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Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems

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ABSTRACT

1. The genus *Castor* comprises two species: the Eurasian beaver *Castor fiber*, and the North American beaver *Castor canadensis*. Both species suffered from overexploitation, but have seen a revival since the 1920s due to increased protection and reintroduction programmes. Increases in the populations and distributions of species that are able to modify ecosystems have generated much scientific interest. Here we review the available literature concerning the possible ecological impact of beaver species in the Old and New World.

2. Beavers, being ecosystem engineers, are among the few species besides humans that can significantly change the geomorphology, and consequently the hydrological characteristics and biotic properties of the landscape. In so doing, beavers increase heterogeneity, and habitat and species diversity at the landscape scale. Beaver foraging also has a considerable impact on the course of ecological succession, species composition and structure of plant communities, making them a good example of ecologically dominant species (e.g. keystone species).

3. Nevertheless, the strength of beavers' impact varies from site to site, depending on the geographical location, relief and the impounded habitat type. Consequently, they may not be significant controlling agents of the ecosystem in all parts of their distribution, but have strong interactions only under certain circumstances. We suggest that beavers can create important management opportunities in the Holarctic, and this review will help land managers determine the likely outcome of beaver activity.

Keywords: biodiversity, *Castor canadensis*, *Castor fiber*, conservation, ecosystem engineers, keystone species

INTRODUCTION

Beavers as ecosystem engineers

Beavers are classified as ecosystem engineers, because their building activities can change, maintain or create habitats by modulating the availability of resources of both biotic and abiotic materials for themselves and for other species (Jones, Lawton & Shachak, 1994; Gurney & Lawton, 1996). Similarly, their foraging activity also alters organic material availability, thus creating habitat for other species, because tree felling by beavers for feeding purposes rarely entails the consumption of the whole plant material. Furthermore, beavers represent a small impasse of evolutionary history and have a unique foraging strategy. As the

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sole member, i.e. the biomass-dominant species, of their occupied functional groups (see Fox & Brown, 1993 and Bellwood & Hughes, 2001 for a definition of functional group), they could also be considered as a candidate keystone species (Davic, 2003). Although beavers have been frequently described as a keystone species (e.g. Naiman, Melillo & Hobbie, 1986), some studies have challenged this role (Nolet, Hoekstra & Ottenheim, 1994; Donkor & Fryxell, 1999), because beavers may decrease the species diversity in lower trophic levels. This can be due to their disproportional selection of less abundant species for complementary mineral sources (Nolet *et al.*, 1994), or the increased importance of dominant plant species, as beavers do not completely shift the plant community composition towards non-preferred species (Donkor & Fryxell, 1999). Nevertheless, beavers probably have a key role in ecosystem processes, because their foraging has a considerable impact on the course of succession, species composition and structure of plant communities (e.g. Huntly, 1995).

Following a period of devastating overexploitation, beavers are once again abundant in North America and are continuing to expand their range in Eurasia. The increase in the population and distribution of a species which is able significantly to modify ecosystems clearly generates considerable scientific and management interest. The aim of this paper is to review the extent of the beavers' ability to modify the physicochemical components and biological properties of ecosystems throughout the Holarctic.

THE GENUS *CASTOR*

Comparison of the two species

The genus *Castor* comprises two species: the Eurasian beaver *Castor fiber*, and the North American beaver *C. canadensis*. The two species are similar both morphologically and behaviourally (e.g. Novak, 1987), and were originally classified as one species. However, distinct karyotypes have been demonstrated (Lavrov & Orlov, 1973). This difference in karyotype probably explains why they do not interbreed successfully (Lahti & Helminen, 1974). The genus of true beavers originated in Eurasia and penetrated into North America during the course of the Pliocene epoch (Lavrov, 1983).

During the 1920s and 1930s, before confirmation that there were two beaver species, North American beavers were introduced to Poland and Finland (Lahti & Helminen, 1974; Ermala, Helminen & Lahti, 1989). They thrived in Finland and spread into parts of Russian Karelia in the 1950s (Danilov, 1992, 1995). Introductions were also made in Russia (Safonov & Saveliev, 1999), along the Seine in France (Richard, 1985), Hungary (Bozsér, 2001a) and Austria (Sieber, 1989). However, North American beavers are probably extinct now in Austria, Hungary, Poland and France (Bozsér, 2001b; Halley & Rosell, 2002). These introductions have provided opportunities for comparative studies on the two beaver species.

Although comparative studies have generally found that the Eurasian beaver demonstrates less building activity than the North American species (Danilov & Kan'shiev, 1982; Danilov, 1995), the effects of their dams on the environment may not differ much (Nolet, 1996). However, two important differences between the species are that the North American beaver may mature earlier and has larger litters than the Eurasian beaver (Lahti & Helminen, 1974; Danilov & Kan'shiev, 1983). In an extensive review, Rosell & Parker (1995), found a mean colony size of 5.2 ± 1.4 S.D. for the North American and 3.8 ± 1.0 S.D. for the Eurasian beaver. Where the two species have been introduced at the same place, the North American beaver often dominates and displaces the Eurasian species (Lahti & Helminen, 1974). This could be associated with the higher reproductive rate of the North American beaver (Danilov & Kan'shiev, 1983). This is supported by studies in Finland, where differences observed in the population growth rates of the two species could not be linked to differences in habitat or food (Lahti & Helminen, 1974). Nevertheless, some Russian evidence suggests that the low litter size in Eurasian beaver may be due to inbreeding depression (Saveljev & Milishnikov, 2002; Saveljev *et al*., 2002). However, Milishnikov (2004) concluded that the effective reproductive size N_e of the minimum Eurasian beaver population in that study was estimated to be equal to three animals. This extremely low value of effective reproductive population size largely explains the high tolerance of Eurasian beaver to inbreeding and striking viability of the species.

MacDonald *et al*. (1995) concluded that studies on North American beavers can provide important clues about the potential effects of Eurasian beavers. This is important for management because the majority of information on the beavers' impact on the environment originates from studies in North America (MacDonald *et al*., 1995; Nolet, 1996). Where Eurasian beavers construct dams and fell trees, they are likely to have similar environmental effects to the North American beavers (MacDonald *et al*., 1995).

Historical and present distribution

Beavers were once found throughout the northern forest belt from Canada and the United States to Europe and Asia. Along this extensive northern range, they are able to occupy a broad spectrum of ecoregions from subtropical to subarctic. Both species suffered from overexploitation, as great value was placed on their pelt and castoreum. In North America, a large proportion of the beaver population at middle and southern latitudes was depleted before 1900 (Hill, 1982). Similarly, it has been estimated that only 1200 Eurasian beavers remained by the early 20th century (Nolet & Rosell, 1998).

To reverse the effects of this overexploitation, beavers on both continents were protected and, from the 1920s, reintroduction programmes were initiated. In North America, after almost four centuries of commercial exploitation, the beaver is once again abundant, and the population in USA is currently estimated to be 6–12 million (Naiman *et al*., 1986). Although the recovery of the Eurasian beaver has been slower, it is continually expanding its range and the current minimum population estimate is 639 000 (Halley & Rosell, 2003).

INFLUENCE ON THE PHYSICOCHEMICAL CHARACTERISTICS OF STREAMS

It is widely recognized that there are strong and continuous interactions between hydrology, geomorphology, water chemistry and temperature (Naiman *et al*., 2000). They are all significant factors that influence aquatic organisms, and they can all be modified by beaver activity.

Hydrological effects

The effect of beaver dams on stream flow will vary according to their location in the catchment. In upland narrow valleys, beaver ponds are generally small; whereas in flood plain areas, even a low dam can flood a relatively large surface area (Johnston & Naiman, 1987). Due to large initial differences in velocity, beaver dams that flood upland areas reduce the kinetic energy of the stream more than those that flood wetlands (Johnston & Naiman, 1987). The age and structural characteristics of the dam can be important, and Meentemeyer & Butler (1999) reported that older beaver dams reduced stream velocity and discharge more efficiently than young dams in low-order streams in Montana. In a second-order stream in Maryland, the creation of a 1.25-ha beaver pond reduced the annual discharge of water by 8% (Correll, Jordan & Weller, 2000).

Although a single beaver dam may have little influence on stream flow, a series of dams can have a significant effect (Grasse, 1951) by moderating the peaks and troughs of the annual discharge patterns. During dry periods, Duncan (1984) reported that up to 30% of the water in an Oregon catchment could be held in beaver ponds. By increasing storage capacity, it has been suggested that large numbers of beaver dams will lead to greater flows during late summer (Parker, 1986), which may result in continual flows in previously intermittent streams (Yeager & Hill, 1954; Rutherford, 1955).

Beaver dams, depending on their number and location, may decrease peak discharge and stream velocity during a run-off event, thereby reducing the erosion potential (Parker, 1986) and the possibility of flooding (Bergstrom, 1985; Harthun, 2000). Associated with the reduction in stream velocity are reductions in the sediment-carrying capacity of the stream and increases in deposition (Naiman, Johnston & Kelley, 1988). Parker (1986) suggested that beaver dams can protect areas from erosive perturbations, if these perturbations are not too great.

Although beaver dams normally reduce the severity of flooding events, they may contribute to them if dam failure occurs (Butler, 1991). The failure of a beaver dam on a small stream in Alberta produced an estimated flood wave which was 3.5 times the maximum discharge recorded over a 23-year period (Hillman, 1998).

Beaver impoundments increase the area of riparian habitat and recharge groundwater by elevating the water table (Bergstrom, 1985; Johnston & Naiman, 1987). The movements of water within bed sediments can be influenced by beaver dams. In a typical convective pattern, stream water penetrates the bed, travels through the sediment along the longitudinal gradient and then upwells back into the river (White, 1990). As pore water moves beneath a beaver dam, it is no longer affected by the pressure of the impounded water. The pressure decreases immediately downstream from the dam, and therefore causes a sharp upwelling of underflowing stream water and upwelling of cooler pore water from deeper in the substrate.

Most studies conclude that beaver dams stabilize stream flow. However, Reid (1952) reported that increased evaporation from beaver ponds in the Adirondacks could reduce the volume of flow. Woo & Waddington (1990) also found that, in the subarctic wetlands of Ontario, the enlargement of the open water area by beaver activities enhanced evaporation in the summer. However, they reported that losses from enhanced evaporation could be offset by the reduction in water loss through run-off in areas with well-maintained dams. Correll *et al.* (2000) suggested that high evapotranspiration by the riparian forest fringing the pond, rather than evaporation, could have been responsible for the reduction in water discharge from a 1.25-ha beaver pond.

Geomorphology

Beavers construct burrows and lodges to enhance their survival (predator avoidance, shelter, thermoregulation), canals to extend feeding areas, food caches to provide a winter food supply and dams to improve their habitat by raising water levels (Zurowski, 1992). These activities affect hydrology, sediment yields and debris accumulation, and therefore have an overall impact on channel morphology.

The discharge regime, structural elements, sediment volume and accumulation pattern of sediment have a great role in shaping the river channel (Gurnell, 1998). Beaver dams are significant structural elements in river channels, greatly influencing discharge regime and sediment transport. Beaver ponds function as sediment traps, and they also accumulate organic matter, especially as anaerobic conditions caused by the restrained stream velocity decrease decay rates (Pollock *et al.*, 1995). A 1.25-ha beaver pond in Maryland reduced annual discharge of total organic carbon by 28% and total suspended solids by 27% (Correll *et al.*, 2000). The organic matter and sediment derives from the stream flow, bank failure, excavation of burrows and canals, collapse of burrows and lodges, primary production in the pond, and organic material from riparian vegetation which could be introduced by beavers, or delivered by other natural means. Although the velocity and discharge of water emerging from beaver ponds are reduced, areas downstream of the dam may have increased potential for erosion due to the trapping of sediments and subsequent release of underloaded water.

Beaver impoundments undergo a process of infilling; therefore the older ponds generally contain more sediment than the recently established ones. Meentemeyer & Butler (1999) found that the depth of sediment ranged from an average 24.6 cm in younger ponds (< 6 years old) to 45 cm in an older pond (> 10 years old) in Glacier National Park, Montana. Accordingly, the sedimentation volume ranged from 9.4 m^3 in a young pond (38 m^2) to 267 m^3 in an older pond (588 m^2). The amount of sediment accumulated in the ponds will vary, depending on the stream discharge, slope, upstream surface material and the extent of erosion-prone areas in the watershed (Meentemeyer & Butler, 1999). For instance, the sediment load within the Matamek and Moise River watersheds, Quebec, differed largely in magnitude from the example above with sediment volumes varying from 35 to 6500 m^3 in the beaver ponds (Naiman *et al.*, 1986). They estimated that the beaver dams constructed on the Matamek River watershed's 2nd–4th-order streams (approx. 322 km) are responsible for the retention of 3.2 million m^3 sediment. If this mass was evenly distributed over the total area of stream bed, it would cover the bottom with 42-cm sediment. Thus, beaver dams and resulting ponds give the channel gradient a stair-step profile, increasing the diversity in channel width and depth (Naiman *et al.*, 1988; Gurnell, 1998). Palaeoecological evidence suggests that, over a million years, entire valley floors have been raised by the continuous sedimentation process in beaver ponds (Rudemann & Schoonmaker, 1938; Ives, 1942).

