disturbance-dependent" avian species are declining throughout the northeastern United States because natural disturbance, historically caused by fire, wind and flooding has been disrupted by human interference (e.g. building of settlements, extirpation of beaver and plantations of wind resistant tree species). Beaver maintain early-successional vegetation creating habitat for many specialist species which are unable to survive in mature woodland stands.
- 4.45. Beaver ponds aren't just advantageous to aquatic birds, raptors may use them for hunting (Carr 1940). Ospreys *Pandion haliaetus* may nest in trees adjacent to ponds (Grover & Baldassarre 1995) and use the littoral zones to hunt (Longcore *et al.* 2006). Standing dead trees can provide ideal raptor perches as well as feeding and nesting sites for woodpeckers (Grover & Baldassarre 1995). Abandoned woodpecker nests are commonly utilised by other species such as tits, flycatchers, owls, and kestrels (Carr 1940; Hilfiker 1991). Reese & Hair (1976) considered beaver ponds to be relatively more valuable to non-waterfowl species after finding the most abundant species present at four beaver-impounded sites was red-winged blackbird *Agelaius phoeniceus*. In total these authors recorded 92 bird species from 31

families across the seasons, concluding that beaver ponds were continually attractive sites to a vast number of non-aquatic avian species.

- 4.46. Edwards & Otis (1999) investigated microhabitat variables important in determining bird group abundance and species richness at six beaver ponds in South Carolina. Usage of ponds by bird groups varied throughout the seasons and this was the most important predictor of abundance of the resident and short distance migrant group. Woodpecker abundance was related to total pond area, whereas vegetation interspersion and plant richness best predicted waterfowl and waterbird abundance respectively. Neotropical bird abundance was best explained by plant richness.

Table 4.3. The effects of beaver activity on bird species

Species	Abundance/ preference	Nesting	Brood Rearing	Foraging	References
American bittern	+				Longcore <i>et al.</i> 2006
American black duck	+		++		Longcore <i>et al.</i> 2006
American woodcock <i>Scolopax minor</i>		+		+	Carr 1940
Belted kingfisher	0				Longcore <i>et al.</i> 2006
Belted kingfisher <i>Ceryle alcyon</i>	+				Grover & Baldassarre 1995
Bitterns		+		+	Salyer 1935; Gibbs <i>et al.</i> 1991
Black ducks <i>Anas rubripes</i>			+		Renouf 1972
Canada geese <i>Branta canadensis</i>	+	+			McCall <i>et al.</i> 1996; Hilfiker, 1991
Chimney swift	-				Longcore <i>et al.</i> 2006
Common goldeneye (American?)	-		-		Longcore <i>et al.</i> 2006
Common loon	-				Longcore <i>et al.</i> 2006
Common merganser	-		+		Longcore <i>et al.</i> 2006
Common nighthawk	0/+				Longcore <i>et al.</i> 2006
Common snipe	+				Longcore <i>et al.</i> 2006
Cormorant <i>Phalacrocorax carbo</i>		+		+	Salyer 1935; Gibbs <i>et al.</i> 1991
Double-crested Cormorant	+				Longcore <i>et al.</i> 2006
Duck sp.	+	+	+	+	Brown <i>et al.</i> 1996; McKinstry <i>et al.</i> 2001
Eastern kingbird	+				Longcore <i>et al.</i> 2006
Egrets		+		+	Salyer 1935; Gibbs <i>et al.</i> 1991
Goldeneye <i>Bucephala clangula</i>		+			Nummi & Hahtola 2008
Great blue heron <i>Ardea herodias</i>	+				Longcore <i>et al.</i> 2006; Grover & Baldassarre 1995
Great blue herons	+	+		+	Foster <i>et al.</i> 2002
Grebes		+		+	Salyer 1935; Gibbs <i>et al.</i> 1991
Green-backed heron <i>Butorides striatus</i>	+				Grover & Baldassarre 1995
Blue-winged teal	+		+		Longcore <i>et al.</i> 2006
Green-winged teal <i>Anas carolinensis</i>			+		Renouf 1972; Longcore <i>et al.</i> 2006
Grey partridge <i>Perdix perdix</i>		+			Carr 1940
Grouse spp.		+		+	Carr 1940
Hawk spp.				+	Carr 1940
Herons <i>Ardea</i> spp.		+		+	Salyer 1935; Gibbs <i>et al.</i> 1991
Hooded mergansers <i>Lophodytes cucullatus</i>	+		++		McCall <i>et al.</i> 1996; Renouf, 1972; Grover & Baldassarre 1995; Longcore <i>et al.</i> 2006
Kingfisher <i>Alcedo atthys</i>		+		+	Salyer 1935; Gibbs <i>et al.</i> , 1991
Mallard <i>Anas platyrhynchos</i>	-/+	+	+		Nummi & Hahtola 2008; Nummi & Poysa 1997; McCall

Species	Abundance/ preference	Nesting	Brood Rearing	Foraging	References
					<i>et al.</i> 1996; Longcore <i>et al.</i> 2006
Mergansers		+		+	Salyer 1935; Gibbs <i>et al.</i> 1991
Osprey	0				Longcore <i>et al.</i> 2006
Osprey <i>Pandion haliaetus</i>		+		+	Nolet <i>et al.</i> 1997
Owl spp.				+	Carr 1940
Pied-billed grebe	+		+		Longcore <i>et al.</i> 2006
Rails <i>Rallus</i> spp.		+		+	Gibbs <i>et al.</i> 1991
Red-winged blackbirds <i>Agelaius phoeniceus</i>	+				Reese & Hair 1976
Ring-necked duck	+		++		Longcore <i>et al.</i> 2006
Shag <i>Phalacrocorax aristotelis</i>		+		+	Salyer 1935; Gibbs <i>et al.</i> 1991
Sora	+		+		Longcore <i>et al.</i> 2006
Spotted sandpiper	0				Longcore <i>et al.</i> 2006
Swan spp.		+			Hilfiker 1991
Teal <i>Anas crecca</i>	+	+			Nummi & Hahtola 2008; Nummi & Poysa 1997
Tree swallow	+				Longcore <i>et al.</i> 2006
Trumpeter swans <i>Cygnus</i> spp.	+				McKelvey <i>et al.</i> 1983
Waterfowl sp.			+		Dieter & McCabe 1989; Nummi 1992; McKinstry <i>et al.</i> 2001
White-tailed eagles <i>Haliaeetus albicilla</i>				+	Nolet <i>et al.</i> 1997
Wigeon <i>Anas penelope</i>	0				Nummi & Poysa 1997
Wild turkey <i>Meleagris gallopavo</i>		+		+	Carr, 1940
Wood ducks <i>Aix sponsa</i>	-/+		++		Hartke & Hepp 2004; Longcore <i>et al.</i> 2006
Woodpecker spp.	+	+		+	Lochmiller 1979; Grover & Baldassarre 1995

+ = positive effect, - = negative effect, 0 = no effect



Table 4.4. The effects of beaver activity on waterfowl

Species	Abundance	Nesting	Brood Rearing	Roosting	Refuge	Foraging	References
Mallard <i>Anas platyrhynchos</i>	-	+					Nummi & Hahtola 2008, Nummi & Poysa 1997
Teal <i>Anas crecca</i>	+	+					Nummi & Hahtola 2008, Nummi & Poysa 1997
Goldeneye <i>Bucephala clangula</i>		+					Nummi & Hahtola 2008
Wigeon <i>Anas penelope</i>	0						Nummi & Poysa 1997
Duck sp.	+	+	+			+	Brown et al. 1996, McKinstry et al. 2001
Waterfowl sp.			+	+			Dieter & McCabe 1989, Nummi 1992

+ = positive effect, - = negative effect, 0 = no effect

## Mammals

- 4.47. Like birds, mammals are likely to be attracted to beaver ponds because of the abundance of prey, along with suitable refuge and breeding sites. In Britain, semi-aquatic mammals such as water voles *Arvicola terrestris*, otters *Lutra lutra*, water shrews *Neomys fodiens* and the introduced North American mink *Mustela vison* may benefit from beaver reintroduction. Otter and mink are known to use both abandoned and active beaver lodges, holes and bank dens as shelter and natal dens (Grasse 1951; Tyurnin 1984; LeBlanc et al. 2007). Water voles use abandoned lodges and burrows (Danilov 1995).
- 4.48. In North America, river otter *Lutra canadensis* territories are frequently associated with beaver ponds (Tyurnin 1984; Reid et al. 1994a; LeBlanc et al. 2007) and otter latrines are recurrently found in the vicinity of bank dens and lodges (Newman & Griffin 1994; Reid et al. 1994a). As well as benefiting from ready-made shelters, otters are able to exploit the abundance of fish, invertebrates, small mammals and amphibians common to beaver impoundments (Rosell et al. 2005). Occasionally otters eat beavers, but these cases are relatively rare (Reid et al. 1994b).
- 4.49. In winter, otters utilise ice holes made by beavers and Reid et al. (1988) found that otters dig passages through dams so gaining under-ice access to adjacent water bodies. This causes water loss from beaver pools, which may concentrate prey under the ice. Benefits to otters seem to be dependent on the activity of beaver, not just beaver-created habitat as LeBlanc et al. (2007) found otter activity was positively correlated with beaver presence. The positive impacts of beaver on otter are so great that Rosell et al. (2005) suggest that the re-establishment of beaver has played a crucial role in preventing the extirpation of otter in some areas of North America.
- 4.50. One possible negative impact of beaver reintroduction on native British fauna is that American mink *Mustela vison* benefit from beaver presence in much the same way that otter do. American mink are already a substantive problem in the UK and have been blamed for the decline of native species, such as the water vole (see Chapter 5). Sidorovich (1992) found that mink density in Belarus was positively correlated with number of beaver sites. Like otter, mink may occasionally kill young beaver (Recker, 1997) although in some areas the two species seem to coexist without conflict (Brzezinski & Zurowski 1992). Nevertheless, recent evidence suggests that otter are dominant competitors over mink. Niche overlap between the two species is high but otter are larger and better adapted to underwater hunting, thus interspecific

competition can force prey switching in mink (Bonesi *et al.* 2004). Furthermore, presence of European otter was shown to significantly reduce mink density in otter release experiments in the Upper Thames catchment (Bonesi & MacDonald 2004).

- 4.51. A lot of research has focused on the interactions between beaver and muskrat *Ondatra zibethicus* (Grasse 1951; Knudsen 1962; McKinstry *et al.* 1997), which cohabit in lodges. However, muskrat are not currently present in the UK and thus interactions between the two species are largely irrelevant to British beaver reintroduction proposals. Nevertheless in North America and Europe muskrat are potential feeding competitors of beaver, often stealing winter caches (Tyurnin 1984). Presumably the absence of this species in Britain may benefit beaver populations to a minor extent.
- 4.52. Presence of beaver can also have positive ecological consequences for terrestrial mammals. Beaver coppicing of riparian vegetation and the subsequent regrowth provides food and shelter for many herbivorous mammals including deer, moose, bear, rabbits and hares (Rosell *et al.* 2005). Wild boar *Sus scrofa* frequent beaver ponds to forage and wallow, although seem to show a preference for partially dried-out sites (Nitsche, 1997). At high densities, boar can inhibit nocturnal beaver movement on land. Dead standing wood created by beaver activity (particularly trees with abandoned woodpecker nests) may provide shelter for small mammals, bats, squirrels and mustelids (Hilfiker 1991). Bats are also likely to benefit from an increase in abundance of invertebrates, commonly associated with beaver pools. Pine martens *Martes martes* may use abandoned lodges and dead tree cavities as denning and resting sites (Rosell & Hovde 1998), whilst simultaneously benefiting from an abundance of prey items. Badger (*Meles meles*) and red fox *Vulpes vulpes* may also use abandoned lodges during the winter (Rosell *et al.* 2005). In the absence of other large carnivores, red fox are likely to be the only significant predator of beaver in England, although mustelids may occasionally take beaver kits.
- 4.53. Relatively few studies have been conducted into the impact of beavers on small mammal populations, but increased invertebrate abundance may prove beneficial to omnivorous and insectivorous species such as mice and shrews (particularly water shrews). Herbivorous water voles are likely to benefit from an increase in riparian grasses, whilst bank voles *Myodes glareolus* are likely to make use of scrubby vegetative cover and find homes in dead wood and tree stumps. Ulevičius & Janulaitis (2007) trapped small mammals in Lithuania and found that relative abundance of small mammals and number of species was higher in beaver lodges than in non beaver sites. Bank voles were by far the most abundant species in both modified and unmodified sites. Suzuki & McComb (2004) found that captures of microtine voles were consistently higher at beaver-occupied areas than unoccupied reaches.

## Part 2: Beaver reintroduction: sites, sources of animals, the concerns of stakeholders, economics, and management

# 5. The identification of suitable regions for candidate reintroduction sites in England

## Summary

5.1. There is abundant knowledge on the habitat requirements of beavers including how much river habitat would be required to support a beaver family, the most appropriate width, gradient, velocity and depth of the river, the composition and profile of the banks, the vegetation required for food and construction, and appropriate floodplain characteristics. As considered elsewhere in the report, it is evident that many if not most of England's rivers would provide suitable habitats to support beavers. We confirmed this by carrying out a preliminary GIS analysis of beaver habitat preference across England's rivers, and we have shown that there are a wide range of potential release sites. Candidate release sites would need to be explored more fully in a second phase of GIS modelling that incorporates more focused (e.g. River Habitat Survey) and higher resolution (e.g. air photo and airborne scanner) data. In addition, more detailed analysis of candidate release sites may take into account anthropogenic and other criteria, such as their proximity to urban or suburban areas, whether they have SAC or SSSI designations, whether beavers are likely to build dams and whether there may be any consequential chance of flooding. Perhaps from the point of view of a pilot reintroduction study, it would be helpful to know which candidate sites would provide restricted dispersal opportunities, especially in the short term. To further this idea, a second phase should also incorporate habitat suitability information into a population- based model that would combine habitat requirements with known life history parameters to simulate beaver population establishment and growth. These models would predict the spread of beaver from the point of release and provide information about potential human-beaver interactions that could be taken into account in the management plan for the site.

## Habitat requirements for reintroduced beavers

- 5.2. Based on the review of beaver habitats in Chapters 2 and 3; we summarise below the most important features of beaver habitats that should be taken into account in selecting candidate beaver release sites:
- **Minimum length of river or lake shore**  
A 2 km length of river or bank with suitable habitat should be sufficient to support a colony of beavers, where habitat is assessed within 20 m of the water's edge.
  - **Channel / Floodplain Downstream Gradient**  
This is the most important physical factor influencing beaver occupation, partly because it is a key control on whether dam construction is necessary to create appropriate habitat. Slope also dictates river energy (and velocity) and so is closely associated with bank materials and flood plain construction/extent. Research on Canadian beavers clearly demonstrates that slopes  $> 0.15$  are unfavourable for beaver and that slopes  $< 0.06$  (preferably  $< 0.03$ ) are favourable.
  - **Bank profile and materials**  
Since European beavers tend to use bank lodges as den sites, the height of banks and the materials from which they are built are important habitat characteristics. Habitats that contain areas of relatively high banks ( $> 1.5$  m above baseflow water level) built of relatively fine materials (earth / loam / peat) are ideal, although shallower ( $> 0.5$  m) coarser (fine gravel) banks could support beaver. Because of the preference for fine bank materials, rock type is likely to be limiting and certainly hard rock areas are likely to be unattractive to beaver unless there are significant fine alluvial deposits in valley bottoms. Bank slope is sometimes specified within a list of beaver habitat requirements, but if a river meets the bank height and calibre requirements, it will support a variety of bank slopes and so slope is unlikely to be limiting.
  - **Water velocity and depth**

Water depth and velocity are both important but are also interrelated aspects of beaver habitat. Their modification underpins dam building activity. Water depth adjacent to the beaver lodge needs to be sufficient for burrow/lodge entrance to be reliably maintained below water level. A general water depth >1 m should be sufficient, but >2 m is preferable. If sufficiently deep water is present then velocity is likely to be low, at least during periods of baseflow.

- **River width**  
Although river width is often reported as a beaver habitat requirement, it is unlikely to be critical. Rivers with low slopes, deep water and high, fine calibre banks are usually wider than those with steeper slopes, shallower water and low, coarse calibre banks. Thus the correlation between river width and beaver occupation does not really indicate dependency.
- **Floodplain characteristics**  
Floodplain width gives an indication of the degree to which beaver construction of dams and canals could extend their habitat laterally. It could be an informative but not crucial habitat variable to consider. However, the presence of lateral water bodies (side channels including artificial ditches, backwaters, cutoffs and other flood plain ponds) greatly increases the suitability of a river reach for beaver occupation.
- **Vegetation**  
Beaver are vegetarian and depend upon vegetation for food and construction materials. Good herbaceous vegetation provides summer food but tree bark is important in winter. Therefore good beaver habitat supports a mix of herbs and favoured tree species (Salicaceae and Betulaceae) within 20 m of the water's edge. Whilst the ideal is approximately 50% closed tree canopy and the ideal tree/shrub dimensions are diameter at breast height (dbh) < 0.15 m, beaver manipulate the vegetation, felling large trees which resprout with smaller shoots and open up the canopy. Thus the crucial element of river margin vegetation is the presence of a good cover of favoured tree species.

- 5.3. Our consideration of British river types (Chapter 3) indicates that beaver could colonise most British river environments but that lowland, low-gradient rivers (Types I, II and III, Table 3.3) offer the best beaver habitat in relation to the above criteria. We have assumed that we are only considering prime beaver habitats as candidate reintroduction sites, since marginal habitats for beavers tend to be those that require most beaver engineering in the form of dam construction and the felling of large trees which result in most reports of beaver-human conflicts (Halley & Rosell 2002).
- 5.4. To complement our consideration of broad river types (Chapter 3), we have compiled national information that was readily available to us on some of the specific criteria noted above. Thus, we have combined information on topographic slope, the river network, and the extent of broadleaf woodland within 1 km of that network, to provide an initial assessment of the spatial distribution of suitable habitats within England.
- 5.5. Throughout Europe, beavers have recolonised agricultural landscapes and areas with high densities of humans (Müller-Schwarze & Sun 2003). This can lead to human-beaver conflict situations that in turn will increase requirements for ongoing management of beavers by wildlife authorities. With this in mind, we have taken it that candidate release sites should not be near urban or suburban areas, or within intensively managed agricultural landscapes. Thus we have identified areas under such land use and excluded them as suitable habitat areas. However, it is crucial to note that analysis of these readily available national data sets has major limitations:
  - the river network excludes lakes and ponds and also the smallest stream channels.
  - our analysis deals with topographic NOT river valley slope and so will include smaller areas of suitable slope than is actually the case.
  - deciduous woodland does not necessarily contain the riparian tree species favoured by beaver (although it is more likely to do so than coniferous woodland).

- specifying sensitive limits on what is urban, suburban or intensive agricultural activity is highly subjective and difficult given the coarse spatial resolution of the national data employed.
- 5.6. Thus the spatial distributions we have generated are informative at a coarse scale and with clear limitations that could only be remedied in a far more detailed study that would best be carried out in relation to selected candidate sites.

## **A preliminary GIS analysis of habitat suitability within England**

- 5.7. Habitat suitability maps based on the criteria discussed above were generated in a Geographical Information System (GIS). Three sources of data were used: a rasterised UK landcover map, a rasterised digital elevation map, and a vectorised river map (Figure 1). All manipulations were performed in GRASS (Westervelt *et al.* 1990). A woodland map was derived from the land cover map, consisting of just the deciduous woodland category. An inland water map was derived from the land cover map (lakes and reservoirs) and the river map. The inland water map was subjected to a 1 km buffer, and the intersection between this map and the woodland map was the basic habitat map for beaver habitat suitability. A topographical slope map was derived from the digital elevation map, and used to generate a 6% slope map (removing all areas with a slope greater than 6%) and a 3% slope map (removing all areas with a slope greater than 3%). The intersection between the slope maps and the beaver habitat suitability maps were the beaver preference maps.
- 5.8. The beaver preference maps were categorised according to the total length of suitable habitat along rivers in each 5 km square across England. Each of these 5 km squares of the land cover map was first assessed for its constituent agricultural land (arable and horticultural categories combined). Two further filters were applied to the maps because of possible conflicts with humans at release sites: (a) urban and suburban areas were omitted because of potential conflicts with humans or their activities, and (b) areas that contained a substantial amount of agriculture were omitted because of potential damage to crops. The median amount of agricultural land across the whole of England was assessed to be 23.8% of each 5 km square, thus squares were excluded from the beaver preference maps altogether if they contained more than 23.8% agricultural land.
- 5.9. Following this filtering process, the squares most suitable for beaver colonisation were considered to be those with a total of 4 or more kilometres of wooded river, and the least suitable those with between 2 and 3 km of wooded river.
- 5.10. The maps derived from studies that have identified factors favoured or avoided by beavers are shown in Figure 5.2. Only deciduous woodland within 1 km of inland water is considered as suitable, after habitat including urban and suburban areas and steep (> 3% or 6%) topological slope has been removed.
- 5.11. The maps of beaver habitat preference are shown in Figure 5.3. To produce these maps, each 5 km square in England was coded for beaver suitability based on habitat, and then squares containing more than the median amount of agricultural land were excluded. Squares coloured in purple contain the greatest amount of habitat suitable for beaver colonisation, although those coloured blue or green may contain enough habitat to support small populations. The most suitable habitat for beavers according to this analysis is (in the south) the Weald of Kent, in the New Forest, Bodmin Moor; (in the west) the Peak District; and (in the north west) the Lake District and the Forest of Bowland; along with a few other locations of less-concentrated suitable habitat. One problem highlighted in these analyses is the proximity of suitable habitat to heavily-populated areas, such as London, Chester, Southampton, and Tunbridge Wells; this analysis only excludes habitat containing urban and suburban areas rather than habitats close to these areas, but this could be addressed in a more detailed study.

## **Where next?**

- 5.12. Our analysis has been aimed at illustrating the potential of GIS and exploring national scale habitat availability, albeit in a rather cruder way. From a modelling point of view, beavers have a wide range of potential release sites across England based on this modelling exercise.

However, the estimates of beaver preference used are quite crude; for example, the dominant species of deciduous woodland is important to beavers rather than simply its presence; and the slope of water catchments rather than simply topological spread is a determinant of beaver suitability. A second phase of GIS modelling that incorporates more focused (e.g. River Habitat Survey) and higher resolution (e.g. air photo and airborne scanner) data would provide a much more detailed assessment of beaver suitability but would involve a far greater data analytical effort and probably the purchase of specific data sets. This phase could also incorporate other criteria, such as proximity to urban or suburban areas, whether the site has SAC or SSSI designations, whether beavers are likely to build dams and whether there was a chance of flooding.

- 5.13. A second study would also incorporate this habitat suitability information into a population-based model (Rushton *et al.* 1997; Suzuki & McComb 1998, Fryxell 2001, South *et al.* 2000, 2001, Rushton *et al.* 2006; Shirley *et al.* 2003, 2007, Maringer & Slotta-Bachmayr 2006). This model would combine the results of the habitat preference study with known life history parameters from both introduced and established beaver populations to simulate beaver population establishment and growth. The model would be subjected to a sensitivity analysis which will reveal those life history parameters to which the model is most responsive. This approach would predict the likely success of a beaver population becoming established; provide population probability density maps of the likely spread of beaver from the point of release; and provide estimates of potential human-beaver conflicts in terms of environmental manipulation and potential damage done to pre-existing resources by the introduced population.
- 5.14. This second phase GIS-modelling studies will enable the identification of release sites (see Macdonald *et al.* 2000) within watersheds that are relatively isolated from other watersheds - this will slow the rate of population expansion. However, the inclusion of suitable sites for dispersing young to establish colonies within a watershed would be beneficial (DeStefano *et al.* 2006). Young dispersers have lower chances of survival in marginal habitat (Campbell *et al.*, 2005). During the initial stages of population expansion, resident territory holders are unlikely to pose problems to the dispersing animals (Fryxell, 2001).

Figure 5.1. Sources of data for beaver habitat preferences maps

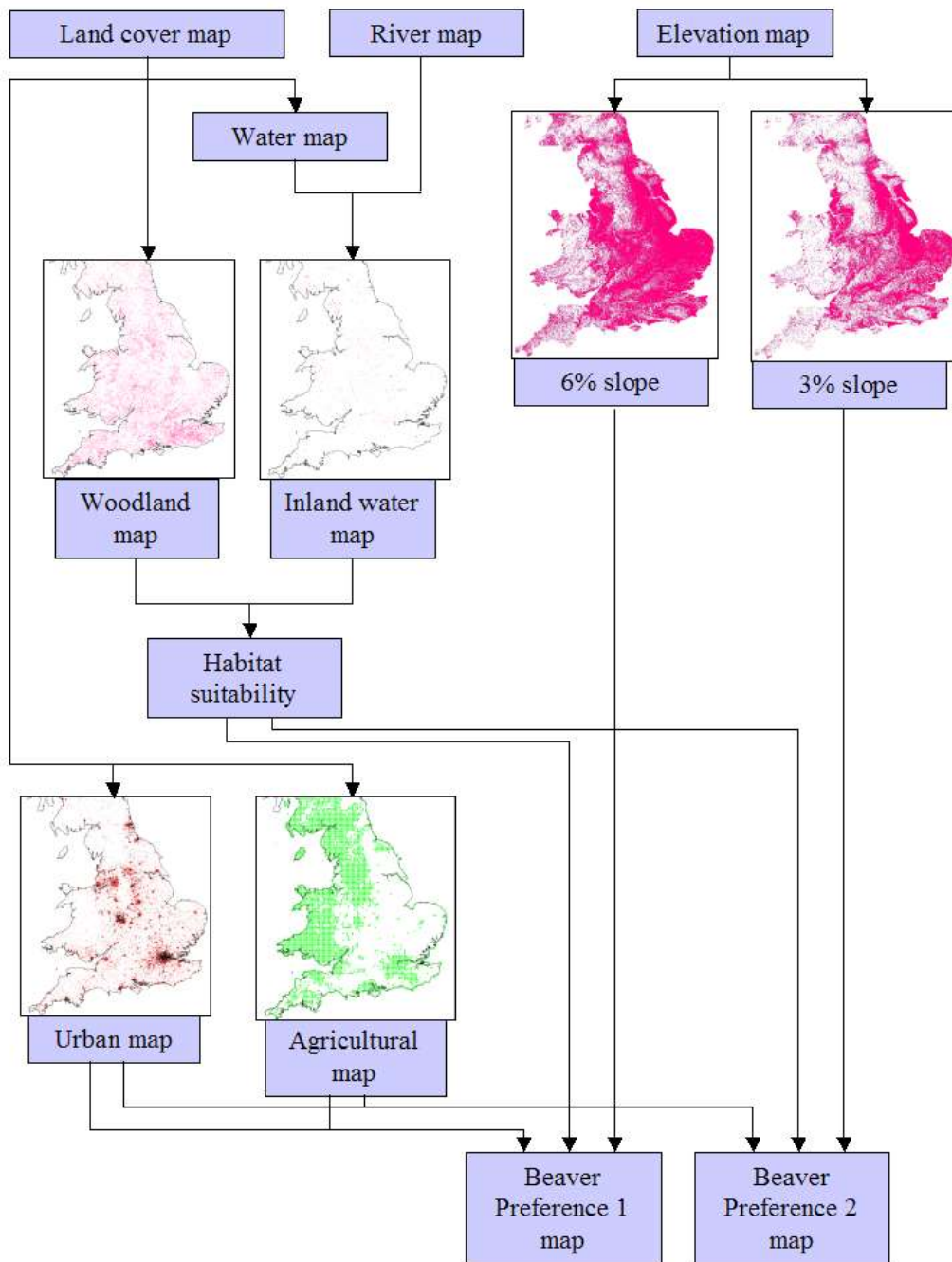




Figure 5.2. Habitat maps of UK indicating regions favoured or avoided by beavers. A) Deciduous woodland; B) Urban and suburban; C) Slope of 3% or less; D) Inland water.

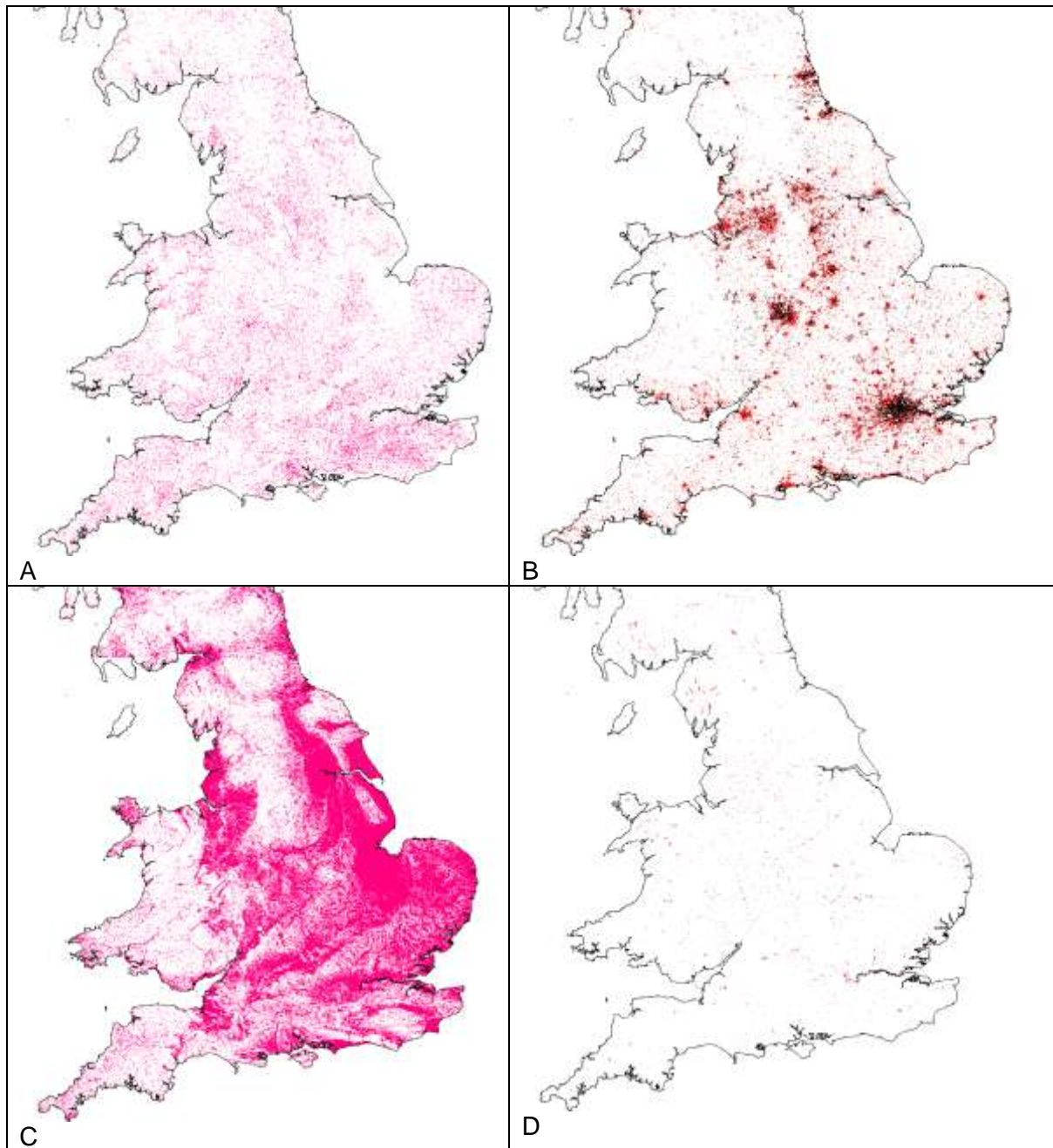
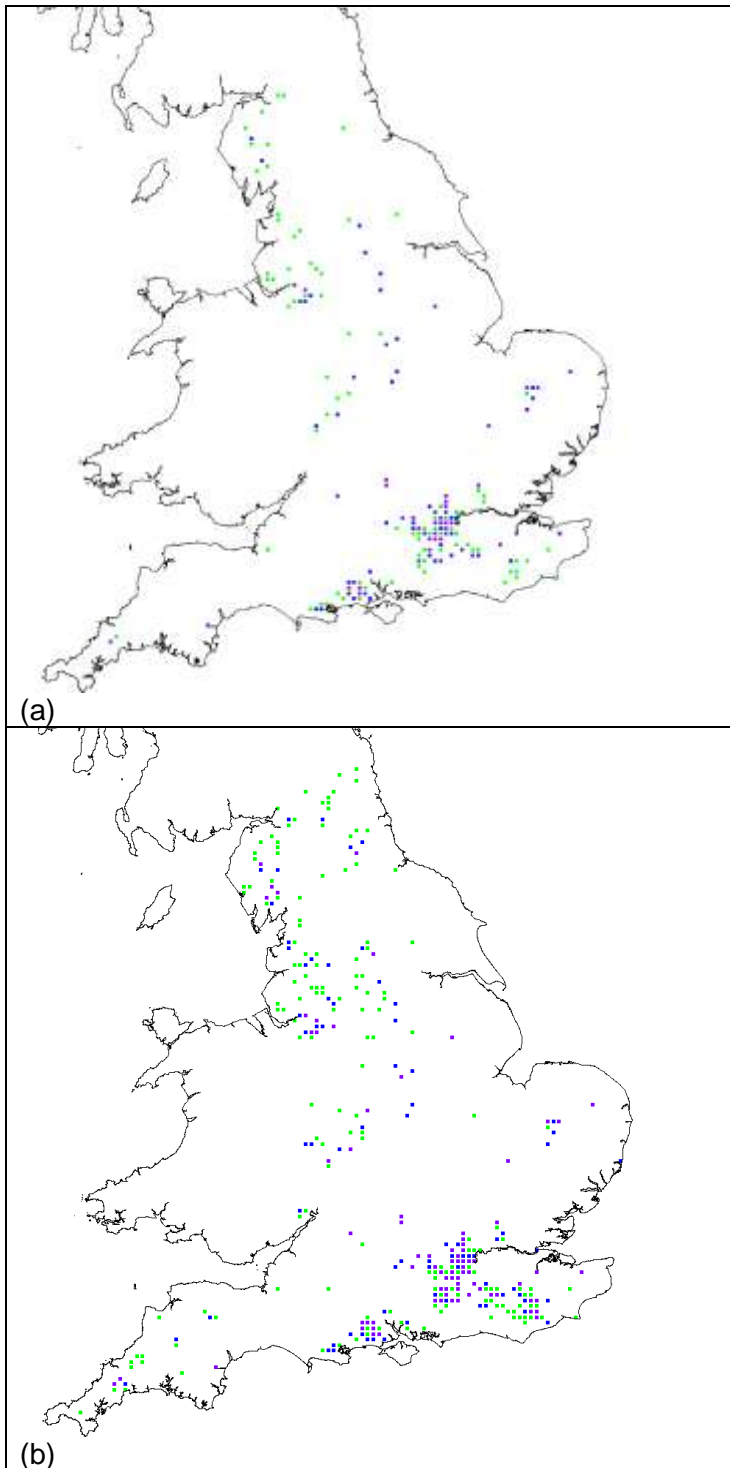


Figure 5.3. Results of the GIS study of beaver habitat suitability. Green indicates at least 2 km of suitable river habitat; blue indicates 3 km of suitable river habitat; and purple indicates 4 km of suitable river habitat in each 5 km square. (a) beaver preference allowing a 3% topological slope; (b) beaver preference allowing a 6% topological slope.



## **6. Beaver reintroductions to England: the legal position by Tony Mitchell-Jones, Natural England**

### **Summary**

- 6.1. The legal status of the beaver in England is complex. In most cases, it is illegal, under the Habitats Regulations, to possess beavers, although this does not apply to captive-bred beavers, as these are not considered to be wild animals. Possession of beavers can be licensed by Natural England.
- 6.2. Releasing beavers into the wild is an offence under the Wildlife & Countryside Act, as the species is not 'ordinarily resident in Great Britain'. In this context, 'into the wild' could probably include releases into large enclosures, where there is potential for impact on native wildlife or habitats.
- 6.3. If beavers are released into the wild in England, they are then considered to be wild animals, owned by no one. Currently, the species is not protected by any UK legislation (other than for the offence of possession), so the reintroduced beavers could be disturbed or killed. The UK would, however, be obliged to protect the species once it became established in the wild.
- 6.4. Once protected, beaver management operations could be licensed by Natural England, under various provisions in the Habitats Regulations. Beaver dams are probably not always protected, as they are not breeding sites or resting places. However, a licence would be needed to destroy one if it affected a nearby breeding site or resting place.

### **Introduction**

- 6.5. As a former native species not currently present in the wild in England, the beaver has a complex legal position.

## **Legislation covering the possession of beavers and their release into the wild.**

### **Possession**

- 6.6. A recent (2007) amendment to regulation 39(2) of the Conservation (Natural Habitats &c.) Regulations 1994 extended the offence of possession to all Habitats Directive Annex IV species instead of just those occurring in the UK (European protected species). This means that it is now an offence to possess, transport, sell or exchange any live or dead beaver or parts of a beaver.
- 6.7. This offence only applies to beavers taken from the wild after 10<sup>th</sup> June 1994 (or if taken in another Member State, the date it became a Member State). In addition, certain populations of beavers are not included in Annex IV, so specimens originating from Estonian, Latvian, Lithuanian, Polish, Finnish and Swedish populations, as well as those taken from outside the EU, may be possessed legally and are not covered by the Habitats Regulations. However, regulation 39(8) makes it clear that the onus lies on the possessor to show that the specimen in question came from an exempt population. Any offspring of exempted beavers born in the wild in Great Britain would not be covered by the defence in regulation 39(8) and so a licence would be needed to possess them legally.
- 6.8. Regulation 39(2) applies only to animals taken from the wild, so the possession of captive-bred beavers would not be an offence, though the onus would be on the possessor to demonstrate that the animal in question had not been taken from the wild (regulation 39(10)).
- 6.9. Licences can be issued by Natural England to permit the possession etc. of live or dead beavers, or parts of beavers, for various purposes, including science, education and conservation. Any beavers imported from other Member States (except from excluded

populations) for the purpose of reintroduction would thus need to be covered by an appropriate possession and transport licence.

## **Release**

- 6.10. Section 14 of the Wildlife and Countryside Act 1981 makes it an offence to release or allow to escape into the wild any animal which -
- (a) is of a kind which is not ordinarily resident in and is not a regular visitor to Great Britain in a wild state; or
  - (b) is included in Part 1 of Schedule 9
- 6.11. Licences can be issued by Natural England, on behalf of the Secretary of State, to permit actions that would otherwise be an offence under this section.
- 6.12. No definition of 'ordinarily resident in Great Britain in a wild state' is included in the Act or has been the subject of judgement by the courts, but it could be taken to mean that the species should have a self-sustaining population in the wild in Great Britain. If this interpretation is correct, then the consequences include:
- If a release into the wild establishes an ordinarily resident population, then subsequent releases do not require a licence. If control over subsequent releases is considered desirable, then it would be necessary to introduce another control mechanism, such as adding the beaver to schedule 9 of the WCA.
  - As section 14 refers to Great Britain, a release into England, Scotland or Wales that established an 'ordinarily resident' population would remove the need for licensing in the other two countries.
- 6.13. The definition of 'into the wild' in this context (only) is considered by Defra and Natural England to apply to animals released into large enclosed areas in some circumstances, such as when the release has the potential to impact on natural or semi-natural habitats or wild species. This area of policy is currently being developed.

## **Other legislative considerations**

- 6.14. Beavers in captivity are covered by the requirements of the Animal Welfare Act 2006. This Act probably also applies to beavers held in large enclosures where the owner of the animals continues to have some control over their welfare.

## **The legislative position of released beavers and beaver management**

### **Current domestic legislation**

- 6.15. If beavers are deliberately released into the wild (or escape and are not pursued) they become wild animals and are no longer owned by anyone. For the purpose of ownership, 'into the wild' probably does not include large fenced enclosures, where the rights of ownership persist as the owner still has a degree of control over the animals (and probably the land). In this case, the owner of these beavers may need two licences, one under section 14 of the WCA to release them 'into the wild' and one under regulation 44 of the Habitats Regulations to possess them.
- 6.16. Once in the wild (i.e. free and not subject to ownership), beavers are not currently protected by UK legislation as the species is not on schedule 2 of the Habitats Regulations. Specimens could, therefore, be taken, killed or injured by anyone, provided they did not breach other legislation (e.g. animal welfare) or use methods of capture prohibited by legislation, such as self-locking snares. However, if a beaver was captured alive or killed and the corpse collected, a licence would be needed to possess it. Although the beaver is included in European Union legislation (the Habitats Directive), this legislation is binding on Member States, not individuals, and so would not provide direct legal protection.

## The Habitats Directive

- 6.17. The beaver is included in Annex IV of the Habitats Directive. Article 12 of the Directive requires Member States to establish a system of strict protection for these species in their natural range. With respect to the latter, the European Commission's Article 12 guidance states *"When a species or habitat spreads on its own to a new area/territory or when a species has been re-introduced into its former natural range (in accordance with the rules in Article 22 of the Habitats Directive), this territory has to be considered part of the natural range. Similarly, the restoration/re-creation or management of habitat areas, as well as certain agricultural and forestry practices, can contribute to the expansion of a habitat or a species and hence its range. However, individuals or feral populations of an animal species introduced deliberately or accidentally by man to locations where they have never occurred naturally, or where they would not have spread to naturally in the foreseeable future, should be considered to be outside their natural range and consequently not covered by the Directive. Vagrant or occasional occurrences would also not be considered as part of the natural range."*
- 6.18. It is likely, therefore, that if beavers have been reintroduced into the wild within their former natural range and established a viable population, the Member State concerned would be obliged to protect the species using its domestic legislation transposing the requirements of Article 12. Great Britain is indisputably within the former natural range of the beaver, so it would be necessary in these circumstances to add the beaver to schedule 2 of the Conservation (Natural Habitats &c.) Regulations for England, Scotland and Wales. If this was not done, the European Commission could begin infraction proceedings against the UK to, ultimately, oblige it to implement the necessary legislation.
- 6.19. Although there is clearly a requirement to protect beavers which have been reintroduced to part of their former natural range, there is arguably a degree of latitude in when this protection needs to be implemented. It could be argued that following initial release(s) and before the establishment of a viable population, there is a period during which assessment of the success and desirability of the venture should take place, and during which the process may be reversed, if necessary.

## Beaver management

- 6.20. The beaver has been widely introduced to parts of its former European range and populations have readily established. One constant lesson from such reintroductions is the need to have a beaver management strategy in place should individual beavers or family groups cause problems for agriculture or forestry.
- 6.21. The possible addition of the beaver to Schedule 2 of the Habitats Regulations has significant implications for the management of the species as it would become illegal to deliberately kill, injure or take beavers or to damage or destroy their breeding or resting places. Should such actions be required for population management purposes, there are two possible licensing routes:
- The licensing authority (Natural England) can grant licences permitting otherwise illegal acts for the purpose of preventing serious damage to crops, timber or any other form of property.
  - Recent amendments to the Habitats Regulations have introduced a new licensing purpose, reflecting a provision in the underlying Directive that has been used in other Member States to allow the management of Annex IV species. The new licensing purpose (regulation 44(2A)) allows the licensing authority to grant licences to permit the taking or possession or control of specimens of Annex IV species, subject to certain safeguards regarding numbers taken, selectivity and supervision.
- 6.22. In both cases, licences could only be issued where there was no reasonable alternative to the proposed action and where the action would not adversely affect the favourable conservation status of the species.
- 6.23. Within parts of its restored range, it is the dams built by beavers that are sometimes associated with damage to forestry or agriculture. Devices are available to manage the water level in beaver dams, but complete dam removal may occasionally be necessary. Dams are

not used by beavers for breeding or resting, so the dam structures themselves are not protected. In some situations, the removal of a dam may have an adverse impact on a nearby beaver burrow or lodge by lowering the water level, so it may be a matter of judgement whether such action would constitute damage to a breeding or resting place. If a proposed dam removal operation is considered to have a damaging effect on a nearby breeding or resting place, a licence may be required in order for the work to be undertaken without committing an offence.

# 7. Parasites, mortality and quarantine and release of beavers

## Summary

7.1. There is no evidence that the reintroduction of beaver into England poses any significant public health risk, providing appropriate quarantine procedures and health checks are followed. It would be prudent to consider public health issues in a post-reintroduction monitoring programme. There is considerable experience of moving and managing captive beaver within England. Importantly, stress should be kept to a minimum during the capture, transportation, quarantine and release of beaver, to minimise disease risks that can be aggravated by a weakened immune system. This should include the simultaneous release of beavers at a target area that does not already hold resident beavers to minimise stress associated with territorial conflict, or alternatively the release of beavers in spatially separated areas. Methods of transporting beavers, and releasing them in their new environment are well-proven.

## Parasites and disease

7.2. Like all wild animals, beavers carry a number of parasites (Table 7.1). A preliminary list from the literature of diseases that are particularly relevant to the reintroduction of beavers and a possible threat to the health of humans and other animal species are: giardiasis, cryptosporidiosis, yersiniosis (including pseudotuberculosis), rabies and tularaemia. At some stage, a full evaluation of all the parasites harboured by the beavers to be translocated would be advisable, with a special focus on parasites alien to the UK.

Table 7.1. Examples of parasites detected in beavers

Group	Infective organism	Useful references
Protozoa	<i>Cryptosporidium</i>	Appelbee <i>et al.</i> 2005
	Giardiasis <i>Giardia lamblia</i> - Beaver fever	Appelbee <i>et al.</i> 2005; Dunlap & Thies 2002; Monzingo & Hibler 1987; Rossell <i>et al.</i> 2001
Virus	Rabies	Belcuore <i>et al.</i> 2002
Bacteria	Tularaemia <i>Francisella tularensis</i>	Tärnvik 2004; Müller <i>et al.</i> 2007
	<i>Streptococcus castoreus</i>	Lawson <i>et al.</i> 2005
	Pseudotuberculosis <i>Yersinia pseudotuberculosis</i>	Hacking & Sileo 1974; Gow 2002
	Leptospirosis	
Fungus	Adiaspiromycosis	Morner <i>et al.</i> 1999
	<i>Chrysosporium parvum</i>	
	<i>Haplosporangium-parvum</i>	Erickson 1949
Helminths	<i>Stichorchis subtriquetrus</i>	Fedynich <i>et al.</i> 1986; Sagar <i>et al.</i> 2005;
	<i>Heterobothriarzia americana</i>	Fedynich <i>et al.</i> 1986
	<i>Dipetalonema</i> sp	Fedynich <i>et al.</i> 1986
	<i>Castorstrongylus castoris</i>	Fedynich <i>et al.</i> 1986
	<i>Travassosius</i> spp.	Fedynich <i>et al.</i> 1986; Lavrov 1983
	<i>Echinococcus multilocularis</i>	Janovsky <i>et al.</i> 2002
Ectoparasites	Beaver beetle <i>Leptinillus validus</i>	Müller-Schwarz & Sun 2003
	Mites <i>Schizocarpus</i> spp.	Müller-Schwarz & Sun 2003

- 7.3. The common, enteric protozoan parasites *Cryptosporidium* spp. and *Giardia* spp. infect humans and a wide range of wild and domestic animals. They are a common cause of protozoal diarrhoea. Infection occurs when parasitic oocysts shed by the infective host are ingested by a susceptible host. Environmental contamination with animal and human faeces provides a possible transmission route to wildlife populations which in turn may act as reservoirs of the infective organisms (Appelbee *et al.* 2005). Transmission may be indirect via ingestion of contaminated food or water (e.g. from streams, lakes, effluent or wastewater), or contact with infected faeces. The latter faecal to oral route is common among humans. In America, infection by *Giardia lamblia* has sometimes been termed beaver fever. It should be noted that other aquatic species such as otters might contribute to the contamination of streams and rivers (Mendez-Hermida *et al.* 2007). The importance of these organisms depends on whether we have the particular species harboured by beaver in England.
- 7.4. Scottish Natural Heritage commissioned a report with respect to the possible impact of these parasites on human health from an introduction of beaver into Scotland (Morrison 2005). *Giardia* spp., *Salmonella* spp., *Cryptosporidium* spp. and faecal *Streptococci* spp. were not isolated from drinking water supplies. However, *Giardia* (1 sample) and *Cryptosporidium* (4 samples) were found in the natural environment and within surface water, indicating the presence of animal faeces in the area. Unfortunately, the analytical methods used did not identify the species of *Cryptosporidium* or *Giardia* detected. The report concluded that, “subject to the animals [beavers] undergoing appropriate quarantine and screening, the release of a limited number of beavers, together with the provision of monitoring and controls, will not pose a significant additional public health risk...and...that the risk of increased human cases of Giardiasis is significantly low and that it should not be considered an obstacle to beaver re-introduction”. However, the report does advocate that monitoring of public health issues should be a key component of any introduction programme.
- 7.5. *Francisella tularensis* (the aetiological agent of tularaemia), is a water-borne bacterium that is carried by a wide range of animal host species such as hares and rabbits, voles, rats and mice, squirrels and beaver, with other susceptible mammalian species such as dogs, cats, sheep and cattle; and incidental hosts including birds, fish and amphibians (see Müller *et al.* 2007, and references therein). Ticks, flies and mosquitoes act as vectors for the infective agent, but the disease can also be contracted by direct contact with contaminated water or infected animals. It is widespread in animals and humans in continental Europe, but has not been reported from the UK (Tärnvik *et al.* 2004). The Canadian beaver is more susceptible to tularemia than the European beaver (Müller-Schwarz & Sun 2003), and epizootics have occurred in North America causing extensive mortality (e.g. Stendland 1953). This is an unpleasant zoonosis (Mörner 1988) that can cause fatal disease in humans, and so it is very important to keep the bacterium out of the UK.
- 7.6. Yersiniosis or pseudotuberculosis caused by the bacterium *Yersinia pseudotuberculosis*, is found in many mammalian hosts, such as dogs, cats, horses, cattle, rabbits, deer, rodents including beaver (Hacking & Sileo 1974), and bird hosts, such as ducks and geese. Three of six captive Bavarian (European) beavers transported to quarantine facilities in Kent died from pseudotuberculosis; the remaining three were euthanased (Gow 2002). Since stressors usually play a part in the development of pseudotuberculosis in animals, this disease may be a significant hazard for the welfare of transported beavers (Mörner 1992 in Mörner *et al.* 1999). The infectious agent *Y. enterocolitica* can cause illness in humans, particularly young children.
- 7.7. Rabies is caused by a virus that attacks the nervous system and later is excreted in saliva. Humans can be infected by, for example, the bite of a dog, bat or monkey. In Western Europe, the virus is mainly carried by the fox but beavers and other wild mammals have been known to carry the virus (e.g. Brakhage & Sampson 1952, Belcuore *et al.* 2002). Strict quarantine regulations prevent the introduction of infected animals into Britain.



