

Forest damage caused by the Canadian beaver (*Castor canadensis*) in South Savo, Finland

Sauli Härkönen

Härkönen, S. 1999. Forest damage caused by the Canadian beaver (*Castor canadensis*) in South Savo, Finland. *Silva Fennica* 33(4): 247–259.

The increasing Canadian beaver (*Castor canadensis*) population has caused forest damage in Finland. However, the occurrence, extent and importance of the damage have not been comprehensively studied. The field inspection was carried out in all of the beaver damage areas (n = 50) in the Anttola, Juva and Pieksämäki game management units in summer 1998. The characteristics of the damage areas, types of damage and the severity of the damage were examined. The size of the damage areas averaged 2.2 ha. The damage areas occurred on peatland forest more (p < 0.05) than expected. The dominant tree species were commercially valuable trees such as Scots pine (*Pinus sylvestris*) (33 %), Norway spruce (*Picea abies*) (18 %) and birches (*Betula* spp.) (47 %). Birch occurred as dominant tree species more (p < 0.05) than expected. The proportion of older forest development classes was considerable. The most important type of damage was flooding (50 %) caused by the damming activity of beavers. The trees were dead or dying in 18 % of the damage areas. It was estimated that the ecosystem engineering performed by beavers was of no importance in 28 % of the damage areas. Prevention of beaver damage has been carried out in 80 % of the damage areas. In the study area, beaver numbers have steadily increased, although the number of beavers taken by hunting and the allowed hunting harvest have sharply increased. It is suggested that the methods used to prevent beaver damage should be improved and a compensation system should be provided by the state for the most damaged areas. Beavers can cause damage to commercial forestry, and this should be taken into account more effectively in the management plans made by the game management districts.

Keywords Canadian beaver, *Castor canadensis*, forest damage, prevention of damage, type of damage

Authors' address South Savo Game Management District, P.O. Box 14, FIN-51901 Juva, Finland

Fax +358 15 452 831 **E-mail** sauli.harkonen@riistanhoitopiirico.inet.fi

Received 29 April 1999 **Accepted** 5 November 1999

1 Introduction

The original beaver species, the European beaver (*Castor fiber* L.) was hunted to extinction in Finland in the late 1860's (Linnamies 1956). Re-introduction of the European beaver and introduction of the Canadian beaver (*C. canadensis* Kuhl) were performed in 1930's (Lahti and Helminen 1969). Two pairs of Canadian beaver were released in Sääminki (Sulkava, Lohikoski) in southeastern South Savo in 1937. The present Canadian beaver population in Finland is composed of the offspring of these two pairs.

The beaver population in Finland has steadily increased. It was estimated that there were 450–500 beavers (both species) in 1955 (Linnamies 1956) and 500–600 beavers in 1960 (Linnamies 1961). It was concluded on the basis of questionnaire surveys that there were 1800–3000 beavers in 1965, 1800–3200 beavers in 1970, 4000–6000 beavers in 1975 (Lahti and Helminen 1980), 2500–4400 beavers in 1980, 2800–4600 beavers in 1985 (Ermala et al. 1989), 9000 beavers in 1995 (Ermala 1996), and 12 000 beavers in 1998 (Ermala et al. 1999). The present beaver population is, however, rather low compared with that in Sweden (100 000 European beavers) and Norway (50 000 European beavers) (Hartman 1999).

Concern has been expressed over the increase in the beaver population and its impact on forest ecosystems (King et al. 1998, Nolet and Rosell 1998). Beavers work as ecosystem engineers (Jones et al. 1994) and can have a long-term influence on the forest landscape. The selective harvesting of deciduous trees and intensive damming activity of beavers cause changes in the succession process (Naiman et al. 1988, Naiman et al. 1994, Pastor and Naiman 1992). These changes can be considered to be forest damage in areas where intensive forestry is practised. In Finland, Linnamies (1956) reported the first damage observations in forests. Lahti and Helminen (1969) estimated that 800 ha of forest had been killed by flooding and an additional 1900 ha of forest affected by higher water levels in 1965. These damage estimates increased along with the increasing beaver population to 2000 ha of dead forest and 2400 ha damaged in 1975 (Lahti and Helminen 1980). In 1998, there was 3682 ha of forest affected by higher water levels (Ermala

et al. 1999). Damage observations have also been reported from Estonia (Laanetu 1995), Lithuania (Mickus 1995) and Sweden (Lavsund 1977).

The estimated beaver number in the South Savo Game Management District (SGMD) has increased considerably during the period 1983–1997 (Härkönen 1999). In 1997, there were approximately 3000 Canadian beavers in SGMD (i.e. 30 % of the total population in Finland). The increasing beaver population has caused damage, especially in forests. This is causing increasing confrontation with man, and population and damage control are required (c.f. Nolet and Rosell 1998). The total area of extensively flooded land (i.e. trees dead or dying) caused by damming activity was 475 ha in 1995 and 320 ha in 1997 in SGMD (Härkönen 1999). Excessively wet areas (i.e. trees suffering and growth diminished) were 580 ha and 600 ha, respectively. Because beaver dams cause flooding and kill the trees, this type of damage can cause considerable economic loss to the forest owner. The debarking and felling of trees by beavers can also be important types of damage. In addition, the dead trees in damage areas provide suitable breeding sites for bark beetles (Col., *Scolytidae*) and can increase the risk of subsequent insect damage in the surrounding forests (Saarenmaa 1978). However, there is no current information about the proportions of different types of damage in SGMD or in Finland.

Canadian beaver hunting was started to prevent damage in Finland in the beginning of the 1960's (Ermala et al. 1989). In this respect, there was a planned overharvesting operation in Northern Karelia in 1970's (Ermala et al. 1989, 1999). Beavers are, however, very easily over-hunted (Nolet and Rosell 1998), and thus successful management of beaver populations should be based on a management plan. Hunting must take place at a sustainable level and, in this respect population demographics and the occurrence and degree of beaver damage, for instance, should be examined (c.f. Ermala et al. 1999, Härkönen 1999).

The aim of the present study was: 1) to survey the characteristics of Canadian beaver damage areas, 2) to determine the types of damage, and 3) to obtain results for management purposes in SGMD.