Similarly, but to a lesser degree, the woody debris accumulated by beavers in streams also increases the patchiness of bed sediment and represents an important in-channel morphological feature. This woody debris controls the transport of sediment and particulate organic matter, and creates conditions for the formation of braided channel, pools and islands. By importing woody debris into streams, beavers play a considerable role in the stabilization of low-order (mainly 1st–5th order) streams (Gurnell, 1998; Naiman *et al.*, 2000).

Beavers can also impact on the drainage network of larger rivers (≥ 5th order), where their alterations to channel geomorphology occurs mainly along river banks and in wide, relatively flat flood plains (Naiman *et al.*, 1986; Gurnell, 1998). In situations where the water level is sufficiently high on the upstream side of the beaver dam for flow diversions to occur across flood plains of very low relief, the river channel might be subdivided into a series of smaller, interconnected channels occupied for shorter or longer periods (Townsend, 1953; Woo & Waddington, 1990). These diversion channels, which can be short or reach a few hundred metres in length, may become permanent routes of water flow if they are utilized enough to allow sufficient down cutting to occur (Woo & Waddington, 1990). By this means, multi-thread channel systems might be created, which accommodate flood flows (Gurnell, 1998).

Water chemistry

Beaver activity can have a significant effect on water quality, although the magnitude and nature of induced changes in water chemistry will be modified by catchment characteristics such as geology, soil type, land use and climate.

Beavers may exert considerable influence on the productivity of fresh waters by altering nutrient levels. Naiman & Melillo (1984) found that beaver ponds stored approximately 1000 times more nitrogen (N) in sediments, per linear metre of stream channel, than riffle areas and that this was solely a function of the amount of sediment accumulated in the different habitats. In the riffle areas of this stream, most of the N input was from allochthonous (terrestrial) sources, mainly deciduous leaves, while in the beaver pond most of the annual input was accounted for by N fixation associated with sediment microbes. Songster-Alpin & Klotz (1995), using electron transport system activity as a measure of microbial biomass and respiration, demonstrated that beaver ponds greatly increased microbial activity along streams. Francis, Naiman & Melillo (1985) estimated that total N accumulation in sediment, per unit area, is enhanced by 9–44 fold by beaver damming a section of stream.

The feeding activities of a colony of six beavers could have contributed as much as 10.3 g $N/m^2/$ year to a beaver pond in Quebec (Naiman & Melillo, 1984). Fallen wood from trees killed by inundation and wood used in dams and lodges would add to this total. This input of organic matter by beaver, augmented by the initial accumulation of flooded forest material, is probably very important to phosphorus (P) and N dynamics, and represents a long-term source of nutrients to the pond water and outflow (Devito & Dillon, 1993).

Beaver ponds were identified as one of the likely sources of the high total organic nitrogen (TON) and total phosphorus (TP) export in forested stream catchments in Ontario (Dillon, Molot & Scheider, 1991). Francis *et al.* (1985) also noted that beaver ponds could act as source or sink for P and N. They found that N fixation may be enhanced downstream of beaver-influenced areas and this was possibly linked to an increase in P levels.

Gross export and absolute retention of P and N in a beaver pond in Ontario were primarily controlled by seasonal variations in run-off (Devito & Dillon, 1993). Positive monthly retention coincided with low run-off and high biotic assimilation during the growing season. Large flow-through of waterborne inputs and flushing of regenerated P and N occurred during peak snowmelt resulting in low annual retention. Prior to the construction of a 1.25-ha beaver pond in Maryland, concentrations of TON and total organic phosphorus (TOP) were significantly correlated with stream discharge, especially in the winter, but subsequent to the pond, there was little relationship with stream discharge (Correll *et al.*, 2000).

In a second-order stream in Wyoming, which was prone to erosion and had a large mineral sediment load, seasonal differences were recorded in water quality following passage through a series of beaver ponds (Maret, Parker & Fannin, 1987). During periods of high flow in spring, concentrations of suspended solids (SS), TP, sodium hydroxide-extractable P (NaOH-P, an index of biologically available P) and total Kjeldahl nitrogen (TKN) were reduced in waterflowing through the beaver ponds. Generally, the amount of SS could explain the variation in TP, TKN and NaOH-P. During low summer flows, when mineral particulate load and deposition were reduced, the beaver ponds did not reduce nutrient levels.

A study of beaver ponds in New York State revealed differences in how individual ponds influenced stream water P concentrations (Klotz, 1998). While some ponds increased soluble reactive P, others decreased it. These differences may have been related to the way in which the biogeochemical cycling of P was influenced by the level of anaerobic conditions in the pond sediments. Klotz (1998) also demonstrated that elevated levels of P may occur for only short distances downstream of the beaver pond.

The anaerobic zones in the sediment interstitial waters of beaver ponds may be enriched in dissolved nutrients. Increased concentrations of these nutrients result in their movement, through turbulent diffusion, into the sediment/water interface (Dahm & Sedell, 1986). The resulting enrichment in this zone stimulates increased primary production. Comparisons of algal production in two streams in New Mexico, one poorly retentive and the other highly retentive due to several decades of beaver activity, found higher algal production in the stream with beavers (Coleman & Dahm, 1990). This was linked to greater nutrient availability at the sediment/water interface due to enhanced retention and processing of organic matter in the hyporheic zone (area in which stream water extends as groundwater throughout the surrounding land). The convective flow patterns associated with pressure changes beneath beaver dams may function to store stream water components temporarily and to bring pore water/stream water to the surface, thereby affecting distributions of surface-dwelling organisms (White, 1990).

Concentrations of dissolved oxygen (DO) can be reduced in waterflowing through beaver impoundments (Naiman *et al*., 1986). However, Smith *et al.* (1991) found that generally, the DO value was increased immediately during outflow from the dam, and complete reoxygenation was achieved within the next 0.25 km of stream. Prolonged deprivation of oxygen, due to the activities of beavers, would not be expected in unpolluted, low-order streams (Smith *et al*., 1991).

Beavers may play an important role in modifying water chemistry in regions where inputs of strong acids from atmospheric pollution are relatively high (Margolis, Castro & Raesly, 2001a). Smith *et al.* (1991) found that generally, pH, acid neutralizing capacity (ANC), dissolved organic carbon (DOC), iron (Fe^{2+}) and manganese (Mn^{2+}) values were elevated, while sulphate (SO_4^{2-}) and ionic forms of aluminium (Al^{n+}) were decreased following passage of water through a beaver impoundment in a second-order Adirondack Mountain stream. Further studies at this site revealed that the beaver pond was also a net annual sink for inlet nitrate (NO_3^-) and silica (H_4SiO_4) and a net annual source of ammonium ions (NH_4^+) (Cirmo & Driscoll, 1993). Similarly, Margolis *et al.* (2001a) found that during the summer, beaver impoundments on Appalachian headwater streams generated ANC and increased pH by acting as sinks for NO_3^- and sources of NH_4^+, iron and manganese.

Losses of ANC, which were associated with Al and basic cation retention, and organic anion release, were more than compensated for by SO_4^{2-} and NO_3^- retention and Fe^{2+} and NH_4^+ release, and this produced a net production of ANC (Cirmo & Driscoll, 1993). They suggested that as beaver pond sediments can store large amounts of organic matter, enhancing the development of anoxic zones which act as sites for ANC generation, the impounded areas provide sites where substantial alterations in water chemistry are possible.

Beaver activity affects biogeochemical cycles and the accumulation and distribution of chemical elements over time and space by altering the hydrological regime (Naiman *et al*., 1994). Only a portion of the chemical elements, derived from retained organic matter and sediment, are exported downstream (except for calcium and magnesium) or returned to the atmosphere (Carbon and N), and substantial standing stocks are accumulated in the pond sediment (Naiman *et al*., 1994).

Water temperature

The effect of beaver activity on water temperature, particularly the creation of impoundments and the harvesting of shade-producing riparian vegetation can vary greatly, depending on the region and site characteristics.

Beaver impoundments in Wisconsin served as heat-collecting units in summer and cold-storage units in winter (Avery, 1983). In the same State, Patterson (1951) found that beaver dams were detrimental in increasing the water temperature of feeder streams which consequently deprived the main river of a supply of cold water. The removal of dams in a low-gradient Wisconsin river generally resulted in an overall decrease in water temperature (Avery, 1992).

Water temperature was often not a main interest of earlier studies, and McRae & Edwards (1994) considered that no clear relationship had been established between different sizes or numbers of impoundments and the degree of stream warming. They found that local differences in vegetative and topographic shading, groundwater inflow contribution and stream volume meant that the thermal effects of beaver impoundments were highly site-dependant. However, their data indicated that large ponds act as thermal buffers, raising downstream water temperatures slightly in some instances, but they also dampened diel fluctuation.

Margolis *et al.* (2001a) found that water temperatures were significantly greater downstream of beaver impoundments, in autumn, spring and summer, in two Appalachian headwater streams. They recorded that water temperatures downstream of beaver impoundments were up to 6 °C warmer in the autumn and spring, and up to 9 °C warmer in the summer.

ECOLOGICAL IMPACTS ON PLANTS

Impact of foraging on plant communities

The beaver is a generalist herbivore, feeding on bark, shoots and leaves of woody plants, terrestrial herbs and forbs, ferns and aquatic vegetation (Wilsson, 1971; Jenkins, 1975; Svendsen, 1980; Nolet *et al.*, 1995; Donkor & Fryxell, 1999). Beavers have the ability to cut mature trees, but they tend to ingest only a proportion of the total biomass harvested. Consequently, beavers are likely to have a larger potential effect on the stand biomass than any other browser within their foraging range (Johnston & Naiman, 1990a). For example, at a pond in Minnesota, Johnston & Naiman (1990a) found that each of the six beavers in an individual colony felled nearly 1.300 kg/ha/year woody plant. This decreased the above ground biomass by over 40% at the pond after 6 years of foraging. Less than one-third of this biomass was consumed, a small part was used for dam and lodge construction, and the rest was left unused. However, biomass reduction is probably less pronounced in ecosystems where the majority of felled trees are immature or where dam construction is unnecessary. As beavers rarely move further than 60 m from the water to forage, their foraging impact is concentrated along narrow shorelines (Barnes & Dibble, 1988; Donkor & Fryxell, 1999; Parker *et al.*, 2001). Furthermore, woody species are not utilized in the same proportion, and beavers generally prefer species belonging to the genera alder *Alnus*, ash *Fraxinus*, birch, cherry *Prunus*, hazel *Corylus*, maple *Acer*, mountain ash *Sorbus*, oak *Quercus*, poplar *Populus*, and willow *Salix* (Curry-Lindahl, 1967; Johnston & Naiman, 1990a; Nolet *et al.*, 1994; Donkor & Fryxell, 1999). Beavers have the ability to fell very large trees, and the largest recorded in Norway and North America had diameters of 58.5 cm and 117 cm (Rosell & Pedersen, 1999).

North American studies demonstrate that, in alluvial vegetation types, the continuous harvesting of early and mid-successional species by beavers can reverse the progress of succession. Moreover, by increasing light penetration and decreasing competition for soil and nutrients, beaver foraging could increase net primary productivity of existing non-preferred woody species (Barnes & Dibble, 1988; Johnston & Naiman, 1990a). Hence, longer-term browsing probably causes deciduous stands to be replaced by shrub zones of unpalatable non-preferred species (Pastor *et al.*, 1988; Johnston & Naiman, 1990a). Though the light gaps created by beavers facilitate the regeneration of both their preferred and avoided food plants, these observations suggest that beaver browsing considerably shifts the species composition of the plant community towards non-preferred species.

In the Biesbosch Nature Reserve of the Netherlands, Nolet *et al.* (1994) studied the impact of beaver foraging on the species composition of a riparian willow forest. They hypothesized that beavers, by creating ephemeral open patches where shade-intolerant plant species could grow, would increase diversity by selective foraging. However, by selectively harvesting the non-willow species, the beavers eventually decreased the diversity of woody species.

Easily digestible trees (willows, alders) are browsed heavily. For production, these early successional trees need high nutrient levels, which are supplemented by their N-rich litter and alluvial sediments, while late successional conifers are able to survive low soil nutrient levels that are maintained by their slowly decomposing litter (Flanagan & van Cleve, 1983; Pastor & Naiman, 1992). Therefore, the impact of selective foraging by beavers through soil nutrient cycles is most relevant in boreal forests where nutrient availability is generally low (Flanagan & van Cleve, 1983) and species differ greatly in palatability, litter quality and growth responses to N. For example, studies in North America demonstrated that beavers influence the stage of vegetational development in boreal conifer forests. By creating light gaps and increasing the availability of nutrients in moist soils, beavers may reverse the succession in the zone next to the water's edge by creating an environment suitable for early successional willows and alders. However, in areas further from the water, beavers may hasten the succession by releasing the pine *Pinus* spp. and spruce *Picea* spp. from understorey competition (Naiman *et al*., 1988; Johnston & Naiman, 1990a).

Effects of selective foraging on tree growth

Mammals can influence the composition, distribution, abundance, form and reproduction of plants in the ecosystem. At the level of the individual plant, herbivory can evoke negative feedback mechanisms, such as enhanced secretion of defensive chemicals (Martinsen, Driebe & Whitham, 1998). Depending on the proximity of the plant to water, beaver foraging caused differences in growth form of even-aged stands of Fremont's cottonwood *Populus fremontii* (McGinley & Whitham, 1985). The cottonwoods furthest from water did not suffer from substantial harvesting and had an upright growth form, and likely reached maturity and reproduced sexually. In contrast, those close to water had a dense, shrub-like growth because the selective harvesting of beavers maintained them in perpetual juvenile condition, and reproduction was predominately vegetative.

Furthermore, after heavy harvesting by beavers, narrowleaf cottonwood *Populus angustifolia* and quaking aspen *P. tremuloides* reproduce clonally by producing adventitious buds by the roots, which sprout around the base of the cut plants (McGinley & Whitham, 1985). Basey, Jenkins & Busher (1988) found that beavers selected against these juvenile-form saplings of quaking aspen, because they had elevated concentrations of a phenolic compound which probably acted as a feeding deterrent. In other cases, the preferred species did not recover soon after beavers abandoned their sites. For example, Barnes & Mallik (2001) did not find any evidence of quaking aspen recovery after 12 years of abandonment. The over-exploited food resources and the negative feedback mechanism of feeding deterrent compounds help to explain how beavers and their preferred food plants have been able to maintain a dynamic equilibrium in riparian forests in the past (Pollock *et al*., 1995).

Effects of beaver dams on plant communities

The size of the dams constructed by beavers is largely dictated by the topography of the site and the availability of building materials. Some exceptionally large North American beaver dams have been recorded, including a 700-m-long dam in Montana (Ives, 1942) and a dam which exceeded a height of 5 m in Wyoming (Grasse & Putnam, 1955). Although there are no records of Eurasian beaver matching these extremes, we have recorded dams more than 3.25 m high in southern Norway (Collen & Gibson, 2001). Beavers can create systems of dams; for example, Zurowski (1989) recorded a colony of beavers constructing 24 dams along a 1300-m section of stream. These dams varied 1.5–60 m in length and they elevated water levels by 20–150 cm.

Damming of streams by beavers is potentially one of the most significant disturbance factors. Other disturbances, like fire and wind, also create clearings, but recovery in such cases is usually rapid as the colonization and growth of a new tree generation occurs within a few years. In contrast, beaver dams cause long-term changes in the ecosystem. Within one cycle of a beaver impoundment, beavers alter the successional stage of the riparian zone in two ways. First, damming raises the water table, thereby causing significant changes to aquatic and riparian ecosystems. Second, following abandonment of sites by beavers, the dams eventually collapse and terrestrial succession begins on the drained mud flats (Nummi, 1989). Nevertheless, beavers sometimes impound sites that are resistant to change. For example, impounded bogs have the ability to float up and down with changes in water level, so the location and extent of these bogs remain relatively unchanged during the course of occupation and abandonment by beavers (Naiman *et al*., 1988).

Beavers' dam streams and the subsequent flooding may kill woody vegetation in one or two growing seasons which increases the surface area of unshaded water. Most woody plants are rapidly stressed by flooding, although willows tolerate flooding for a longer period (Nummi, 1989). However, the pond edges create favourable conditions for moisture demanding plants, such as willow and alder.

Beaver ponds are usually shallow with little current, and resulting sedimentation allows sunlight to reach aquatic primary producers (Klotz, 1998). Further, beaver ponds retain a large proportion of nitrate, silicate and phosphate by trapping sediments and organic matter. The enhanced nutrient levels can facilitate the growth of aquatic vegetation (Correll *et al*., 2000).

Ray, Rebertus & Ray (2001) studied the successional sequence of aquatic vegetation in beaver ponds in peatland areas. These peatland impoundments were not connected to permanent open waters, so they were less prone to washout events and were isolated from rapid colonization of macrophyte species from inflowing sources. The ponds were first colonized by free-floating, easily dispersible genera like duckweed (*Lemna* spp., *Spirodela* spp.), watermeal *Wolffia* spp. and bladderwort *Utricularia* spp. They were most abundant in young impoundments (4–6 years old) and declined afterwards. By the end of the first decade, submersed macrophyte species (pondweeds *Potamogeton* spp., hornwort *Ceratophyllum demersum*, waterstarwort *Callitriche vulgaris*) colonized the impoundments and peaked in ponds of intermediate age (10–40 years). Representatives of floating-leaved macrophyte communities (watershield *Brasenia schreberi*, water lily *Nymphaea* spp., and yellow water lily *Nuphar lutea*) appeared last, probably because of the dispersal characteristics of these species. However, once introduced, they increased in abundance until the ponds were 40 years old (Ray *et al*., 2001). In the first 40–50 years, the species turnover was only 85%, probably due to the effective dispersal of many macrophyte species, and the high internal heterogeneity within beaver ponds that facilitates the long coexistence of numerous species. During this period, the species richness increased linearly, and up to 75% of the total richness found in surrounding lakes appeared in the ponds. However, after 40 years, the richness and diversity stabilized or even declined, possibly due to competition for light between canopy-forming floating-leaved macrophytes and submersed vegetation, and to herbivory (Ray *et al*., 2001).

Beavers often leave their ponds due to a reduction in food supply. In the absence of regular maintenance, the dams will ultimately collapse (Pollock *et al*., 1995). However, if dams resist structural failures during floods for long time periods, the gradual sedimentation in these ponds eventually results in the development of gently sloping, organically rich alluvial plains, so-called beaver meadows (Gurnell, 1998; Meentemeyer & Butler, 1999).

Following drainage, sediments and organic matter trapped on the upstream side of the dam begin to change. The soil becomes more aerobic and nutrients are released due to the mineralization of organic matter (Correll *et al*., 2000). Unless they are reflooded, beaver meadows undergo plant and soil succession (Pollock *et al.*, 1995; Terwilliger & Pastor, 1999). However, Remillard, Gruendling & Bogucki (1987) reported that the return interval of beaver disturbance is approximately 10–30 years in the Adirondacks. Thus, reoccupation may take place at any seral state, converting the vegetation to an early successional stage.

Upon abandonment, ponds drain gradually. The upstream end and lateral margins of the site drain first, while standing water persists near the lodge and dam. Therefore, zones of open water, mud flats, wet meadows and dry meadows coexist soon after abandonment (McMaster & McMaster, 2000). In the Adirondacks and Massachusetts, abandoned ponds which are not recolonized, develop into either open meadows dominated by grasses and sedges, or shrubby swamps dominated by alder, spirea *Spirea* spp., holly *Ilex* spp. and Viburnum *Viburnum* spp. (McMaster & McMaster, 2001; Wright, Jones & Flecker, 2002). As the meadow matures, a new channel will develop in the bottom sediments reforming the stream (Naiman *et al.*, 1988), but it will probably take another century for the stream to approach a new biogeochemical quasi-equilibrium. Several factors, like an unsuitable hydrologic regime or competition from grasses and herbivory, may account for the persistence of meadows. However, an important mechanism preventing the colonization of a new generation of conifers was described by Terwilliger & Pastor (1999). They provided evidence that an ectomycorrhizal fungi, which was required for the growth and survival of fir *Abies* spp. and spruce, was lacking in beaver meadows. The disappearance of the ectomycorrhizal fungi is likely due to the anaerobic conditions during flooding at active beaver sites, and their dispersal is largely connected to the movements of mycophagous small mammals. Their study indicated that the disperser of the fungi is the red-backed vole *Clethrionomys gapperi*, and that dispersal was limited by the habitat use patterns of this species. As a consequence, despite close proximity to seed sources, no woody plant invasion was recorded in beaver meadows over a 70-year period in Voyageurs National Park, Minnesota (Johnston & Naiman, 1990b). Therefore, beavers may alter the successional dynamics of riparian ecosystems by extending the area of a stable community (Pollock *et al.*, 1995).

IMPACT AT THE LANDSCAPE SCALE

Beavers can alter large areas of the landscape by damming streams. In areas of Quebec where the beaver population is largely unexploited, they can influence as much as 30–50% of the total length of 2nd–4th (approximately 1–2 m to 10–15 m wide) order streams (Naiman & Melillo, 1984). Within a 298-km^2 area of the Kabetogame Peninsula, Minnesota, the total area converted to ponds and meadows by beavers increased from 1% to 13% of the landscape (Naiman *et al.*, 1994), as the beaver population increased from near extinction to a density of more than 1 colony per km^2 (Johnston & Naiman, 1990c). By contrast, in a predominantly coniferous forested area (35 km^2) in southern Norway, which had a well-established beaver population, only 0.2% of the total area was flooded (Parker *et al.*, 2001). In the central Oregon Coast Range, Stack & Beschta (1989) demonstrated that beaver can alter the characteristics of stream pools, as sections with beaver dams typically had larger residual pools than reaches without beaver. Thus, river corridors, which are rather narrow and well-defined elements of the landscape, become wider, geomorphologically more complex and biologically more diverse and more productive zones of the landscape in the presence of beavers (Correll *et al.*, 2000). This alteration is well illustrated by McKinstry, Caffrey & Anderson (2001), who found that the width of the riparian zone averaged 33.9 m in streams with beaver ponds compared with 10.5 m in streams without such ponds.

The size of wetland areas created by beavers depends on local topography (width of channel and riparian zone, stream gradient) and whether the dam is restricted in-channel or extends across the flood plain. As a result of dam building by beavers, the riparian ecosystem increases, and different types of wetland communities develop along stream channels. Pollock *et al.* (1995) reported that on the Kabetogama Peninsula, Minnesota, the riparian system included 32 different plant communities, ranging from aquatic to forested wetland communities at different successional stages due to dam building activity. Therefore, by creating more or fewer open wetland patches in the forest matrix, beavers increase landscape heterogeneity. Moreover, the repeated occupation and abandonment of sites with the concomitant impact of dam-building and selective foraging, plus periodic human disturbances, make the landscape a dynamic, ever-changing system (McMaster & McMaster, 2001).

Besides the impact on community-level diversity, species diversity is also increased by beavers at the landscape scale, although species richness within single beaver sites may decline. The floristic diversity of beaver-influenced riparian ecosystems is determined by the diversity of pre-impounded vegetation, the spatial heterogeneity of environmental parameters caused by the temporally complex discharge regimes, and the impact of beavers' selective foraging in the riparian zone (Naiman *et al.*, 1988; Pollock *et al.*, 1995). Based on the estimates of Wright *et al.* (2002), wetlands created or modified by beavers may contribute to as much as 25% of the total vascular plant species richness in the riparian zone, and create favourable conditions for many species which otherwise would be excluded.

Wright *et al.* (2002) predicted that the impact of beavers on species richness might be less relevant in landscapes where lentic freshwater habitats independent of beaver activity occur. They also predicted that the total species richness would decrease if beaver-modified wetlands dominated the riparian ecosystem, as the number of unengineered patches may not be sufficient to support their entire complement of species.

Naiman *et al.* (2000) concluded that beavers can greatly affect the structure (channel morphology, vegetation characteristics), diversity (habitat, species), and function (productivity, connectivity, resistance and resilience to perturbations) of river corridors. They assumed that streams have relatively low resilience to disturbances, partly because they lack spatial heterogeneity (Naiman *et al.*, 1986). Therefore, beaver dams are important functional elements in river channels, and the resulting beaver ponds function as large-mass, slow-turnover components of the corridor buffering the ecosystem from perturbations (Naiman *et al.*, 1986).

ECOLOGICAL IMPACT ON OTHER SPECIES OF ANIMALS

Aquatic invertebrates

Generally, in small streams, beaver activity will create pond habitat at the expense of riffle or glide habitat, and the ponds will favour lentic species rather than the original lotic animals. McDowell & Naiman (1986) found that the typical low-order stream invertebrate community of a small stream in Quebec was replaced by assemblages which were functionally more similar to large-order systems. Specifically, the running water communities of the non-impounded sites were dominated by blackflies (Simuliidae), chironomids Tanytarsini (Chironomidae), scraping mayflies (Ephemeroptera), and net-spinning caddis flies (Trichoptera). Following impoundment by beaver, these species were replaced by two different groups of chironomids Tanypodinae and Chironomini (Chironomidae), predatory dragonflies (Odonata), sludge worms (Tubificidae), and filtering mussels (Pelecypodae).

Margolis, Raesly & Shumway (2001b) found that the major difference in taxonomic structure between impounded and above-impounded assemblages in two Appalachian streams was the dominance of midges, segmented worms (Oligochaeta) within the impoundments. Similarly, in a recently formed beaver pond in Ontario, Sprules (1941) recorded an increase in midges, while obligate lotic species, including mayflies, caddis flies, stoneflies (Plecoptera) and some true flies (Diptera), died or migrated. However, while beaver alterations to a German stream resulted in the disappearance of some species, it also accommodated a significantly higher number of species of dragonflies, damsel flies, caddis flies and some snails and mussels (Harthun, 1999).

By contrast, the situation on the dam structure itself, depending on site characteristics, can be different. In a low-gradient meandering stream in Alberta, Clifford, Wiley & Casey (1993) found that the invertebrate community of the dam was typical of a free-flowing environment. In particular, the dam had a large proportion of simuliid larvae, but other sections in the stream had a fauna more characteristic of slow-flowing or lentic environments. In slow-flowing streams, beaver dams can therefore have an important role in maintaining a lotic fauna.

The heterogeneity of the invertebrate fauna in a stream in Germany was found to be highest in the dam structure compared with the free-flowing stream and the beaver pond (Rolauffs, Hering & Lohse, 2001). They reported that the median emergence density of invertebrates in the dam was 3.2 times higher than the stream, and 5.5 times higher than the pond section, and the density of emerging caddis flies in particular was increased in the dam. Their results demonstrate that beavers increase the patchiness of the stream not only in terms of habitat and taxa composition, but also in terms of productivity. Adler & Mason (1997), working in Saskatchewan streams, also found that beaver dams were important sites for black fly production.

Beavers are also capable of influencing the invertebrate fauna of lakes. Many boreal headwater lakes in Ontario have limited littoral invertebrate habitat features, and beaver lodges can provide important structures in such environments. France (1996) recorded that the richness and abundance of 10 benthic macroinvertebrate taxa were higher near beaver lodges compared with other littoral zone sites which consisted of sand and rock. He argued that the presence of beavers is important for structuring the littoral communities in these headwater Canadian Shield lakes.

In some situations, the activity of beavers may be of particular importance to the conservation of endangered species. The Hungerford crawling water beetle *Brychius hungerfordi*, a rare North American species, is often associated with the area downstream of beaver dams. The removal of existing dams upstream from populations of these beetles is considered to represent a significant threat to them (U.S. Fish and Wildlife Service, 1994). By contrast, inundation from beaver dams is reported to present a significant danger to the threatened Louisiana pearlshell mussel *Margaritifera hembeli* (U.S. Fish and Wildlife Service, 1993). As this mussel must live in flowing waters, the inundation of water and accumulations of silt caused by the construction of a dam is likely to kill these bivalves. Also, this mussel requires a host fish to complete its life cycle, and it has been suggested that beaver dams may present barriers to migrations of the host fish (Johnson & Brown, 1998).

Beaver ponds may remain for considerable periods of time even after the beavers have moved to new locations. Such abandoned ponds may continue to provide suitable habitat for a wide range of invertebrates. Crane flies (Tipulidae) were found to be an important component of the aquatic fauna of a series of beaver ponds in Alberta which had been abandoned for about 10 years (Pritchard & Hall, 1971; Hodkinson, 1975a). Other macro fauna commonly occurring in these ponds included sludge worms, midges, soldier flies (Stratiomyidae), caddis flies, alder flies (Sialidae), backswimmers (Notonectidae), water boatmen (Corixidae), predacious diving beetles (Dytiscidae), water scavenging beetles (Hydrophilidae), and water striders (Gerridae). Additional studies in these beaver ponds focused on energy flows, and they were described as being highly accretive heterotrophic ecosystems (Hodkinson, 1975b, c).

Beaver activity normally leads to an increased input and storage of organic material and sediment in the impounded areas (Francis *et al.*, 1985). Associated with this, there can be an increase in the density and biomass of the invertebrate community and changes in the relative importance of the different invertebrate functional feeding groups (McDowell & Naiman, 1986). They found that the total density and biomass of invertebrates in impounded sites could be 2–5 times greater than riffle sites in spring and summer, although no differences were found in the autumn.

Low-order sites, with natural riparian vegetation, receive large inputs of coarse particulate organic matter (CPOM) from terrestrial sources, and the shredders (consumers of CPOM) are generally a very important group among the invertebrate fauna of such streams (Vannote *et al.*, 1980). In beaver-impounded sections of such streams, however, the relative importance of shredders decreases, even though large quantities of CPOM are available (Margolis *et al.*, 2001b). McDowell & Naiman (1986) suggested this may be due to inadequate velocity and substrate types for the shredders. This is partly supported by work in a low-gradient boreal stream where a Plecopteran shredder *Amphinemura* was only found at the dams where flow rates were greater (Clifford *et al.*, 1993).

McDowell & Naiman (1986) also reported that collectors [consumers of fine particulate organic matter (FPOM) gathered from the substrate] and predators were most abundant in impounded sites, and that filterers (consumers of FPOM filtered from the water) remained important, but the taxa changed compared with non-impounded areas. While much of the CPOM and the FPOM is supplied by the autumnal fall of leaves from riparian trees, there can be important contributions of fresh leaves, derived from beaver activity, entering the water at other times of the year. Stout & Taft (1985) reported that high beaver activity was one of the reasons for commonly finding fresh speckled alder *Alnus incana rugosa* leaves in Michigan streams. These green leaf inputs may also provide an important food source for invertebrate fauna.

Terrestrial invertebrates

Close relationships have developed between certain invertebrates and the activities of beavers. For example, most of the fruit fly species group *Drosophila virilis* are semiobligatory commensals of the beaver (Spieth, 1979). These flies require the rotting bark of a limited number of deciduous tree species as ovipositional substrates, and these substrates are typically abundant at beaver sites. Spieth (1979) suggested that the increase in both species of beaver has also resulted in a proportional increase in populations of these fruit flies.

By altering the species structure of woodlands, beaver may also affect the distribution and dispersal of terrestrial invertebrates. McNeel (1964) found that white pine *Pinus strobus* trees planted in the partial shade of aspen trees were free of white pine weevil *Pissodes strobi*, while those planted in an adjacent open area had been severely attacked. However, beavers colonized the area, felled the aspen, and in the absence of these trees, the previously shaded pines were subsequently attacked by the weevils.

Beavers also exert indirect effects on their trophic webs. Regrowth of cottonwood trees following cutting by beavers results in trees with much higher levels of phenolic glycosides. These chemicals serve as a defence against mammalian herbivores, but leaf beetles *Chrysomela confluens* are attracted to the regrowth. Leaf beetles sequester the chemicals for their own defence and develop faster on a diet of resprouted cottonwood compared with first growth (Martinsen *et al.*, 1998).

The amount of dead wood in forests increases as greater areas are flooded by the beavers' dams, and this can help certain bark beetles (Scolytidae) (Saarenmaa, 1978).

Fish

In small streams that are easily dammed, beavers can alter many of the habitat features which are crucial to fish survival, growth and reproduction. These beaver-created alterations can be either beneficial or detrimental, depending on the population density of the beavers and the prevailing constraints on local fish species composition and abundance (Collen & Gibson, 2001).

Beaver dams, by reducing flow rates, reduce the silt loads of water, and this is a potential benefit for salmonids which require clean gravel for spawning. However, following damming, long stretches of streambed can be covered by silt, and potentially important spawning areas may be damaged (Knudsen, 1962), although it is likely that trout downstream will benefit from reduced sediment loads (Grasse, 1951). Swanston (1991) also noted that the viability of spawning areas could be reduced if they are covered with deeper, slow-moving water as a result of beaver activity. Silt deposition regularly occurred in beaver ponds in Utah, but Rasmussen (1941) reported that, in areas where the average stream gradient was 2.2%, damage to spawning areas was minimal and extensive areas of spawning gravel remained.

For many species of salmonids, the ability to migrate both upstream and downstream is essential. Spring spawners (cutthroat trout *Oncorhynchus clarki* and rainbow trout *O. mykiss*) usually negotiated beaver dams (Rasmussen, 1941; Grasse, 1951). However, autumn spawners (brook charr *Salvelinus fontinalis* and/or brown trout *Salmo trutta*) could be blocked during low-flow conditions when the dams are in a good state of repair (Cook, 1940; Rupp, 1955). Rupp (1955), however, concluded that as trout habitat was well distributed throughout his study site, extensive seasonal migration was probably unimportant, but this would not be so at sites where free access was essential and where even delaying obstacles could present problems. In a California stream containing brown trout, brook charr and rainbow trout, the former was found to be the most inclined to cross beaver dams (Gard, 1961). He concluded that some trout are able to cross dams in both directions, but movements were influenced by river flow conditions. Although beaver dams presented some obstacles to colonizing fish (coho *Oncorhynchus kisutch* and sockeye salmon *O. nerka*) (Murphy *et al.*, 1989) and adult Atlantic salmon *Salmo salar* (Cunjak & Therrien, 1998), high flows may allow some passage. Water flow conditions, dam characteristics and the size and species of fish are important in determining the degree of difficulty presented by beaver dams to fish passage.

The beaver-induced changes to aquatic invertebrates, which are important food items for fish, and changes to riparian and stream habitats resulting from beaver activity, can have important consequences for fish populations. In small streams in Sweden, Hägglund & Sjöberg (1999) found that brown trout were larger in beaver ponds compared with those in riffle sections, and they also suggested that beaver ponds are likely to provide habitat for larger trout in small streams during periods of drought. Similarly, brook charr, coho and sockeye salmon were significantly larger in beaver ponds than those in un-impounded stream sections (Rutherford, 1955; Murphy *et al.*, 1989). In Maine headwater sites, Rupp (1955) reported that ninespine sticklebacks *Pungitius pungitius* were more abundant in beaver ponds than in the open stream, and they featured prominently in the diet of 15–25 cm brook charr.

Where water temperatures are well below the critical values for trout, beaver-induced increases in temperature may enhance trout production (Rasmussen, 1941; Huey & Wolfrum, 1956). However, where beaver activity raises water temperature above the optimum preferenda of salmonids, it may produce adverse conditions for trout (Cook, 1940; Adams, 1949), and may result in a shift to other species (Bailey & Stephens, 1951). Beaver impoundments served as heat-collecting units in summer and cold-storage units in winter, which markedly affected the survival of resident trout in Wisconsin (Avery, 1983).

Beaver ponds can provide important winter habitat for many stream fishes and in streams lacking deep pools, the importance of these impoundments increases (Cunjack, 1996). Beaver ponds in Oregon benefited coho salmon during the winter (Nickelson *et al.*, 1992), and also during summer flow conditions (Leidholt-Bruner, Hibbs & McComb, 1992). Similar benefits were recorded for sockeye salmon during the summer period in Alaskan streams (Murphy *et al.*, 1989). Bryant (1984) found that coho salmon in south-east Alaskan streams were also able to exploit the additional habitat created by beaver ponds.

Knudsen (1962) reported that mudminnows *Umbra limi* often increase in beaver ponds due to the large volume of water, increased forage space and warmer waters. Pike *Esox lucius* were also found to increase in number in beaver ponds in Wisconsin, particularly in large ponds with abundant shallow grassy areas, but the beaver dams may act as barriers to pike movements (Knudsen, 1962). Hanson & Campbell (1963) suggested that beaver ponds could provide important refuges for fish in times of low flow, and consequently serve as reservoirs for recolonizing streams. In the same way, beaver ponds in Minnesota can support a high production of juvenile creek chub *Semotilus atromaculatus*, and the summer dispersal of these age-0 fish from the ponds is an important factor controlling the population structure of creek chub in the adjacent stream (Schlosser, 1998). A similar situation occurred with minnow *Phoxinus phoxinus* fry in beaver ponds in Swedish forest streams (Hägglund & Sjöberg, 1999).

The reintroduction of beavers to Carolina was considered to have had a detrimental effect on the distribution and current status of the sandhills chub *Semotilus lumbee* and the pinewoods darter *Etheostoma mariae* (Rohde & Arndt, 1991). However, they found that the dusky shiner *Notropis cummingsae*, which favoured lentic waters, remained following intensive beaver activity. In small streams in Sweden, minnows were more common in beaver-affected sections than in reference sections, while the opposite was found for brown trout (Hägglund & Sjöberg, 1999).

Beaver activity may also influence lake-dwelling fish. France (1997) found that in boreal headwater lakes in Ontario, the abundance of northern redbelly dace *Phoxinus eos*, finescale dace *P. neogaeus*, fathead minnows *Pimephales promelas*, white suckers *Catostomus commersoni*, brook sticklebacks *Culaea inconstans*, and slimy sculpins *Cottus cognatus* were significantly elevated near beaver lodges compared with the more typical sand-and-rock littoral zone habitats of these lakes. He reported that 15% of the total standing crop of littoral fishes was associated with beaver lodges in his study lakes.

Although beaver ponds can be important sites for communities of warm water fish in streams, these populations may be different from those found in natural lakes in a river system. Keast & Fox (1990) found that a small shallow beaver pond in Ontario lacked the range of habitat types and associated fish species that occurred in nearby lake environments. They concluded that the size, depth and reduced recolonization potential of beaver ponds resulted in fish communities which contained fewer species and individuals of small body size when compared with lake communities.

Environmental changes produced by beaver activity were responsible for a change in dominance from brook charr to yellow perch *Perca flavescens* at a site in Ontario (Balon & Chadwick, 1979). Here, the activities of the beaver may have resulted in a major shift from fish which use stones and gravel for spawning to a dominance by other fish species that spawn on submerged plant surfaces or other substrata. Similarly, following beaver activity in streams which were generally considered to be marginal for trout in west Virginia, other species, such as minnows, chubs and suckers (Catostomidae), could out-compete and displace trout (Bailey & Stephens, 1951).

Amphibians

Frogs and toads (Anura), and tailed amphibians (Caudata) propagate, often profusely, in the shallow parts of beaver ponds. In boreal headwater lakes with limited amounts of vascular macrophytes, green frog *Rana clamitans* tadpoles and red-spotted newt *Notophthalmus viridescens* were found to be significantly more abundant near beaver lodges compared with other littoral zone areas of the lake (France, 1997). Metts, Lanham & Russell (2001) showed that in western South Carolina, the abundance of frogs and toads was significantly higher at beaver ponds than at un-impounded stream reaches. However, salamanders were less abundant in beaver impoundments likely due to their preference for small, free-flowing streams and to the presence of predatory fish.

In the Piedmont of South Carolina, Russel *et al*. (1999) found that the richness and total abundance of amphibians were not significantly different among new beaver ponds (5 years old), old beaver ponds (10 years old) and un-impounded streams, although several species of frogs and toads were captured predominately or exclusively at beaver ponds. Amphibian community overlap and diversity were also similar among the three habitats.

Beavers may also affect the development and physiology of amphibians. Skelly & Freidenburg (2000) reported that larvae of wood frog *Rana sylvatica* responded rapidly to changes in their environment induced by beavers. They found that the average temperature and the peak temperature of beaver-modified open wetlands can be 2 °C and 15 °C higher than in shaded wetlands, respectively. As a response, the critical thermal maxima of wood frogs has increased in a short time (< 36 years) in beaver wetlands.

Reptiles

Turtles (Chelonia) and water snakes *Natrix* spp., *Nerodia* spp. may utilize beaver ponds (Hilfiker, 1991). Metts *et al*. (2001) found that reptile richness and diversity were significantly higher at beaver ponds compared with those in un-impounded streams in western South Carolina. They associated a higher abundance of turtles in beaver impoundments to their preference for shallow, slow-flowing or standing water, abundant aquatic vegetation and soft organic substrates. The richness and abundance of reptiles were significantly higher at old beaver ponds compared with new beaver ponds and un-impounded streams. The degree of community reptile overlap was relatively low, with significant differences in diversity among all three habitats (Russel *et al*., 1999).

Birds

Beaver ponds produce an abundance of invertebrates that provide protein- and calcium-rich foods for breeding pairs of birds, nesting females and their broods (Danell & Sjöberg, 1982; Nummi, 1984; Whitman, 1987; McKinstry *et al*., 2001). Removal of trees by beavers from the riparian zone can increase the density and height of the grass–forb–shrub layer, which enhances waterfowl nesting cover adjacent to ponds. Beaver-impounded wetlands offer interspersion of cover and open water for isolation of territorial pairs (Ringelman & Longcore, 1982), as well as brood-rearing habitat (Carr, 1940; Beard, 1953; Brenner, 1960; Ringelman & Longcore, 1982). Beaver ponds also provide excellent roosting habitats for migratory and wintering waterfowl during autumn and winter (Arner & Hepp, 1989; Dieter & McCabe, 1989).

Grover & Baldassarre (1995) surveyed 70 wetlands in New York State during winter and spring 1992, and found that those occupied by beaver contained significantly more species and a greater average number of species than inactive or potential sites of the same size. The active sites had more open water, standing dead trees, surface water and flooded emergents. Peterson & Low (1977) found that adult waterfowl preferred beaver ponds larger than 0.4 ha over natural catchment basins of the same size.

Edwards & Otis (1999) examined the seasonal community composition and discerned microhabitat variables associated with bird group abundance and richness at six beaver ponds in South Carolina. The resident/short distance migrant group and the neotropical migrant group were most abundant in the spring seasons and waterfowl were less abundant. In autumn and winter, the resident/short distance migrant group was most abundant at all ponds with the exception of one that had very high use by waterfowl. Vegetation interspersion, patch evenness, plant richness and total area were most important in explaining abundance of waterfowl, waterbirds, neotropical migrants and woodpeckers (Picidae), respectively.

Beaver ponds provide wetland habitats and therefore play an important role in attracting ducks (McKinstry *et al.*, 2001). Further, the shallow water along beaver pond edges warms quickly and provides an excellent supply of plant particles, seeds and invertebrates for foraging ducks (Brown, Hubert & Anderson, 1996). Nevertheless, Brown *et al.* (1996) found that beaver ponds associated with duck usually have a surface area exceeding 1000 m^2.

Wetlands and ponds created by beaver provide important habitats for duck species, especially for teal *Anas crecca*, mallard *Anas platyrhynchos*, goldeneye *Bucephala clangula* (Nummi, 1987) and black ducks *Anas rubripes* (Ringelman & Longcore, 1982; Ringelman, Longcore & Owen, 1982; Whitman, 1987; Diefenbach & Owen, 1989), and in less productive regions in particular, for rearing duck broods (Beard, 1953; Renouf, 1972; Rudqvist, 1977; Ringelman & Longcore, 1982; Nummi, 1989, 1992; Nummi & Pöysä, 1995). Nummi (1984) found that benthic invertebrates played an important role in the increase in duck brood numbers in beaver flowages. As the flooded area aged (> 5 years), both the density of invertebrates and duck broods decreased (see also Kadlec, 1962; Danell & Sjöberg, 1982).

Beaver activity has an important influence on the development of ponds used by trumpeter swans *Cygnus* spp. (McKelvey, Dennington & Mossop, 1983). Swans and Canada geese *Branta canadensis* often build nests on the tops of lodges (Brenner, 1960; Hilfiker, 1991).

Dead, decaying trees in flooded beaver impoundments may provide nesting and feeding sites for woodpeckers (Grover & Baldassarre, 1995). Abandoned woodpecker nests provide valuable nesting cavities for many other birds, including flycatchers (*Ficedula* spp., *Empidonax* spp.), tree swallows *Tachycineta bicolor*, tits *Parus* spp., wood ducks *Aix sponsa*, goldeneyes, mergansers *Mergus* spp., owls (Titonidae, Strigidae) and kestrels *Falco tinnunculus* (Carr, 1940; Hilfiker, 1991). Lochmiller (1979) found that woodpeckers used beaver ponds more frequently than a control area without beaver ponds.

Piscivores, such as herons *Ardea* spp., grebes (Podicipedidae), cormorant *Phalacrocorax carbo*, shag *Phalacrocorax aristotelis*, bitterns *Botaurus* spp., egrets *Egretta* spp., mergansers and kingfishers *Alcedo atthys*, hunt for fish in beaver ponds (Salyer, 1935), which also provide nesting sites (Gibbs *et al.*, 1991). Grover & Baldassarre (1995) reported that hooded mergansers *Lophodytes cucullatus*, green-backed heron *Butorides striatus*, great blue heron *Ardea herodias* and belted kingfisher *Ceryle alcyon* occurred more frequently in wetlands where beaver were active than at sites with no beaver activity.

Standing dead trees may provide important perching sites for raptors (Grover & Baldassarre, 1995). Ospreys *Pandion haliaetus* hunt for fish in beaver ponds and may nest in trees close to the pond, while white-tailed eagles *Haliaeetus albicilla* may hunt for beaver kits (see

Nolet *et al.*, 1997). Hawks *Buteo* spp. and *Accipiter* spp. (e.g. red-shouldered hawks *B. lineatus*) and owls may increase their hunting success for birds and mice (Muridae) around beaver ponds (Carr, 1940), and hobbies *Falco subbuteo* may hunt for dragonflies (F. Rosell, personal observation).

Wetlands dominated by emergent vegetation and influenced by beaver, provide nesting and foraging sites for several marsh birds such as rails *Rallus* spp. (Gibbs *et al.*, 1991). Carr (1940) noted large numbers of song sparrows *Melospiza melodia* and marsh birds along with other non-game birds utilizing beaver ponds. The northern yellow-throat *Geothlypis trichas brachydactyla* and the yellow warbler *Dendroica petechia* were typical summer residents, especially of deserted beaver sites.

Reese & Hair (1976) showed that the structural complexity of beaver ponds was highly attractive to a large number of birds year-round, and concluded that the ponds value to waterfowl was minor when compared with their value to other species of birds. They identified 92 bird species (31 families and 2346 individuals) at four beaver ponds, the most abundant species being red-winged blackbirds *Agelaius phoeniceus*. Aquatic and terrestrial insects thrive in/along beaver ponds, providing a food base for such songbirds as song sparrow, tree swallows and cedar waxwings *Bombycilla cedrorum*.

The damp shores of beaver ponds provide suitable feeding places for American woodcock *Scolopax minor* and tree felling by beavers provides openings for singing and nesting sites. Grey partridge *Perdix perdix* and towhee *Pipilo* spp. thrive in the ground cover around beaver ponds (Carr, 1940). Open areas in woodlands created by beaver provide nesting, loafing, feeding and dusting places for wild turkeys *Meleagris gallopavo* and grouse (Tetraonidae) (Carr, 1940).

Semiaquatic mammals

Beaver ponds provide semiaquatic mammals with an abundant supply of prey, stable water levels, den sites and refuge from human disturbance. Accordingly, muskrat *Ondatra zibethicus*, water voles *Arvicola terrestris*, North American mink *Mustela vison* and otter (*Lutra* spp. and *Lontra canadensis*) may use abandoned or active beaver lodges, bank dens or holes for shelter and breeding (Leighton, 1933; Grasse, 1951; Tyurnin, 1984; Müller-Schwarze, 1992; Danilov, 1995; Rosell & Parker, 1996). Muskrats may also eat food remains left by beaver (Grasse, 1951), and in winter, they may use beaver air holes and food caches (Tyurnin, 1984). Knudsen (1962) and Rutherford (1955) recorded that muskrats more frequently used beaver ponds than wetlands above or below the ponds. For the beaver, cohabitation with the muskrat and water voles seems to be primarily a negative relationship, since they are feeding competitors to some extent (Leighton, 1933; Tyurnin, 1984).

Mink hunt in beaver ponds for fish, crayfish *Astacus* and muskrats (Bailey & Stephens, 1951; Grasse, 1951; Rutherford, 1955; Danilov, 1992, 1995). A positive correlation between numbers of beaver sites and densities of mink has commonly been observed in Belarus. Mink profit from ice-free access to water in winter around beaver lodges and burrows, and they use lodges as marking places (Sidorovich, 1992). Zurowski & Kammler (1987) found that feral mink often choose beaver lodges as their winter home. Recker (1997) reported that mink may kill young beavers, but Brzezinski & Zurowski (1992) found that in an area of Poland where these two species coexisted, mink did not prey on young beaver.

Beaver and otter territories frequently overlap (Tyurnin, 1984), and the presence of beavers is thought to be beneficial to otters. Since otters live in wetland habitats both modified and unaltered by beavers, Polecha (1989) described their relationship as facultative commensal. Dubuc, Krohn & Owen (1988, 1990) found that otters in Maine selected watersheds with a high proportion of beaver-influenced streams. Beaver bank dens and lodges made up 32% and 6%, respectively, of otter den and resting sites in Idaho (Melquist & Hornocker, 1983).

Otters hunt in beaver ponds for small mammals, fish, crayfish and amphibians, and they rest on top of lodges and dams (see, e.g. Green, 1932; Vogt, 1981; Tumlison, Karnes & King, 1982; Danilov, 1992, 1995). Tyurnin (1984) recorded water vole remains more frequently in otter faeces within the limits of beaver colonies than outside. Although otters may kill beaver (Green, 1932), this seems to be rare.

In winter, otters make use of air holes made in the ice by beavers (Tyurnin, 1984) and profit from ice-free access to water around beaver lodges and burrows. They also use lodges as marking places (Reid, Herrero & Code, 1988; Sidorovich, 1992). Beaver bank dens and lodges have also been associated with otter latrines (Greer, 1955; Newman & Griffin, 1994). Furthermore, Reid *et al.* (1988) found that otters dig passages through dams, thereby gaining access to the lake or pond and allowing under-ice movements between adjacent water bodies. They hypothesized that this dam rifting would increase the area available for effective foraging and also enhance prey density by decreasing water volume (see also Green, 1932).

Beaver activity positively influence otter habitat (Tumlison *et al.*, 1982). In regions of marginal otter habitat, or where otter habitat destruction is occurring, beavers play a major role in preventing extirpation of the otter. It has been suggested that the recent increase in the otter population in parts of the USA is due to the re-establishment of beaver populations (Tumlison *et al.*, 1982; see also Vogt, 1981).

Terrestrial mammals

Hawkes (1973) describes the positive ecological consequences that beaver have on elk (also known as red deer in Europe) *Cervus elaphus* and moose *Alces alces* (also known as elk in Europe) habitat. In areas of dense forest, beaver meadows provide succulent vegetation for many species, including white-tailed deer *Odocoileus virginianus*, moose and bears *Ursus* spp. (Bailey & Stephens, 1951; Müller-Schwarze, 1992). Often the bulk of the trees felled by beavers remain where they fall. The bark and branches of these trees increase the food supply for species such as roe deer *Capreolus capreolus*, red deer/elk, white-tailed deer and moose during autumn and winter. Also, the regrowth of aspen, birch and rowan are highly preferred food for these species (Cook, 1940; Grasse, 1951; Danilov, 1992; Safonov & Saveljev, 1992; Danilov, 1995). Moose often feed on aquatic plants such as water lilies in beaver ponds (Grasse, 1951; Hilfiker, 1991), and may find relief there from biting insects (Müller-Schwarze, 1992). Beaver ponds may also provide water for several species during dry periods (Hawkes, 1973).

Beaver territories in river flood plains, ox-bow lakes and ditches provide favourable conditions for wild boar *Sus scrofa*. Fourteen of 20 beaver sites were regularly visited by wild boar in Dessau, Germany (Nitsche, 1997). Patches where beaver fell trees are frequently visited by foraging wild boar. Partially dried-out beaver ponds are favoured by wild boar searching for rhizomes of water lilies and reeds, and provide good wallowing sites. Beaver and boar rarely disturb each other, but large numbers of wild boar on a beaver territory may restrict beaver activity on land at night (Nitsche, 1997).

Other wildlife, such as bark-feeding mice, pocket gophers (Geomyidae), rabbits and hares (Leporidae), will also find shelter and food around beaver ponds (Hawkes, 1973). Rutherford (1955) stated that beavers, by creating openings in forests, increased the amount of ecotone, which may improve habitat for snowshoe hares *Lepus americanus*.

Abandoned woodpecker holes in trees killed by beaver activity provide homes for cavity-nesting mammals, such as mice, martens *Martes* spp., squirrels (Sciuridae), chipmunks

Tamias and bats (Chiroptera) (Hilfiker, 1991). Moreover, bats roost under exfoliating bark of dead snags in beaver ponds (Menzel *et al.*, 2001). Bats also find good hunting for insects around beaver ponds (Solheim, 1987).

Beaver created habitat attracts raccoons *Procyon lotor*, since such areas contain many of its favourite foods (Müller-Schwarze, 1992). It has been suggested by Bailey & Stephens (1951) that the increase of the beaver may be partly responsible for the parallel increase in raccoons. Badgers *Meles meles* and red foxes *Vulpes vulpes* have been observed to occupy abandoned beaver lodges during winter (F. Rosell, personal observation).

Beaver lodges can also function as a breeding chamber for predators, like bobcat *Lynx rufus* (Lovallo, Gilbert & Gehring, 1993). Pine marten *Martes martes* (Rosell & Hovde, 1998) has also been reported to use abandoned beaver lodges as resting sites.

Beaver can be an important prey item for both wolves *Canis lupus* (e.g. Shelton & Peterson, 1983) and black bear *Ursus americanus* (Smith, Trauba & Anderson, 1994). Andersone (1999) reported that beaver appeared to be the most important food item for wolves in Latvia during summer, and that beaver became an important alternative prey when ungulate populations were low. Also considered potential predators, though probably only having minimal effects on beaver populations, are grizzlies (also known as brown bear) *Ursus arctos*, coyotes *Canis latrans*, wolverines *Gulo gulo*, mountain lion *Felis concolor*, lynx *Lynx lynx*, bobcat, red fox, pine marten and dog *Canis familaris* (Engelhart & Müller-Schwarze, 1995; Rosell, Parker & Kile, 1996).

CONCLUSIONS

The description of the beaver as an ecosystem engineer is well documented (Jones *et al.*, 1994), and many studies have been conducted concerning the impact of both their building activities and foraging strategies. Numerous manifestations of beaver building activity, such as dams, canals, burrows, lodges and foodcaches, can affect the physical habitat (Woo & Waddington, 1990; Naiman *et al.*, 1994; Pollock *et al.*, 1995; Gurnell, 1998; Meentemeyer & Butler, 1999), thereby directly or indirectly influencing certain species negatively or positively in the community. These non-trophic effects are responsible for the major portion of the beavers' influence on the ecosystem (Pollock *et al.*, 1995). However, beavers also have the ability to cut mature trees; they forage selectively and their repeated removal of above-ground plant tissues can result in significant changes in plant growth form (McGinley & Whitham, 1985; Basey *et al.*, 1988; Barnes & Mallik, 2001). Although the beavers' keystone status has been challenged (Nolet *et al.*, 1994; Donkor & Fryxell, 1999), beavers obviously have a considerable impact on the course of succession, the species composition and structure of plant communities (Barnes & Dibble, 1988; Johnston & Naiman, 1990a; Pastor & Naiman, 1992; Nolet *et al.*, 1994; Donkor & Fryxell, 1999; Barnes & Mallik, 2001) and the presence of animal species requiring substrates abundant at beaver sites (e.g. dead trees, rotting bark) for their survival and reproduction (Spieth, 1979; Martinsen *et al.*, 1988; Hilfiker, 1991; Menzel *et al.*, 2001).

Beavers occupy a geographical range extending from tree line to sea level and the subarctic to the subtropics, and therefore influence many ecosystems (Halley & Rosell, 2002). However, beavers do not necessarily act as significant controlling agents of the ecosystem throughout their distribution. The interaction intensity will apparently vary in space and time, resulting in a concomitant change in the species' importance to the community (e.g. Paine, 1995). Namely, the strength of beavers' impact depends on the geographical location, the relief and the impounded habitat type just as much as on beaver density at the landscape scale.

As an ecosystem engineer, beavers can create important management opportunities in the Holarctic. The number of threatened species is increasing globally, and can result in conservation effort being focused on the management of individual species. While this may be effective for the species concerned, it does not necessarily contribute effectively to the enhancement and protection of the overall biodiversity of ecosystems. One way to overcome this problem could be to manage entire ecosystems, thereby protecting all the inhabitants at the same time (Simberloff, 1996). The management of ecosystem engineers is likely to help meet the challenge of single species management and ecosystem management. These species have a large impact on other species in their assemblage, mainly through patch-creation in otherwise closed communities (Jones *et al*., 1994); therefore their management may play a crucial role in the maintenance of populations of other species. However, some species may be adversely affected by the activities of ecosystem engineers, and this should be considered when assessing their overall influence on ecosystems.

This review demonstrates the beavers' wide ranging ability to influence habitats and species. As they have an extensive potential geographical distribution, and are once again a common animal in some regions, it is important to be aware of their possible roles in shaping ecosystems.

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REFERENCES

Adams, A.K. (1949) Beavers versus trout. *Michigan Conservation*, **18**, 15–16.

Adler, P.H. & Mason, P.G. (1997) Black flies (*Diptera: Simuliidae*) of East-central Saskatchewan, with description of a new species and implications for pest management. *Canadian Entomologist*, **129**, 81–91.

Andersone, Ź. (1999) Beaver: a new prey of wolves in Latvia? Comparison of winter and summer diet of *Canus lupus* Linnaeus, 1758. In: *Beaver Protection, Management and Utilization in Europe and North America* (Ed. by P.E. Busher & R.M. Dzieciolowski), pp. 103–108. Kluwer Academic/Plenum Publishers, New York.

Arner, D.H. & Hepp, G.R. (1989) Beaver pond wetland: a southern perspective. In: *Habitat Management for Migrating and Wintering Waterfowl in North America* (Ed. by L.M. Smith, R.L. Pederson & R.M. Kaminski), pp. 117–128. Texas Tech University Press, Lubbock.

Avery, E.L. (1983) A bibliography of beaver, trout, wildlife, and forest relationships with special references to beaver and trout. *Technician Bulletin*, 137, 1–23. Wisconsin Department of Natural Resources, Madison, WI.

Avery, E.L. (1992) Effects of removing beaver dams upon a northern Wisconsin brook trout stream. *Wisconsin Department of Natural Resources*, **Study No. 406**, 1–59.

Bailey, R.W. & Stephens, R.F. (1951) Some effects of beaver on fish and wildlife. *West Virginia Conservation*, **15**, 11–16.

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, W.J. & Dibble, E. (1988) The effects of beaver in riverbank forest succession. *Canadian Journal of Botany*, **66**, 40–44.

Barnes, D.M. & Mallik, A.U. (2001) Effects of beaver, *Castor canadensis*, herbivory on streamside vegetation in Northern Ontario watershed. *The Canadian Field-Naturalist*, **115**, 9–21.

Basey, J.M., Jenkins, S.H. & Busher, P.E. (1988) Optimal central-place foraging by beavers: tree-size selection in relation to defensive chemicals of quaking aspen. *Oecologia*, **76**, 278–282.

Beard, E.B. (1953) The importance of beaver in waterfowl management at the Seney National Refuge. *Journal of Wildlife Management*, **17**, 398–436.

Bellwood, D.R. & Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science*, **292**, 1532–1534.

Bergstrom, D. (1985) Beavers: biologists 'rediscover' a natural resource. *Forestry Research West*, 1–5, United States Department of Agriculture, Forest Service.

Bozsér, O. (2001a) History and reintroducion of the beaver *(Castor fiber)* in Hungary, with special regard to the floodplain of the Danube in Gemenc area. In: *The European Beaver in a New Millennium* (Ed. by A. Czech & G. Schwab), pp. 44–46. *Proceedings of the Second European Beaver Symposium, 27–30 September 2000, BiałOvieża, Poland.* Carpathian Heritage Society, Kraków.

Bozsér, O. (2001b) *Hódok az Óvilágban.* WWF-füzetek 19 [in Hungarian].

Brenner, F.J. (1960) Canada geese nesting on a beaver lodge. *The Auk*, **77**, 476–477.

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.

Bryant, M.D. (1984) The role of beaver dams as coho salmon habitat in southeastern Alaska streams. In: *Proceedings of the Olympic Wild Fish Conference* (Ed. by J.M. Walton & D.D. Houston), pp. 183–192. Peninsula College, Fisheries Technology Program, Port Angeles, Washington.

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.

Butler, D.R. (1991) Beavers as agents of biogeomorphic change: a review and suggestions for teaching exercises. *Journal of Geography*, **90**, 210–217.

Carr, W.H. (1940) Beaver and birds. *Bird Lore*, **42**, 141–146.

Cirmo, C.P. & Driscoll, C.T. (1993) Beaver pond geochemistry – acid neutralising capacity generation in a headwater wetland. *Wetlands*, **13**, 277–292.

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*, **71**, 1439–1447.

Coleman, R.L. & Dahm, C.N. (1990) Stream geomorphology: effects on periphyton standing crop and primary production. *Journal of the North American Benthological Society*, **9**, 293–302.

Collen, P. & Gibson, R.J. (2001) The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystem and riparian habitats, and the subsequent effects on fish – a review. *Reviews in Fish Biology and Fisheries*, **10**, 439–461.

Cook, D.B. (1940) Beaver trout relations. *Journal of Mammalogy*, **21**, 397–401.

Correll, D.L., Jordan, T.E. & Weller, D.E. (2000) Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry*, **49**, 217–239.

Cunjack, 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.

Curry-Lindahl, K. (1967) The beaver, *Castor fiber* Linnaeus, 1758 in Sweden – extermination and reappearance. *Acta Theriologica*, **12**, 1–15.

Dahm, C.N. & Sedell, J.R. (1986) The role of beaver on nutrient cycling in streams. *Journal of the Colorado–Wyoming Academy of Science*, **18**, 32.

Danell, K. & Sjöberg, H. (1982) Successional patterns of plants, invertebrates and ducks in a manmade lake. *Journal of Applied Ecology*, **19**, 395–409.

Danilov, P.I. (1992) Introduction of North-American semiaquatic mammals in Karelia and its consequences for aboriginal species. *Semiaquatische Säugetiere*. *Wissenschaftliche Beiträge Universität Halle*, **1**, 267–276.

Danilov, P.I. (1995) Canadian and European beavers in Russian northwest (distribution, number, comparative ecology). In: *Proceedings of the Third Nordic Beaver Symposium* (Ed. by A. Ermala & S. Lahti), pp. 10–16. Iiomats, Finland, 15–17 September 1992. Finnish Game and Fisheries Research Institute, Helsinki.

Danilov, P.I. & Kan'shiev, V.Y. (1982) Some morphological and ecological features of the Eurasian and North American beaver in the USSR north west. *Fauna: Ecologiyaptic (Mlekopitajvscic)*. Severo-Zapada SSSR, Petrozavodsk, pp. 109–123.

Danilov, P.I. & Kan'shiev, V.Y. (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.

Davic, R.D. (2003) Linking keystone species and functional groups: a new operational definition of the keystone species concept. *Conservation Ecology*, **7**, r11.

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 Science*, **50**, 2222–2234.

Diefenbach, D.R. & Owen, R.B.J.R. (1989) A model of habitat use by breeding American black ducks. *Journal of Wildlife Management*, **53**, 383–389.

Dieter, C.D. & McCabe, T.R. (1989) Factors influencing beaver lodge-site selection on a prairie river. *American Midland Naturalist*, **122**, 408–411.

Dillon, P.J., Molot, L.A. & Scheider, W.A. (1991) Phosphorus and nitrogen export from forested stream catchments in central Ontario. *Journal of Environmental Quality*, **20**, 857–864.

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.

Dubuc, L.J., Owen, R.B.J.R. & Krohn, W.B. (1988) *Ecology of River Otter on Mount Desert Island, Maine.* Report to National Park Service, North Atlantic Region, Boston, Mass.

Dubuc, L.J., Krohn, W.B. & Owen, R.B.J.R. (1990) Predicting occurrence of river otters by habitat on Mount Desert Island, Maine. *Journal of Wildlife Management*, **54**, 594–599.

Duncan, S.L. (1984) Leaving it to beaver. *Environment*, **26**, 41–45.

Edwards, N.T. & Otis, D.L. (1999) Avian communities and habitat relationships in South Carolina Piedmont beaver ponds. *American Midland Naturalist*, **141**, 158–171.

Engelhart, A. & Müller-Schwarze, D. (1995) Responses of beaver (*Castor canadensis* Kuhl) to predator chemicals. *Journal of Chemical Ecology*, **21**, 1349–1364.

Ermala, A., Helminen, M. & Lahti, S. (1989) Some aspects of the occurrence, abundance and future of the Finnish beaver population. *Suomen Riista*, **35**, 108–118.

Flanagan, P.W. & van Cleve, K. (1983) Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Canadian Journal of Forest Research*, **13**, 795–817.

Fox, B.J. & Brown, J. (1993) Assembly rules for functional groups in North American desert rodent communities. *Oikos*, **67**, 358–370.

France, R.L. (1996) Stable carbon and nitrogen isotopic evidence for ecotonal coupling between boreal forests and fishes. *Ecology of Freshwater Fish*, **6**, 78–83.

France, R.L. (1997) The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. *Canadian Journal of Zoology*, **75**, 1009–1113.

Francis, M.M., Naiman, R.J. & Melillo, J.M. (1985) Nitrogen fixation in subarctic streams influenced by beaver (*Castor canadensis*). *Hydrobiologia*, **121**, 193–202.

Gard, R. (1961) Effects of beavers on trout in Sagehen Creek, California. *Journal of Wildlife Management*, **25**, 221–242.

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.

Grasse, J.E. (1951) Beaver ecology and management in the Rockies. *Journal of Forestry*, **49**, 3–6.

Grasse, J.E. & Putnam, E.F. (1955) Beaver management and ecology in Wyoming. *Wyoming Game and Fish Communication Bulletin*, **6**, Cheyenne.

Green, H.U. (1932) Observations on the occurrence of otter in the Riding Mountain National Park, Manitoba, in relation to beaver life. *The Canadian Field-Naturalist*, **46**, 204–206.

Greer, K.R. (1955) Yearly food habits of the river otter in the Thompson Lakes region, northwestern Montana, as indicated by scat analysis. *American Midland Naturalist*, **54**, 299–313.

Grover, A.M. & Baldassarre, G.A. (1995) Bird species richness within beaver ponds in south-central New York. *Wetlands*, **15**, 108–118.

Gurnell, A.M. (1998) The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography*, **22**, 167–189.

Gurney, W.S.C. & Lawton, J.H. (1996) The population dynamics of ecosystem engineers. *Oikos*, **76**, 273–283.

Hägglund, Å. & Sjöberg, G. (1999) Effects of beaver dams on the fish fauna of forest streams. *Forest Ecology and Management*, **115**, 259–266.

Halley, D. & Rosell, F. (2002) The beaver's reconquest of Eurasia: status, population development and management of a conservation success. *Mammal Review*, **32**, 153–178.

Halley, D. & Rosell, F. (2003) Population and distribution of European beavers (*Castor fiber*). *Lutra*, **46**, 91–101.

Hanson, W.D. & Campbell, R.S. (1963) The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a north Missouri stream. *American Midland Naturalist*, **69**, 136–149.

Harthun, M. (1999) The influence of the European beaver (*Castor fiber albicus*) on the biodiversity (*Odonata*, *Mollusca*, *Trichoptera*, *Ephemeroptera*, *Diptera*) of brooks in Hesse (Germany). *Limnologica*, **29**, 449–464.

Harthun, M. (2000) Influence of the damming-up by beavers (*Castor fiber albicus*) on physical and chemical parameters of highland brooks (Hesse, Germany). *Limnologica*, **30**, 21–35.

Hawkes, F.W. (1973) Elk, moose, and beaver. *Pacific Discovery*, **26**, 12–15.

Hilfiker, E.L. (1991) *Beavers, Water, Wildlife and History*. Windswept Press, Interlaken, New York.

Hill, E.P. (1982) Beaver (*Castor canadensis*). In: *Wild Mammals of North America: Biology, Management, and Economics* (Ed. by J.A. Chapman & G.A. Feldhamer), pp. 256–281. John Hopkins University Press, Baltimore and London.

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.

Hodkinson, I.D. (1975a) A community analysis of the benthic insect fauna of an abandoned beaver pond. *Journal of Animal Ecology*, **44**, 533–551.

Hodkinson, I.D. (1975b) Dry weight loss and chemical changes in vascular plant litter of terrestrial origin, occurring in a beaver pond ecosystem. *Journal of Ecology*, **63**, 131–142.

Hodkinson, I.D. (1975c) Energy flow and organic matter decomposition in an abandoned beaver pond ecosystem. *Oecologia*, **21**, 131–139.

Huey, W.S. & Wolfrum, W.H. (1956) Beaver–trout relations in New Mexico. *The Progressive Fish-Culturist*, **18**, 70–74.

Huntly, N. (1995) How important are consumer species to ecosystem functioning? In: *Linking Species and Ecosystem* (Ed. by C.G. Jones & J.H. Lawton), pp. 72–83. Chapman & Hall, New York.

Ives, R.L. (1942) The beaver–meadow complex. *Journal of Geomorphology*, **5**, 191–203.

Jenkins, S.H. (1975) Food selection by beavers: a multidimensional contingency table analysis. *Oecologia*, **21**, 157–173.

Johnson, P.D. & Brown, K.M. (1998) Intraspecific life history variation in the threatened Louisiana pearlshell mussel, *Margaritifera hembeli*. *Freshwater Biology*, **40**, 317–329.

Johnston, C.A. & Naiman, R.J. (1987) Boundary dynamics of the aquatic–terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecology*, **1**, 47–57.

Johnston, C.A. & Naiman, R.J. (1990a) Browse selection by beaver: effects on riparian forest composition. *Canadian Journal of Forest Restoration*, **20**, 1036–1043.

Johnston, C.A. & Naiman, R.J. (1990b) The use of a geographic information system to analyze long-term landscape alteration by beaver. *Landscape Ecology*, **4**, 5–19.

Johnston, C.A. & Naiman, R.J. (1990c) Aquatic patch creation in relation to beaver population trends. *Ecology*, **71**, 1617–1621.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Kadlec, J.A. (1962) The effects of a drawdown on a waterfowl impoundment. *Ecology*, **43**, 267–280.

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.

Klotz, R.L. (1998) Influence of beaver ponds on the phosphorus concentration of stream water. *Canadian Journal of Fisheries and Aquatic Science*, **55**, 1228–1235.

Knudsen, G.J. (1962) Relationship of beaver to forests, trout and wildlife in Wisconsin. *Wisconsin Conservation Department, Technical Bulletin*, no. 25, Madison, 50 pp.

Lahti, S. & Helminen, M. (1974) The beaver *Castor fiber* (L.) and *Castor canadensis* (Kuhl) in Finland. *Acta Theriologica*, **19**, 177–189.

Lavrov, L.S. (1983) Evolutionary development of the genus *Castor* and taxonomy of the contemporary beavers of Eurasia. *Acta Zoologica Fennica*, **174**, 87–90.

Lavrov, L.S. & Orlov, V.N. (1973) Karyotypes and taxonomy of modern beavers (*Castor, Castoridae, Mammalia*). *Zoologische Zhurnal*, **52**, 734–742.

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 two coastal Oregon streams. *Northwest Science*, **66**, 218–223.

Leighton, A.H. (1933) Notes on the relation of beavers to one another and to the muskrat. *Journal of Mammalogy*, **14**, 27–35.

Lochmiller, R.L. (1979) Use of beaver ponds by southeastern woodpeckers in winter. *Journal of Wildlife Management*, **43**, 263–266.

Lovallo, M.J., Gilbert, J.H. & Gehring, T.M. (1993) Bobcat, *Felis rufus*, dens in an abandoned beaver, *Castor canadensis*, lodge. *The Canadian Field-Naturalist*, **107**, 108–109.

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.

McDowell, D.M. & Naiman, R.J. (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, **8**, 481–489.

McGinley, M.A. & Whitham, T.G. (1985) Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). *Oecologia*, **66**, 558–562.

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.

McMaster, R.T. & McMaster, N.D. (2000) Vascular flora of beaver wetlands in western Massachusetts. *Rhodora*, **102**, 175–197.

McMaster, R.T. & McMaster, N.D. (2001) Composition, structure, and dynamics of vegetation in fifteen beaver-impacted wetlands in western Massachusetts. *Rhodora*, **103**, 293–320.

McNeel, W. (1964) Beaver cuttings in aspen indirectly detrimental to white pine. *Journal of Wildlife Management*, **28**, 861–863.

McRae, G. & Edwards, C.J. (1994) Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for brook trout habitat. *Transactions of the American Fisheries Society*, **123**, 641–656.

Maret, T.J., Parker, M. & Fannin, T.E. (1987) The effect of beaver ponds on the nonpoint source water quality of a stream in southwestern Wyoming. *Water Research*, **21**, 263–268.

Margolis, B.E., Castro, M.S. & Raesly, R.L. (2001a) The impact of beaver impoundments on the water chemistry of two Appalachian streams. *Canadian Journal of Fisheries and Aquatic Science*, **58**, 2271–2283.

Margolis, B.E., Raesly, R.L. & Shumway, D.L. (2001b) The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. *Wetlands*, **21**, 554–563.

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.

Meentemeyer, R.K. & Butler, D.R. (1999) Hydrogeomorphic effects of beaver dams in Glacier National Park, Montana. *Physical Geography*, **20**, 436–446.

Melquist, W.E. & Hornocker, M.G. (1983) Ecology of river otters in west-central Idaho. *Wildlife Monographs.* no. 83, 60 pp.

Menzel, M.A., Carter, T.C., Ford, W.M. & Chapman, B.R. (2001) Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the Upper Coastal Plain of South Carolina. *American Midland Naturalist*, **145**, 112–119.

Metts, B.S., Lanham, J.D. & Russell, K.R. (2001) Evaluation of herpetofaunal communities on upland stream and beaver-impounded streams in the upper Piedmont of South Carolina. *American Midland Naturalist*, **145**, 54–65.

Milishnikov, A.N. (2004) Population-genetic structure of beaver (*Castor fiber* L., 1758) communities and estimation of effective reproductive size N_e of an elementary population. *Russian Journal of Genetics*, **40**, 772–781.

Müller-Schwarze, D. (1992) Beaver waterworks. *Natural History*, **5**, 52–53.

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.J. & Melillo, J.M. (1984) Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia*, **62**, 150–155.

Naiman, R.J., Melillo, J.M. & Hobbie, J.E. (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, **67**, 1254–1269.

Naiman, R.J., Johnston, C.A. & Kelley, J.C. (1988) Alteration of North American streams by beaver. *Bioscience*, **38**, 753–762.

Naiman, R.J., Pinnay, G., Johnston, C.A. & Pastor, J. (1994) Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology*, **75**, 905–921.

Naiman, R.J., Elliott, S.R., Helfield, J.M. & O'Keefe, T.C. (2000) Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. *Hydrobiologia*, **410**, 79–86.

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 Science*, **49**, 783–789.

Nitsche, K.A. (1997) Wild boar (*Sus scrofa*) and beaver (*Castor fiber*) relations. In: *Proceedings of the First European Beaver Symposium* (Ed. by K. Pachinger), p. 16. 15–19 September 1997. Institute of Ecology, Faculty of Natural Sciences Comenius University, Bratislava, Slovakia.

Nolet, B.A. (1996) *Management of the Beaver (Castor fiber): Towards Restoration of Its Former Distribution and Ecological Function in Europe?* Council of Europe, Strasbourg, 25 October 1996, 29 pp.

Nolet, B.A. & Rosell, F. (1998) Come back of the beaver *Castor fiber*: an overview of old and new conservation problems. *Biological Conservation*, **83**, 165–173.

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., Van Der Veer, P.J., Evers, E.G.J. & Ottenheim, M.M. (1995) A linear programming model of diet choice of free-living beavers. *Netherlands Journal of Zoology*, **45**, 315–337.

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.

Novak, M. (1987) Beaver. In: *Wild Furbearer Management and Conservation in North America, Ontario* (Ed. by M. Novak, J.A. Baker, M.E. Obbard & B. Malloch), pp. 283–312. Ontario Ministry of Natural Resources, Ontario.

Nummi, P. (1984) Majava-altaiden merkityksestä vesilintupoikueille. *Suomen Riista*, **31**, 47–53.

Nummi, P. (1987) Majavamalli vesilintujen elinympäristön hoidossa. *Suomen Riista*, **34**, 22–30.

Nummi, P. (1989) Simulated effects of the beaver on vegetation, invertebrates and ducks. *Annales Zoologici Fennici*, **26**, 43–52.

Nummi, P. (1992) The importance of beaver ponds to waterfowl broods: an experiment and natural tests. *Annales Zoologici Fennici*, **29**, 47–55.

Nummi, P. & Pöysä, H. (1995) Habitat use by different-aged duck broods and juvenile ducks. *Wildlife Biology*, **1**, 181–187.

Paine, R.T. (1995) A conservation on refining the concept of keystone species. *Conservation Biology*, **9**, 962–964.

Parker, M. (1986) Beaver, water quality and riparian systems. *Proceedings of the Wyoming Water and Streamside Zone Conference.* Wyoming Water Research Centre, University of Wyoming, Laramie, **1**, 88–94.

Parker, H., Haugen, A., Kristensen, Ø., Myrum, E., Kolsing, R. & Rosell, F. (2001) Landscape use and economic value of Eurasian beaver (*Castor fiber*) on a large forest in southeast Norway. In: *Proceedings of the First Euro-American Beaver Congress* (Ed. by P. Busher & Y. Gorshkov), pp. 77–95. First Euro-American Beaver Congress, 24–28 August 1999. Transactions of the Volga-Kama National Nature Zepovednik, Kazan, Russia.

Pastor, J. & Naiman, R.J. (1992) Selective foraging and ecosystem processes in boreal forests. *The American Naturalist*, **139**, 690–705.

Pastor, J., Naiman, R.J., Dewey, B. & McInnes, P. (1988) Moose, microbes, and the boreal forest. *Bioscience*, **38**, 770–777.

Patterson, D. (1951) *Beaver–trout Relationships*. Wisconsin Conservation Department, Division of Fish Management. Investigational Report No. 822, 34 pp.

Peterson, S.R. & Low, J.B. (1977) Waterfowl use of Unita Mountain wetlands in Utah. *Journal of Wildlife Management*, **41**, 112–117.

Polecha, P.J. (1989) More evidence of a commensal relationship between the river otter and the beaver. In: *Proceedings of the Tenth International Symposium on Biotelemetry* (Ed. by C.J. Amlaner), pp. 217–236. University of Arkansas Press, Fayetteville, Arkansas.

Pollock, M.M., Naiman, R.J., Erickson, H.E., Johnston, C.A., Pastor, J. & Pinay, G. (1995) Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. In: *Linking Species and Ecosystem* (Ed. by C.G. Jones & J.H. Lawton), pp. 117–126. Chapman & Hall, New York.

Pritchard, G. & Hall, H.A. (1971) An introduction to the biology of craneflies in a series of abandoned beaver ponds, with an account of the life cycle of *Tipula sacra* Alexander (*Diptera; Tipulidae*). *Canadian Journal of Zoology*, **49**, 467–482.

Rasmussen, D.I. (1941) Beaver trout relationship in the Rocky Mountain region. *Transactions of the Fifth North American Wildlife Conference*, **5**, 256–263.

Ray, A.M., Rebertus, A.J. & Ray, H.L. (2001) Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany*, **79**, 487–499.

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, K.A. (1952) Effect of beaver on trout waters. *Maryland Conservation*, **29**, 21–23.

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.

Remillard, M.M., Gruendling, G.K. & Bogucki, J.D. (1987) Disturbance by beaver (*Castor canadensis* Kuhl) and increased landscape heterogeneity. *Ecological Studies Analysis and Synthesis*, **64**, 103–122.

Renouf, R.N. (1972) Waterfowl utilization of beaver ponds in New Brunswick. *Journal of Wildlife Management*, **36**, 740–744.

Richard, P.B. (1985) Peculiarities on the ecology and management of the Rhodanian beaver (*Castor fiber* L.). *Zeitschrift für Angewandte Zoologie*, **72**, 143–152.

Ringelman, J.K. & Longcore, J.R. (1982) Movements and wetland selection by brood-rearing black ducks. *Journal of Wildlife Management*, **46**, 615–621.

Ringelman, J.K., Longcore, J.R. & Owen, R.B. (1982) Breeding habitat selection and home range of radio-marked black ducks (*Anas rubripes*) in Maine. *Canadian Journal of Zoology*, **60**, 241–248.

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. & Hovde, B. (1998) Pine Marten, *Martes martes*, as a Eurasian beaver, *Castor fiber*, lodge occupant and possible predator. *The Canadian Field-Naturalist*, **112**, 535–536.

Rosell, F. & Parker, H. (1995) *Beaver Management: present practice and Norway's future needs*. (In Norwegian with English summary.) Bø, Norway, 137 pp.

Rosell, F. & Parker, H. (1996) The beaver's (*Castor* spp.) role in forest ecology: a key species returns (in Norwegian with English summary). *Fauna*, **49**, 192–211.

Rosell, F. & Pedersen, K.V. (1999) *Bever*. Landbruksforlaget, Oslo, Norway.

Rosell, F., Parker, H. & Kile, N.B. (1996) Causes of mortality in beaver (*Castor fiber & canadensis*). (In Norwegian with English summary.) *Fauna*, **49**, 34–46.

Rudemann, R. & Schoonmaker, W.J. (1938) Beaver dams as geologic agents. *Science*, **88**, 523–525.

Rudqvist, L. (1977) *Bäverdammar som andfågelbiotoper*. Institutt for Skogszoologi, Uppsala.

Rupp, R.S. (1955) Beaver–trout relationship in the headwaters of Sunkhaze Stream, Maine. *Translocations of American Fishery Society*, **84**, 75–85.

Russel, K.R., Moorman, C.E., Edwards, J.K., Metts, B.S. & Guynn, D.C. Jr. (1999) Amphibian and reptile communities associated with beaver (*Castor canadenis*) 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.

Saarenmaa, H. (1978) The occurrence of bark beetles (*Col. Scolytidae*) in a dead spruce stand flooded by beavers (*Castor canadensis* Kuhl). *Silva Fennica*, **12**, 201–216.

Safonov, V.G. & Saveljev, A.P. (1992) Ecological peculiarities of the most eastern beaver population *Castor fiber* L. in Eurasia. *Semiaquatische Säugetiere, Wissenschaftliche Beiträge Universität Halle*, **1**, 157–167.

Safonov, V.G. & Saveliev, A.P. (1999) Beavers in CIS: resources, translocation and trapping. In: *Proceedings of the First Euro-American Beaver Congress* (Ed. by P. Busher & Y. Gorshkov), pp. 22–39. First Euro-American Beaver Congress, 24–28 August 1999. Transactions of the Volga-Kama National Nature Zepovednik, Kazan, Russia.

Salyer, J.C. (1935) Preliminary report on the beaver trout investigation. *American Game*, **24**, 13–15.

Saveljev, A. & Milishnikov, A. (2002) Biological and genetic peculiarities of cross-composed and aboriginal beaver populations in Russia. *Acta Zoologica Lituanica*, **12**, 397–402.

Saveljev, A.P., Stubbe, M., Stubbe, A., Unzhakov, V.V. & Kononov, S.V. (2002) Natural movement of tagged beavers in Tyva. *Russian Journal of Ecology*, **33**, 434–439.

Schlosser, I.J. (1998) Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia*, **113**, 260–268.

Shelton, P.C. & Peterson, R.O. (1983) Beaver, wolf and moose interactions in Isle Royale National Park, USA. *Acta Zoologica Fennica*, **174**, 265–266.

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.

Sieber, J. (1989) Biber in Oberösterreich: eine aktuelle Bestandsaufnahme an Inn und Salzach. *Jahrbücher Oberösterreichischer Museum-Verein*, **134**, 277–285.

Simberloff, D. (1996) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation*, **83**, 247–257.

Skelly, D.K. & Freidenburg, L.K. (2000) Effects of beaver on the thermal biology of an amphibian. *Ecology Letters*, **3**, 483–486.

Smith, D.W., Peterson, R.O., Drummer, T.D. & Sheputis, D.S. (1991) Over-winter activity and body temperature patterns in northern beavers. *Canadian Journal of Zoology*, **69**, 2178–2182.

Smith, D.W., Trauba, D.R. & Anderson, R.K. (1994) Black bear predation on beavers on an island in Lake Superior. *American Midlland Naturalist*, **132**, 248–255.

Solheim, R. (1987) Barskogsøkologi og zoologiske verneinteresser – tilpasninger og habitatkrav hos insekter, fugler og pattedyr i et dynamisk økosystem. *Økoforsk Utredning*, **8**, 1–117.

Songster-Alpin, M.S. & Klotz, R.L. (1995) A comparison of electron transport system activity in stream and beaver pond sediments. *Canadian Journal of Fisheries and Aquatic Science*, **52**, 1318–1326.

Spieth, H.T. (1979) The virilis group of *Drosophila* and the beaver *Castor*. *The American Naturalist*, **114**, 312–316.

Sprules, W.M. (1941) The effect of a beaver dam on the insect fauna of a trout stream. *Transactions of the American Fisheries Society*, **70**, 236–248.

Stack, W.R. & Beschta, R.L. (1989) Factors influencing pool morphology in Oregon coastal streams. *Headwaters Hydrology, American Water Resources Association, Hydrological Symposium, Missoula, Montana*, **1**, 401–411.

Stout, R.J. & Taft, W.H. (1985) Growth patterns of a chironomid shredder on fresh and senescent tag alder leaves in two Michigan streams. *Journal of Freshwater Ecology*, **3**, 147–153.

Svendsen, G.E. (1980) Seasonal change in feeding patterns of beaver in southern Ohio. *Journal of Wildlife Management*, **44**, 285–290.

Swanston, D.N. (1991) Natural processes. In: *Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats* (Ed. by W.R. Meehan), pp. 139–179. American Fisheries Society Special Publication 19, Bethesda, Maryland.

Terwilliger, J. & Pastor, J. (1999) Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. *Oikos*, **85**, 83–94.

Townsend, J.E. (1953) Beaver ecology in western Montana with special reference to movements. *Journal of Mammalogy*, **34**, 459–479.

Tumlison, R., Karnes, M. & King, A.W. (1982) The river otter in Arkansas. II. Indications of beaver facilitated commensal relationship. *Arkansas Academy of Science Proceedings*, **36**, 73–75.

Tyurnin, B.N. (1984) Factors determining numbers of the river beavers (*Castor fiber*) in the European North. *Soviet Journal of Ecology*, **14**, 337–344 (Translated from *Ekologiya*, **6**, 43–51).

U.S. Fish and Wildlife Service (1993) Endangered and threatened wildlife and plants; determination to reclassify the Louisiana pearlshell (*Margaritifera hembeli*) from endangered to threatenened. *Federal Register*, **58**, 49935–49937.

U.S. Fish and Wildlife Service (1994) Endangered and threatened wildlife and plants; determination of endangered status for Hungerford's crawling water beetle (*Brychius hungerfordi*). *Federal Register*, **59**, 10580–10584.

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 Science*, **37**, 130–137.

Vogt, B. (1981) What ails the river otter? *National Wildlife*, **19**, 25–28.

White, D.S. (1990) Biological relationships to convective flow patterns within stream beds. *Hydrobiologia*, **196**, 149–158.

Whitman, W.R. (1987) Estimating black duck production on beaver ponds in the Maritimes, 1976–1977. *Canadian Wildlife Service*, **60**, 32–34.

Wilsson, L. (1971) Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). *Viltrevy*, **8**, 115–266.

Woo, M.K. & Waddington, J.M. (1990) Effects of beaver dams on sub-arctic wetland hydrology. *Arctic*, **43**, 223–230.

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.

Yeager, L.E. & Hill, R.R. (1954) Beaver management problems in western public lands. *Transactions of the North American Wildlife and Natural Resources Conference*, **19**, 462–479.

Zurowski, W. (1989) Dam building activity of beavers on the mountainous streams. *Proceedings of the Fifth International Theriological Congress, Rome*, **1**, 316–317.

Zurowski, W. (1992) Building activity of beavers. *Acta Theriologica*, **37**, 403–411.

Zurowski, W. & Kammler, J. (1987) American mink (*Mustela vison* Schreber, 1977) in beaver's sites. *Przeglad Zoologiczny*, **31**, 513–521.

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