## Post-release mortality in beavers

7.8. Nolet *et al.* (1997) have considered the main causes of mortality in beaver transported from Germany to the Netherlands between 1988 and 1994. Twenty-two of forty-three animals (51%) fitted with radiocollars were found dead, and the causes of death investigated (Table 7.2). Infectious diseases, especially pseudotuberculosis and leptospirosis were the most common causes of death, and these took their toll one to three months after release. In support of the statements above, the authors hypothesised that the stress of translocation had weakened the immune system and they recommended that stress be kept to a minimum in animals being translocated [and reintroduced], that good hygiene is maintained, and that the beavers should be vaccinated against pseudotuberculosis and leptospirosis. Other causes of mortality included traffic and boat trauma, and injuries that could have been caused by other vehicles, or maybe other beavers. Two animals succumbed to pneumonia.

Table 7.2. Causes of mortality in beavers found dead after being translocated to the Netherlands from Germany (from Nolet *et al.* 1997).

Beaver No.	Sex	Age(yr)	Survival (days)	Diagnosis	Bacteriology
1	M	Adult	21	Tooth wear	
2	M	1.5	24	Leptospirosis	
3	F	1.5	26	Leptospirosis	
4	F	Adult	31	Leptospirosis	serovar <i>icterohaemorrhagiae</i>
5	F	8	32	Yersiniosis	<i>Yersinia</i> <i>pseudotuberculosis</i>
6	M	1.5	34	Trauma with incised wound	No pathogens
7	M	2.5	40	Obstruction of lumen by implant	
8	F	2.5	42	Yersiniosis	<i>Yersinia pseudo</i> <i>tuberculosis</i>
9	F	1.5	55	Yersiniosis	<i>Yersinia</i> <i>pseudotuberculosis</i>
10	F	0.5	65	Predation by sea eagle	
11	F	1.5	85	Yersiniosis	<i>Yersinia entocolitica</i>
12	M	5	102	Unknown	
13	M	2.5	122	Cachexic	No pathogens
14	F	8	154	Pneumonia	No pathogens
15	M	Adult	159	Pneumonia	
16	F	1	187	Blunt trauma	No pathogens
17	F	13	221	Boat victim	
18	F	1	266	Blunt trauma	No pathogens
19	M	1.5	346	Traffic victim	
20	M	11	366	Unknown	
21	F	21	630	Avian tuberculosis	<i>Mycobacterium avium</i> type 2
22	M	17	2028	Tooth wear	

7.9. Interestingly, Nolet *et al.* (1997) compared their findings with two studies on beaver mortalities that had been carried out in the source populations on the Elbe (Table 7.3). On the Elbe, animals dying from human-related activities were probably over-represented in the samples because animals dying from disease would have been less easily found. The two studies on the Elbe also produced different results, with large numbers of beavers dying from avian tuberculosis in the 1950 study and large numbers dying from beaver bites, pneumonia (both attributed to poor water quality), liver and internal diseases in the 1977 study. However,

pseudotuberculosis and leptospirosis were not detected in either study, reinforcing the idea that factors related to the translocation process were linked to the occurrence of these infectious diseases in the beavers that were moved. The authors suggest that the procedure of releasing beavers over a number of years resulted in territorial conflicts that added to the stress and high initial mortalities. They concluded that, “*one should aim at a simultaneous release of as many animals as possible, or sequentially release animals in areas which are spatially separated*”.

Table 7.3. Causes of beaver deaths from two studies on the River Elbe (Hinze 1950 and Piechocki 1977, both in Nolet et al. 1977) and those that had been translocated to the Netherlands (from Nolet et al. 1997).

<b>Mortality cause</b>	<b>Hinze (1950)</b>	<b>(%)</b>	<b>Piechocki (1977)</b>	<b>(%)</b>	<b>Nolet et al. (1997)</b>	<b>(%)</b>
Killed	23		40		0	
Traffic victim	3		10		4	
Accidentally caught	4		9		0	
Incised wound	0		0		1	
Poisoned	0		3		0	
Transmitter	0		0		1	
Dog bites	7		5		0	
<b>Human factors</b>	<b>37</b>	<b>50.7</b>	<b>67</b>	<b>39.9</b>	<b>6</b>	<b>30</b>
Beaver bites	0		30		0	
Pneumonia	2		18		2	
Liver diseases	0		11		0	
Intestinal diseases	1		8		0	
Periostitis	0		4		0	
Avian tuberculosis	25		0		1	
Yersiniosis	0		3		4	
Leptospirosis	0		0		3	
Flukes	0		1		0	
<b>Diseases</b>	<b>28</b>	<b>38.4</b>	<b>75</b>	<b>44.6</b>	<b>10</b>	<b>50</b>
Old age	0		10		2	
Flooding	8		7		0	
Winter victims	0		7		1	
Predation	0		0		1	
Under felled tree	0		2		0	
<b>Biological factors</b>	<b>8</b>	<b>11</b>	<b>26</b>	<b>15.5</b>	<b>4</b>	<b>20</b>
<b>Unknown</b>	<b>42</b>		<b>48</b>		<b>2</b>	
Total known	73	63.5	168	77.8	20	90.9

## Quarantine and licenses

7.10. Peter Smith from WildWood, Kent has kindly provided details of licenses required and the health checks and quarantine procedures carried out on European beavers brought into WildWood from Germany. Most licenses and reports needed for importing and holding beavers in England come under The Animal Health Act 1981 and The Rabies (Importation of Dogs, Cats and Other Mammals) Order 1974 (as amended). These include:

- an Import Licence from DEFRA;
- an Authorisation of Quarantine Premises (DEFRA);
- a Boarding Document (DEFRA) – a licence for landing at an approved port/airport in Great Britain;

- a Report by the Carrying Agent(s) of the arrival of imported animal(s) at the authorised place of detention (DEFRA);
- Report by a Veterinary Surgeon or Medical Supervisor of the arrival of imported animal(s) at the authorised place of detention (DEFRA)
- A Licence for the Possession of a European Protected Species (EPS) is also required from Natural England.

7.11. Before the animals were moved to WildWood from Germany, a German vet inspected the beavers and issued a European licence indicating they were fit for travel. In fact, the beavers were screened for a number of diseases both before and after they arrived in England, and during the six month quarantine period (Jeremy Stattersfield, Peter Smith pers. comm.). Tests included:

- Tularaemia -*Francisella tularensis* serology
- *Yersinia pseudotuberculosis*
- *Yersinia enterocolitica* - serology or preferably faecal examination
- Leptospirosis - *Leptospira* appropriate serotype antibody levels
- Faecal examination for protozoa and worm infestations
- Tests for Rickettsia and a flavivirus called Omsk Haemorrhagic Fever were to be considered if infections were likely in the source area.

7.12. Methods of moving and keeping beavers in quarantine are well established (Gow 2002); they will not be considered here.

## Release protocols

7.13. The methods for releasing beavers at target sites are well-proven from work carried out in both Norway and Britain (Gow 2002). Generally, a soft-release<sup>10</sup> is recommended as a precautionary method to allow for a period of acclimatisation by the animals to the new conditions. Beavers can be retained in small ponds by encircling these with wire mesh fencing or electrified sheep netting (Gow 2002). These can be removed after a week or two, or longer if necessary. The beavers are provided with an artificial lodge at the side of the pond made of wooden boxes or straw bales with bitumen-coated roofing card about 1 m long by 1 m wide by 1.5 m high. The lodge is covered with wood, grass tussocks and mud to create a mound. The entrance to the lodges should be set next to the water's edge and initially blocked with a fence of willow stakes driven down into the ground. The beaver will gnaw through these quickly to get to the water. A back entrance to the lodge allows the beavers to be transferred from their travelling crates to the lodge. Bedding from the crates together with apples should be placed in the lodge (Gow 2002). Eventually the beavers will build their own lodges in their new environment.

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<sup>10</sup> A 'soft' release involves a period of confinement of individuals at the release site until they become acclimatised to their new environment (e.g. Hardman & Moro 2006). Food, water and maybe a predator-proof retreat are provided. In contrast, a 'hard' release involves the immediate release of the individuals into the wild.

# 8. Phylogeographic history of European beaver populations and identification of suitable source populations for reintroduction

## Summary

- 8.1. The Eurasian beaver was once native to Britain but became extinct a long time ago, maybe as long ago as the end of the twelfth century in England and Wales, although it may have persisted for longer in parts of northern England. It is not known which of the European subspecies inhabited Britain, or whether it was a unique but now extinct subspecies. At present, it appears unlikely that we will be able to find out more about this through genetic analysis of museum material. The general advice is that the source population for reintroductions should be the geographically closest surviving form (IUCN 1998). Most beaver reintroduced populations in Europe are of mixed subspecific origin and many have been successful. This would suggest that it does not matter where the reintroduced beavers come from, but it is important to preserve the remaining unmixed, genetically distinct subspecies which may possess important local adaptations. Studies have shown that the remaining relic beaver populations in Europe are genetically distinct and should be treated as management units for conservation.
- 8.2. Based on a study of their genetics there are nine named subspecies of beavers currently alive that belong to two main groups: a western European group consisting of three subspecies and an eastern group consisting of six subspecies. It appears that the subspecies from the western group would be the most appropriate for reintroductions into Britain. *C. fiber galliae* (from the Rhone in France) or *C. fiber albicus* (from the Elbe in Germany) are the geographically closest populations for reintroductions into England and would be most suited for introductions to southern England as they are adapted to lowland habitats. *C. fiber fiber* from Scandinavia maybe more appropriate for Scotland because they are adapted to a more extreme climate and habitat. However, because potential European source populations may be of mixed subspecific origin, it is recommended that DNA sampling and mtDNA genotyping of reintroduced animals are carried out as part of the reintroduction protocol.

## Introduction

- 8.3. Beavers are the largest of the squirrel-like rodents with extant populations distributed across part of the Nearctic and Palaearctic ecozones, including in the latter both western and eastern Europe, central Asia, Russia and north-western China. Despite this widespread occurrence and the potential for sub-structuring of populations along the river systems and lakes that they inhabit, just two species are currently recognised in a single genus (*Castor*) in the family Castoridae. These are the North American beaver *Castor canadensis* and the European (or Eurasian) beaver *Castor fiber*. Like other rodents, the fossil record of beavers is relatively old with the earliest ancestor of the Eurasian beaver thought to be *Steneofiber* of the Oligocene epoch (dated at about 32 million years ago). The extant genus *Castor* has its origins in Europe in the Pliocene between five and 1.8 million years ago and subsequently spread into North America. More recently during the Pleistocene (10,000 years ago) Canadian and European beavers coexisted with other, giant forms of beaver (*Castoroides* and *Trogotherium* respectively), now extinct. Although the two living species *C. canadensis* and *C. fiber* are very similar in appearance, they are chromosomally distinct (with  $2n = 40$  in *C. canadensis* and 48 in *C. fiber*), and there are also differences in cranial morphology. Interbreeding between the two has not been recorded and thus there appears to be a clear taxonomic distinction in accordance with the biological species concept. At a species level, decisions regarding translocations and reintroductions within a particular continent are therefore straightforward, although Canadian beavers have been released in Europe (Halley & Rosell 2002). However, at the subspecific level there is much greater diversity and it is apparent that local

differentiation of populations commonly occurs, and that ideally this should be considered when making management decisions (see below). Beavers thus have a complex and dynamic history with their distribution initially influenced by climate change and cycles of ice ages. More recent demographic processes are characterised by population bottlenecks and the effects of genetic drift arising from large-scale regional extinctions and range reductions due to hunting. These have been followed by uncoordinated reintroductions and translocations that have confused the historical distributions across the entire range of the genus (for a review of this in European beavers see Halley & Rosell 2002).

## Taxonomy

- 8.4. In the North American beaver 24 or 25 subspecies are generally recognised (Gabrys & Wazna 2003). However, local extinctions, reintroductions and translocations together with intra-subspecific hybridisation have affected the genetic purity of most, if not all of these lineages. Similarly, the current distribution and composition of the Eurasian beaver has been heavily influenced by a long history of hunting leading to local and regional extinctions, followed in some areas by uncoordinated and haphazard attempts at translocations and reintroduction. These factors have thus overridden any historic population structure that may have existed. Furthermore, subspecific taxonomy of the Eurasian beaver has been confused in the past due to incorrect application of the rules laid out by the International Code of Zoological Nomenclature. In a recent attempt to clarify the situation by resolving controversial and incorrect nomenclatural decisions, a review by Gabrys and Wazna (2003) recognised nine subspecies of *C. fiber* (Table 8.1.). Their exact ranges have not been accurately determined, and further examination of types and molecular genetic investigations were recommended by Gabrys and Wazna (2003) in order to further validate the taxonomy listed in Table 8.1. This especially applies to the eastern European taxa where *C. f. vistulanus*, *C. f. belorussicus* and *C. f. orientoeuropaeus* have been viewed as various combinations of one, two and three subspecies.
- 8.5. Around the end of the 19th century, numbers of the Eurasian beaver crashed to around 1200 animals in eight isolated populations. As a result of protection, natural recovery and intervention by programmes of reintroduction that started in 1922, during the 20th century there has been a rapid recovery. In their 2002 review, Halley and Rosell quoted a minimum population estimate of 593,000, together with around 12,500 North American beavers established in Russian Karelia and Finland. The eight relic populations of the Eurasian beaver that survived the population crash are reported by Nolet and Rosell (1998) to be found in the following locations: the Rhone Delta of France (corresponding to *C. f. galliae*); on the middle Elbe region of Germany (*C. f. albicus*); Telemark in southern Norway (*C. f. fiber*); the Dnepr River system with the rivers Pripjat and Beresina in Belarus and Ukraine (*C. f. belorussicus*); the Woronesh-Don river system of Russia (*C. f. orientoeuropaeus*); the Konda and Soswa rivers of the east Ural region of Russia (*C. f. pohlei*); the upper Jenissej and Azas rivers of Russia (*C. f. tuvinicus*), and the Bulgan River in Mongolia (*C. f. birulai*). The correspondence of these relic populations with the named subspecies (most of which were described *after* the population crash) is probably no coincidence - an observation noted by Halley and Rosell (2002). Presumably this is a result of genetic drift and founder effects arising from the small remnant populations, a hypothesis supported by genetic studies.

Table 8.1. A current subspecific taxonomy for Palaearctic beavers (adapted from Gabrys & Wazna 2003). Eastern and Western haplogroups determined by mitochondrial DNA sequence analysis representing two major evolutionary significant units are also indicated (Durka *et al.* 2005).

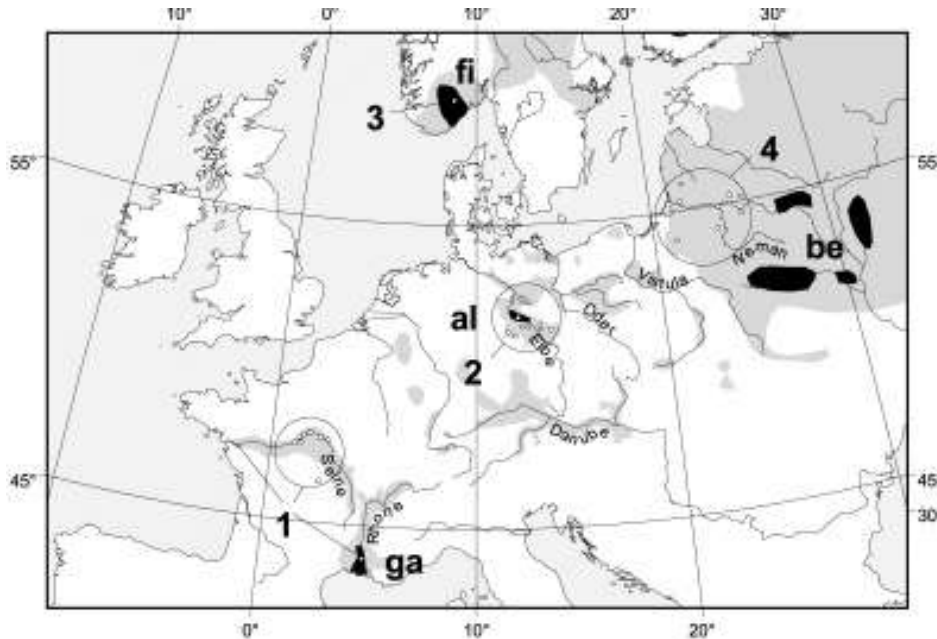
Subspecies	Type reference	Common name	Haplogroup
<i>C. f. fiber</i>	Linneaus, 1798	Scandinavian beaver	Western
<i>C. f. galliae</i>	Geoffroy, 1803	Rhone beaver	Western
<i>C. f. albicus</i>	Matschie, 1907	Elbe beaver	Western
<i>C. f. vistulanus</i>	Matschie, 1907	Vistula beaver	Eastern
<i>C. f. pohlei</i>	Serebrennikov, 1929	Western Siberian (Uralian)	Eastern

<i>C. f. birulai</i>	Serebrennikov, 1929	beaver Mongolian beaver	Eastern
<i>C. f. tuvinicus</i>	Lavrov, 1969	Yenisei (Tuvian) beaver	Eastern
<i>C. f. belorussicus</i>	Lavrov, 1981	Belorussian beaver	Eastern
<i>C. f. orientoeuropaeus</i>	Lavrov, 1981	Eastern European beaver	Eastern

## Genetic diversity and phylogenetic relationships

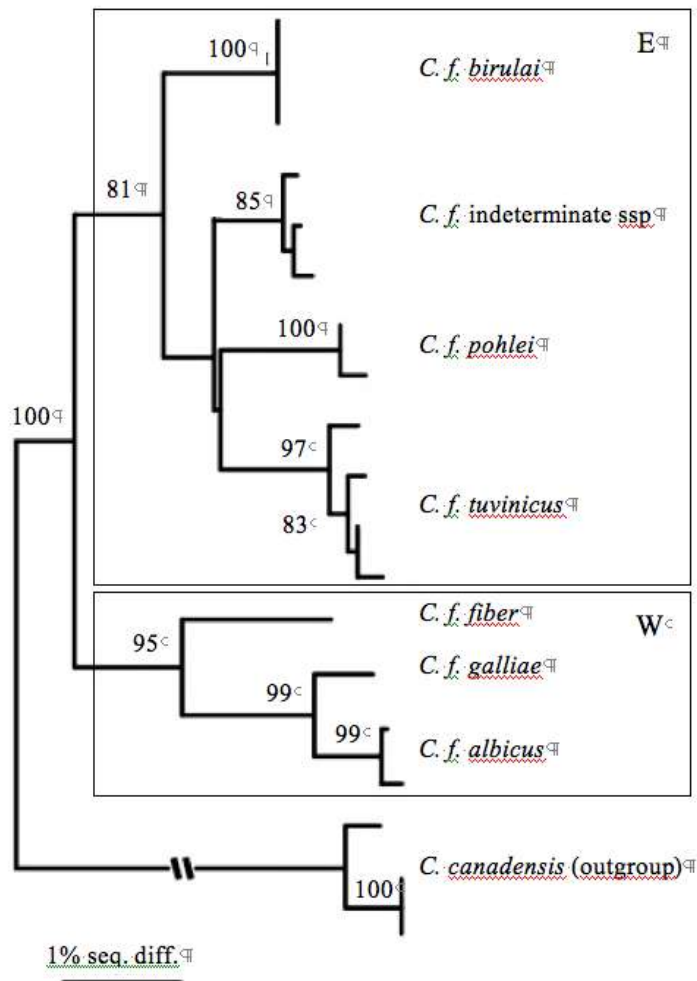
- 8.6. Recent extensive molecular phylogenetic studies based on mitochondrial DNA (mtDNA) sequence data indicate that the existing eight relic populations of the Eurasian beaver in France, Germany, Norway, Belarus, Russia, Ukraine, Mongolia and China resolve as clades that support the subspecific classification shown in Table 8.1. (Durka *et al.* 2005; Ducroz *et al.* 2005; Figure 8.1.). Mitochondrial DNA haplotypes were found to be distributed in a population specific pattern, and two major mtDNA lineages, a western and an eastern haplogroup were recognised by Durka *et al.* (2005). The tree topology generated by their analysis appears to be robust as bootstrap support for these lineages and clades (indicated in Figure 8.2.) was high, ranging from 81 to 100%, despite the fact that overall levels of genetic divergence were generally low between subspecies/populations. For example, the net sequence divergence between pairs of subspecies at the mitochondrial D-loop locus, normally the most variable region of mtDNA, ranged from 1.03% between *C. f. albicus* and *C. f. galliae* (western haplogroup) to a maximum of 5.09% between *C. f. albicus* and *C. f. tuvinicus* (eastern haplogroup). Overall, sequence differences were greater among the eastern populations, and this was confirmed by further data obtained from the mitochondrial cytochrome *b* gene: there was no sequence variation detected at this locus between *C. f. albicus* and *C. f. galliae*, while a maximum value of just 0.7% was noted among comparisons within some of the eastern populations, and between the eastern and western populations (Durka *et al.* 2005). In addition to the low levels of sequence divergence among haplotypes, haplotype diversity itself was extremely low. Within the western haplogroup just one haplotype was detected both among the seventeen samples from the French beaver population (*C. f. galliae*), and the nineteen samples from Norway (*C. f. fiber*). Out of the 27 individuals of *C. f. albicus* sampled from Germany, just two haplotypes were revealed, although one was present at a frequency of 0.96.

Figure 8.1. Map showing distribution of relic *C. fiber* populations (dark shading) together with the current range (adapted from Durka *et al.* 2005). The Eastern evolutionary significant unit/haplogroup as determined by Durka *et al.* (2005) corresponds to sampling areas labelled 1, 2 and 3 or *C. f. galliae* (ga), *C. f. albicus* (al) and *C. f. fiber* (fi) respectively. Part of the range of the Western haplogroup is also shown, corresponding to *C. f. belorussicus* (be) and the nearest area (4) sampled by Durka *et al.* (2005).



- 8.7. The observed low levels of sequence divergence within and between *C. fiber* populations indicate recent common ancestry for the existing subspecies, while the lack of haplotype diversity seen in the western haplogroup appears to be due to a recent bottleneck, in all likelihood the population crash at the beginning of the 20th century. The extreme genetic structuring reported by Durka *et al.* (2005) where no haplotypes were shared between any pairs of relic populations, and the close similarity of haplotypes within populations (where variation existed) suggests two scenarios that are not mutually exclusive. Firstly, a cessation of gene flow among populations following the population crash, or secondly, an underlying historical genetic structure arising from the life history and dispersal habits of the beaver, restricting them to the watersheds of major river systems. The identification of two clear phylogroups (eastern and western) strongly suggests the existence of at least two refugia during the last glacial period, and possibly more in the eastern part of the beaver's range (Durka *et al.* 2005).
- 8.8. Because of its maternal pattern of inheritance the geographical structuring of genetic variation revealed by mtDNA will be affected by the dispersal patterns and population size of females, and may not necessarily be reflected in markers from the nuclear genome. Although studies are limited, nuclear genetic markers so far also reveal differences between western and eastern populations. DNA fingerprints of Beavers from Scandinavia were found to have very low variation at the normally highly variable minisatellite loci, while major histocompatibility complex (MHC) genes, also normally highly variable, were monomorphic.

Figure 8.2. Neighbour-joining phylogram based on mitochondrial DNA D-loop sequences for Palaearctic beavers (adapted from Durka *et al.* 2005). The two major evolutionary significant units are the Eastern (E) and Western (W) reciprocally monophyletic haplogroups. The three haplotypes in the clade labelled *C. f. indeterminate ssp* were samples taken at some distance from the relic populations of *C. f. belorussicus* and *C. f. orientoeuropaeus*, and were therefore not assigned to a specific taxon. The tree is rooted with the Canadian beaver as an outgroup. The tree is rooted with the Canadian beaver as an outgroup.



- 8.9. The MHC is important in both the adaptive immune response and recognition and selection of mates (Edwards & Hedrick 1998). In contrast, eastern populations from locations in Russia showed high polymorphism at minisatellite loci and variation in allozymes, but this was not reflected at MHC loci (Ellengren *et al.* 1993; Milishnikov *et al.* 1994, 1997; Milishnikov & Saveljev 2001; Babik *et al.* 2005). While selectively neutral loci such as minisatellites are useful markers for genetic variation in the genome as a whole, it is also important to quantify genes that may confer a selective advantage, such as those within the MHC. Numerous studies have shown that sections of the MHC to be under strong positive selection giving rise to high levels of heterozygosity (Edwards & Hedrick 1998). This can even occur in highly inbred/bottlenecked populations, for example, the San Nicholas Island fox completely lacks variation at normally hypervariable genetic loci but had surprisingly high levels of heterozygosity at MHC loci (Aguilar *et al.* 2004). This unexpected observation is thought to be due to intense balancing selection (selection for heterozygotes) at these fitness-related genes, and Aguilar *et al.* (2004) suggest that one goal of the genetic management of populations should be the maintenance of genetic diversity at the MHC. Conversely, the aforementioned studies of beaver have shown that while neutral loci may be polymorphic in some eastern populations, the MHC shows a distinct lack of variation across its geographic range. Babik *et al.* (2005) examined the Class II MHC DRB locus, one of the most variable parts of the genome, and found just 10 unique alleles among the 74 beavers that were sampled. Furthermore the only population found to be polymorphic was in western Siberia, where 4 alleles were detected among 10 individuals. Each remaining population studied (which were



also studied by Durka *et al.* 2005) was found to be fixed for a different MHC allele. This observation has implications for decisions on UK reintroductions (see below).

## Summary and recommendations for source populations for UK introductions

- 8.10. Although it was once also indigenous to Britain, the Eurasian beaver is believed to have become extinct as long ago as the end of the twelfth century in England and Wales, but isolated populations in the highlands of Scotland persisted into the sixteenth century (for review see Kitchener and Conroy, 1997, and references therein). Although much uncertainty exists on the exact dates, it seems unlikely that skins or other remains of UK beavers of known provenance exist in any museum collections. It is therefore not known which of the European subspecies inhabited Britain, or whether a unique but now extinct subspecies was present. The prospect of addressing this question through analysis of DNA taken from suitable museum material is remote. Although such an approach has been successful in genotyping extinct populations of the highly endangered Mauritian kestrel (Groombridge 2000), currently it would appear that only sub-fossil and archaeological specimens remain for UK beavers. DNA work with such material is generally not possible, but morphometric analysis might be feasible. However, whether enough samples are available, and whether there is enough subspecific variation in morphology to make unambiguous judgements on the taxonomy of the samples, remains unknown.
- 8.11. It is normally suggested that the source population for reintroductions should be the geographically closest surviving form (Halley & Rosell 2002 and references therein; Durka *et al.* 2005). Most reintroduced populations in Europe are of mixed subspecific origin (Halley & Rosell 2002), and it could be argued that this being the case, and because these populations are generally thriving, careful sourcing of populations is not important. On the other hand, there is a strong case to be made to attempt to preserve the remaining unmixed, genetically distinct subspecies, not least because these may possess important local adaptations. The study of Durka *et al.* (2005) showed clearly that the remaining relic populations in Europe are genetically structured and distinct and should therefore be treated as management units for conservation. MacDonald *et al.* (1995) suggest that *C. fiber galliae* or *C. fiber albicus* would not only be the geographically closest populations for reintroductions into the UK, but also be best suited for introductions to southern Britain as they are adapted to a lowland habitat. They further recommended that for reintroductions in Scotland, *C. fiber fiber* are more likely to be adapted to the prevailing harsher climate and habitat. We agree with this and in the light of the recent genetic study by Durka *et al.* (2005) it is clear that, based on current knowledge, choices for source populations from the genetically unmixed subspecies of the western haplogroup are limited due to their lack of diversity. We concur with the view expressed by Aguilar *et al.* (2004) that maintenance of genetic diversity at the MHC and other fitness-related genes should be considered when making management decisions on translocations and reintroductions of beavers. Unfortunately at present this is not possible with European beavers if we want to maintain subspecific integrity and choose geographically close populations for UK introductions. All potential source populations of *C. fiber fiber*, *C. fiber galliae*, and *C. fiber albicus* are genetically distinct but monomorphic for the mtDNA haplotypes and MHC alleles so far isolated (although two mtDNA haplotypes are present in separate populations of *C. fiber albicus*). Given our present knowledge either *C. fiber galliae* or *C. fiber albicus* should be chosen for introductions to southern UK, and because European populations may be of mixed subspecific origin, DNA sampling and mtDNA genotyping to identify genetically pure subspecies would be also highly desirable.

# 9. Public perceptions and stakeholder responses

## Summary

- 9.1. While review of the literature and of recent public consultations suggests broad but shallow support from the public at large, the majority of stakeholders consulted for this project are supportive, at least in principle, of reintroducing European beaver to England. Along with the potential for eco-tourism, various improvements to ecosystem services were the most commonly perceived benefit of reintroducing beaver. Concerns centred on the system for regulating and managing introduced populations and on their potential to cause flooding, damage woodland and crops, and affect fish. Any future reintroduction plans must involve extensive public consultation, backed by clear and trustworthy information about the management and likely environmental impacts of reintroduced beaver.

## Introduction

- 9.2. Local public acceptance is key to the success of ecological restoration efforts (e.g. Naughton-Treves *et al.* 2003; Zimmerer & Young 1998). Not only can opposition from local groups compromise restoration plans and the licensing approvals on which they depend, but reintroduced species or the restored habitats on which they depend may also face deliberate sabotage, if they do not enjoy sufficient popular support. Such resistance points to the fact that the 'success' of any reintroduction must be judged not simply in scientific terms of species abundance and ecosystem functioning, but also in terms of how those impacts are perceived and understood by the public and other stakeholders. Perceptions are social facts. Whatever their relationship to received scientific opinion, public perceptions of the potential impacts of any beaver reintroduction are a material consideration that will need to be addressed by any future reintroduction plan.
- 9.3. In order to scope out the likely public perceptions of and stakeholder responses to any proposed reintroduction of beaver, this feasibility study reviewed the extant literature about public attitudes to wildlife and biodiversity in general as well as the findings about public perceptions of beaver in particular from the recent consultations in Scotland and other research. This desk-based work then informed the design of a structured interview schedule that was used to consult with key stakeholders to identify their concerns about, as well as perceived benefits of, any potential beaver re-introduction.

## Attitudes and perceptions of the general public

- 9.4. Past research suggests that there is broad but shallow support among the general public across the UK for wildlife conservation (Bremner and Park 2007, Macnaghten 1995, Nilsen *et al.* 2006, Wilson 2004). The latest Defra (2007a) survey of Public Attitudes and Behaviours toward the Environment found that although people were concerned about biodiversity loss, it was not an issue they thought much about. While nearly 80% of respondents agreed or strongly agreed with the statement, 'I do worry about the changes to the countryside in the UK and the loss of native plants and animals', only a minority thought 'a great deal' (6%) or a 'fair amount' (25%) about the issue. The plurality (36%) thought only 'a little', while a further 32% had 'not really given this issue any thought before'.
- 9.5. Although beaver do not have the same public profile of such iconic species as pandas, whales, or tigers (Walpole & Leader-Williams 2002), they possess many features associated with nonhuman charisma (Lorimer 2007). As such there are reasons to expect the reintroduction of beavers to enjoy broad, if shallow, support among the general public. Unlike many invertebrate species, beavers are comparatively easy for amateurs to detect and identify, while as mammals they are easy to anthropomorphise. There is a long and very well documented history of sentimentality about small mammals in England, going back to the Victorian era children's books of Beatrix Potter and the like (Ritvo 1987). Moreover as

herbivores (and relatively cuddly ones at that) beavers do not raise anxieties about public safety and livestock depredation associated with large carnivores like the wolf or lynx, whose introduction and conservation, nevertheless, enjoy strong levels of public support, at least among urban populations, across Europe (Wilson 2004, Buller 2003, Ericsson & Heberlein 2003).

- 9.6. For these reasons, the response from the general public to any proposed beaver reintroduction is likely to be similar to that of the pine marten (Bright *et al.* 2000), whose reintroduction was supported by nearly 90% of the general public surveyed. In a small experimental study in Scotland, over 70% of respondents surveyed by Philip & MacMillan (2005) supported the reintroduction of native species. When asked specifically about reintroducing beaver, the most commonly cited reasons included the basic principle of reintroducing once native species (identified by 27% of respondents), environmental benefits (25%), such as to biodiversity and water quality, and boosts to tourism (23%).
- 9.7. That suggestion about the comparative popularity of beaver is borne out by a systematic review of UK press coverage of beavers in the period 1998-2008. A search of the ProQuest UK database of 68 national and regional newspapers found 80 articles featuring the term 'beaver'. Most of the coverage of beaver reintroductions was favourable, with celebratory headlines such as 'Back from the Dead' (*Independent* 10.04.08), 'The buck-toothed eco-warriors' (*The Times* 22.03.03), and 'Blighty Beavers Build First Dam' (*The Sun* 11.06.08). Although the opposition of some local groups was reported in coverage of the political debate over the Scottish reintroduction, it was dwarfed by more favourable coverage pointing to biodiversity benefits and to the glories of restoring a once extinct species. Likewise several pieces in the Travel sections highlighted the pleasures of eco-tourist trips to beaver enclosures in Kent and Scotland. The affectionate and curious tone of beaver coverage, which was broadly supportive of their re-introduction, stands in marked contrast to the media coverage of wild boar populations in southern England. Whereas there was no media discussion of the disease or biosecurity risks posed by reintroducing beaver, wild boar were cast as a potential menace to public health and safety as well as to livestock and crops (Goulding & Roper 2002). Given the well recognized potential for adverse media coverage to amplify public perceptions of risk (Pidgeon *et al.* 2003), any proposed beaver reintroduction scheme will need a carefully designed media and public communication strategy.
- 9.8. The results of this literature review into public perceptions of beaver and of species reintroductions more generally are consistent with those of recent public consultations elsewhere in the UK over proposals to reintroduce European beavers. In 1998, Scottish Natural Heritage commissioned a survey of 2141 people across Scotland. It found 63% supported reintroducing beavers, with only 12% against and 25% without a view (Scott Porter Research & Marketing Ltd 1998). A subsequent, 2001 public consultation near the proposed Knapdale site for a trial reintroduction found similar levels of public support (65% in favour) but larger and arguably more entrenched levels of opposition, with 27.5% of respondents opposed (SNH 2001). In the most recent public consultation by the Wildlife Trust (2007), 73% of all respondents favoured plans to reintroduce beaver to Knapdale, whereas 57% of the subset of local respondents were opposed. Some limited public consultations about beaver reintroductions have also been undertaken in Wales, but results have not yet been published.
- 9.9. While more research would be required to ascertain the views of the general public in England, there are good reasons to assume that there would be broad but shallow support from the public at large for the general idea of reintroducing beaver in England. However it is also clear that this support is likely to be relatively 'soft'. Members of the general public are neither particularly interested in nor well-informed about the issue. This suggests that the responses of stakeholder groups and other opinion leaders will be key both to the success of any proposed reintroduction and to shaping broader public perceptions of it.

## **Views of key stakeholders and interest groups**

- 9.10. The views of key stakeholders about the feasibility of reintroducing European beaver to England were ascertained through telephone interviews conducted in the spring and early summer of 2008. The list of organizations to consult was drawn up in consultation with the

project funders. Several organizations either refused comment or proved unable to provide a response within the allotted time. The list of those ultimately responding is provided below in Table 9.1.

Table 9.1. List of organizations formally consulted

Anglers' Conservation Association(ACA)	Association of Drainage Authorities (ADA)	Association of River Trusts (ART)
British Association for Shooting and Conservation (BASC)	British Waterways	Centre for Ecology & Hydrology (CEH)
Confederation of Forest Industries (ConFor)	Campaign to Protect Rural England (CPRE)	Country Land & Business Association (CLA)
Environment Agency	Forestry Commission (FC)	Game and Wildlife Conservation Trust (GCT)
Kent Wildlife Trust	National Farmers Union (NFU)	National Gamekeepers Organisation (NGO)
National Trust (NT)	Pond Conservation	Royal Society for the Protection of Birds (RSPB)
Salmon and Trout Association (STA)	Woodland Trust (WT)	

- 9.11. Representatives of each of those organizations were identified from the personal contacts of the research team and advisory board and from the lists of those previously contacted by Natural England about the issue.
- 9.12. Interviews were conducted using a standard interview protocol of six questions:
- Does your organisation have a formal position on the feasibility and impacts of reintroducing the European beaver to England? If so would you care to share it with us?
  - What, if any, concerns would your organisation have about any potential reintroduction?
  - How might those concerns be allayed or addressed?
  - What, if any, benefits would you associate with the reintroduction of the European beaver to England?
  - How might these benefits be best achieved?
  - Are there any locations within England that you would see as either particularly well suited or inappropriate for hosting any proposed reintroduction?
- 9.13. Of the 20 respondents interviewed, 9 expressed support for reintroducing beaver, with 5 opposed and a further 6 expressing no clear-cut view. It should be noted, however, that many organisations, particularly the smaller, less professionalised ones, have yet to consider the issue. At the time of our survey, only two organisations, the Environment Agency and the Salmon & Trout Association, had gone so far as to prepare a formal position paper on the issue of reintroducing beaver to Britain, though with the granting of a licence for a trial reintroduction in Scotland, and consultations under way in Wales, it is likely that more will follow suit. There were also clear differences between those individuals and organisations with a strong scientific and technical grounding and those without, who were more likely both to raise issues, such as alleged fish predation by beavers, without any scientific foundation and to express a desire for more official information from Natural England about the issue. Thus the views described below may well change in the event of an actual consultation over any concrete reintroduction proposal. Indeed a number of organizations expressed the desire for much more information to inform their response to any future consultation over actually reintroducing beaver to any particular locality.

## Perceived benefits of beaver reintroductions

- 9.14. The benefits of reintroducing beaver mentioned by respondents are listed in Table 9.2. Unlike the members of the general public interviewed by Philip & MacMillan (2005), none of our respondents advanced any de-ontological arguments for reintroduction as a matter of principle. Those in favour of beaver introduction tended to focus on concrete benefits rather than on the rights of the beaver or the moral or aesthetic 'goodness' of reintroducing them. This utilitarian focus may be partly a function of our survey design, as well as the preference of scientific policy officers for the factual register of impacts over a more 'subjective' and value-laden one of principles.

Table 9.2. Perceived benefits of beaver reintroductions

<b>Potential benefits cited by respondents</b>	<b>Number mentioning</b>
Ecological improvements to water quality, habitat, biodiversity	11
Economic potential from ecotourism	10
Inspire public appreciation for the environment	7
Ameliorate flood risk	3
Forest regeneration	5

- 9.15. Apart from those groups so implacably opposed to beaver reintroduction as to deny any benefits at all, there was a fair bit of consensus about what the benefits are likely to be. The most common cited benefits were ecological. All but one of those in favour of beaver reintroduction pointed to their potential to improve riparian ecosystem services. Even some organisations otherwise antipathetic to beaver re-introduction recognized that they would bring some ecological benefits, such as improvements to the habitats, biodiversity, and water quality of English watercourses. However, appreciation of these ecological benefits depends upon scientific training. Water quality improvements, for example, cannot be directly apprehended by the senses while the role of beavers in re-engineering bankside trees and other vegetation occurs so slowly, that it requires some training and careful observation to appreciate. It is noteworthy that the larger, more professionalised stakeholder groups, whose representatives had scientific training, most consistently appreciated the ecological benefits of beaver reintroductions. For lay people these ecological benefits will not necessarily be self-evident. Indeed one of our respondents explained that while she personally saw the potential ecological benefits of beaver reintroduction, she thought the rank and file membership of her organisation would require some convincing. This suggests the importance of a clear and carefully designed communication strategy for any future consultation over proposed reintroduction plans.
- 9.16. Ten respondents also cited the potential for economic benefits stemming from eco-tourism. Compared to other mammals beaver are relatively easy to observe, and the volume of media interest suggests that they would attract visitors. Indeed one large land owning interest group is hopeful that beaver would help draw visitors and revenue that could be used to fund other projects that would allow visitors to enjoy the countryside in many different ways (e.g. building paths and interpretation centres). A recent study estimated the potential tourist benefits from beaver to the local economy in Wales at £2-4 million/year (Campbell *et al.* 2007). The valuation methods used in such studies are notoriously uncertain, so such estimates must be treated with caution. Realising those tourist benefits will require any trial reintroduction to be located so as to be relatively accessible to visitors.
- 9.17. In addition to the direct economic benefits from beaver related tourism, several large conservation organizations were also hopeful about the educational benefits and the potential for visitors coming to see beavers being encouraged develop a richer appreciation of ecosystem function more generally.

## Stakeholder concerns

- 9.18. Respondents also raised a number of concerns about the reintroduction of European beaver to England, which are summarised in Table 9.3. Many of these concerns were also raised by

organisations otherwise supportive of beaver reintroduction. As such they cannot be dismissed as mere rationalisation for opposition to reintroduction.

- 9.19. Stakeholders raised a number of linked concerns about the legal status and management regime for dealing with introduced beaver. There was uncertainty about how any nuisance animals would be dealt with and by whom. Even those supporting a potential reintroduction warned they might take a different view if reintroduced beavers were to be treated as a protected species that could not be removed if found to cause nuisance. But how would any nuisance animals be dealt with? Would landowners be allowed to remove and kill problem animals, for instance? While a few informants favoured that, others believed it would be better if there were a scheme to trap and relocate nuisance beavers, though others raised concerns about the delays and cumbersome application process this might involve. There was widespread agreement on the need for these questions about the management of any introduced beavers to be clarified and clearly communicated as part of the consultation over any planned introduction.

Table 9.3. Perceived concerns of beaver reintroductions

Concerns cited by respondents	Number mentioning
Compensation scheme to pay for damages	12
Legal status of and liability for managing nuisance animals	9
Management and responsibility for nuisance animals	9
Local flooding	9
Damage to crops, woodlands, and grazing	7
Effects on fish populations from beaver dams and beavers 'eating fish'	4
Disease and biosafety risk to livestock and native biota	3
Hazards posed by beaver burrows to livestock, farm machinery and ramblers	2
Obstruction to paths, canals and waterways from beaver dams and debris	2
Effects on landscapes potentially already vulnerable to climate change	1

- 9.20. There were also concerns raised about civil liability for damage caused by beavers. Two informants worried about being sued by third parties injured by fallen trees or tripping in holes dug by beavers on their land. But much more common were questions about whether and how landowners might be compensated for damage they themselves might suffer from beaver.
- 9.21. A dozen informants advocated a government compensation scheme, as is common in some European countries, to pay landowners for any damages inflicted by reintroduced beavers. Experience with compensation schemes for large carnivores suggests they are publicly popular, at least in the first instance (Naughton-Treves *et al.* 2003), and can be important in helping to establish or protect small populations of rare or threatened species (Cope *et al.* 2003). In addition to the long-term cost implications, however, critics of such schemes also complain that compensation schemes can lead to a moral hazard by discouraging land owners from adapting their activities to the presence of wildlife (Bulte & Rondeau 2005). Nyhus *et al.* (2003) identify some key determinants for the success of any compensation programme.
- 9.22. Such concerns about the management of any reintroduced beaver populations were compounded by a general lack of confidence in the ability of Government to manage any reintroduction properly. There is the perception among at least some stakeholders that past reintroductions in England have been badly managed. Without prompting several respondents commented that once a species has been reintroduced, often with support from Defra, there is a tendency for central government then to wash its hands of any problems associated with its

subsequent management. Accordingly 9 informants recommended the importance of active local involvement in the planning and management of any proposed beaver reintroduction.

- 9.23. In terms of substantive ecological impacts, the most common concern was about the potential for beavers to cause local flooding, either directly through dam building, blocking culverts or tunnelling into flood defences, or indirectly by raising local water tables or releasing debris that could interfere with drainage systems. This issue was raised by nearly half of all respondents (9 out of 20). As one informant noted, contemporary drainage and canal infrastructures were not designed with beavers in mind, and so those responsible for managing such systems are concerned about the potential impacts of beaver upon them. Flooding can also damage standing timber. The consequences of such flooding are particularly severe for small woodland owners who could see a substantial portion of their holdings damaged by a single beaver pond. The potential impacts of local flooding on farmland was also a common concern, not just for farming and land owner interests, but also for those supportive of beaver introduction but concerned about alienating local landowners whose support is key to any successful reintroduction. The possibility that beaver dams might flood agricultural lands was also a common concern; this included concern about the impact of beavers' canals and burrows that affect the productivity of lands. These canals are also seen as a possible way beavers would access cereal crops and create problems.
- 9.24. Informants also expressed concern about a variety of other ecological impacts of beaver reintroduction. Five informants mentioned the potential for beavers to eat crops, plantation woodlands, and ornamental vegetation. Three expressed concerns about biosafety and the possibility that beavers, like badgers, might spread TB or other diseases to livestock, or even human populations. Others wondered about the confidence with which the ecological impacts of beaver on the landscape could be predicted. Though perhaps once native, beaver have not been extant in England for at least five centuries, probably longer in many places. Accordingly one opponent argued that beavers should really be treated as an introduced species and, on a precautionary basis, subject to a much higher regulatory standard than those associated with 'reintroduced species', which they believed the current legislative framework assumes should go ahead unless proven unsafe or undesirable. Several people wondered whether reintroducing beaver might result in similar havoc as the coypu, which proved so damaging and difficult to eradicate once introduced to Norfolk and eastern England. In terms of building stakeholder confidence, several informants recommended some careful pilot studies in areas where beaver could be easily controlled, or eliminated, if they proved troublesome.
- 9.25. Fishing interests, in particular, were worried about the effects of beaver on recreational fish populations. While some, scientifically trained informants were optimistic about the potential for beavers to improve water quality, and thus fish stocks, others feared the effects of dams on spawning fish populations and even that beaver, like otters, might prey on fish. Other organisations, not necessarily associated with angling activities, were also worried that impacts on fish migration could degenerate into conflicts over the accessibility of lands. In other words, some were worried that large land owners could limit access to their properties in order to protect the fish remaining in the rivers next to their land. Powerful lobbies can have more influence than small organisations in accessing rivers for activities other than angling.
- 9.26. Some of these concerns, such as the alleged fish eating habits of the herbivorous beaver (a myth mentioned more than once!) have no scientific or factual basis, and might be addressed through an information strategy accompanying the consultation over any planned re-introduction. Indeed, a number of stakeholders, particularly the smaller and less well-resourced organizations, wanted to have more information about the European beaver to help them decide upon a formal policy position on the issue.
- 9.27. However, research in risk communication suggests that the success of such communication campaigns depends heavily upon the trustworthiness and perceived competence and credibility of the information source (Lofstedt 2005, Cvetkovich & Winter 2003). Given the concerns expressed about the competence and over-confidence of Defra and Natural England, any communication strategy will require careful planning. In particular, attention will need to be paid to the appearance of partiality and conflict of interest should Natural England become involved, itself, in any future proposals to reintroduce beaver, given its dual role as both regulator and potential advocate of any such application. One opponent of beaver

reintroductions noted bitterly that in Scotland, Scottish Natural Heritage has set itself up as judge and jury of its own licensing application in what was condemned as a 'sham' process. Given the importance of trust to public perceptions of risk, it may be advisable that the objective factual information to accompany any public consultations over reintroducing beaver be provided by a third parties, perhaps from the university sector, or other highly trusted institutions, like the Natural History Museum, rather than Natural England or from any bodies involved in actually making or judging an application to re-introduce beaver.

## Conclusions and recommendations

- 9.28. While a few interest groups are intractably opposed, the majority of organisations interviewed for this project, like the general public at large, are likely to be cautiously, sometimes even enthusiastically, supportive of any proposals to reintroduce European beaver to England. To maximize the benefits of any reintroduction and minimize the concerns, it is important to highlight the recommendations made by stakeholders themselves about how they would like to see any future reintroduction managed. In particular, there is clear consensus on four points:
- I. Any future reintroduction should be piloted in some small, controlled areas, where the impacts of beaver could be assessed, and if necessary, reversed by the removal of beavers. Some demonstration projects would both provide scientific data about their likely impacts and an educational opportunity to win over doubters and build wider public support. It is important to recognize that many of the concerns expressed about the beaver are at least in part a function of unfamiliarity, which pilot projects would help to address.
  - II. The legal status and management responsibility for any pilot introduction must be clear. Many stakeholders would like to see some sort of compensation scheme to help assure worried landowners, and others, that damages from beaver will be minimized and that any nuisance animals will be dealt with promptly and efficiently, preferably at no cost to the parties suffering the nuisance. Defining clear guidelines about when, how, by whom, and at whose expense problem animals would be trapped and removed was regarded as essential by several organisations.
  - III. The details of any specific reintroduction plans must include extensive public consultations. To be meaningful, consultations must take place early enough in the planning process to have a substantive influence on the details of whether, where, when, and how beavers are introduced and managed. As well as being the 'right' thing to do, many informants argued that involving affected parties in the plans would ensure that local concerns were met and opposition was minimized.
  - IV. Public consultations must be supported by some objective and trustworthy information about the European beaver and their likely impacts on the landscape. Realizing the economic and educational benefits of reintroducing the beaver also requires facilities so that visitors can come see and learn about them.
- 9.29. While there was consensus on those four basic principles, informants offered two contrasting views on where any pilot reintroduction would best be located. On the one hand there was the view that beaver should be placed in areas with low human population density and far from large settlements, so to reduce the potential for conflict between beaver and people. On the other hand, there was the alternative view that realizing the full economic, as indeed the ecological, benefits of reintroducing beaver would require putting them in some accessible areas, perhaps floodplains or brownfield, post-industrial landscapes, where the beaver, as a keystone species, can make a real difference with a good chance of delivering demonstrable public benefit.



# 10. The financial costs and benefits of reintroducing beavers

## Summary

- 10.1. There are an appreciable number of studies that have looked at the socioeconomic and financial costs of the loss of ecosystem services associated with a loss of biodiversity. However, there is only one study from Germany to have considered beaver introductions, and then only in relation to self-purification of the river. Although based on several assumptions, the indication is that considerable financial benefits will accrue from nitrogen retention after beavers have been introduced, and one could extend that generality to other ecosystem services such as flood alleviation and erosion control, although financial estimates based on the Replacement Cost Method still have to be done. Considerable financial benefits can also be gained from tourism and recreation, even though this may depend on how tourism is managed.
- 10.2. The available evidence suggests that financial costs resulting from damage to trees, ditches, dykes, ponds, roads and flooding of agricultural land, as a result of beaver reintroductions are low, and that mitigation costs are small and more than offset by the financial benefits in a full Cost-Benefit Analysis (CBA). Nevertheless, because the monetary values of all ecosystem service benefits have not been fully quantified, damage control and mitigation will be seen to be of primary economic importance. Moreover, the distribution of financial costs and benefits of beaver reintroductions will be biased towards different sectors of society or stakeholders (e.g. foresters and farmers versus organisations involved in wastewater treatment and flood control respectively). Consequently, the medium term financial implications of beaver introductions must be taken into account in a full CBA during the planning stage of a beaver reintroduction programme.

## Introduction

- 10.3. In economic terms, the costs and benefits of conservation initiatives such as species reintroductions are complex and not easy to estimate, but nevertheless critically important (e.g. Adams 2004). One of the more obvious benefits is from wildlife tourism, or ecotourism, which is tourism designed to have minimal social and environmental impacts (Adams 2004). Although beavers are mostly active at night, they can sometimes be seen during daylight hours, especially during the summer, and, of course, they leave many noticeable signs of their presence, such as dams, canals, lodges and felled wood. Beaver ecotourism has been popular in European countries such as Denmark, Belgium and Germany (e.g. Bräuer 2006, Gaywood *et al.* 2008). Traditionally there are also benefits that arise from beaver products such as meat, fur and castoreum, although these are unlikely to be relevant if beavers are to return to England. However, there are equally important but less tangible benefits accruing from ecosystem services provided by beavers. These refer to benefits to humans that arise from, for example, improving water quality or alleviating flooding. The financial benefits here relate to savings made by the government or environmental organisations that would otherwise have to pay for these services. On the other side of the equation there are costs with managing beaver populations and dealing with possible impacts such as damage to crops or highly valued trees, blocking culverts and digging in embankments. In this chapter we explain how the financial costs and benefits of reintroducing beavers may be estimated, and give an indication of what the balance sheet may look like based on present knowledge.

## Financial benefits

- 10.4. The Total Economic Value (TEV) conceptual framework for ecosystem goods and services looks at the benefits that are provided to humans by the stock of natural capital (Defra 2007b, POST 2007) and breaks down values into use values (e.g. consumptive values) and non-use values (e.g. intangible human benefits). Applying this framework (see POST 2007) to beaver

introductions into England, the following values can be identified (after MASR (2005), also see POST 2007):

- 1 Use values
  - a. Direct use values
    - i Extractive use values of beavers: food, castoreum and fur;
    - ii Non extractive use values of beavers: tourism and recreation;
  - b. Indirect use values
    - i Indirect support and protection to human activities: ecosystem services; provided by beavers such as creation of wetlands, water storage, improved water quality, erosion control, and sediment deposition;
- 2 Non-use values
  - a. Altruistic value – derived from knowing that others can enjoy beavers and the ecosystems in which they live;
  - b. Bequest value – passing on ecosystems services provided by beavers to future generations;
  - c. Existence value – the satisfaction to humans knowing that beavers have been reintroduced and therefore now exist again in England;
- 3 Option values - future uses, presently unforeseen.

10.5. Methods to carry out a Cost Benefit Analysis (CBA) on beaver include:

- 1 Market prices for ecosystem goods and services, e.g. meat, fur, castoreum;
- 2 Non market values for ecosystem services:
  - a. Cost methods, such as the cost of damage caused by the loss of an ecosystem service (e.g. expenditure to prevent that damage, the Damage Cost Avoided Method DCAM, or the cost of replacing the ecosystem service, the Replacement Cost Method, RCM<sup>11</sup>). Lower costs to maintain ecosystem services may be revealed after reintroduction of beavers;
  - b. Revealed preference methods, for example, travel and access costs that tourists are willing to pay (the Contingent Valuation Method, CVM<sup>12</sup>);

10.6. In contrast to the situation in North America and some parts of Europe (Busher & Dzieciolowski 1999, Baker & Hill 2003, Müller-Schwarze & Sun 2003), direct, extractive use values providing market prices for beaver goods are unlikely to apply in England, as hunting is unlikely to be an option.

10.7. Non-market ecosystem services are difficult to cost, but CVM and RCM valuation methods have been combined to illustrate how a cost benefit analysis can be applied to a beaver reintroduction in the Spessart Mountains in Germany in 1987/88 (Table 10.1.). In addition to reintroducing beaver, the reintroduction programme aimed to revitalise the flood plain. Eighteen beavers were released and buffer strips were bought and managed. The scheme was successful and the population of beavers is now viable.

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<sup>11</sup>The DCAM and RCM are related and estimate values of ecosystem services based on either the costs of avoiding damages due to lost services or the cost of replacing ecosystem services (or of providing substitute services.) respectively. They assume that the costs of avoiding damages or replacing ecosystems or their services provide useful estimates of the value of these ecosystems or services.

<sup>12</sup> The contingent valuation method (CVM) is used to estimate economic use and non-use values for ecosystem and environmental services. It is based on surveying peoples opinions and asking how much are they willing to pay, *contingent* on a specific scenario and description of the environmental service.

Table 10.1. Ecosystem goods and services affected by the beaver reintroduction, classified according to the Millennium Assessment categories (MASR, 2005) – (from Bräuer 2006).

<b>Observed changes [1]</b>		
<b>Direct consequences</b>	<b>Cultural services</b>	<b>Contingent Valuation Method</b>
	Conservation of an endangered species	
	Conservation of an endangered ecosystem	
	Increased biodiversity	
	<b>Recreation and tourism (observation)</b>	
	Beaver and succession species	
	Landscape impression of the river (alteration in the structure of the river bed)	
	Landscape impression of the floodplain (Succession on buffer strips)	
<b>Indirect consequences</b>	<b>Regulating services</b>	<b>Replacement Cost Method</b>
	Self purification of the river	
	[Flood protection (lower running velocity)]	
	[Flood protection (additional space for retention)]	
	[Erosion control (riverine vegetation)]	<b>Market Prices</b>
	<b>Provisioning Services (Damage in cultural landscape)</b>	
	Flooding of agricultural land	
	Damage to forestry	
Damage to hydraulic engineering (dykes, drainage channels)		
[1] Consequences in brackets [] were not quantified		

10.8. The study looked at revenues from nitrogen regulation in relation to purification of the river and from recreation and tourism. Nitrogen retention was estimated for the river and the flooded areas on the floodplains. Dam building by beavers resulted in the creation of 13 pools and ponds. Bräuer (2006) estimated the additional nitrogen retention of 2800 kgN per annum in the river and of 1900 kgN per annum in the floodplains (Table 10.2.). Note that estimates on the impact of increased nitrogen retention for the overall river and its water quality were not possible, but since German rivers suffer from high nutrient load, the reductions were believed to have an overall positive effect of the quality of the ecosystem. The economic value of the nitrogen retention and ecosystem service was calculated by working out what the cost of reducing the same amount of nitrogen through technical solutions using (1) agri-environmental schemes to reduce fertiliser application (estimated at €2.56 /kgN) and (2) an end-of-the pipe solution where the nitrogen is removed in a sewage plant (estimated marginal costs of €7.68 /kgN). Thus the value of the ecosystem service accounted for (1) €12,000/year (agri-environmental) or (2) €36,000/year (sewage). Taking into account the establishment of the beaver population, and for an assumed duration of the programme of 25 years, the lower estimate of nitrogen removal was extrapolated to €250,300 (Table 10.3.).

Table 10.2. Additional N-Retention in river and the floodplain. Results of minimum and maximum and mean (Bräuer 2006).

		Mean	Min [1]	Max [1]
River	[k N/year]	2800	210	3600
Floodplain	[kg N/year]	1900	640	3100
Project duration [2]	[kg N/25 years]	115,633	66,354	164,991

[1] Population development is considered during the project duration (1987-2012)

10.9. Using the CVM approach, visitors were asked to say how much they were willing to pay for the conservation programme in the form of a nature tax. Bräuer (2006) found this to vary between €0.74 and €1.11 per person per day's visit to the Spessart Mountains. Taking into account the number of visitors to the area of the reintroduction, increased revenues from tourism were estimated as ~€550,000 per year or € 17,251,700 for the duration of the project (Table 10.3.). In a similar exercise, Campbell *et al.* (2007) questioned people involved in research, management and tourism of beavers in Europe, and, by looking at revenue currently generated by wildlife attractions in England, they estimate that a beaver site could potentially provide a net income of £1.25 million to £2 million a year (Table 10.4.)<sup>13</sup>.

## Cost-benefit analysis

10.10. The cost-benefit analysis (CBA) of the Germany reintroduction programme over the 25 year period included fixed costs for land purchase (€1,200,000) and acquiring beavers at the beginning of the programme as well as compensation payments to local stakeholders and administration and management costs (€ 600,000) (Table 10.3.). From this analysis, the benefits accrued clearly exceed the costs of the reintroduction programme. Campbell *et al.* (2007) also show the clear monetary benefits that might be forthcoming from beaver ecotourism. However, other regulating services (e.g. flood control) and costs resulting from beaver damage and flooding of agricultural land (Table 10.1.), would need to be estimated for a full CBA.

Table 10.3. Cost-Benefit Analysis of the programme for an assumed duration of 25 years (Bräuer 2006).

	Position	Economic effects (€)
Costs	Initiation costs of the programme (land purchase, beavers, etc)	1,244,500
	Income effects of local stakeholders (compensation payments)	1,200 <sup>2</sup>
	Administration and management (personal costs)	634,000
	<i>Sum costs</i>	<i>1,879,700</i>
Benefits	Cultural services, recreation and tourism	17,251,700
	Regulating service (N-Retention)	250,300
	<i>Sum benefits</i>	<i>17,502,000</i>
	Total	15,622,300
<sup>2</sup> The original value for the calculations was 5 DM		

<sup>13</sup> Campbell *et al.* (2007) should be consulted on the details about how they estimated the potential economic impact of beavers on wildlife tourism in Britain.

Table 10.4. Projected income from a beaver reintroduction site based in England. Total income was calculated from the net regional income, based on the 'Wildlife Attraction: Visitor Expenditure Model' <sup>14</sup> (from Campbell *et al.* 2007).

Region	Mean annual no. of visitors to a wildlife attraction	Number of visitors used in model	Net impact in region	Mean admission charge	Potential admission income	Total income
East (24)	102,315	102,270	£1,090,613	£7.41	£757,820	£1,848,433
East Midlands (3)	110,502	110,600	£1,270,801	£7.41	£819,546	£2,090,347
North East (3)	24,028	23,970	£260,377	£7.41	£177,617	£437,994
North West (7)	203,738	203,740	£2,206,766	£7.41	£1,509,713	£3,716,479
South East (11)	135,150	135,240	£1,595,056	£7.41	£1,002,128	£2,597,184
South West (18)	241,132	241,070	£2,879,909	£7.41	£1,786,328	£4,666,237
West Midlands (5)	41,552	41,475	£483,700	£7.41	£307,329	£791,029
Yorkshire and Humber (1)	21,036	21,100	£4,350	£7.41	£156,351	£380,701
MEAN			£1,223,946		£814,604	£2,066,050

- 10.11. In England flood alleviation as a result of dam building could be a very beneficial ecosystem service. Five million people, in two million properties, live in flood risk areas in England and Wales (Environment Agency 2008). Figures for annual damage from flooding could rise from the present level of £1 billion to about £25 billion in the future in the worst-case scenario. More effective land management will be needed to reduce the risks in most scenarios (Future Flooding Report 2004<sup>15</sup>). Beaver dams reduce peak flows and permit a gradual release of water, and maintain or elevate the water table. Müller-Schwarze & Sun (2003) give several examples of how beavers have been used to revitalise riparian ecosystems and ameliorate flooding in North America.
- 10.12. The balance between costs and benefits is one of public perception as well as monetary value. In Wyoming, land managers were concerned that beaver caused problems when they ring-barked trees, blocked irrigation ditches and culverts, flooded pastures, roads, crops, and timber. However, 45% of private landowners with beaver on their land and all public land managers were interested in using beaver for riparian management (McKinstry & Anderson 1999 in Baker & Hill 2003).
- 10.13. Campbell *et al.* (2007) have provided a preliminary analysis of market prices associated with mitigation costs and beaver management by asking experts in research and management in mainland Europe. They found that conflict between beaver and human land use to be generally low and costs generally low (Figure 10.1). Public perception of beavers was generally positive (76% responses, N=17) and only occasionally negative (6%). Conflict between beavers and humans was in the main low and localised (Table 10.5). Information on the management of beavers from this study is considered in Chapter 12.

<sup>14</sup> The 'Wildlife Attraction: Visitor Expenditure Model' provides a tool for estimating the economic impact generated by tourists visiting a given attraction. It is not a substitute for the detailed survey work and economic analysis, but does provide a starting point or benchmark for estimating the impact of visitors to wildlife attractions : taken from: <http://www.ukbap.org.uk/ebg/library.asp>. Note there are many assumptions that underpin the model.

<sup>15</sup> Foresight: Future Flooding Report. Office of Science and Technology

Figure 10.1. Frequency of reported costs of each beaver population by land-use category \* = median or typical cost range for the land-use (from Campbell *et al.* 2007). Note beaver populations varied from 20 to >100,000.

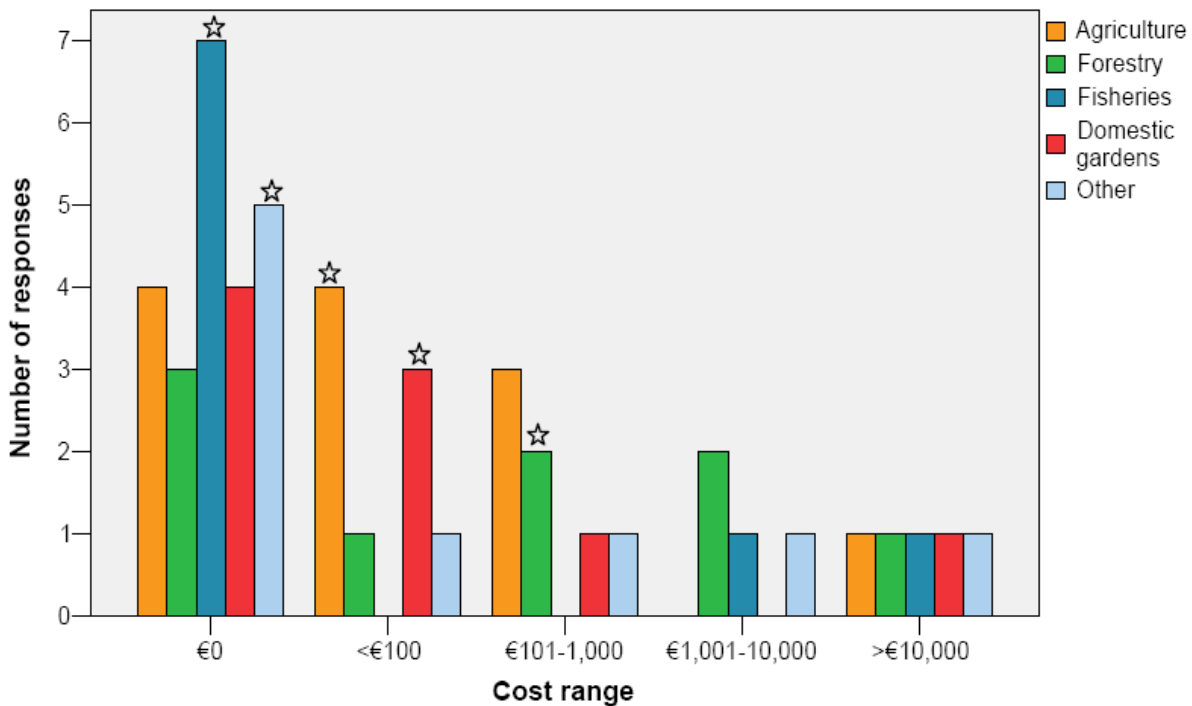


Table 10.5. Costs and perceptions according to land-use categories from 18 replies to questionnaires sent to managers and researchers of beaver populations in Europe (Campbell *et al.* 2007).

	Land-use				
	Agriculture	Forestry	Fisheries	Domestic gardens	Other land-use
% of respondents with concerns before reintroduction	38	38	7	0	22
Median costs (Euros) per beaver population	1-100	101-1000	0*	1-100	0**
Conflict as a result of...	foraging on crops; loss of agricultural land due to flooding	foraging on trees; loss of forest land/trees due to flooding	damage to fish ponds	occasional felling of ornamental trees; occasional flooding	damage to banks and dykes
Scale of conflict	Localised and small scale	Localised and small scale	Very localised	Localised and very small scale	Rare

\*two reports of costs, one due to a breached fish pond

\*\*three incidences of damage to dykes and pond banks in the Netherlands and the Czech Republic

# 11. Beaver management

## Summary

11.1. Methods to control beavers are well-established and can be used to control beavers subsequent to reintroductions, and to mitigate any detrimental impacts. Thus, providing funding is secured and appropriate management strategies are in place before release, there are minimal risks associated with reintroducing beaver into the English countryside. Most beaver-human interactions tend to occur within a narrow zone alongside the water's edge and careful management of this zone can minimise or avoid conflicts. Flood prevention can commonly be achieved by installing beaver-proof culverts or devices that control water levels, or by dam removal. Damage to vegetation or crops can be reduced by using physical (e.g. fencing) or chemical (e.g. repellents) barriers. In extreme cases, problem individuals or family groups may be removed by live-trapping or netting, and either translocated or, as a last resort, culled.

## Introduction

- 11.2. Since the early part of the 20<sup>th</sup> century, beaver reintroductions have taken place in many European countries, and by the beginning of the 21<sup>st</sup> century they could be found throughout most of Continental Europe (Chapter 1). The recovery of beaver populations in many places has been sufficiently successful that local and national authorities have had to introduce management schemes to reduce further population growth (see the various chapters in Busher & Dzieciolowski 1999). Different countries adopt slightly different approaches to the regulation and management of beaver populations. For example, one of the most straightforward management programmes is found in Sweden. Here, beavers are hunted with rifles between 1<sup>st</sup> October and 15<sup>th</sup> May; there is no bag limit. Shotguns are not permitted, live traps rarely employed and the use of conibear traps<sup>16</sup> is tightly regulated. These regulations are in place to prevent capture of non-target species, notably otters (Hartman 1999). Hunting for sport is unlikely to occur if beavers were reintroduced to England. Therefore, in this section we predominantly consider the possible types of management and mitigation that might occur in this country after beavers have been reintroduced. We also discuss mitigation measures that should be considered in the target area before beavers are released. Issues surrounding the health and welfare of beavers involved in translocated programmes, and of the general public, have been considered in Chapter 8.
- 11.3. Generally, the management of beaver distribution should operate at the watershed scale (Halley & Rosell 2002) and the landscape context of candidate reintroduction sites should be considered with respect to future management options. Many beaver-human conflicts are local in nature with both costs and benefits recognised by landowners (see Macdonald *et al.* 1995; Chapters 10 and 11). Public opinion is an important consideration when choosing methods to control beaver damage. Many people have an emotional attachment to wild animals and oppose control methods that may cause pain, suffering, or death (Baker & Hill 2003).
- 11.4. In Europe most beaver–human conflicts are caused by beavers feeding on cultivated plants such as crops and trees, or, occasionally, blocking culverts and drainage pipes or, through their dam building activities, flooding roads, forests and agricultural land (see Chapters 3, 11, Richard 1985; Heidecke & Klenner-Fringes 1992 in Halley & Rossell 2002; Rosell & Parker 1995 in Halley & Rossell 2002). Beavers that come into conflict with humans are generally called *nuisance beavers*.

## Flood control

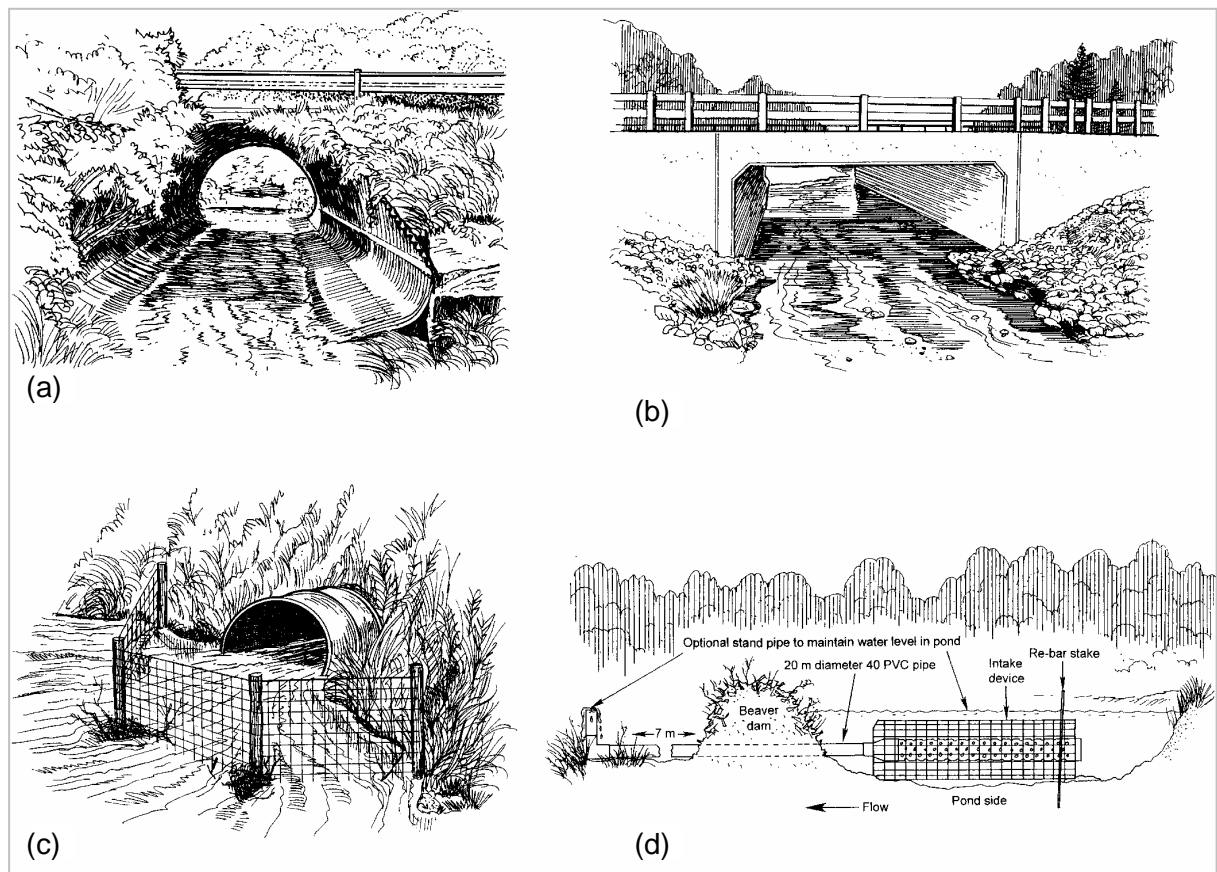
11.5. Damage occurs when beavers block culverts or impound water against the beds of roads or railways, causing flooding. Prevention of flooding can often be managed by installation of beaver-proof road culverts and other water control structures, by inserting flow control devices

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<sup>16</sup> Body-holding traps that clamp onto various parts of the body of an animal – they do not generally kill animals swiftly.

in dams or by removing dams completely (see Figure 11.1; MacDonald *et al.* 1995; Rosell & Pedersen 1999). Techniques for minimising or preventing beavers from blocking road drains include using oversized pipe-arch culverts (Figure 11.1A), low-profile box culverts (Figure 11.1B), and various designs of beaver exclosure fencing (Figure 11.1C) which prevent beavers from building a dam at the upstream end of a road drain (Hammerson 1994; Jensen *et al.* 1999 in Baker & Hill 2003). Flow control devices installed in existing beaver dams have been very effective at mitigating damage to roads or other developments, while maintaining the ecological and aesthetic values of beaver presence. For example, the Clemson beaver pond leveler (Figure 11.1D) can control the water level in beaver ponds by using tubes or similar structures laid perpendicular to the dam, with the upstream end porous and protected from blocking by beaver (Buech 1985, Hammerson 1994, Olson & Hubert 1994). The most widely used method to control flooding is to remove problem beaver dams. Removing problem dams may only be temporarily effective since beaver may rebuild dams within a few days if building materials are available. Making sites unsuitable to beaver is possible but may not be acceptable to landowners (Baker & Hill 2003).

Figure 11.1. Examples of water control structures used to manage Canadian beaver impacts (Baker & Hill 2003; adapted in part from Jensen *et al.* 1999).



## Riparian zone management

- 11.6. Most beaver conflicts with humans occur in a very narrow riparian zone: 75% within 20 m (Heidecke & Klenner-Fringes 1992 in Halley & Rossell 2002), and almost all within c. 100 m, of the water's edge. Nolet & Rosell (1998) suggested that restitution of at least 20 m wide zones of natural vegetation along the banks of waterways is the best way of dealing with beaver feeding damage. Current moves throughout Europe to conserve and regenerate the riparian zone around rivers, for other conservation and flood control motives, have the side-effect of both creating beaver habitat and reducing the scope for conflict with many human activities (Collen 1995; Peterken & Hughes 1995). Removing food and construction trees from alongside ditches, canals and waterways could prevent beavers settling in those areas.



## Repellents and wire fencing

11.7. Feeding damage can be reduced by chemical repellents (slaked lime, quick lime, linseed oil or predator odours), or fencing along boundaries or around individual trees (Richard 1985, Rosell & Czech 2000). In one study, beaver avoided aspen that had been painted with an extract of red maple (Müller-Schwarze *et al.* 1994). Predator odours may be a useful management tool for preventing beaver damage. For example, when painted on aspen logs, there was a strong preference against the odours of faeces from coyote, lynx, and river otter (Engelhart and Müller-Schwarze 1995). Any repellent used in England would have to have appropriate approval under the Control of Pesticides Regulations 1986. Wire mesh fencing around individual trees is a very simple and effective way of preventing damage to those trees. Fencing in general, including single-wire electric fencing, can keep beavers out of protected areas, although it can be expensive.

## Traffic collisions

11.8. With an increasing population, traffic collisions are an important cause of beaver mortality (see Chapter 8). This was found, for example, in Croatia as beavers moved to find new habitats (Sager *et al.* 2005). As with otters, fencing where roads pass close to watercourses may reduce traffic collisions (Philcox *et al.* 1999).

## Animal control

### Culling beavers

11.9. As well as hunting beavers as game animals, killing unwanted individuals is frequently the most effective way of reducing beaver damage. However, it is becoming more unacceptable to the public (Baker & Hill 2003). Available control methods include shooting, snaring, and trapping with body-hold or leghold traps; poison baits, such as strychnine and 1080, are not approved for this purpose in the UK. Live trapping would be the most effective method of controlling unwanted beavers in England, and it would enable beavers to be translocated rather than killed; this would be more acceptable to the general public (Baker & Hill 2003). Methods for controlling beaver or minimising their damage may require training and licensing.

### Live-trapping and netting

11.10. Beavers can be captured alive using a variety of different types of traps, snares or nets (see Rosell & Kvinlaug 1998, Gow 2002, Müller-Schwarze. & Haggart 2005). Traps may be set on the sides of banks or in shallow water. In some cases, beaver can be captured by nets or by hand after being flushed from lodges or dens by dogs or other means (Hill 1982; Rosell & Hovde 2001). In large river systems or lakes, surface-swimming beaver can be captured using a dip net. A dive net can be pushed down over the top of swimming beaver in shallow water, after locating them with the aid of spotlights and headlights from a motorboat (Rosell & Hovde 2001).

11.11. Live trapping methods are well-proven. Mature, resident beavers are relatively easy to locate, allowing traps to be set along their trails and paths. Locating suitable trap sites for immature dispersing beavers can be more problematic. In America, trapper created mounds, where beavers may leave territorial scent marks, are considered a good place to set traps<sup>17</sup>. Other suitable places would include at lodges and dams (Schulte & Müller-Schwarze 1999). Traps may be left unbaited in places frequently visited by beavers, or they can be baited (Rosell & Kvinlaug 1998). A variety of baits have been used, including poplar and willow stems, poplar oil, aspen twigs, castoreum, apple and carrot (e.g. Rosell & Kvinlaug 1998, Gow 2002). In sites where inundation of timber is the primary problem, timing of trapping is also important. In this case, it may be most effective to eradicate problem beaver colonies by the end of May and continue to remove immigrants from June to September, or until dispersal rates are relatively low (Houston *et al.* 1995).

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<sup>17</sup> See Beaver Control at <http://www.bugspray.com/catalog/products/page563.html>

## Fertility control

- 11.12. Chemosterilents and surgical sterilization have also been evaluated for beaver control, but remain impractical for treating wild populations on a large scale (Hill 1982, Hammerson 1994 in Baker & Hill 2003; Müller-Scwarze & Sun 2003).

## The effectiveness of control

- 11.13. Beavers live in small family groups and their movements and dispersal are constricted by the necessity to remain in close proximity to water, making them relatively straightforward to control. Beavers are territorial, and breed relatively slowly for a rodent thus, reintroduced populations are likely to be substantially easier to manage than other comparative mammalian species. For example, beavers are monogamous and have up to three offspring per year. In contrast, both coypu and muskrat, large semi-aquatic rodents that have invaded Europe (see Chapter 5), produce several litters a year of up to six or more young (Perry 1982, Gosling & Baker 2008). This slower rate of population increase will make beaver populations easier to contain if required (see Gosling & Baker 1989, Macdonald *et al.* 1995). It is notable that coypu and muskrat are the only two mammalian species that have been successfully eradicated from mainland Britain. The success of both campaigns was partially due to the restricted range of these species because of their close association with aquatic habitats (Gosling & Baker, 1989).
- 11.14. Live trapping techniques are time consuming but effective at catching beavers, with a high rate of success (Macdonald *et al.* 1995)<sup>18</sup> Resident beavers have predictable habits and leave clear signs of their presence, thus guiding the control operator on where to place traps. Transients or floaters may be more troublesome to catch quickly. However, if the necessity should arise, skilled control operators should be able to remove or eradicate beavers expeditiously.

## Methods used to manage beavers in Europe

- 11.15. As mentioned above, detailed examples of beaver management in different European countries can be found in Busher & Dzieciolowski (1999). The results from a small questionnaire study by Campbell *et al.* (2007) on how frequently they are utilised in relation different types of land-use are shown in Table 11.1. Fencing followed by dam removal and the installation of flow devices were the most common methods. Culling was occasionally used.

Table 11.1. Management techniques used in beaver conflict situations in relation to different types land use in terms of number of responses to a questionnaire sent out to 14 beaver managers and researchers in Europe (from Campbell *et al.* 2007). Note that repellents to protect trees were not mentioned by respondents in this study.

Land-use	Cull	Trans- location	Dam removal	Flow devices	Fencing	Compen- sation	Other
Agriculture	3	3	6	4	2	1	0
Forestry	3	0	7	2	3	1	0
Fisheries	1	1	4	1	0	0	0
Gardens	2	0	4	0	9	0	0
Other	2	2	3	1	0	0	2
No. respondents	3	4	7	4	9	1	2
% using technique	23	31	54	31	69	8	15

<sup>18</sup> Rosell & Kvinlaug (1998) hypothesise that European beavers are more difficult to catch than Canadian beavers, although this seems to be simply based on the notion that, *North American species often are less shy and thereby easier to trap than their European counterpart.*

## Management and the reintroduction programme

11.16. Methods to manage beavers or their impacts are well established and should prove effective in reducing any potential risks associated with releasing beavers into the English countryside. If used in an approved way, these management strategies should allay the concerns of landowners, the public and other interested parties. The recommended strategy is to adopt an integrated management approach – this refers to the use of a combination of different techniques to ensure the overall success of a management programme. It is recommended that a local management committee comprising representatives from different sectors of society (e.g. stakeholders, landowners, scientists) should be set up to oversee and monitor the success or otherwise of the reintroduction programme. In addition, for each candidate reintroduction site, the following work will be required:

- To carry out a detailed habitat analysis of sites and the surrounding landscape.
- To carry out a simulation of population growth of the introduced beavers at each site over a period of at least 5 years, and identify the most likely routes, throughout the landscape, that population expansion would follow within this time.
- To carry out an assessment of how the habitat might be modified by beavers, particularly within 20 m of the riverbank, and identify possible human-conflict situations. The latter should be discussed with local landowners and stakeholders.
- To identify trees, drains and culverts that might need protection from beavers and erect tree guards, exclusion fences or deploy repellents as necessary.
- To draw up contingency plans, including the necessary equipment, to remove beavers if required, insert water control devices in beaver ponds or carrying out other habitat management.
- To design a programme to monitor the introduced beavers for a period of at least five years.
- To estimate the costs of managing and monitoring the beavers at each site, both in the short and medium term, and identify sources of funding to pay for that management. Identify the control operators/wildlife managers who would be responsible for carrying out these activities.

11.17. It should be noted that, if there are no major barriers such as dams, beavers will spread throughout the entire river system, although movement between watersheds may be limited. If it is considered necessary, containment of the spread of beavers at a release site in England would require an ongoing trapping effort and this should be recognized at the outset of the reintroduction programme.

# Part 3: Beaver reintroductions and the way forward

# 12. Beaver reintroductions to England

## Summary

- 12.1. The evidence gathered in this report clearly shows that it is feasible to reintroduce beavers into England and that many benefits are likely to accrue, not least the potential for beavers to assist with river and floodplain restoration. Moreover, the success of reintroductions elsewhere in Europe has demonstrated the feasibility of putting in place measures to deal with any possible adverse consequences. A second phase of consultation and actions concerning beaver reintroductions to England should focus on education of the wider public about beavers, investigation of specific candidate sites for releasing beavers, drawing up detailed management plans and costings, and, if agreed by all interested parties, releasing beavers within the umbrella of pilot studies. Not only would this be a first step in the possible restoration of a native species, but also such studies would offer an unparalleled opportunity to assess and quantify the benefits that beavers could bring in terms of ecosystem services. This would not only be valuable information with regard to beavers, but would also improve our understanding of the economic, social and ecological value of ecosystem services generally.

## Mammal introductions and reintroductions

- 12.2. Many species of plants and animals have been eliminated from parts or all of their historical range, through overexploitation or habitat destruction by humans. Examples of mammals that have disappeared from Britain within the last 2000 years include: lynx *Lynx lynx* (probable date of extinction ~200 AD), brown bear *Ursus arctos* (~500 AD), wolf *Canis lupus* (~1700 AD), and wild boar *Sus scrofa* (~1500 AD) (Yalden 1999). In previous chapters we have seen that the same was true for European beaver, not only in Britain but across Europe. By the beginning of the 20th century European beavers survived in only eight refuge areas (Halley & Rosell 2002). Since then, beavers have made a remarkable recovery and returned to many of their former haunts as a result of legal protection, translocation and reintroduction programmes, and natural re-colonisation. A similar picture can be drawn for Canadian beaver in North America (e.g. Müller-Schwarze & Sun 2003).
- 12.3. Although patterns of land-use are likely to have changed since beavers disappeared across much of Europe, their return indicates that preferred food and habitat are still widely available to support viable populations. In addition, other animals do not appear to have moved in to significantly occupy the niche space of the beaver in its absence. For example, there is no evidence of competition between beavers and introduced coypu or introduced muskrat in Europe. Rather like beavers, these species are large semi-aquatic, burrowing rodents with herbivorous or omnivorous food habits, respectively. In fact, in their native North America muskrats have been recorded mixing with beavers inside beaver lodges (Hill 1982, Müller-Schwarze & Sun 2003). Introduced coypu and muskrat were eliminated from England many years ago, but they continue to flourish in Europe. Another relevant factor is that beavers appear to tolerate living in close association with humans, for example, within suburban areas and intensively managed landscapes.
- 12.4. Britain is one of only a handful of European countries where wild beavers are currently not present, and there has been great interest in restoring the species to our countryside within the last 20 years. For any reintroduction initiative, it is important to establish why the species in question disappeared in the first place. In the case of beavers and the other mammal species above, the reason was over-hunting. However, hunting beavers for sport or beaver products (fur, castoreum) in England is unlikely, and this check to population growth would no longer be a factor. Moreover, natural predators (e.g. wolf, lynx) are absent, and although introduced mink may take young beavers, their impact is considered of minor importance in North America (Hill 1982). The most likely mortality factors for beavers reintroduced into England, therefore, would appear to be disease, possibly starvation in some instances, road casualties, and control measures resulting from human-beaver interactions.

- 12.5. Another species with no natural predators that has already made an unscheduled return to the English countryside is wild boar *Sus scrofa*. Several feral populations have become established in recent years and numbers are likely to increase. Although the risk of wild boar being involved in the transmission of exotic disease to domestic pigs is considered low (Defra 2008a), the long-term impacts of wild boar are unclear, and crop damage at a local scale could be significant. It is salient that Defra (2008a) have put the onus on managing wild boar down to local communities and landowners. The question of responsibility for the control and management of a 'reinstated' species, both in the short and the long-term, is clearly a major concern for stakeholders in relation to beaver reintroductions in England. Thus, although, the main aim of a re-introduction programme is to establish a viable, free-ranging population of a species (or subspecies or race), which has become globally or locally extinct in the wild (IUCN 1998), consideration of wider issues must form part and parcel of the reintroduction programme.

## Key points concerning reintroducing beavers to Britain

- 12.6. The IUCN have established a set of guidelines on reintroductions (IUCN 1998), and any reintroduction of beavers to England should comply with the key recommendations made in those guidelines. These considerations are briefly summarised in Table 12.1. with cross-reference to the chapters of the report where further information can be found.

## Reintroducing beavers to England

- 12.7. The conclusion from this report is clear in that it is feasible to carry out reintroduction of beavers into England. Although this was a similar conclusion reached by Macdonald *et al.* (1995) in their detailed review on the feasibility of reintroducing beavers to Britain some 18 years ago, a substantive amount of new evidence supporting this conclusion has accrued over the intervening time period and has been detailed in this report. There is also a considerable body of expertise and practical knowledge about handling, holding in captivity and releasing beavers that has developed in recent years. Furthermore, the approval by the Scottish Parliament for the reintroduction of beavers into Scotland on 25<sup>th</sup> May 2008 after more than 10 years of detailed study and consultation reinforces the proposition that it is feasible to reintroduce beavers into England (also see Gaywood *et al.* 2008).
- 12.8. So, although entirely feasible, should beavers be reintroduced to England in the near future? Naturally, any reintroductions should be carried out as pilot studies. In this sense, there is an excellent opportunity, not just to trial replacing a native species that has died out because of the actions of humans, but to carry out detailed studies on the economic benefits that beavers may bring, as well as possible negative impacts on the environment and human activities, such as damage to trees, rivers, crops and wildlife. The ecosystem services, such as water purification, flood and natural hazard regulation, provided by these natural ecosystem engineers may be considerable and very beneficial to humans, but, as is evident from Chapter 10, our knowledge is limited and this aspect needs to be carefully researched, assessed and quantified. The information forthcoming would be relevant to our understanding of the economic, social and ecological value of ecosystem services in general (see Defra 2008b<sup>19</sup>).

## Characteristics of candidate release sites

- 12.9. The following should be considered as requirements for candidate release sites:
- Sympathetic land managers and conservation designations if present.
  - Good beaver habitat (e.g. low-moderate flows, presence of aquatic, semi-aquatic vegetation, bankside trees and bushes) within wetlands and/or river system with the potential for the beaver population to grow and expand across neighbouring areas within at least a five-year period.
  - Wetlands/river system with natural barriers to unlimited expansion so that containment, control or eradication is achievable if required
  - Located away from urban/suburban areas to avoid high level of interaction with humans.

<sup>19</sup> Defra: Ecosystem Services <http://www.ecosystemservices.org.uk/ecoserv.htm>, accessed 25<sup>th</sup> October 2008

- River system with headwater catchments of moderate elevations to assess effectiveness of beaver dams and managing flood risk should dams fail.
- Capacity to use fencing to prevent stock infiltrating the bankside habitats or to prevent beavers moving onto agricultural land or woodland.
- Capacity to study changes in animal and plant biodiversity before and after reintroduction, and to carry out genotyping of beavers.
- Use of degraded/partially degraded or flood-risk habitats to demonstrate potential restoration of natural habitat features and the water table, flood alleviation and water purification of beavers, beaver dams and beaver ponds.
- Capacity to physically manage potential ecotourism.

## What next?

12.10. The way seems clear to move to a second phase of consultation and actions concerning beaver reintroductions to England, focusing on education of the wider public about beavers, investigating specific candidate sites for releasing beavers, drawing up detailed management plans and costings, and, if agreed by all interested parties, releasing beavers within the umbrella of pilot studies. Following the general considerations listed in Table 12.1., we propose that the following actions need to be taken into account in any plan to reintroduce beavers into England:

### Education

- To prepare and disseminate educational material about beavers, their habits, ecosystem services, possible impacts and management, to gain a consensus of approval for a pilot reintroduction programme or programmes;

### Legal aspects

- To review legislative mechanisms to protect and manage beaver populations in England, and draw up proposals to amend the legal status of beavers as necessary;

### Who is responsible

- To consider who will be responsible for the release and management of beavers and set up grant-aid schemes to offset any financial costs of management and mitigation;

### Candidate release sites and consultation

- To select candidate sites for detailed habitat analysis, population modelling and the production of a human-beaver interaction risk analysis;
- To carry out a local consultation exercise of local stakeholders, including landowners and the general public, at each candidate site and gain their approval;
- To determine which site or sites are most suitable for beaver reintroductions and explore the costs and benefits of such a reintroduction;

### Source of beavers and quarantine

- To determine the costs, time frame, source of beavers and quarantine holding facilities that will be used for each candidate site, and to obtain the necessary licences and permits to carry out the importation, quarantine and release of beavers;

### Research, monitoring and management

- To produce detailed guidance on costs, research (including that into ecosystem services), and monitoring to be carried out at each site and to establish a local management group to oversee and monitor the release;
- To carry out pre-emptive management at the candidate site(s) (e.g. protect vulnerable trees and crops);

### Funding and implementation of reintroduction

- To raise sufficient funds to carry out the reintroduction programme;
- To import the beavers and place into quarantine with appropriate health checks;
- To prepare the site(s) for a soft release. After six months of quarantine, release the beavers and start monitoring for a period lasting at least five years;
- To publicise locally and nationally the presence and conservation importance of the return of beavers to England.

Table 12.1. Considerations for a successful beaver reintroduction (based on IUCN 1998) with cross reference to chapters in the report.

<b>Considerations for a successful reintroduction</b>		<b>Chapter</b>
<b>1</b>	<b>Beaver natural history</b> Many studies of beavers in Europe and North America have been carried out, especially within the last 20 years, consolidating previous knowledge.	1,2
<b>2</b>	<b>Source populations for reintroductions</b> Source population for reintroductions should be the geographically closest surviving form.	8
<b>3</b>	<b>Candidate release sites</b> A preliminary analysis clearly indicates that there is a wide range of potential release sites across England. A further phase of GIS habitat modelling study that incorporates catchment-scale data is required to select sites for pilot studies.	5
<b>4</b>	<b>Strategy for release</b> Methods for the capture, marking, transportation, health screening, quarantine and release of beavers are known and have been well rehearsed across Continental Europe and in England.	6,7
<b>5</b>	<b>Post release monitoring and research</b> Economic, population and behavioural studies of beavers for at least 5 years after release are recommended. In particular, a pilot reintroduction of beavers into England would be an excellent opportunity to carry out a full cost-benefit analysis of beavers in relation to ecosystem services, ecotourism, control and mitigation.	7,8,9,11
<b>6</b>	<b>Beavers and the law</b> This has been reviewed - for future protection and management of released beavers, licensing authorities should give consideration to adding beavers to schedule 2 of the Conservation (Natural Habitat) Regulations, and schedule 9 of the Wildlife and Countryside Act.	6
<b>7</b>	<b>Managing human-beaver interactions</b> A management plan should be prepared in advance as an integral part of a beaver reintroduction programme. This should include criteria to assess the success of the reintroduction, monitoring of the population and an evaluation of possible environmental impacts. This should include financial costs and benefits, grant aid and compensation schemes. Each reintroduction should be overseen by a local management committee comprising stakeholders, landowners and scientists.	3,4,10,11
<b>8</b>	<b>Public consultation, addressing concerns and ecotourism</b> Public consultation exercises are essential to seek public views on beaver reintroductions into England both nationally and locally. At the same time, the consultation exercise should inform the public about beavers, their ecology and behaviour, possible environmental effects, how a reintroduction would be carried out and the safeguards that would be built into the scheme.	9,10,11



## 13. References

- ADAMS, A. K. 1949. Beavers versus trout. *Michigan Conservation*, 18, 15-16.
- ADAMS, W. M. 2004. *Against extinction: the story of conservation*. London: Earthscan.
- AGUILAR, A., ROEMER, G., DEBENHAM, S., BINNS, M., GARCELON, D. & WAYNE, R. 2004. High MHC diversity maintained by balancing selection in an otherwise genetically monomorphic mammal. *Proceedings of the National Academy of Sciences, USA*, 101, 3490-3494.
- ALLEN, A. W. 1983. Habitat suitability index models: Beaver. . U.S. Department of the Interior, Fish and Wildlife Service.
- ANDERSON, C. B. & ROSEMOND, A. D. 2007. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia*, 154, 141-153.
- ANDERSON, C. B., PASTUR, G., LENCINAS, M., WALLEM, P., MOORMAN, M. & ROSEMOND, A. 2009. Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. *Mammal Review*, 39, 33-52.
- APPELBEE, A. J., THOMPSON, R. C. A. & OLSON, M. E. 2005. *Giardia* and *Cryptosporidium* in mammalian wildlife - current status and future needs. *Trends in Parasitology*, 21, 370-376.
- APPLE, L. 1982. The use of beavers in riparian/aquatic habitat restoration in a cold desert, gullycut stream: a case history. In: *Proceedings, 18th annual meeting Colorado: Wyoming Chapter, American Fisheries Society* (Ed. by Whaley, R.), pp. 29-35. Laramie, Wyoming.
- ATWOOD, E. J. 1938. Some observations on adaptability of Michigan beavers released in Missouri. *Journal of Wildlife Management*, 2, 165-166.
- EVERY, E. L. 1983. A bibliography of beaver, trout, wildlife, and forest relationships with special references to beaver and trout. *Technician Bulletin, Wisconsin Department of Natural Resources, Madison, WI.*, 137, 1-23.
- BABIK, W., DURKA, W. & RADWAN, J. 2005. Sequence diversity of the MHC DRB gene in the Eurasian beaver (*Castor fiber*). *Molecular Ecology*, 14, 4249-4257.
- BAILEY, R. W. 1954. Status of beaver in West-Virginia. *Journal of Wildlife Management*, 18, 184-190.
- BAKER, B. W., HILL, E. P. 2003. Beaver (*Castor canadensis*). In: *Wild Mammals of North America: Biology, Management, and Conservation*. (Ed. by Feldhamer, G. A., Thompson, B. C., Chapman, J. A. ), pp. 288-310. Baltimore, Maryland, USA.: The Johns Hopkins University Press.
- BALON, E. K. & CHADWICK, E. M. P. 1979. Reclamation of a perch lake: a case study using density estimates and the guild concept. *Archiv für Hydrobiologie*, 85, 543-547.
- BARNES, D. M. & MALLIK, A. U. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. *Journal of Wildlife Management*, 61, 1371-1377.
- BARNES, D. M. & MALLIK, A. U. 2001. Effects of Beaver, *Castor canadensis*, herbivory on streamside vegetation in a northern Ontario watershed. *Canadian Field-Naturalist*, 115, 9-21.
- BASEY, J. M. & JENKINS, S. H. 1995. Influences of predation risk and energy maximization on food selection by beavers (*Castor canadensis*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 73, 2197-2208.
- BEIER, P. & BARRETT, R. 1987. Beaver habitat use and impact in Truckee River Basin, California. *Journal of Wildlife Management*, 51, 794-799.
- BELCUORE, T., CONTI, L., WIERSMA, S., CHILDS, J., RUPPRECHT, C., HANLON, C., KREBS, J. & GUERRA, M. 2002. Rabies in beaver - Florida 2001. *The Journal of the American Medical Association*, 51, 3202-3203.
- BERGERUD, A. & MILLER, D. 1977. Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology*, 55, 1480-1492.

- BERGSTROM, D. 1985. Beavers: ecologists rediscover a natural resource. (Ed. by United States Department of Agriculture, F. S.).
- BERTOLO, A., MAGNAN, P. & PLANTE, M. 2008. Linking the occurrence of brook trout with isolation and extinction in small Boreal Shield lakes. *Freshwater Biology*, 53, 304-321.
- BLUZMA, P. 2003. Beaver abundance and beaver site use in a hilly landscape (eastern Lithuania). *Acta Zoologica Lituanica*, 13, 8-14.
- BONESI, L. & MACDONALD, D.W. 2004. Differential habitat use promotes sustainable coexistence between the specialist otter and the generalist mink. *Oikos*, 106, 509-519.
- BOYCE, M. S. 1983. Habitat ecology of an unexploited population of beavers in interior Alaska. In: *Worldwide furbearer conference proceedings* (Ed. by Chapman, J. A. & Pursley, D.), pp. 155-186. Falls Church, Virginia: Donnelly.
- BRAKHAGE, G. K. & SAMPSON, F. W. 1952. Rabies in beaver. *Journal of Wildlife Management*, 16, 226-226.
- BRÄUER, I. 2006. Annex 9. Restoring ecosystem services by reintroducing a keystone species - case study on the cast and benefits of beaver reintroduction in Germany. In: *Value of Biodiversity: documenting EU examples where biodiversity loss has led to the loss of ecosystem services* (Ed. by Kettunen, M. & ten Brink, P.), p. 131. Brussels, Belgium: Final report for the European Commission. Institute for European Environmental Policy (IEEP).
- BRAYTON, D. S. 1984. The beaver and the stream. *Journal of Soil and Water Conservation*, 39, 108-109.
- BREMNER, A. & PARK, K. 2007. Public attitudes to the management of non-invasive species in Scotland. *Biological Conservation*, 139, 306-314.
- BRIGHT, P., HALLIWELL, E. & MITCHELL-JONES, T. 2000. Return of the Pine Marten to England. London: People's Trust for Endangered Species, London.
- BROOKS, R., FLEMING, M. & KENNELLY, J. 1980. Beaver colony response to fertility control: evaluating a concept. *Journal of Wildlife Management*, 44, 568-575.
- BROSCHART, M., JOHNSTON, C. & NAIMAN, R. 1989. Predicting beaver colony density in boreal landscapes. *Journal of Wildlife Management*, 53, 929-934.
- BROWN, D. J., HUBERT, W. A. & ANDERSON, S. H. 1996. Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. *Wetlands*, 16, 127-133.
- BRZEZINSKI, M. & ZUROWSKI, W. 1992. Spring diet of the American mink *Mustela vison* in the Mazurian and Brodnica Lakelands, northern Poland. *Acta Theriologica*, 37, 193-198.
- BRZEZINSKI, M. & ZUROWSKI, W. 1992. Spring diet of the American mink *Mustela vison* in the Mazurian and Brodnica Lakelands, northern Poland. *Acta Theriologica*, 37, 193-198.
- BUECH, R. 1985. Methodologies for observing beavers (*Castor canadensis*) during the activity period. In: *Nocturnal mammals: techniques for study* (Ed. by Brookes, R. P.). Pennsylvania: Pennsylvania State University School for Resources Research.
- BULLER, H. 2003. Where the wild things are: the evolving iconography of rural fauna. *Journal of Rural Studies*, 10, 131-141.
- BULTE, E. & RONDEAU, D. 2005. Why compensating wildlife damages may be bad for conservation. *Journal of Wildlife Management*, 69, 14-19.
- BUSHER, P. & DZIECIOLOWSKI, R. 1999. *Beaver protection, management, and utilisation in Europe and North America*. New York: Kluwer Academic/Plenum Publishers.
- BUSHER, P. E. 1987. Population parameters and family composition of beaver in California. *Journal of Mammalogy*, 68, 860-864.
- BUSHER, P. E., WARNER, R. J. & JENKINS, S. H. 1983. Population-density, colony composition, and local movements in 2 Sierra Nevada beaver populations. *Journal of Mammalogy*, 64, 314-318.

- BUTLER, D. R. 1995. *Zoogeomorphology : animals as geomorphic agents*. Cambridge: Cambridge University Press.
- BUTLER, D. R. 2006. Human-induced changes in animal populations and distributions, and the subsequent effects on fluvial systems. *Geomorphology*, 79, 448-459.
- BUTLER, D. R. & MALANSON, G. P. 1995. Sedimentation-rates and patterns in beaver ponds in a mountain environment. *Geomorphology*, 13, 255-269.
- BUTLER, D. R. & MALANSON, G. P. 2005. The geomorphic influences of beaver dams and failures of beaver dams. *Geomorphology*, 71, 48-60.
- BUTTS, W.L., (2001) Scientific note: beaver ponds in upstate New York as a source of anthropophilic mosquitoes. *Journal of the American Mosquito Control Association*, 17, 85.
- CAMPBELL, R., DUTTON, A. & HUGHES, J. 2007. Economic Impacts of the beaver. p. 24. Oxford: University of Oxford.
- CAMPBELL, R. D., ROSELL, F., NOLET, B. A. & DIJKSTRA, V. A. A. 2005. Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? *Behavioral Ecology and Sociobiology*, 58, 597-607.
- CARR, W. H. 1940. Beaver and birds. *Bird Lore*, 42, 141-146.
- CASEY, A., KRAUSMAN, P., SHAW, W. & SHAW, H. 2005. Knowledge of and attitudes toward mountain lions: a public survey of residents adjacent to Saguaro National park, Arizona. *Human Dimensions of Wildlife*, 10, 29-38.
- CLIFFORD, H. F., WILEY, G. M. & CASEY, R. J. 1993. Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 71, 1439-1447.
- COLE, M., KITCHENER, A. & YALDEN, D. 2007. Eurasian beaver. In: *Mammals of the British Isles 4th Edition* (Ed. by Harris, S. & Yalden, D.), pp. 72-76. Southampton, UK: The Mammal Society.
- COLES, B. 2006. *Beavers in Britain's Past*. Oxford, UK: Oxbow Books.
- COLLEN, P. 1995. The reintroduction of beaver (*Castor fiber* L.) to Scotland: an opportunity to promote the development of suitable habitat. *Scottish Forestry*, 49, 206-217.
- COLLEN, P. & GIBSON, R. J. 2001. The general ecology of beavers (*Castor spp.*), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. *Reviews in Fish Biology and Fisheries*, 10, 439-461.
- COOK, D. 1940. Beaver-trout relations. *Journal of Mammalogy*, 21, 397-401.
- COOPER, D. J., DICKENS, J., HOBBS, N. T., CHRISTENSEN, L. & LANDRUM, L. 2006. Hydrologic, geomorphic and climatic processes controlling willow establishment in a montane ecosystem. *Hydrological Processes*, 20, 1845-1864.
- COPE, D., PETTIFOR, R., GRIFFIN, L. & ROWCLIFFE, J. 2003. Integrating farming and wildlife conservation: the Barnacle Goose Management Scheme. *Biological Conservation*, 110, 113-122.
- CORBETT, G. 1978. The mammals of the Palaearctic Region: a taxonomic review. p. 314. London: British Museum (Natural History).
- COSGROVE, P. J., YOUNG, M. R., HASTIE, L. C., GAYWOOD, M. & BOON, P. J. 2000. The status of freshwater pearl mussel *Margaritifera margaritifera* Linn. in Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 10, 197-208.
- CUNJAK, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Science*, 53 (Suppl. 1), 267-282.
- CUNJAK, R. A. & THERRIEN, J. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. *Fisheries Management and Ecology*, 5, 209-223.
- CUNNINGHAM, J. M., CALHOUN, A. J. K. & GLANZ, W. E. 2006. Patterns of beaver colonization and wetland change in Acadia National Park. *Northeastern Naturalist*, 13, 583-596.

- CURRY-LINDAHL, K. 1967. The Beaver, *Castor fiber* Linnaeus, 1758 in Sweden - Extermination and Reappearance. *Acta Theriologica*, 12, 1-15.
- CURTIS, P. D. & JENSEN, P. G. 2004. Habitat features affecting beaver occupancy along roadsides in New York state. *Journal of Wildlife Management*, 68, 278-287.
- CVETKOVICH, G. & WINTER, P. 2003. Trust and social representations of the management of threatened and endangered species. *Environment and Behavior*, 35, 286-307.
- DANILOV, P. I., KAN'SHIEV, V.YA. 1983. The state of populations and ecological characteristics of European (*Castor fiber* L.) and Canadian (*Castor canadensis* Kuhl.) beavers in the northwestern USSR. *Acta Zoologica Fennica*, 174, 95-97.
- DANILOV, P. I. 1992. Introduction of North-American semiaquatic mammals in Karelia and its consequences for aboriginal species. *Semiaquatiscche Säugetiere. Wissenschaftliche Beiträge Universität Halle*, 1, 267-276.
- DANILOV, P. I. 1995. Canadian and European beavers in Russian Northwest. In: *The Third Nordic Beaver Symposium*, pp. 10-16. Helsinki: Mekrijarvi Research Station, Ilomantsi, Finland.
- DEFRA. 2007a. 2007 Survey of Public Attitudes and Behaviours Toward the Environment <http://www.defra.gov.uk/environment/statistics/pubatt/download/pubattsum2007.pdf>. London: Defra.
- DEFRA. 2007b. An introductory guide to valuing ecosystem services. London: Department for Environment, Food and Rural Affairs.
- DEFRA. 2008a. Feral wild boar in England. p. 57: Department for Environment, Food and Rural Affairs, London.
- DEFRA. 2008b. Ecosystem Services <http://www.ecosystems-services.org.uk/ecoserv.htm>, accessed 25<sup>th</sup> October 2008
- DEGRAAF, R. M. & YAMASAKI, M. 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management*, 185, 179-191.
- DEPARTMENT OF TRADE AND INDUSTRY. 2004. The Foresight Future Flooding Report. London: Office of Science and Technology.
- DESTEFANO, S., KOENEN, K. K. G., HENNER, C. M. & STRULES, J. 2006. Transition to independence by subadult beavers (*Castor canadensis*) in an unexploited, exponentially growing population. *Journal of Zoology*, 269, 434-441.
- DEVITO, K. J. & DILLON, P. J. 1993. Importance of runoff and winter anoxia to the P and N dynamics of a beaver pond. *Canadian Journal of Fisheries and Aquatic Sciences*, 50, 2222-2234.
- DIETER, C. D. & MCCABE, T. R. 1989. Factors influencing beaver lodge-site selection on a prairie river. *American Midland Naturalist*, 122, 408-411.
- DONKOR, N. T. & FRYXELL, J. M. 1999. Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. *Forest Ecology and Management*, 118, 83-92.
- DONKOR, N. T. & FRYXELL, J. M. 2000. Lowland boreal forests characterization in Algonquin Provincial Park relative to beaver (*Castor canadensis*) foraging and edaphic factors. *Plant Ecology*, 148, 1-12.
- DOUCET, C. M. & FRYXELL, J. M. 1993. The effect of nutritional quality on forage preference by beavers. *Oikos*, 67, 201-208.
- DUCROZ, J. F., STUBBE, M., SAVELJEV, A. P., HEIDECHE, D., SAMJAA, R., ULEVICIUS, A., STUBBE, A. & DURKA, W. 2005. Genetic variation and population structure of the Eurasian beaver *Castor fiber* in Eastern Europe and Asia. *Journal of Mammalogy*, 86, 1059-1067.
- DUGMORE, A. R. 1914. *The romance of the beaver: being the history of the beaver in the Western Hemisphere*. London: William Heinemann.
- DUNCAN, S. L. 1984. Ecology - leaving it to beaver. *Environment*, 26, 41-45.

- DUNLAP, B. G. & THIES, M. L. 2002. Giardia in beaver (*Castor canadensis*) and nutria (*Myocastor coypus*) from east Texas. *Journal of Parasitology*, 88, 1254-1258.
- DURKA, W., BABIK, W., DUCROZ, J. F., HEIDECKE, D., ROSELL, F., SAMJAA, R., SAVELJEV, A. P., STUBBE, A., ULEVICIUS, A. & STUBBE, M. 2005. Mitochondrial phylogeography of the Eurasian beaver *Castor fiber* L. *Molecular Ecology*, 14, 3843-3856.
- EDWARDS, N. T. & OTIS, D. L. 1999. Avian communities and habitat relationships in South Carolina Piedmont beaver ponds. *American Midland Naturalist*, 141, 158-171.
- EDWARDS, S. & HEDRICK, P. 1998. Evolution and Ecology of MHC molecules: from genomics to sexual selection. *Trends in Ecology and Evolution*, 13, 306-311.
- ELLENGREN, H., HARTMAN, G., JOHANSSON, M. & ANDERSSON, L. 1993. Major histocompatibility complex monomorphism and low-levels of dna-fingerprinting variability in a reintroduced and rapidly expanding population of beavers. *Proceedings of the National Academy of Sciences of the United States of America*, 90, 8150-8153.
- ENGELHART, A. & MULLER-SCHWARZE, D. 1995. Responses of beaver (*Castor canadensis* Kuhl) to predator chemicals. *Journal of Chemical Ecology*, 21, 1349-1364.
- ENVIRONMENT\_AGENCY. 2008. Flooding. <http://www.environment-agency.gov.uk/subjects/flood/>.
- ERICKSON, A. B. 1949. The fungus (*Haplosporangium-parvum*) in the lungs of the beaver (*Castor canadensis*). *Journal of Wildlife Management*, 13, 419-&.
- ERICSSON, G. & HEBERLEIN, T. 2003. Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. . *Biological Conservation*, 111, 149-159.
- ERMALA, A., HELMINEN, M. & LAHTI, S. 1989. Some aspects of the occurrence, abundance and future of the Finnish beaver population (summary only). *Suomen Riista*, 35, 108-118.
- EROME, G. 1984. La typologie des gites du castor rhodanien, *Castor fiber*. *La Terre et la Vie*, 39, 55-76.
- FARRAR, G. B. 1971. The beaver: the conservationist! *Defenders of Wildlife News*, 46, 205-206.
- FEDYNICH, A. M., PENCE, D. B. & URUBEK, R. L. 1986. Helminth fauna of beaver from central Texas. *Journal of Wildlife Diseases*, 22, 579-582.
- FOSTER, D. R., MOTZKIN, G., BERNARDOS, D. & CARDOZA, J. 2002. Wildlife dynamics in the changing New England landscape. *Journal of Biogeography*, 29, 1337-1357.
- FRANCE, R. L. 1997. The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 75, 1009-1013.
- FRYXELL, J. M. 2001. Habitat suitability and source-sink dynamics of beavers. *Journal of Animal Ecology*, 70, 310-316.
- FUSTEC, J., CORMIER, J.-P. . 2007. Utilisation of woody plants for lodge construction by European beaver (*Castor fiber*) in the Loire valley, France. *Mammalia*, 71 11-15.
- FUSTEC, J., LODE, T., LE JACQUES, D. & CORMIER, J. P. 2001. Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. *Freshwater Biology*, 46, 1361-1371.
- GABRYS, G. & WAZNA, A. 2003. Subspecies of the European beaver *Castor fiber* Linnaeus, 1758. *Acta Theriologica*, 48, 433-439.
- GAMBORG, C. & SANDØE, P. 2004. Beavers and biodiversity: the ethics of ecological restoration. In: *Philosophy and Biodiversity* (Ed. by Oksanen, M. & Pietarinen, J.), pp. 217-236. Cambridge: Cambridge University Press.
- GARD, R. 1961. Effects of beavers on trout in Sagehen Creek, California. *Journal of Wildlife Management*, 25, 221-242.
- GAYWOOD, M., BATTY, D. & GALBRAITH, C. 2008. Reintroducing the European Beaver in Britain. *British Wildlife*, 19, 381-391.

- GIBBS, J. P., LONGCORE, J. R., MCAULEY, D. G. & RINGELMAN, J. K. 1991. Use of wetland habitats by selected nongame water birds in Maine. *U.S. Fish and Wildlife Service, Fish and Wildlife Research*, 9, 1-57.
- GORMAN, M. L. 2007. Restoring ecological balance to the British mammal fauna. *Mammal Review*, 37, 316-325.
- GOSLING, L. & BAKER, S. 1989. The eradication of coypu and muskrats from Britain. *Biological Journal of the Linnean Society*, 38, 39-51.
- GOSLING, L. & BAKER, S. 2008. Coypu. In: *Mammals of the British Isles: Handbook 4th Edition* (Ed. by Harris, S. & Yalden, D.), pp. 159-165. Southampton: The Mammal Society.
- GOULDING, M. & ROPER, T. 2002. Press responses to the presence of free-living Wild Boar (*Sus scrofa*) in southern England. *Mammal Review*, 32, 272-282.
- GOW, D. 2002. The quarantine and captive management of European beaver *Castor fiber*. p. 20: Report for Scottish Natural Heritage.
- GRASSE, J. E. 1951. Beaver ecology and management in the Rockies. *Journal of Forestry*, 49, 3-6.
- GROOMBRIDGE, J. J., JONES, C. G., BRUFORD, M. W. & NICHOLS, R. A. 2000. 'Ghost' alleles of the Mauritius kestrel. *Nature*, 403, 616.
- GROVER, A. M. & BALDASSARRE, G. A. 1995. Bird species richness within beaver ponds in south-central New-York. *Wetlands*, 15, 108-118.
- GURNELL, A. & PETTS, G. 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. *Freshwater Biology* 47: 581-600., 47, 581-600.
- GURNELL, A., PIÉGAY, H., SWANSON, F. & GREGORY, S. 2002. Large wood and fluvial processes. *Freshwater Biology*, 74, 601-619.
- GURNELL, A. M. 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography*, 22, 167-189.
- HAARBERG, O. & ROSELL, F. 2006. Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. *Journal of Zoology*, 270, 201-208.
- HACKING, M. & SILEO, M. 1974. *Yersinia enterocolitica* and *Yersinia pseudotuberculosis* from wildlife in Ontario *Journal of Wildlife Diseases*, 10, 452-457.
- HAGGLUND, A. & SJOBERG, G. 1999. Effects of beaver dams on the fish fauna of forest streams. *Forest Ecology and Management*, 115, 259-266.
- HALLEY, D. J. & ROSELL, F. 2002. The beaver's reconquest of Eurasia: status, population development and management of a conservation success. *Mammal Review*, 32, 153-178.
- HAMMERSON, G. 1994. Beaver (*Castor canadensis*) ecosystem alterations, management and monitoring. *Natural Areas Journal*, 14, 44-57.
- HARDMAN, B. & MORO, D. 2006. Optimising reintroduction success by delayed dispersal: Is the release protocol important for hare-wallabies? *Biological Conservation*, 128, 403-411.
- HÄRKÖNEN, S. 1999a. Forest damage caused by the Canadian beaver (*Castor canadensis*) in South Savo, Finland. *Silva Fennica*, 33, 247-259.
- HÄRKÖNEN, S. 1999b. Management of the North American beaver *Castor canadensis* on the South-Savo management district, Finland (1983-1997). In: *Beaver protection, management and utilisation in Europe and North America* (Ed. by PE, B. & Dzieciolowski, R.), pp. 2-16. New York: Kluwar Academic / Plenum Publishers.
- HARTKE, K. M. & HEPP, G. R. 2004. Habitat use and preferences of breeding female wood ducks. *Journal of Wildlife Management*, 68, 84-93.
- HARTMAN, G. 1994. Long-term population development of a reintroduced beaver (*Castor fiber*) population in Sweden. *Conservation Biology*, 8, 713-717.
- HARTMAN, G. 1996. Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. *Journal of Zoology*, 240, 317-325.

- HARTMAN, G. 1999. Beaver management and utilisation in Scandinavia. In: *Beaver protection, management, and utilisation in Europe and North America* (Ed. by Busher, P. & Dzieciolowski, R.), pp. 1-6. New York: Kluwer Academic/Plenum Publishers.
- HARTMAN, G. & AXELSSON, A. 2004. Effect of watercourse characteristics on food-caching behaviour by European beaver, *Castor fiber*. *Animal Behaviour*, 67, 643-646.
- HERING, D., GERHARD, M., KIEL, E., EHLERT, T. & POTTGIESSER, T. 2001. Review study on near-natural conditions of Central European mountain streams, with particular reference to debris and beaver dams: Results of the "REG meeting" 2000. *Limnologica - Ecology and Management of Inland Waters*, 31, 81-92.
- HERR, J. & ROSELL, F. 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). *Journal of Zoology*, 262, 257-264.
- HILFIKER, E. L. 1991. *Beavers, water, wildlife and history*. New York.: Windswept Press, Interlaken.
- HILL, E. 1982. Beaver. In: *Wild Mammals of North America* (Ed. by Chapman, J. A. a. F., G.A. ), pp. 256-281.
- HILLMAN, G. R. 1998. Flood wave attenuation by a wetland following a beaver dam failure on a second order boreal stream. *Wetlands*, 18, 21-34.
- HODGDON, H. & LANCIA, R. 1983. Behavior of the North American beaver, *Castor canadensis*. *Acta Zoologica Fennica*, 174, 99-103.
- HOLMES, N., BOON, P. & ROWELL, T. 1999. *Vegetation communities of British rivers: a revised classification*. Peterborough: JNCC.
- HOUSTON, A., PELTON, M. & HENRY, R. 1995. Beaver immigration into a control area. *Southern Journal of Applied Forestry*, 19, 127-130.
- HOWARD, R. & LARSON, J. 1985. A stream habitat classification system for beaver. *Journal of Wildlife Management*, 49, 19-25.
- HUEY, W. S. & WOLFRUM, W. H. 1956. Beaver-trout relations in New Mexico. *The Progressive Fish-Culturist*, 18, 70-74.
- IUCN. 1998. Guidelines for re-introductions. Gland, Switzerland and Cambridge UK: Prepared by IUCN/SSC Reintroduction Specialist Group IUCN.
- JANOVSKY, M., BACCIARINI, L., SAGER, H., GRONE, A. & GOTTSTEIN, B. 2002. *Echinococcus multilocularis* in a European beaver from Switzerland. *Journal of Wildlife Diseases*, 38, 618-620.
- JENKINS, S. 1980. A size-distance relation in food selection by beavers. *Ecology*, 61, 740-746.
- JOHNSON, P. 1984. The dam builder is at it again! *National Wildlife*, 22, 8-15.
- JOHNSTON, C. & NAIMAN, R. 1987. Boundary dynamics of the aquatic-terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecology*, 1, 47-57.
- KEAST, A. & FOX, M. G. 1990. Fish community structure, spatial-distribution and feeding ecology in a beaver pond. *Environmental Biology of Fishes*, 27, 201-214.
- KETTUNEN, M. & TEN BRINK, P. 2006. Value of biodiversity: documenting EU examples where biodiversity loss has led to the loss of ecosystem services. p. 131. Brussels, Belgium: The Institute for European Environmental Policy (IEEP).
- KINDSCHY, R. 1985. Response of red willow to beaver use in Southeastern Oregon. *Journal of Wildlife Management*, 49, 26-28.
- KING, S. L., KEELAND, B. D. & MOORE, J. L. 1998. Beaver lodge distributions and damage assessments in a forested wetland ecosystem in the southern United States. *Forest Ecology and Management*, 108, 1-7.
- KITCHENER, A. C. & CONROY, J. W. H. 1997. The history of the Eurasian beaver *Castor fiber* in Scotland. *Mammal Review*, 27, 95-108.
- KNUDSEN, G. J. 1962. *Relationship of beaver to forests, trout and wildlife in Wisconsin*. Madison: Wisconsin Conservation Department, Technical Bulletin.

- LAHTI, S. & HELMINEN, M. 1974. The beaver *Castor fiber* (L.) and *Castor canadensis* (Kuhl) in Finland. *Acta Theriologica*, 19, 177-189.
- LARSON, J. S., GUNSON, J.R. 1983. Status of the beaver in North America. *Acta Zoologica Fennica*, 174, 91-93.
- LAVROV, L. S. 1983. Evolutionary development of the genus *Castor* and taxonomy of the contemporary beavers of Eurasia. *Acta Zoologica Fennica*, 174, 87-90.
- LAWSON, P. A., FOSTER, G., FALSEN, E., MARKOPOULOS, S. J. & COLLINS, M. D. 2005. *Streptococcus castoreus* sp nov., isolated from a beaver (*Castor fiber*). *International Journal of Systematic and Evolutionary Microbiology*, 55, 843-846.
- LEBLANC, F. A., GALLANT, D., VASSEUR, L. & LEGER, L. 2007. Unequal summer use of beaver ponds by river otters: influence of beaver activity, pond size, and vegetation cover. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 85, 774-782.
- LEIDHOLT-BRUNER, K., HIBBS, D. E. & MCCOMB, W. C. 1992. Beaver dam locations and their effects on distribution and abundance of Coho salmon fry in 2 coastal Oregon streams. *Northwest Science*, 66, 218-223.
- LIZARRALDE, M., ESCOBAR, J. & DEFERRARI, G. 2004. Invader species in Argentina: A review about the beaver (*Castor canadensis*) population situation on Tierra del Fuego ecosystem. *Interciencia*, 29, 352-+.
- LIZARRALDE, M. S. 1993. Current status of the introduced beaver (*Castor canadensis*) population in Tierra-del-Fuego, Argentina. *Ambio*, 22, 351-358.
- LONGCORE, J. R., MCAULEY, D. G., PENDELTON, G. W., BENNATTI, C. R., MINGO, T. M. & STROMBORG, K. L. 2006. Macroinvertebrate abundance, water chemistry, and wetland characteristics affect use of wetlands by avian species in Maine. *Hydrobiologia*, 567, 143-167.
- LONGCORE, T., RICH, C. & MULLER-SCHWARZE, D. 2007. Management by assertion: Beavers and songbirds at Lake Skinner (Riverside County, California). *Environmental Management*, 39, 460-471.
- LORIMER, J. 2007. Nonhuman charisma. *Environment and Planning D: Society and Space*, 25, 911-932.
- LOWRY, M. M. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon, University of Oregon.
- MACDONALD, D. & TATTERSALL, F. 1999. Beavers in Britain: planning reintroduction. In: *Beaver protection, management and utilisation in Europe and North America* (Ed. by Busher, P. & Dzieciolowski, R.), pp. 77-102. New York: Kluwer Academic/Plenum Publishers.
- MACDONALD, D. W. & BARRETT, P. 1993. Collins Field Guide to Mammals. Harper Collins.
- MACDONALD, D. W., TATTERSALL, F. H., BROWN, E. D. & BALHARRY, D. 1995. Reintroducing the European beaver to Britain: Nostalgic meddling or restoring biodiversity? *Mammal Review*, 25, 161-200.
- MACDONALD, D. W., TATTERSALL, F. H., RUSHTON, S., SOUTH, A. B., RAO, S., MAITLAND, P. & STRACHAN, R. 2000. Reintroducing the beaver (*Castor fiber*) to Scotland: a protocol for identifying and assessing suitable release sites. *Animal Conservation*, 3, 125-133.
- MACNAGHTEN, P. 1995. Public attitudes to countryside leisure: a case study on ambivalence. *Journal of Rural Studies*, 11, 135-148.
- MARGOLIS, B. E., RAESLY, R. L. & SHUMWAY, D. L. 2001. The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. *Wetlands*, 21, 554-563.
- MARINGER, A. & SLOTTA-BACHMAYR, L. 2006. A GIS-based habitat-suitability model as a tool for the management of beavers *Castor fiber*. *Acta Theriologica*, 51, 373-382.
- MARTINSEN, G. D., DRIEBE, E. M. & WHITHAM, T. G. 1998. Indirect interactions mediated by changing plant chemistry: Beaver browsing benefits beetles. *Ecology*, 79, 192-200.



- MASR. 2005. Millennium Ecosystem Assessment Report. Washington DC: The MA, World Resources Institute.
- MCCALL, T. C., HODGMAN, T. P., DIEFENBACH, D. R. & OWEN, R. B. 1996. Beaver populations and their relation to wetland habitat and breeding waterfowl in Maine. *Wetlands*, 16, 163-172.
- MCDOWELL, D. M. & NAIMAN, R. J. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, 68, 481-489.
- MCKELVEY, R. W., DENNINGTON, C. M. & MOSSOP, D. 1983. The status and distribution of trumpeter swans (*Cygnus buccinator*) in the Yukon. *Arctic*, 36, 76-81.
- MCKINSTRY, M. C., CAFFREY, P. & ANDERSON, S. H. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of the American Water Resources Association*, 37, 1571-1577.
- MCKINSTRY, M. C., KARHU, R. R. & ANDERSON, S. H. 1997. Use of active Beaver, *Castor canadensis*, lodges by Muskrats, *Ondatra zibethicus*, in Wyoming. *Canadian Field-Naturalist*, 111, 310-311.
- MCNEEL, W. 1964. Beaver cuttings in aspen indirectly detrimental to white pine. *Journal of Wildlife Management*, 28, 861-863.
- MCTAGGART, S. T. & NELSON, T. A. 2003. Composition and demographics of beaver (*Castor canadensis*) colonies in central Illinois. *American Midland Naturalist*, 150, 139-150.
- MEDIN, D. E. 1990. Bird populations in and adjacent to a beaver pond ecosystem in Idaho. *Usda Forest Service Intermountain Research Station Research Paper*, U1-U6.
- MENDEZ-HERMIDA, F., GOMEZ-COUSO, H., ROMERO-SUANCES, R. & ARES-MAZAS, E. 2007. *Cryptosporidium* and *Giardia* in wild otters (*Lutra lutra*). *Veterinary Parasitology*, 144, 153-156.
- METTS, B. S., LANHAM, J. D. & RUSSELL, K. R. 2001. Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the upper Piedmont of South Carolina. *American Midland Naturalist*, 145, 54-65.
- MILISHNIKOV, A. N., LIKHNOVA, O. A., NIKONOVA, O. A., LAVROV, V. L. & ORLOV, V. N. 1994. Allozyme variability in the European beaver *Castor fiber* 1758 (*Castoridae, Rodentia*) from the Voronezh-State-Nature-Reserve. *Genetika*, 30, 529-534.
- MILISHNIKOV, A. N. & SAVEL'EV, A. P. 2001. Genetic divergence and similarity of introduced populations of European beaver (*Castor fiber* L., 1758) from Kirov and Novosibirsk oblasts of Russia. *Russian Journal of Genetics*, 37, 108-111.
- MILISHNIKOV, A. N., SAVELEV, A. P. & LIKHNOVA, O. P. 1997. Allozyme variation in European beaver (*Castor fiber* L, 1758) inhabiting Berezina and Cheptsya rivers. *Genetika*, 33, 674-680.
- MITCHELL, S. C. & CUNJAK, R. A. 2007. Stream flow, salmon and beaver dams: roles in the structuring of stream fish communities within an anadromous salmon dominated stream. *Journal of Animal Ecology*, 76, 1062-1074.
- MONZINGO, D. L. & HIBLER, C. P. 1987. Prevalence of *Giardia* sp. In a beaver colony and the resulting environmental contamination. *Journal of Wildlife Diseases*, 23, 576-585.
- MORGAN, L. 1868. *The American beaver and his works*. Philadelphia: J.B. Lippincott & co.
- MÖRNER, T., AVENAS, A. & MATTSSON, R. 1999. Adiaspiromycosis in a European beaver from Sweden. *Journal of Wildlife Diseases*, 35, 367-370.
- MÖRNER, T., SANDSTRÖM, G. & MATTSON, R. 1988. Comparison of sera and lung extracts for surveys of wild animals for antibodies against *Francisella tularensis* biovar *palaeartica*. *Journal of Wildlife Diseases*, 24, 10-14.
- MORRISON, A. 2005. Trial re-introduction of the European beaver to Knapdale: public health monitoring 2001–3. . p.14: Scottish Natural Heritage
- MÜLLER, W., BOCKLISCH, H., SCHÜLER, G., HOTZEL, H., NEUBAUER, H. & OTTO, P. 2007. Detection of *Francisella tularensis* subsp. *holarctica* in a European brown hare (*Lepus europaeus*) in Thuringia, Germany. *Veterinary Microbiology*, 123, 225-229.

- MÜLLER-SCHWARZE, D. & SUN, L. 2003. *The beaver: natural history of wetland engineers*: Cornell University Press.
- MÜLLER-SCHWARZE, D. & HAGGART, D. P. 2005. From the field: A better beaver trap - new safety device for live traps. *Wildlife Society Bulletin*, 33, 359-361.
- MÜLLER-SCHWARZE, D., SCHULTE, B., SUN, L., MÜLLER-SCHWARTZE, A. & MÜLLER-SCHWARZE, C. 1994. Red maple (*Acer rubrum*) inhibits feeding by beaver (*Castor canadensis*). *Journal of Chemical Ecology*, 20, 2021-2034.
- MURPHY, M. L., HEIFETZ, J., THEDINGA, J. F., JOHNSON, S. W. & KOSKI, K. V. 1989. Habitat utilisation by juvenile Pacific salmon (*Onchorynchus*) in the glacial Taku River, southeast Alaska. . *Canadian Journal of Fisheries and Aquatic Science*, 46, 1677-1685.
- NAIMAN, R., JOHNSTON, C. & KELLEY, J. 1988. Alteration of North American Streams by Beaver. *Bioscience*, 38, 753-762.
- NAIMAN, R., MELILLO, J. & HOBBIE, J. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, 67, 1254-1269.
- NAIMAN, R. J., PINAY, G., JOHNSTON, C. A. & PASTOR, J. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology*, 75, 905-921.
- NAUGHTON-TREVES, L., GROSSBERG, R. & TREVES, A. 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, 17, 1500-1511.
- NEWMAN, D. G. & GRIFFIN, C. R. 1994. Wetland use by river otters in Massachusetts. *Journal of Wildlife Management*, 58, 18-23.
- NICKELSON, T. E., RODGERS, J. D., JOHNSON, S. L. & SOLAZZI, M. F. 1992. Seasonal-changes in habitat use by juvenile Coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 783-789.
- NILSEN, E., MILNER-GULLAND, E., SCHOFIELD, L., MYSTERUD, A., N.CHR, S. & COULSON, T. 2007. Wolf reintroduction to Scotland: public attitudes and consequences for red deer management. *Proceedings of the Royal Society B: Biological Sciences*, 274, 995-1002.
- NITSCHKE, K. A. 1997. Wild boar (*Sus scrofa*) and beaver (*Castor fiber*) relations. In: *Proceedings of the First European Beaver Symposium* (Ed. by Pachinger, K.), p. 16. Bratislava, Slovakia.: Institute of Ecology, Faculty of Natural Sciences Comenius University.
- NOLET, B. A. & BAVECO, J. M. 1996. Development and viability of a translocated beaver *Castor fiber* population in the Netherlands. *Biological Conservation*, 75, 125-137.
- NOLET, B. A., BROEKHUIZEN, S., DORRESTEIN, G. M. & RIENKS, K. M. 1997. Infectious diseases as main causes of mortality to beavers *Castor fiber* after translocation to the Netherlands. *Journal of Zoology*, 241, 35-42.
- NOLET, B. A., HOEKSTRA, A. & OTTENHEIM, M. M. 1994. Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. *Biological Conservation*, 70, 117-128.
- NOLET, B. A. & ROSELL, F. 1994. Territoriality and time budgets in beavers during sequential settlement. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 72, 1227-1237.
- NOLET, B. A. & ROSELL, F. 1998. Comeback of the beaver *Castor fiber*. An overview of old and new conservation problems. *Biological Conservation*, 83, 165-173.
- NOVAK, M. 1977. Determining average size and composition of beaver families. *Journal of Wildlife Management*, 41, 751-754.
- NUMMI, P. 1984. Majava-altaiden merkityksestä vesilintupoikueille. *Suomen Riista*, 31, 47-53.
- NUMMI, P. 1992. The importance of beaver ponds to waterfowl broods - an experiment and natural tests. *Annales Zoologici Fennici*, 29, 47-55.
- NUMMI, P. & HAHTOLA, A. 2008. The beaver as an ecosystem engineer facilitates teal breeding. *Ecography*.

- NUMMI, P. & POYSA, H. 1997. Population and community level responses in Anas-species to patch disturbance caused by an ecosystem engineer, the beaver. *Ecography*, 20, 580-584.
- NUMMI, P., ELMBERG, J., PÖYSÄ, H., GUNNARSON, G. & SJÖBERG, K. 2005. Varhaiset tavit asuttavat parhaat järvet ja menestyvät parhaiten. [Breeding success of teals varies for different lakes] Suomen Riista **51**: 27-34.
- NYHUS, P., OSOFSKY, S., FERRARO, P., MADDEN, F. & FISCHER, H. 2003. Bearing the costs of human-wildlife conflict: the challenges of compensation schemes. In: *People and Wildlife, Conflict or Coexistence?* (Ed. by Woodroffe, R., Thirgood, S. & Rabinowitz, A.), pp. 107-121. Cambridge: Cambridge University Press.
- PARKER, H. & RONNING, O. C. 2007. Low potential for restraint of anadromous salmonid reproduction by beaver *Castor fiber* in the Numedalslagen River catchment, Norway. *River Research and Applications*, 23, 752-762.
- PARKER, J. D., CAUDILL, C. C. & HAY, M. E. 2007. Beaver herbivory on aquatic plants. *Oecologia*, 151, 616-625.
- PARKER, M., WOOD, F., SMITH, B. & ELDER, R. 1985. Erosional downcutting in lower order riparian ecosystems: have historical changes been caused by the removal of the beaver? In: *Riparian ecosystems and their management: reconciling conflicting uses* (Ed. by Johnson, R. R.), pp. 35-38. Fort Collins, Colorado, USA.: U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station.
- PAYNE, N. F. 1982. Colony size, age, and sex structure of Newfoundland beaver. *Journal of Wildlife Management*, 46, 655-661.
- PERRY JR., R. 1982. Muskrats In: *Wild Mammals of North America: Biology, Management and Economics* (Ed. by Chapman, J. & Feldhamer, G.), pp. 282-325. Baltimore, Maryland, USA: John Hopkins University Press.
- PETERKEN, G. F. & HUGHES, F. M. R. 1995. Restoration of floodplain forests in Britain. *Forestry*, 68, 187-202.
- PHILCOX, C., GROGAN, A. & MACDONALD, D. 1999. Patterns of Otter *Lutra lutra* road mortality in Britain. *Journal of Applied Ecology*, 36, 748-762.
- PHILIP, L. & MACMILLAN, D. 2005. Exploring Values, Context and Perceptions in Contingent Valuation Studies: The CV Market Stall Technique and Willingness to Pay for Wildlife Conservation. *Journal of Environmental Planning and Management*, 48, 257-274.
- PIDGEON, N., KASPERSON, R. & SLOVIC, P. 2003. *The Social Amplification of Risk* Cambridge: Cambridge University Press.
- POLLOCK, M. M., BEECHIE, T. J. & JORDAN, C. E. 2007. Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surface Processes and Landforms*, 32, 1174-1185.
- POST. 2007. Ecosystem services. Parliamentary Office of Science and Technology.
- PUPININKAS, S. 1999. The state of the beaver (*Castor fiber*) population and characteristics of beaver sites in eastern Lithuania. *Acta Zoologica Lituanica*, 9, 20-26.
- RACKHAM. 1986. *The History of the Countryside*. London: J.M. Dent and Sons.
- RASMUSSEN, D. I. 1941. Beaver trout relationship in the Rocky Mountain region. *Transactions of the Fifth North American Wildlife Conference*, 5, 256-263.
- REBERTUS, A. J. 1986. Bogs as beaver habitat in north-central Minnesota. *American Midland Naturalist*, 116, 240-245.
- RECKER, W. 1997. Seltene todesursache des bibers, *Castor fiber* der mink, *Mustela (Lutrola) vision*, als Prädator des bibers im Bau. *Säugetierkundliche Mitteilungen*, 39, 87.
- REESE, K. P. & HAIR, J. D. 1976. Avian species diversity in relation to beaver pond habitats in the Piedmont region of South Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, 30, 437-447.

- REID, D. G., CODE, T. E., REID, A. C. H. & HERRERO, S. M. 1994a. Food-habits of the river otter in a boreal ecosystem. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 72, 1306-1313.
- REID, D. G., CODE, T. E., REID, A. C. H. & HERRERO, S. M. 1994b. Spacing, movements, and habitat selection of the river otter in boreal Alberta. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 72, 1314-1324.
- REID, D. G., HERRERO, S. M. & CODE, T. E. 1988. River otters as agents of water-loss from beaver ponds. *Journal of Mammalogy*, 69, 100-107.
- RENOUF, R. N. 1972. Waterfowl utilization of beaver ponds in New Brunswick. *Journal of Wildlife Management*, 36, 740-&.
- RICHARD, P. 1955. Bièvres constructeurs de barrages. *Mammalia*, 19, 293-301.
- RICHARD, P. 1967. Le déterminisme de la construction des barrages chez le castor du Rhône. *La Terre et la Vie*, 4, 339-470.
- RICHARD, P. 1983. Mechanisms and adaption in the constructive behaviour of the beaver (*C. fiber* L.). *Acta Zoologica Fennica*, 174, 105-108.
- RICHARD, P. B. 1985. Peculiarities of the ecology and management of the Rhodanian Beaver (*Castor fiber* L.). *Zeitschrift für Angewandte Zoologie*, 72, 143-152.
- RITVO, H. 1987. *The Animal Estate: The English and Other Creatures in the Victorian Age*. Cambridge, MA: Harvard University Press.
- ROBEL, R. J. & FOX, L. B. 1993. Comparison of aerial and ground survey techniques to determine beaver colony densities in Kansas. *Southwestern Naturalist*, 38, 357-361.
- ROBEL, R. J., FOX, L. B. & KEMP, K. E. 1993. Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. *Wildlife Society Bulletin*, 21, 415-421.
- ROBERTS, T. & ARNER, D. 1984. Food habits of beaver in East-Central Mississippi. *Journal of Wildlife Management*, 48, 1414-1419.
- ROHDE, F. C. & ARNDT, R. G. 1991. Distribution and status of the sandhills chub, *Semotilus lumbee*, and the pinewoods darter, *Etheostoma mariae*. *Journal of the Elisha Mitchell Science Society*, 107, 61-70.
- ROLAUFFS, P., HERING, D. & LOHSE, S. 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia*, 459, 201-212.
- ROSELL, F., KVINLAUG, J.K. 1998. Methods for live-trapping beaver (*Castor spp.*). *Fauna Norvegica. Serie A.*, 19, 1-28.
- ROSELL, F., BOZSER, O., COLLEN, P. & PARKER, H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, 35, 248-276.
- ROSELL, F. & CZECH, A. 2000. Responses of foraging Eurasian beavers *Castor fiber* to predator odours. *Wildlife Biology*, 6, 13-21.
- ROSELL, F. & HOVDE, B. 1998. Pine marten, *Martes martes*, as a Eurasian Beaver, *Castor fiber*, lodge occupant and possible predator. *Canadian Field-Naturalist*, 112, 535-536.
- ROSELL, F. & HOVDE, B. 2001. Methods of aquatic and terrestrial netting to capture Eurasian beavers. *Wildlife Society Bulletin*, 29, 269-274.
- ROSELL, F. & PARKER, H. 1995. Forvaltning av bever: dagens tilstand og fremtidig behov. (Beaver management: present practice and Norway's future needs.)
- ROSSELL, F., ROSEF, O. & PARKER, H. 2001. Investigations of waterborne pathogens in Eurasian beaver (*Castor fiber*) from Telemark County, southeast Norway. *Acta Veterinaria Scandinavica*, 42, 479-482.
- RUEDEMANN, R. & SCHOONMAKER, W. 1938. Beaver-dams as geologic agents. *Science*, 88, 523-525.

- RUPP, R. S. 1955. Beaver-trout relationship in the headwaters of Sunkhaze Stream, Maine. *Translocations of American Fishery Society*, 84, 75-85.
- RUSHTON, S., P. LURZ, R. FULLER & P. GARSON (1997) Modelling the distribution and abundance of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *Journal of Applied Ecology*, **34**, 1137-1154.
- RUSHTON, S. P., P. W. W. LURZ, J. GURNELL, P. NETTLETON, C. BRUEMMER, M. D. F. SHIRLEY & A. W. SAINSBURY (2006) Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiology and Infection*, **134**, 521.
- RUSHTON, S., M. SHIRLEY, D. MACDONALD & J. REYNOLDS (2006) Effects of culling fox populations at the landscape scale: a spatially explicit population modelling approach. *Journal of Wildlife Management*, **70**, 1102.
- RUSSELL, K. R., MOORMAN, C. E., EDWARDS, J. K., METTS, B. S. & GUYNN, D. C. 1999. Amphibian and reptile communities associated with beaver (*Castor canadensis*) ponds and unimpounded streams in the Piedmont of South Carolina. *Journal of Freshwater Ecology*, 14, 149-158.
- RUTHERFORD, W. H. 1955. Wildlife and environmental relationships of beavers in Colorado forests. *Journal of Forestry*, 53, 803-806.
- SAGER, H., KONJEVIC, D., GRUBESIC, M., JANICKI, Z., SEVERIN, K. & BECK, R. 2005. *Stichorchis subtriquetrus* in European beaver from Croatia: first report. *European Journal of Wildlife Research*, 51, 63-64.
- SCHLOSSER, I. J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology*, 76, 908-925.
- SCHLOSSER, I. J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia*, 113, 260-268.
- SCHULTE, B. & MÜLLER-SCHWARZE, D. 1999. Understanding North American beaver behavior as an aid to management. In: *Beaver protection, management, and utilisation in Europe and North America* (Ed. by Busher, P. & Dzieciolowski, R.). New York.: Kluwer Academic/Plenum.
- SCOTT PORTER RESEARCH & MARKETING LTD. 1998. Re-introduction of the European beaver to Scotland: results of a public consultation. Edinburgh: Scottish Natural Heritage Research.
- SCOTTISH GOVERNMENT, THE. 2008. The reintroduction of beavers. Edinburgh.
- SCOTTISH NATURAL HERITAGE. 2001. Proposed trial reintroduction of beaver to Knapdale: report on local consultation, 30 March. Edinburgh: Scottish Natural Heritage. Last accessed 7 July 2008 from: <http://www.snh.org.uk/pdfs/strategy/beaversappendix2.pdf>.
- SCOTTISH WILDLIFE TRUST. 2007. Trial reintroduction of the European beaver to Knapdale, Mid-Argyll: Local consultation report. Scottish Wildlife Trust. [http://www.swt.org.uk/Uploads/Downloads/BeaverConsultationReport\\_Dec07.pdf](http://www.swt.org.uk/Uploads/Downloads/BeaverConsultationReport_Dec07.pdf)
- SHEAIL, J. 2003. Government and the management of an alien pest species: a British perspective. *Landscape Research*, 28, 101-111.
- SHIRLEY, M. D. F., LURZ, P. W. W. & RUSHTON, S. P. 2007. Modelling the population dynamics of hedgehogs on the Outer Hebrides with a view towards eradication. Edinburgh: Rep. No. 15365. Scottish Natural Heritage. .
- SHIRLEY, M. D. F., RUSHTON, S. P., SMITH, G. C., SOUTH, A. B. & LURZ, P. W. W. 2003. Investigating the spatial dynamics of bovine tuberculosis in badger populations: evaluating an individual-based simulation model. *Ecological Modelling*, 167, 139-157.
- SIDOROVICH, V. E. 1992. Influence of amelioration works on densities of semiaquatic mammals in Yaselda river basin. *Vesci Akademii Navuk Belarusi. Seriya Biyalagichnykh Navuk*, 2, 48-52.
- SIDOROVICH, V. E., JEDRZEJEWSKA, B. & JEDRZEJEWSKI, W. 1996. Winter distribution and abundance of mustelids and beavers in the river valleys of Bialowieza Primeval Forest. *Acta Theriologica*, 41, 155-170.

- SIGOURNEY, D. B., LETCHER, B. H. & CUNJAK, R. A. 2006. Influence of beaver activity on summer growth and condition of age-2 Atlantic salmon parr. *Transactions of the American Fisheries Society*, 135, 1068-1075.
- SJÖBERG, G. 1999. Ecosystem engineering in forest streams - invertebrate fauna in beaver ponds [abstract]. In: *European-American Mammal Congress*, p. 158. Santiago de Compostela, Spain: Santiago de Compostela: Universidad de Spain.
- SKELLY, D. K. & FREIDENBURG, L. K. 2000. Effects of beaver on the thermal biology of an amphibian. *Ecology Letters*, 3, 483-486.
- SKEWES, O., GONZALEZ, F., OLAVE, R., AVILA, A., VARGAS, V., PAULSEN, P. & KONIG, H. E. 2006. Abundance and distribution of American beaver, *Castor canadensis* (Kuhl 1820), in Tierra del Fuego and Navarino islands, Chile. *European Journal of Wildlife Research*, 52, 292-296.
- SMITH, D. W. & PETERSON, R. O. 1991. Behavior of beaver in lakes with varying water levels in Northern Minnesota. *Environmental Management*, 15, 395-401.
- SMITH, M. E., DRISCOLL, C. T., WYSKOWSKI, B. J., BROOKS, C. M. & COSENTINI, C. C. 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack mountains, New York. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 69, 55-61.
- SOUTH, A., RUSHTON, S. & MACDONALD, D. 2000. Simulating the proposed reintroduction of the European beaver (*Castor fiber*) to Scotland. *Biological Conservation*, 93, 103-116.
- SOUTH, A. B., RUSHTON, S. P., MACDONALD, D. W. & FULLER, R. 2001. Reintroduction of the European beaver (*Castor fiber*) to Norfolk, UK: a preliminary modelling analysis. *Journal of Zoology*, 254, 473-479.
- SPIETH, H. T. 1979. Virilis group of *Drosophila* and the beaver *Castor*. *American Naturalist*, 114, 312-316.
- STENDLAND, M. 1953. Report of Minnesota beaver die-off. *Journal of Wildlife Management*, 17, 376-377.
- STEVENS, C. E., PASZKOWSKI, C. A. & FOOTE, A. L. 2007. Beaver (*Castor canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. *Biological Conservation*, 134, 1-13.
- STEVENS, C. E., PASZKOWSKI, C. A. & SCRIMGEOUR, G. J. 2006. Older is better: Beaver ponds on boreal streams as breeding habitat for the wood frog. *Journal of Wildlife Management*, 70, 1360-1371.
- SUZUKI, N. & MCCOMB, B. C. 2004. Associations of small mammals and amphibians with beaver-occupied streams in the Oregon coast range. *Northwest Science*, 78, 286-293.
- SUZUKI, N. & MCCOMB, W. C. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon coast range. *Northwest Science*, 72, 102-110.
- TAMBETS, M., JARVEKULG, R., VEEROJA, R., TAMBETS, J. & SAAT, T. 2005. Amplification of negative impact of beaver dams on fish habitats of rivers in extreme climatic condition. Abstract only *Journal of Fish Biology*, 67, 275-276.
- TÄRNVIK, A., PRIEBE, H.-S. & GRUNOW, R. 2004. Tularaemia in Europe: An epidemiological overview. *Scandinavian Journal of Infectious Diseases* 36, 350-355.
- TOWNSEND, J. 1953. Beaver ecology in Western Montana with special reference to movements. *Journal of Mammalogy*, 34, 459-479.
- TOWNSEND, P. & BUTLER, D. 1996. Patterns of landscape use by beaver on the lower Roanoke river floodplain, North-Carolina. *Physical Geography*, 17, 253-269.
- TYURNIN, B. N. 1984. Factors determining numbers of the river beavers (*Castor fiber*) in the European North. *Soviet Journal of Ecology*, 14.
- ULEVIČIUS, A. & JANULAITIS, M. 2007. Abundance and species diversity of small mammals on beaver lodges. *Ekologija*, 53, 38-43.

- VANNOTE, R. L., MINSHALL, G. W., CUMMINS, K. W., SEDELL, J. R. & CUSHING, C. E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130-137.
- VINES, G. 2007a. Don't fear the beaver. *New Scientist*, 195, 42-45.
- VINES, G. 2007b. The beaver: destructive pest or climate saviour? *New Scientist*, 2618, 42-45.
- WALLACE, J. B., WEBSTER, J. R. & MEYER, J. L. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 2120-2137.
- WALPOLE, M. & LEADER-WILLIAMS, N. 2002. Tourism and flagship species in conservation. *Biodiversity and Conservation*, 11, 543-547.
- WARREN, E. R. 1927. *The beaver: Its work and its ways*. London: Bailliere, Tindall & Cox.
- WESTERVELT, J., SHAPIRO, M., GORAN, W. & GERDES, D. 1990. Geographic Resource Analysis Support System, Version 4.0 User's Reference manual. USACERL ADP Report N-87/22, 1990.
- WHITE, D. 1990. Biological relationships to convective flow patterns within stream beds. *Hydrobiologia*, 196, 149-158.
- WILSON, C. 2004. Could we live with reintroduced large carnivores in the UK? . *Mammal Review*, 34, 211-252.
- WOO, M. K. & WADDINGTON, J. M. 1990. Effects of beaver dams on sub-arctic wetland hydrology. *Arctic*, 43, 223-230.
- WOODROFFE, G. 2005. A trial reintroduction of the European Beaver. *British Wildlife*, 16, 381-384.
- WOODROFFE, G. 2006. Mammals. *British Wildlife*, 17, 194.
- WRIGHT, J. P., FLECKER, A. S. & JONES, C. G. 2003. Local vs. landscape controls on plant species richness in beaver meadows. *Ecology*, 84, 3162-3173.
- WRIGHT, J. P., JONES, C. G. & FLECKER, A. S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, 132, 96-101.
- YALDEN, D. 1999. *The History of British Mammals*. London: T. & A.D. Poysner Ltd.
- ZIMMERER, K. & YOUNG, K. 1998. *Nature's Geography: New Lessons for Conservation in Developing Countries*. Madison University of Wisconsin Press
- ZUROWSKI, W. 1992. Building activity of beavers. *Acta Theriologica*, 37, 403-411.
- ZUROWSKI, W. & KASPERCZYK, B. 1986. Characteristics of a European Beaver Population in the Suwalki Lakeland. *Acta Theriologica*, 34, 311-321.