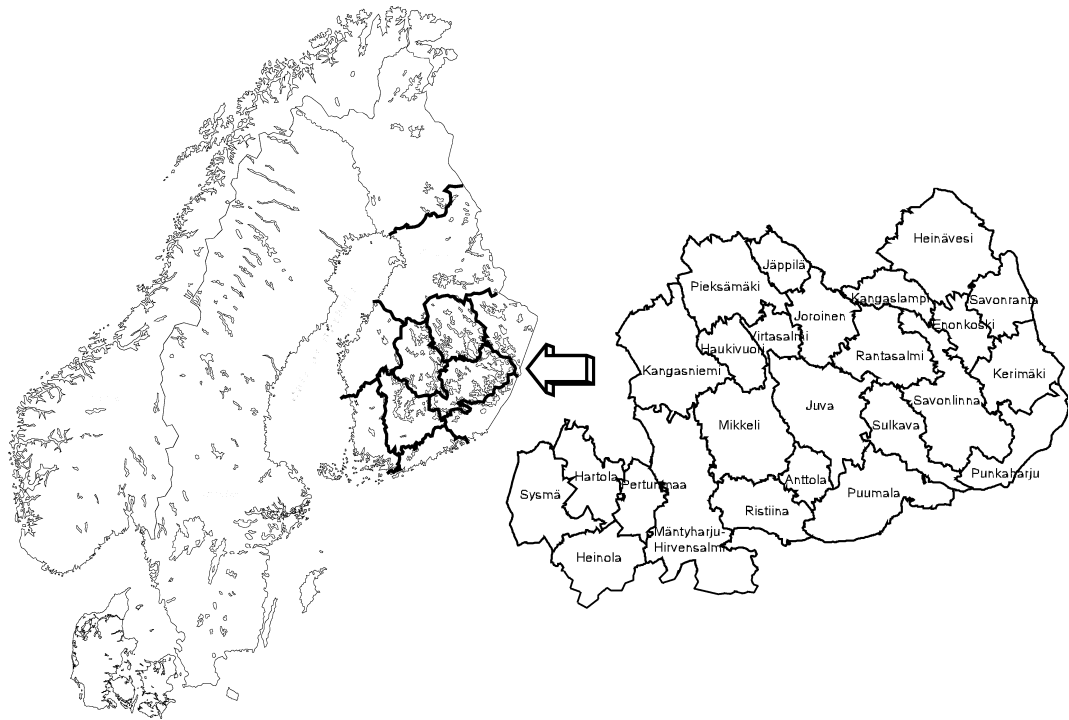


Fig. 1. The study areas in the Anttola, Juva and Pieksämäki game management units belonging to the South Savo Game Management District.

2 Material and Methods

The study was performed in the Anttola, Juva and Pieksämäki game management units in the region of South Savo, southcentral Finland (Fig. 1). The total land area in the region of South Savo is 1.45 million ha. Eighty-six percent of this area is forestry land (including peatland forest area) (Tomppo et al. 1998). The forests are intensively managed and are mainly privately owned (79 %). Forest companies (11 %), the Finnish Forest and Park Service (5 %) and others (e.g. communes and the church) (5 %) are minor forest owners. The growing stock volume (m^3/ha) consists of Scots pine (*Pinus sylvestris* L.) (41 %), Norway spruce (*Picea abies* (L.) Karsten) (41 %), birch (*Betula* spp.) (14 %), and other deciduous tree species (4 %). Pine occurs as the dominant tree species over 54.8 % of the forest land area (Tomppo et al. 1998). Spruce (35.5 %), birch (9.0 %) and other deciduous tree species

(0.7 %) are other dominant tree species. The proportion of young thinning stands is relatively high (33 %). The proportions of young stands, advanced thinning stands and mature stands are 23 %, 26 % and 18 %, respectively. The forests in the area are growing on relatively fertile sites. According to the forest site type classification (Cajander 1909), the forest site type distribution in the South Savo region is: Oxalis-Maianthemum type (2 %), Oxalis-Myrtillus type (30 %), Myrtillus type (47 %), Vaccinium type (16 %), and Calluna and Cladonia types combined (5 %).

Lakes, rivers and small streams provide very good habitats for the beaver. There are about 38 000 km land/water edge in the area of the SGMD. In 1997, the occurrence of forest damage caused by the Canadian beaver and the density of the Canadian beaver population in SGMD were estimated by means of a questionnaire survey (Härkönen 1999). The results of this ques-

Table 1. The classifications used in describing beaver damage areas.

Variable	Classification
Main category	1 = mineral soil site, 2 = peatland forest
Dominant tree species of the forest stands	1 = Scots pine, 2 = Norway spruce, 3 = birch, 4 = other
Forest site type	1 = Oxalis-Myrtillus type or better (OMT), 2 = Myrtillus type (MT), 3 = Vaccinium type or worse (VT)
Peatland forest category	1 = spruce mire, 2 = pine mire
Forest development class	A = young stand, B = young thinning stand, C = advanced thinning stand, D = mature stand
Type of damage	1 = extensively flooded area, i.e. trees were dead or dying, 2 = excessively wet area, i.e. trees were suffering and growth diminished, 3 = felled trees, 4 = extensively flooded area and felled trees, 5 = excessively wet area and felled trees, 6 = agricultural land, 7 = road and forest
Duration of damage	1 = < 1 year, 2 = 1–2 years, 3 = > 2 years
Severity of damage	1 = no importance, 2 = growth diminished and trees will die, 3 = growth diminished and patchily occurring dead trees, 4 = dead trees

tionnaire formed the basis for the field inspections. All of the beaver damage areas ($n = 50$, 110 ha) in forestry land in the game management units of Anttola, Juva and Pieksämäki were inspected (i.e. total sampling). This sampling corresponded 12 % of total damage area (920 ha) in SGMD (Härkönen 1999). The damage areas in Anttola, Juva and Pieksämäki can be considered to be in average category in relation to damage occurrence and beaver density in the area of SGMD (Härkönen 1999).

The following characteristics were determined in each damage area: main category, dominant tree species of the forest stands, forest site type, peatland forest category, forest development class, average height of dominant tree species (m), size of damage area (ha), type of damage, duration of damage, and severity of damage (Table 1). The greatest distance (m) between the water and the site of the felled trees was also measured. Peatland forest site types were included to the comparable forest site type.

Damage areas with a high water level were only visually inspected. Whenever possible, the damage areas were also sampled using a systematic line-plot method (e.g. Lääperi & Löyttyneemi 1988). A total of 13 damage areas in Pieksä-

mäki, 4 in Juva, and 8 in Anttola were inspected by the line-plot method. The plot size was 20 m². The tree species, height (m), feeding signs on tree (1 = debarking, 2 = felled tree), and the effect of flooding on tree condition (1 = none, 2 = slight damage, 3 = considerable damage, i.e. growth diminished and tree will die, 4 = dead) were determined. Basal area (m²/ha) was measured using a relascope. The growing stock volume was calculated according to the average height and basal area of the trees. The result was multiplied by the size of the damage area in order to obtain the growing stock volume per damage area.

Enquiries were also made in order to determine whether the destruction of problem dams or hunting is carried out to reduce the damage probability. In Finland, the destruction of problem dams is freely allowed during 15 June–15 September. Otherwise, a license is required for destruction of problem dams or hunting and is granted by the local game management districts. The hunting season is open during 20 August–30 April.

Beaver numbers in the Anttola, Juva and Pieksämäki game management units during the period 1994–1997 were estimated on the basis

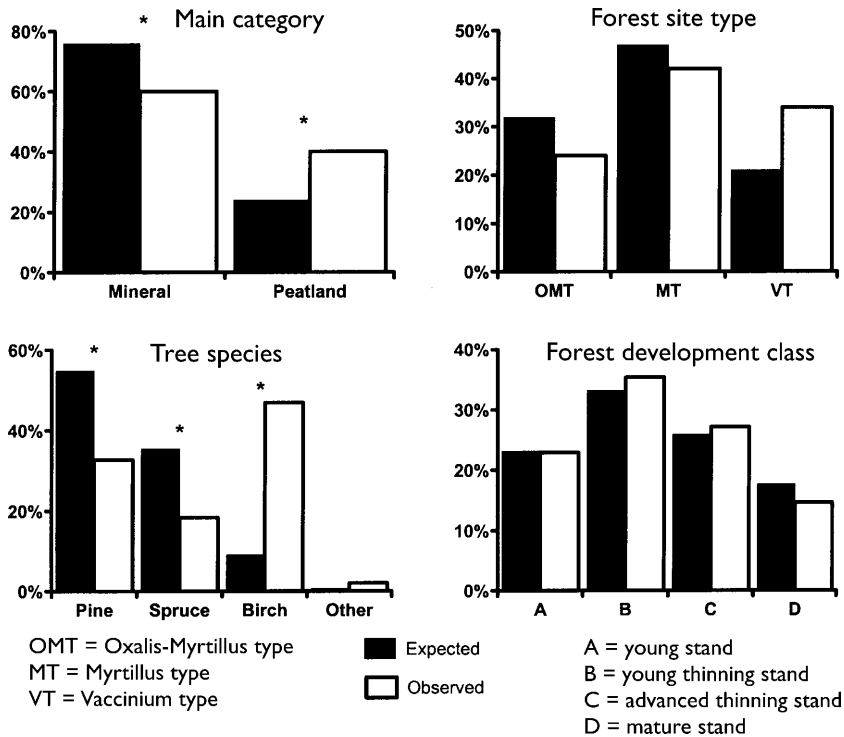


Fig. 2. The expected and observed distribution of characteristics of beaver damage areas. The expected values are based on Tomppo et al. (1998). Bonferroni Z-statistics: * $p < 0.05$.

of the questionnaire surveys conducted by SGMD (c.f. Härkönen 1999). Hunting statistics were prepared using the data gathered by SGMD.

Chi-square goodness-of-fit analysis was used to test the hypotheses that characteristics of damage areas corresponded to expected patterns based on habitat availability (Neu et al. 1974). At least 50 observations are required for adequate power in hypothesis testing when availabilities are known (Allredge and Ratti 1986). Bonferroni Z-statistic as modified by Neu et al. (1974) was used to determine which habitat types in damage areas occurred in proportions greater or less ($p < 0.05$) than availability. The size of the damage area and the height of the dominant tree species were statistically analysed by one-way ANOVA. In addition, proportional data are presented for game management units, because the management of the Canadian beaver population is based on the decisions made by local game managers.

3 Results

The average size of the beaver damage areas was 2.2 ha (± 0.3 S.E.). The damage areas in Anttola were relatively small (1.2 ha ± 0.3 S.E.). The respective value for Pieksämäki was 2.7 ha (± 0.6 S.E.) and for Juva 2.5 ha (± 0.4 S.E.). However, there was no significant difference in the size of the damage areas between the study areas (ANOVA, $F = 2.35$, $p = 0.11$).

Chi-square goodness-of-fit tests revealed that characteristics of beaver damage areas in relation to main category ($G^2 = 6.26$, $p = 0.02$) and dominant tree species ($G^2 = 50.0$, $p < 0.001$) differed significantly from expected (Fig. 2). The damage areas occurred on peatland forest more ($p < 0.05$) and on mineral soil sites less ($p < 0.05$) than expected. In damage areas, birch occurred as dominant tree species more ($p < 0.05$) than expected, whereas pine and spruce occurred as dominant tree species less ($p < 0.05$) than

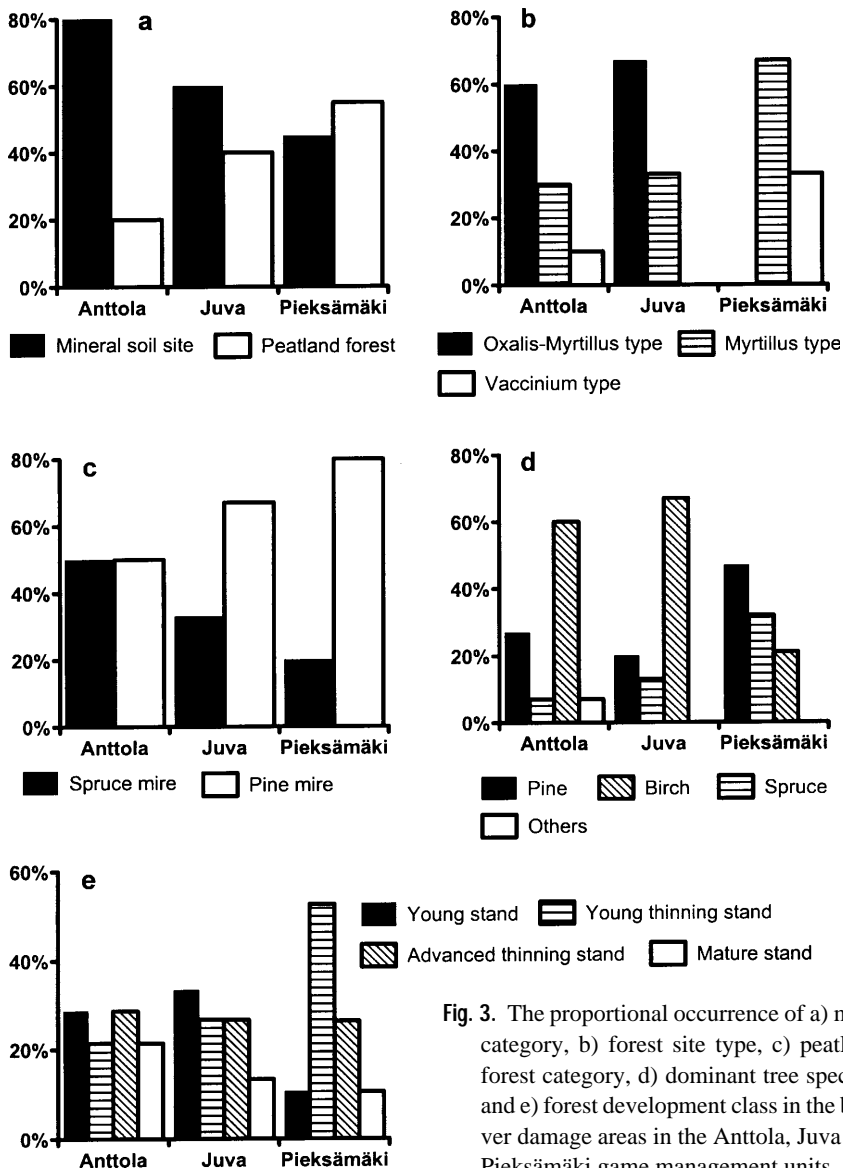


Fig. 3. The proportional occurrence of a) main category, b) forest site type, c) peatland forest category, d) dominant tree species, and e) forest development class in the beaver damage areas in the Anttola, Juva and Pieksämäki game management units.

expected. There were no differences in characteristics of beaver damage areas in relation to forest site type ($G^2 = 4.75, p = 0.09$) and forest development class ($G^2 = 0.58, p = 0.99$).

The damage areas mainly occurred on mineral soil sites (60 %). The proportion of peatland forest was 40 %. In Anttola, the damage areas were mainly on mineral soil sites, whereas the proportion in peatland forest was considerable in Pieksämäki and Juva (Fig. 3 a).

The damage areas on mineral soil sites were restricted to relatively fertile forest site types. The proportions of Oxalis-Myrtillus type, Myrtillus type, and Vaccinium type were 43 %, 43 %, and 14 %, respectively. Juva and Anttola especially had a high proportion of damage on the Oxalis-Myrtillus type (Fig. 3 b).

Damage areas in the peatland forest category were mainly on pine mires (72 %). The proportion of spruce mires was 28 %. The proportion of

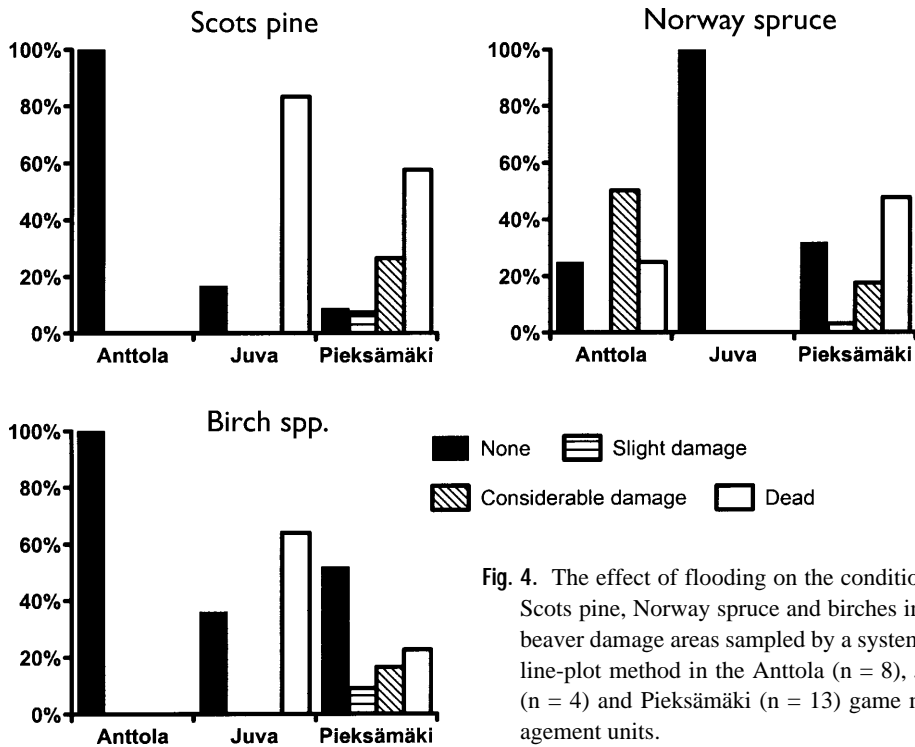


Fig. 4. The effect of flooding on the condition of Scots pine, Norway spruce and birches in the beaver damage areas sampled by a systematic line-plot method in the Anttola ($n = 8$), Juva ($n = 4$) and Pieksämäki ($n = 13$) game management units.

damage on pine mires was considerable in Pieksämäki (Fig. 3 c).

The dominant tree species in the damage areas were birch (47 %), pine (33 %), spruce (18 %) and others (aspen *Populus tremula* L.) (2 %). Birch dominance was rather high in Anttola and Juva (Fig. 3 d). The average height of the dominant tree species in the damage areas ($13.8 \text{ m} \pm 1.0 \text{ S.E.}$) did not differ between the study areas (ANOVA, $F = 0.53$, $p = 0.59$).

The damage areas mainly occurred in young thinning stands (35 %) and in advanced thinning stands (27 %). Also the proportion of mature stands (15 %) was relatively high. In Pieksämäki, the proportion of young thinning stands was highest (Fig. 3 e), and in Juva and Anttola the affected forest development classes were more evenly distributed.

The growing stock volume per damage area was $126 \text{ m}^3 (\pm 45 \text{ S.E.})$ in pine-dominated stands, $227 \text{ m}^3 (\pm 64 \text{ S.E.})$ in spruce-dominated stands and $100 \text{ m}^3 (\pm 0 \text{ S.E.})$ in birch-dominated stands. The effect of flooding on the condition of commercially valuable tree species was greatest in

Juva and Pieksämäki (Fig. 4). However, the result would have been different if damage areas with a high water level would also have been inspected by the systematic line-plot method.

The most common type of damage was an excessively wet area (38 %) caused by intensive damming activity. The proportions of extensively flooded area, felled trees and excessively wet area and felled trees were 12 %, 24 % and 16 %, respectively. Other types of damage were negligible. The proportion of excessively wet areas was highest in Juva, whereas felled trees was the most important type of damage in Anttola (Fig. 5 a). The greatest distance between the water and the site of the felled trees was 150 m, and the average distance 47 m. Beaver feeding signs were mainly observed on aspen (Table 2). There were no feeding signs on pine and spruce. Debarking only occurred on birch and aspen.

The ecosystem engineering performed by beavers was estimated to be of no importance in 28 % of the damage areas. The growth had diminished and the trees will die in 12 % of the damage areas. The growth had diminished and there

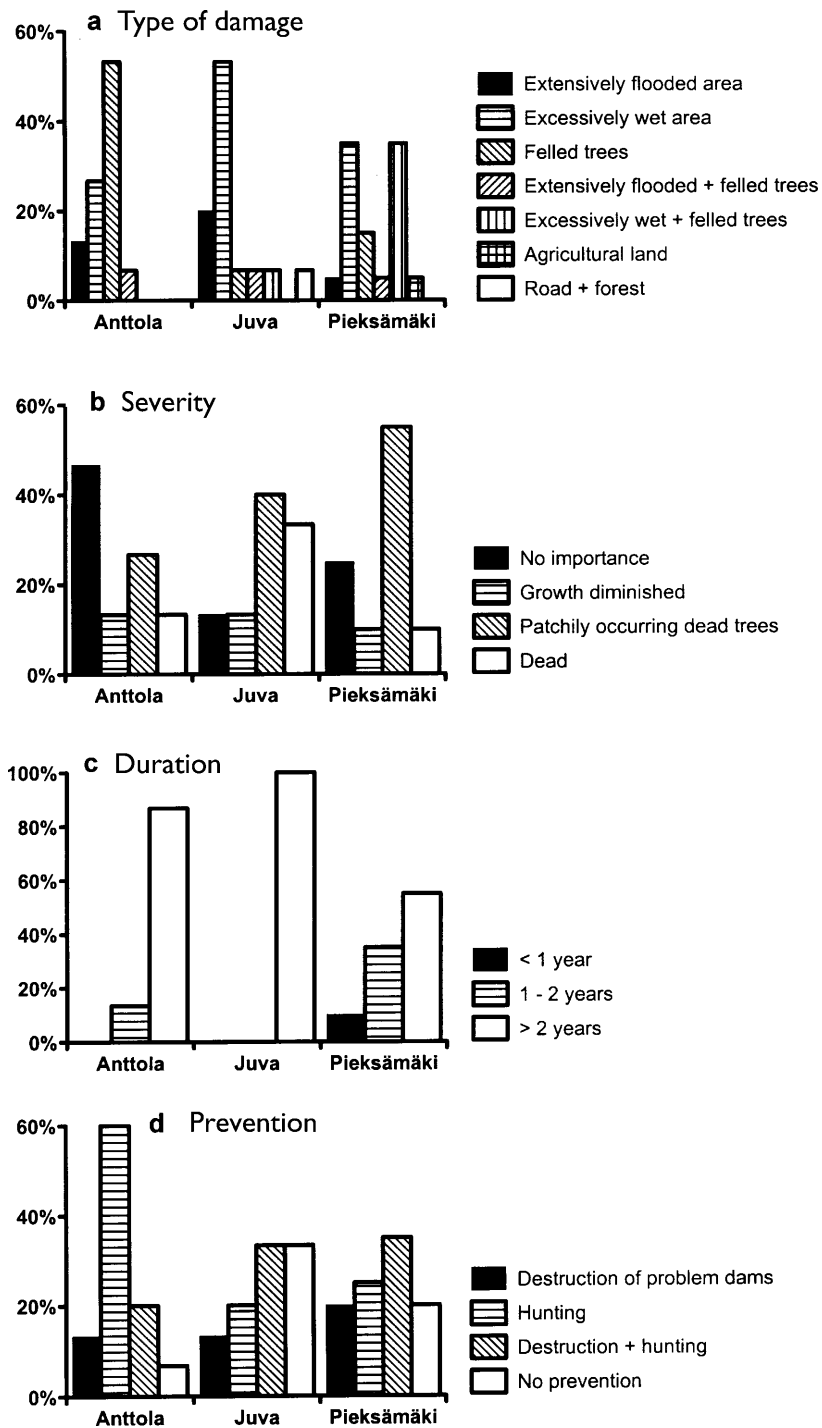


Fig. 5. The proportional occurrence of a) type of damage, b) severity of damage, c) duration of damage, and d) prevention of damage in the beaver damage areas in the Anttola, Juva and Pieksämäki game management units.

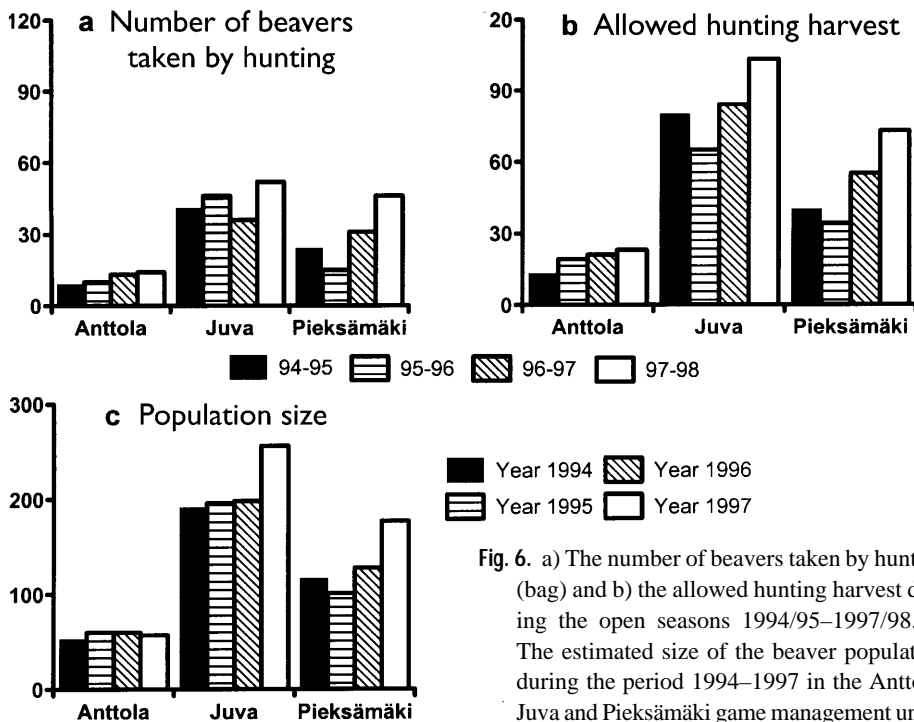


Fig. 6. a) The number of beavers taken by hunting (bag) and b) the allowed hunting harvest during the open seasons 1994/95–1997/98. c) The estimated size of the beaver population during the period 1994–1997 in the Anttola, Juva and Pieksämäki game management units.

Table 2. The density (stems/ha) and height (m) of different tree species in beaver damage areas sampled by a systematic line-plot method ($n = 25$). In addition, the number of trees debarked and felled by beavers (per ha) are presented. Means are given with their standard errors.

Tree species	Density	Height	Debarked	Felled
Scots pine	647±223	9.2±1.8	0	0
Norway spruce	930±206	5.4±1.2	0	0
Birch spp.	1520±221	5.5±0.9	4±4	158±104
Aspen	1264±443	2.6±0.5	20±15	928±335
Willow spp.	551±159	1.9±0.2	0	40±31
Rowan	569±268	2.0±0.3	0	100±82
Grey alder	487±217	2.2±0.3	0	23±13

were already sporadic patches of dead trees in 42 % of the damage areas. Trees were dead in 18 % of damage areas. The severity of damage was lowest in Anttola (Fig. 5 b). In Juva, the trees were already dead in 33 % of the damage areas. In Pieksämäki, the situation will be the same after a few years.

Beaver damage had occurred for more than two years running in 78 % of the damage areas. Especially in Juva, but also in Anttola, the dam-

age had occurred for several years (Fig. 5 c). In Pieksämäki, there were also new damage areas.

There was no prevention of beaver damage in 20 % of the damage areas. When prevention was used, the most widely used prevention method was hunting (43 %). The destruction of problem dams (20 %) and the hunting and destruction of problem dams together (37 %) were other prevention methods used. In Anttola, the prevention of beaver damage occurred in 93 % of the dam-

age areas (Fig. 5 d). The respective value in Pieksämäki was 80 % and in Juva 67 %. The combined use of the destruction of problem dams and hunting was the most common prevention method in Pieksämäki and Juva, whereas hunting was the most important method in Anttola.

The number of beavers taken by hunting (bag) has increased by 92 % in Pieksämäki, 27 % in Juva and 56 % in Anttola during the period 1994–1998 (Fig. 6 a). Simultaneously, the allowed hunting harvest has increased by 83 %, 29 % and 77 %, respectively (Fig. 6 b). Despite hunting, the beaver numbers in Juva and Pieksämäki have clearly increased during the period 1994–1997 (Fig. 6 c). In Anttola, the estimated beaver population has remained more constant.

4 Discussion

In Finland forests are intensively managed for commercial purposes. In this respect, mammalian species that feed heavily on trees are considered as damaging agents if feeding kills the tree, causes a reduction in growth or impairs the technical quality of the wood. In Finland, Sweden and Norway, moose (*Alces alces* L.) browsing causes considerable economic loss to forest owners especially in high-density winter range areas (Lavsund 1987). Hares and voles can also cause some damage. In Finland, there has also been an increasing frequency and extent of forest damage caused by the Canadian beaver in the region of South Savo (Härkönen 1999). Beaver damage is problematic and causes a considerable amount of public discussion because the damage is not compensated by the state as is the case for moose damage. For this reason, the capacity of forest owners to tolerate beaver damage is relatively low, even though the total area damaged (ca. 900 ha) by beavers in relation to the total land area (1.45 million ha) in South Savo is negligible and occurs in a very patchy fashion (Härkönen 1999). The damage can, however, be of significant importance for forest owners, because the average area managed by private forest owners is only approximately 34 ha in South Savo. In this respect, I suggest that the state should provide compensation at least for the most severely damaged stands (c.f. Nolet and Rosell 1998).

The importance and economic value of the damage depend on the characteristics of the area and the type of damage. In Sweden, forest damage caused by beavers normally occurs on unproductive or marginal sites in relation to forestry, and the damage is more severe in flat terrain than in hilly or mountaneous areas (Lavsund 1977). In this study, the severity of the damage was lowest in Anttola. This can be explained by relatively hilly landscape, intensive prevention of damage and relatively stable beaver numbers. The most severe damage occurred in Juva where the beaver damage has occurred for more than two years running in all of the damage areas. In this study, the beaver damage areas mainly occurred on relatively fertile forest land such as *Oxalis-Myrtillus* type and *Myrtillus* type. In addition, in the damage areas the dominant tree species were commercially valuable tree species such as Scots pine, Norway spruce and birches, and the proportions of older forest development classes were also considerable. In contrast, the tree species growing in damage areas in Sweden are, in most cases, marginal deciduous trees which have no commercial value (Lavsund 1977). In this study, the ecosystem engineering performed by beavers was of no importance in 28 % of the damage areas. The most important form of damage, in which the trees were dead or dying, occurred in 18 % of the damage areas. In these areas, the economic loss can be relatively high. However, the total economic value (FIM/damage area) could not be calculated because the growing stock volume was not divided into logs or pulpwood of commercially valuable tree species. In addition, dead trees may also have some value as pulpwood or fuelwood.

On the other hand, when the economic aspects were ignored, positive effects could be found. For example, the occurrence of dead trees offering breeding sites for bark beetles (Saarenmaa 1978) can increase the biodiversity. In addition, beavers can have both negative and positive effects on species richness and abundances at the small scale (Jones et al. 1997). Resprout growth arising from the stumps and roots of beaver-cut trees contain more defensive chemicals than normal juvenile growth (Martinsen et al. 1998). However, defoliator beetles were attracted to resprout growth because the beetles were better defended against

their predators than those fed nonresprout growth. The patch disturbance caused by beavers may also benefit some waterfowl species, even though species-dominance relationships may change (Nummi and Pöysä 1997).

Beavers are central-place foragers (McKinley and Whitham 1985, Basey et al. 1988). Beavers feed relatively close to their lodges, mainly on aquatic and herbaceous plant species. During the autumn food caching period, beavers also cut woody plant species. In this study, the greatest distance between the water and the site of the felled trees was 150 m, with an average distance of 47 m. It can be concluded that this type of damage is of little importance because the number of stems cut by beavers was relatively low and the cutting was not directed at the commercially valuable tree species (c.f. Linnamies 1956, Lahti 1966). In special cases, if beavers fell trees near to summer cottages, beaver damage can alter the aesthetic value of area (Lavsund 1977). Debarking of trees by beavers was also negligible. Linnamies (1956) and Lahti and Helminen (1969) reported that beavers can even debark large pines. In this study, I did not observe any debarking of pine or spruce. In USA, at Caddo Lake, most of the beaver damage to trees was restricted to the peeling or stripping of bark, which is believed to have minimal effect on tree survival (King et al. 1998). Beaver feeding selection among woody plants can be explained on the basis of energetic profitability (Doucet and Fryxell 1993, Fryxell and Doucet 1993). Thus, deciduous tree species such as aspen, birches and willows (*Salix* spp.) are favoured in the diet (Linnamies 1956, Lahti 1966) if their availability is high enough in relation to the consumption. This was also evident from the feeding signs observed in this study.

The most important type of damage was flooding caused by damming activity. In this study, flooding damage was separated into extensively flooded areas and excessively wet areas. The damage has occurred over several years and the trees were dead or dying in extensively flooded areas. Spruce is especially sensitive to flooding damage (c.f. Saarenmaa 1978). The trees were also suffering in excessively wet areas, but the duration of damage was shorter. The damage is total in extensively flooded area, but the prevention of damage is still possible in excessively

wet areas. According to this study, there have been attempts to prevent beaver damage in 80 % of the damage areas. The most commonly used prevention method was hunting. In several of the damage areas a combination of hunting and the destruction of problem dams has also been used. The destruction of problem dams is, however, difficult because the beavers almost immediately repair the dam. Thus, destruction should be as complete as possible, if the goal is to achieve a long-lasting effect. More sophisticated methods such as fertility control and chemical repellents need more research (see Nolet and Rosell 1998). Thus, I believe that a combination of hunting and the destruction of problem dams would be the best method for preventing beaver damage. However, the prevention of damage should be started at an earlier stage than the attempts made, for example, in the inspected damage areas in Juva. This means that the activity of beavers should be closely followed. The prevention of damage should be started immediately after the first signs of flooding.

In spite of hunting, the beaver numbers have increased in the study area. This could mean that the damage probability has also increased. However, I suggest that the damage probability has in fact decreased because hunting licenses are directed specifically at those areas where damage occurs (c.f. Härkönen 1999). In addition, the licenses permitting the destruction of problem dams are relatively easily available for areas where economically significant damage is expected to occur. There is also an open season during 15 June – 15 September when a license is not needed for the destruction of dams. However, more information and guidance are needed to ensure that the forest owners have enough knowledge about the possible prevention methods. In addition, attention should be paid to increase public awareness in relation to the occurrence, distribution and management of Canadian beaver populations.

The Canadian beaver harvest has clearly increased in Finland since the 1980's (Ermala 1996). For example, the number of beavers taken by hunting was approximately 1300 individuals in the 1997–98 open season. In South Savo, the respective value was 508 individuals (39 % of the total bag in Finland). This means that the

value of the Canadian beaver as a game animal in SGMD is considerable and is still increasing. At present, the management of beavers in Finland is based on the management plans drawn up by the local game management districts. The aim of the plan in SGMD is to maintain the Canadian beaver population at a sustainable level through hunting. Simultaneously, the occurrence and extent of damage should be kept as low as possible. The results obtained in this study show that the main aim has been achieved. However, the occurrence and extent of damage are relatively significant for private forest owners, if they are practising commercial forestry. In this respect, compensation should be provided by the state for the most damaged areas. In addition, the risk of damage should be taken more effectively into account in the management plans for areas where the beaver numbers are still relatively low but in the increasing phase. More attempts should also been made to improve the methods for preventing beaver damage.

Acknowledgements

I would like to thank Minna Turunen and Lasse Nykänen for their skillfull assistance with the fieldwork. I would also like to thank the private forest owners for their help during the field inspections. I also thank Aslak Ermala and one anonymous reviewer for their valuable comments on the manuscript, and John Derome for revising the English. This work was supported financially by grant from William, Bertta, and Erkki Lyllys Foundation (Finnish Cultural Foundation).

References

- Allredge, J.R. & Ratti, J.T. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 50: 157–165.
- Basey, J.M., Jenkins, S.H. & Busher, P.E. 1988. Optimal central-place foraging by beavers: tree size selection in relation to defencive chemicals of quaking aspen. *Oecologia* 76: 278–282.
- Cajander, A.K. 1909. Über Waldtypen. *Acta Forestalia Fennica* 1. 175 p. (In German).
- Doucet, C.M. & Fryxell, J.M. 1993. The effect of nutritional quality on forage preference by beavers. *Oikos* 67(2): 201–208.
- Ermala, A. 1996. Euroopanmajava (*Castor fiber*), kanadanmajava (*Castor canadensis*). In: Linden, H., Hario, M. & Wikman, M. (eds.). *Riistan jäljille. Riista- ja kalatalouden tutkimuslaitos, Edita, Helsinki*. p. 30–33. (In Finnish with English summary).
- , Helminen, M. & Lahti, S. 1989. Majaviemme levinneisyyden ja runsauden vaihteluista sekä tulevaisuuden näkymistä. Summary: Some aspects of the occurrence, abundance and future of the Finnish beaver population. *Suomen Riista* 35: 108–118.
- , Lahti, S. & Vikberg, P. 1999. Majavakanta edelleen kasvussa – saalismäärä jo lähes 2500 yksilöä. *Metsästäjä* 48(4): 28–31. (In Finnish).
- Fryxell, J.M. & Doucet, C.M. 1993. Diet choice and the functional response of beavers. *Ecology* 74(5): 1297–1306.
- 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. p. 7–14.
- Hartman, G. 1999. Beaver management and utilization in Scandinavia. In: Busher, P.E. & Dzieciolowski, R.M. (eds.). *Beaver protection, management, and utilization in Europe and North America*. Kluwer Academic, Plenum Publishers, New York. p. 1–6.
- Jones, C.G., Lawton, J.H. & Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386.
- 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78(7): 1946–1957.
- King, S.L., Keeland, B.D. & Moore, J.L. 1998. Beaver lodge distributions and damage assessments in a forested wetland ecosystem in the southern United States. *Forest Ecology and Management* 108(1–2): 1–7.
- Laanetu, N. 1995. The status of European beaver (*Castor fiber* L.) population in Estonia and its influence on habitats. In: Ermala, A. & Lahti, S. (eds.). *Proceedings of the 3rd Nordic Beaver Symposium*. Finnish Game and Fisheries Research Institute, Helsinki. p. 34–40.
- Lääperi, A. & Löyttyniemi, K. 1988. Hirvituhot vuosina 1973–1982 perustetuissa männyn viljelytaimi-

- koissa Uudenmaan-Hämeen metsälautakunnan alueella. Summary: Moose (*Alces alces*) damage in pine plantations established during 1973–1982 in the Uusimaa-Häme Forestry Board District. *Folia Forestalia* 719: 13 p.
- Lahti, S. 1966. Majavan ravinnonvalinnasta ja ravinnon käytöstä. Summary: On the food habits of the beaver (*Castor* spp.) in northern Finland. *Suomen Riista* 18: 7–19.
- & Helminen, M. 1969. Suomen majavien istutus-historiasta ja kannan levinneisyys 1960-luvulla. Summary: History of reintroductions and present population status of the beaver in Finland. *Suomen Riista* 21: 67–75.
- & Helminen, M. 1980. Suomen majavien levinneisyyden muutokset vuosina 1965–1975. Summary: The status of European and Canadian beavers in Finland in 1965–75. *Suomen Riista* 27: 70–77.
- Lavsund, S. 1977. Bäverskador i Sverige. Summary: Beaver damages in Sweden. In: Lavsund, S. (ed.). Proceedings from the Nordic Symposium on the Beaver 1975, September 23–26, Ramsele, Sweden. p. 103–105.
- 1987. Moose relationships to forestry in Finland, Norway and Sweden. *Swedish Wildlife Research, Supplement 1*: 229–244.
- Linnamies, O. 1956. Majavien esiintymisestä ja niiden aiheuttamista vahingoista maassamme. *Suomen Riista* 10: 63–86. (In Finnish).
- 1961. Majavakantamme viimeaikaisista muutoksista. Summary: Recent changes in Finnish beaver (*Castor*) population. *Suomen Riista* 14: 159–160.
- Martinsen, G.D., Driebe, E.M. & Whitham, T.G. 1998. Indirect interactions mediated by changing plant chemistry – beaver browsing benefits beetles. *Ecology* 79(1): 192–200.
- McKinley, 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.
- Mickus, A. 1995. The European beaver (*Castor fiber* L.) in Lithuania. In: Ermala, A. & Lahti, S. (eds.). Proceedings of the 3rd Nordic Beaver Symposium. Finnish Game and Fisheries Research Institute, Helsinki. p. 44–45.
- Naiman, R.J., Johnston, C.A. & Kelley, J.C. 1988. Alteration of North American streams by beaver. *BioScience* 38(11): 753–762.
- , Pinay, G., Johnston, C.A. & Pastor, J. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* 75(4): 905–921.
- Neu, C.W., Byers, C.R. & Peek, J.M. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 32(3): 541–545.
- Nolet, B.A. & Rosell F. 1998. Comeback of beaver *Castor fiber* – an overview of old and new conservation problems. *Biological Conservation* 83(2): 165–173.
- Nummi, P. & Pöysä, H. 1997. Population and community level responses in *Anas*-species to patch disturbance caused by an ecosystem engineer, the beaver. *Ecography* 20(6): 580–584.
- Pastor, J. & Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139(4): 690–705.
- Saarenmaa, H. 1978. Kaarnakuoriaisten (Col., Scolytidae) esiintyminen eräässä kanadanmajavan (*Castor canadensis* Kuhl) aiheuttaman tulvan seurauksena kuolleessa metsikössä. Summary: The occurrence of bark beetles (Col., Scolytidae) in a dead spruce stand flooded by beavers (*Castor canadensis* Kuhl). *Silva Fennica* 12(3): 201–216.
- Tomppo, E., Katila, M., