Habitat dynamics of beaver Castor canadensis at two spatial scales

Authors: Hyvönen, Terho, and Nummi, Petri

Source: Wildlife Biology, 14(3) : 302-308

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2008)14[302:HDOBCC]2.0.CO;2

Habitat dynamics of beaver *Castor canadensis* at two spatial scales

Terho Hyvönen & Petri Nummi

Hyvönen, T. & Nummi, P. 2008: Habitat dynamics of beaver *Castor canadensis* at two spatial scales. - Wildl. Biol. 14: 302-308.

We studied habitat dynamics of the Canadian beaver *Castor canadensis* in a boreal forest landscape in southern Finland at two scales: the beaver pond level and the landscape level. To explore the changes in tree species composition due to beaver browsing and flooding, six abandoned beaver ponds were sampled (537 sample plots altogether). For habitat dynamics at the landscape scale, the variation in the flooded area and the number of active beaver colonies were recorded during 18 years (1980-1998). At the pond level, flooding appeared to effect more rapid and more pronounced changes in woody growth production than browsing. Coniferous trees were particularly susceptible to flooding, and deciduous trees were more susceptible to browsing. Deciduous trees dominated during succession following a flooding. At the landscape level, mean occupation time of a colony site was found to be short (2.6 years), and the mean area of beaver impoundments was small (0.14% of the total area). Recolonisation of habitats occurred on average nine years after previous abandonment. A reason for the short occupation time may have been scarcity of food. The results suggest that both browsing and flooding should be considered when studying the dynamics of woody growth used by beavers.

Key words: beaver, boreal forest, Castor canadensis, disturbance dynamics, landscape ecology

Terho Hyvönen, MTT Agrifood Research Finland, Plant Production Research, FI-31600 Jokioinen, Finland - e-mail: terho.hyvonen@mtt.fi
Petri Nummi, Department of Forest Ecology, P.O.B. 27, FI-00014, University of Helsinki, Finland - e-mail: petri.nummi@helsinki.fi

Corresponding author: Terho Hyvönen

Received 15 February 2005, accepted 7 November 2007

Associate Editor: Jon E. Swenson

Animals that modify their habitats act as natural disturbance regimes in ecosystems. Though varying in type, intensity, frequency and extent, disturbance regimes are typical of every ecosystem (Pickett & White 1985). The disturbance regime created by each animal is linked to its population dynamics, and may thus itself be very dynamic (Johnston 1995).

Beavers *Castor* spp. are known for their ability to modify habitats and are therefore identified as 'ecosystem engineers' (Jones et al. 1994). Habitat modification caused by beavers affects their food resources, e.g. woody plants, both directly from browsing and indirectly through flooding. Beavers select mainly deciduous trees for food and building material, and concentrate their browsing near the lodge (Fryxell & Doucet 1990, Johnston & Naiman 1990b). This leads to changes in the tree species composition around ponds (e.g. Barnes & Dibble 1988, Johnston & Naiman 1990b, Nolet et al. 1994).

Beavers usually build a dam, which creates a pond (Naiman et al. 1988, Barnes & Dibble 1988, Pollock et al. 1995). Flooding affects nitrogen dynamics and other soil properties (Naiman et al. 1994) and kills most trees within a couple of years (Nummi 1989).

The population dynamics of beavers at the landscape scale have been found to be related to food availability at the local scale (Fryxell 2001). The forest succession of abandoned beaver ponds and their immediate surroundings can therefore be expected to have profound effects on the population dynamics of beavers. Pastor & Naiman (1992) hypothesised that selective browsing of deciduous trees by beavers may lead forest succession towards the dominance of coniferous species. If so, the availability of woody plants preferred by beavers could decline in the long term. Recent findings on the short-term effects of browsing on forest structure, however, do not support this hypothesis (Donkor & Fryxell 1999), as small gaps created by browsing may facilitate the regeneration of both preferred and non-preferred species.

The effects of damming are often neglected in studies of beaver habitat food abundance changes, even though damming can have both spatially and temporally more pronounced effects than browsing (Naiman et al. 1988, Nummi 1992, Pollock et al. 1995). As coniferous trees are more susceptible to anoxia following flooding than deciduous trees (Gill 1970), a short-term flooding could provide a competitive advantage for deciduous trees (see Nummi 1989), thus changing the relative availability of coniferous and deciduous trees to beavers. Flooding, however, usually kills most trees, thereby converting late or mid-successional forest stands to early successional stands after abandonment. In both cases, the proportion of deciduous trees can be expected to increase. The dynamics of forest succession in abandoned beaver ponds and their effect on the production of woody plants favoured by beavers have not been studied, though it may be of central importance for beaver dynamics at the landscape scale.

We studied the dynamics of beaver pond construction and forest regrowth following abandonment both at the individual pond scale and at the landscape scale. First, we quantified the relative importance of browsing and flooding on the forest structure in previously flooded areas. Second, the forest succession of abandoned beaver ponds was explored. Third, the annual variation in a flooded area and number of occupied beaver colonies were studied at the landscape scale.

Material and methods

Study area

Our study area was situated in Evo, southern Finland (61°10'N, 25°05'E), which belongs to the southern boreal vegetation zone (Ahti et al. 1968). The area is a barren watershed region consisting of approximately 100 small (areas of 1-20 ha) lakes and ponds that are interconnected by creeks. The topography of the area varies from 125 m to 185 m a.s.l. The total study area was 7,200 ha of which bogs formed 815 ha and open water area 458 ha. Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* were the dominant tree species in the study area and they contributed 46.9 and 39.0% of the tree volume, respectively (Kallonen et al. 1999). Deciduous trees contributed 12.5% of the tree volume (Kallonen et al. 1999). In most bogs and other moist sites, Norway spruce and downy birch *Betula pubescens* were the dominant trees species. In shrub, field and ground layers, the dominant species were willows *Salix* spp., *Ledum palustre* and *Sphagnum* mosses, respectively.

The native beaver was hunted to extinction in the study area during the 19th century. Two pairs of European beavers *Castor fiber* were introduced to the area in 1935 (Linnamies 1956). As a result of this introduction, there were nine lodges (1-2 of the lodges being occupied at a time) and 15-18 individuals in 1955 (Linnamies 1956). In 1957, one pair of Canadian beavers *Castor canadensis* was introduced to the study area (Lahti 1983), and today, the beaver population in the area consists of Canadian beavers solely. A typical beaver pond in the study area is one in which beavers have dammed the outlet of a small lake or pond, and the riparian zone is flooded.

Habitat dynamics

Of the former beaver ponds that differed in flooding duration and time since flooding, six were selected for the study in July 1996 (Table 1). The ponds were selected based on a minimum former flooding area (i.e. zone of dead trees) 10 m wide around the pond. For each pond, a number of 'sampling zones' at least 10 m wide were established parallel to the shoreline. The number and length of zones for each pond were dependent on the size of the former flooding area. Within each zone, at least 10 sampling plots were located randomly. The sampling plots covered at least 25% but at the most 75% of the former flooding area. In total, 537 sample plots were included in the study (see Table 1).

Table 1. Data on the six beaver ponds studied at Evo, Finland, in 1996.

	Pond area before flooding (ha)	Flooded area (ha)	Duration of flooding (years)	Number of dry years after flooding	Number of sample plots
Pond I	0.4	1.8	1	10	89
Pond II	3.2	3.5	4	15	179
Pond III	0.6	1.3	2	8	76
Pond IV	2.7	2.6	5	10	49
Pond V	2.0	1.6	2	13	76
Pond VI	1.0	2.4	2	5	68
Mean	1.7	2.2	2.7	10.2	89.5

We measured tree stem diameter at stump height (~30 cm above ground level) for tree species with woody stems (living and dead) and beaver-browsed stumps. Basal area, i.e. the cross section area of the stems of all trees in a stand, was calculated based on these measurements. One sampling plot consisted of three concentric circles with radii of 1.25, 2.5 and 5.0 m, respectively. The smallest sampling plot included stems and stumps of 2-5 cm in diameter, the second of 6-20 cm, and the largest of >20 cm. The number of all trees and shrubs <2 cm in stem diameter was counted, and the length of the five longest stems was measured from the smallest sampling plot. All dead trees (other than browsed) were considered dead because of flooding, and stems with a diameter of <2 cm were considered as regrowth after flooding.

To compare the relations of the deciduous and coniferous trees, importance values (see Johnston & Naiman 1990b) were calculated for stems with a diameter of >2 cm as: Importance value $IV_i = (RF_i + RD_i + RB_i)/3$ where RF_i = Relative Frequency, i.e. the percentage of plots where species i occurred; RD_i = Relative Density, i.e. percentage of stems of the species i out of all stems; and RB_i = Relative Basal area, i.e. percentage of total basal area of the species i out of the pooled basal area. We used ANCOVA to determine differences in densities and maximum lengths of the deciduous and coniferous trees in the regrowth (i.e. trees of <2 cm in diameter), and 'Years after flood' was used as a covariate in the analyses. Both density and length data were log(x+1)-transformed prior to analysis.

Landscape dynamics

Beaver colonies and the amount of flooded area in the study area were recorded annually during 1980-1998. The total area of bogs in the study area and the area flooded yearly by beavers were measured from 1:20,000 scale maps using a Geographical Information System. Areas that were defined as bogs on the maps were considered as potential areas for beaver flooding. Hunting data were obtained from the regional game management agency (J. Rauhala, pers. comm.).

Results

Habitat dynamics

On average, more birch, alder *Alnus* spp. and willow (included in the group 'others') were killed by flood-

Table 2. Percentages of living, dead and browsed trees species with diameters of >2 cm at stump height on ground previously flooded by beavers at Evo, Finland, in 1996, expressed as a proportion of the total basal area (m^2 ha^{-1}).

	Pond I	Pond II	Pond III	Pond IV	Pond V	Pond VI	Average
LIVING							
Pinus sylvestris	25.0	2.5	5.4	2.4	1.0	-	6.1
Picea abies	2.6	7.5	0.7	2.8	-	-	2.3
Betula spp.	42.3	31.7	35.1	21.8	8.7	0.1	23.3
Alnus spp.	0.6	8.0	1.8	14.3	14.6	-	6.6
Other	-	0.8	-	-	8.0	0.3	1.5
DEAD							
Pinus sylvestris	10.1	7.9	15.0	10.4	23.1	42.3	18.1
Picea abies	14.0	16.7	9.9	30.5	1.2	29.1	16.9
Betula spp.	1.9	13.8	17.9	3.0	12.6	24.3	12.3
Alnus spp.	0.2	2.1	1.6	5.1	19.3	1.7	5.0
Other	0.2	0.3	-	-	3.7	0.3	0.8
BROWSED							
Pinus sylvestris	-	-	-	-	0.2	-	0.03
Picea abies	-	-	-	-	-	-	-
Betula spp.	2.4	8.3	12.3	6.9	3.5	1.9	5.9
Alnus spp.	0.7	0.3	0.2	2.9	2.7	-	1.1
Other	-	0.2	-	-	1.6	0.1	0.3
Total basal area (m^2 ha^{-1})	1436	2910	1226	1095	1440	1411	1586

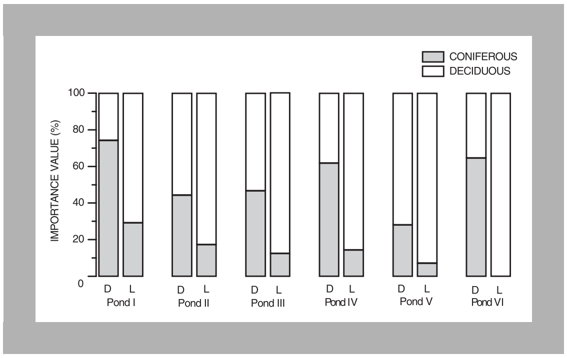

Figure 1. Importance values (in %) of dead (D) and living (L) coniferous and deciduous trees (with diameters of > 2 cm) in the six study ponds at Evo, Finland, in 1996.

ing than by browsing (Table 2). In all ponds, a large proportion of trees (with a diameter of > 2 cm) had died due to flooding (see Table 2). Coniferous trees appeared to be more susceptible to flooding than deciduous trees. Especially spruce had suffered from flooding: the proportion of dead trees was higher for spruce than for pine (see Table 2). As a whole, the forest structure changed towards the dominance of deciduous trees in all ponds (Fig. 1). In pond VI, living coniferous trees (with a diameter of > 2 cm) were completely eliminated due to damming by beavers (see Fig. 1). As the pond had been flooded for only two years (see Table 1), the change had been rapid.

In the regrowth (with a diameter of < 2 cm), deciduous trees had higher density ($F_{TREES} = 40.9$, df = 1, $P < 0.001$; $F_{YEARS} = 43.9$, df = 1, $P < 0.001$) and were taller ($F_{TREES} = 351.7$, df = 1, $P < 0.001$; $F_{YEARS} = 18.9$, df = 1, $P < 0.001$) than coniferous trees (Fig. 2). No clear pattern in regeneration related to the age of

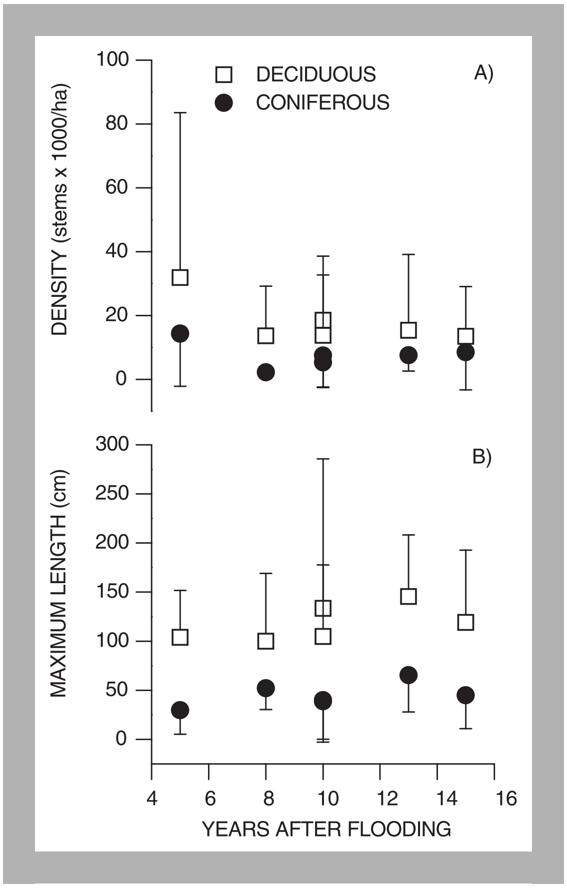

Figure 2. Density (A; in stems × 1000/ha) and maximum length (B; in cm) of the trees in the regrowth expressed as average and SD of the six ponds at Evo, Finland, in 1996. Years after flooding refer to the six individual ponds (see Table 1).

beaver pond was detected. The most frequent species in the regrowth were downy birch and Norway spruce (Table 3). In the study ponds, birches, the

Table 3. Frequencies of occurrence (expressed as percentages of sample plots in which the species occurred) of tree species in the regrowth of the six ponds at Evo, Finland, in 1996.

Tree species	Pond I	Pond II	Pond III	Pond IV	Pond V	Pond VI	Average
Alnus glutinosa	-	6.7	-	10.2	-	-	2.8
Alnus incana	2.2	11.7	13.2	-	7.9	10.3	7.6
Betula pendula	-	2.2	2.6	4.1	13.2	45.6	11.3
Betula pubescens	86.5	63.7	72.4	51.0	47.4	98.5	69.9
Juniperus communis	1.1	-	-	-	1.3	-	0.4
Picea abies	56.2	57.0	14.5	44.9	18.4	70.6	43.6
Pinus sylvestris	20.2	12.3	10.5	4.1	18.4	42.6	18.2
Populus tremula	-	-	-	2.0	-	10.3	2.1
Prunus padus	50.6	11.7	32.9	10.2	1.3	-	17.8
Salix aurita	4.5	25.1	9.2	2.0	3.9	19.1	10.6
Salix caprea	-	-	-	-	-	7.4	1.2
Salix cinerea	-	-	2.6	-	-	2.9	0.9
Salix myrsinifolia	1.1	5.5	-	-	26.3	17.6	8.4
Salix phylicifolia	4.5	16.8	25.0	2.0	21.1	19.1	14.8
Salix spp.	5.6	4.5	-	8.2	19.7	19.1	9.5
Sorbus aucuparia	2.2	7.3	1.3	12.2	3.9	16.2	7.2

most common tree species in the regrowth, had regenerated with seedlings. Only in a few cases were resprouts observed and no such case was observed in the sample plots. Regeneration of birches was most pronounced in ponds in which the effect of flooding was strongest (i.e. where the former vegetation had died out completely).

Landscape dynamics

The number of beaver colonies in the study area varied between two and nine during the study period. The average density of occupied colonies for the entire study area was 12.4 km^2/active colony or 0.08 colonies/km^2. Hunting did not seem to have affected the population systematically (Fig. 3). The number of beavers shot averaged 2.4 individuals/year (range: 0-7 individuals) during the study period, which averages about 15% of the population (assuming that the average number of individuals per beaver colony is 2.8 individuals in Finland; A. Ermala, pers. comm.).

During our study period, a mosaic of 30 beaver sites differing in age had been formed. The number of active beaver colonies was 5.8 at the time, and the occupation time was 2.6 years (after exclusion of ponds in which hunting had affected the occupation time, the average was 2.8 years; Table 4). A typical beaver pond in the study area was one in which beavers had dammed the outlet of a small lake and this led to inundation of the riparian zone. Sometimes, parts of the rivers and creeks were flooded too. The total flooded area averaged 1.23% (range: 0.20-1.90%) of the total bog area, and 0.14% (range: 0.02-0.22%) of the whole study area. The total flooded area and the number of colonies were correlated ($r = 0.765$, $P < 0.001$, $N = 19$). During the study years, there were four cases of recolonisation of a beaver settlement, and they happened on average nine years (range: 6-13 years) after previous abandonment.

Table 4. Data on the dynamics of beaver colonies at Evo, Finland, during 1980-1998.

	Average	SD	N	Minimum	Maximum
Occupation time (in years)	2.6	1.7	33	1.0	9.0
Number of active colonies	5.8	1.8	19	2.0	9.0
Total flooded area (in ha)	9.9	0.3	19	1.4	15.8
Pond size (in ha; i.e. flooded area)	1.7	1.2	41	0.1	4.5

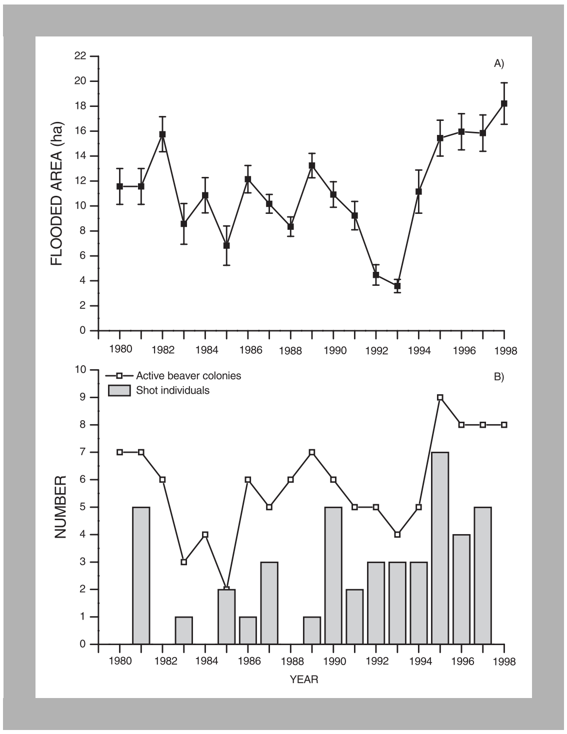

Figure 3. Amount of flooded area expressed as average and SD (A), and the numbers of beaver colonies occupied and individuals shot (B) in the study area at Evo, Finland, during 1980-1998.

Discussion

Flooding appeared to be a more important factor affecting forest structure than browsing. Coniferous trees proved to be more susceptible to flooding than deciduous trees, which is in accordance with previous findings (Gill 1970, Nummi 1989). As found in our study, also previous studies reported that tree species suffer from the effects of flooding after just two years (Nummi 1989). Beavers are known to use deciduous trees (of small diameters) in their diet, favouring aspen and willows (e.g. Barnes & Dibble 1988, Johnston & Naiman 1990b). The small amount of browsed trees reported in our results may have been a consequence of the fact that we measured only trees with a diameter > 2 cm, and it is known also from our study area that beavers browse small trees in considerable amounts (Lahti 1972). Furthermore, beavers might have browsed outside our sampling area (Johnston & Naiman 1987) or might have used other food sources, e.g. aquatic plants (Lahti & Helminen 1974).

We found the tree species composition of abandoned beaver ponds to be potentially favourable for beavers recolonising the sites. This finding contradicts results of previous studies which only considered the effects of browsing on the tree species composition (e.g. Barnes & Dibble 1988, Donkor & Fryxell 1999). Previous studies of beaver disturbance have reported multi-successional pathways of beaver habitats from areas with higher population densities and longer periods of flooding than ours (Remillard et al. 1987, Johnston & Naiman 1990a). In these studies, some of the habitat changes were irreversible and influenced beavers negatively (e.g. leading from forest to bog). Our results indicate that a short-term beaver disturbance can change the forest structure and tree species composition in a favourable direction (i.e. leading to dominance of decidiuous trees) for many browsing mammals including beavers themselves (*cf.* Pastor & Naiman 1992). The reason for the diverging results might be that different population densities of beavers might influence habitat dynamics differently. In our area, the average density of occupied colonies was low, i.e. 0.08 colonies/km^2, which is quite similar to the density reported earlier from Finland (0.10 colonies/km^2; Härkönen 1999), and below the density gradient found in North America (0.15-4.6 colonies/km^2; Parker et al. 2002). At high population densities with longer flooding times, the amount of 'virgin' habitat may decrease due to irreversible habitat changes, and the time it takes for habitats to recover gets longer.

The landscape mosaic created by beavers in our study area proved to be very dynamic: the average occupation time of a patch was 2.6 years. In previous studies, beavers have been reported to occupy the same areas for much longer times, even decades (Johnston & Naiman 1990a). However, many of these studies have been conducted in temperate forests of North America where the deciduous tree resources are more abundant than in the boreal Finland. Likewise, European beavers may stay in one place for a longer time because they build less and, thus, presumably use woody resources less heavily (Danilov & Kan'shiev 1983, Ruusila 1997). In our study area, hunting might have shortened the occupation time in a few places and likely has lowered the density of active beaver colonies. However, short occupation times seemed merely to be a result of scarce resources. The most popular browsed tree species were downy birch, alders *Alnus glutinosa* and *Alnus incana* and willows, while aspen *Populus tremula*, which is one of beavers' most preferred tree species as winter food (see Bryant & Kuropat 1980), was rare. It seems that a disturbance regime maintained by beavers has higher disturbance frequencies in the boreal than in the temperate vegetation zone, which may be partly due to lower amount of resources of the boreal forest area.

Although the number of active beaver colonies in our study area was rather small (Parker et al. 2002), almost half of the ponds were influenced by beaver flooding during our 19-year study period. Furthermore, deciduous trees along the shores of quite a number of additional ponds were affected by slight beaver browsing. A mosaic of beaver patches in various stages increases the structural diversity of boreal forest. The disturbance regime and pattern of successional stages of beaver patches depend on the density of the beaver population and the vegetation of the area. In our study area, the density of the beaver population and the resource levels were rather low. Most patches were therefore dry most of the time, but new flowages were also created quite often; especially considering that the beaver population was small. In the previous studies conducted in North America, occupation times have varied from much more (Johnston & Naiman 1990a) to comparable with our results (Fryxell 2001). In areas with more resources, the wet phases would dominate the mosaic due to longer occupation times.

Acknowledgements - we are indebted to Petri Timonen for assistance in the fieldwork and to the Finnish Game Foundation for funding him. We are indebted to the staff of Evo Game Research Station for their participation in the collection of data, and to Jyri Rauhala for supplying data on the hunting.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. - Annales Botanici Fennici 5: 169-211.

Barnes, W.J. & Dibble, E. 1988: The effects of beaver in riverbank forest succession. - Canadian Journal of Botany 66: 40-44.

Bryant, J.P. & Kuropat, P.J. 1980: Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. - Annual Review of Ecology and Systematics 11: 261-285.

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.

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.

Fryxell, J.M. 2001: Habitat suitability and source-sink dynamics of beavers. - Journal of Animal Ecology 70: 310-316.

Fryxell, J.M. & Doucet, C.M. 1990: Provisioning time and central-place foraging in beavers. - Canadian Journal of Zoology 69: 1308-1313.

Gill, C.J. 1970: The flooding tolerance of woody species - a review. - Forest Abstracts 31: 671-688.

Härkönen, S. 1999: Management of the North American beaver (Castor canadensis) on the South-Savo Game Management District, Finland (1983-1997). - In: Busher, P.E. & Dzieciolowski, R.M. (Eds.); Beaver Protection, Management and Utilization in Europe and North America. Kluwer Academic, Plenum Publishers, New York, pp. 7-14.

Johnston, C.A. 1995: Effects of animals on landscape patterns. - In: Hansson, L., Fahrig, L. & Merriam, G. (Eds.); Mosaic landscapes and ecological processes. Chapman & Hall, London, UK, pp. 57-80.

Johnston, C.A. & Naiman, R.J. 1987: Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. - Landscape Ecology 1: 47-57.

Johnston, C.A. & Naiman, R.J. 1990a: Aquatic patch creation in relation to beaver population trends. - Ecology 71: 1617-1621.

Johnston, C.A. & Naiman, R.J. 1990b: Browse selection of beavers: effects on riparian forest composition. - Canadian Journal of Forestry Research 20: 1036-1043.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994: Organisms as ecosystem engineers. - Oikos 69: 373-386.

Kallonen, S., Liljeroos, H. & Timonen, P. 1999: Evon alue-ekologinen suunnitelma. Metsähallitus. - Oy Edita Ab, Helsinki, Finland, 77 pp. (In Finnish).

Lahti, S. 1972: Majavat. - In: Siivonen, L. (Ed.); Suomen Nisäkkäät 1. - Otava, Keuruu, Finland, pp. 285-308. (In Finnish).

Lahti, S. 1983: Majavat. - In: Koivisto, I. (Ed.); Suomen Eläimet: Nisäkkäät, Weilin+Göös, Espoo, Finland, pp. 117-123. (In Finnish).

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

Linnamies, O. 1956: Majavien esiintymisestä ja niiden aiheuttamista tuhoista. - Suomen Riista 10: 63-68. (In Finnish).

Naiman, R.J., Johnston, C.A. & Kelley, J.C. 1988: Alteration of North American streams by beaver. - BioScience 38: 753-762.

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

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.

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.

Parker, H., Rosell, F. & Gustavsen, Ø. 2002: Errors associated with moose-hunter counts of occupied beaver Castor fiber lodges in Norway. - Fauna Norvegica Serie A 22: 23-31.

Pastor, J. & Naiman, R.J. 1992: Selective foraging and ecosystem processes in boreal forests. - American Naturalist 139: 690-705.

Pickett, S.T.A. & White, P.S. (Eds.) 1985: The ecology of natural disturbance and patch dynamics. - Academic Press, Orlando, Florida, USA, 425 pp.

Pollock, M.M., Naiman, R.J., Erickson, H.E., Johnston, C.A., Pastor, J. & Pinay, G. 1995: Beavers as Engineers: Influences on Biotic and Abiotic Characteristics of Drainage Basins. - In: Jones, C.G. & Lawton, J.H. (Eds.); Linking species and ecosystems. Chapman and Hall, New York, USA, pp. 117-126.

Remillard, M.M., Gruendling, G.K. & Bogucki, D.J. 1987: Disturbance by beaver (Castor canadensis Kuhl) and Increased Landscape Heterogeneity. - In: Turner, M.G. (Ed.); Landscape Heterogeneity and Disturbance. Springer-Verlag, New York, USA, pp. 103-122.

Ruusila, V. 1997: Kanadan-ja euroopanmajavan reviirikäyttäytymisestä ja metsästyksen vaikutuksesta majavapopulaatioon. - M.Sc. thesis University of Joensuu, 33 pp. (In Finnish).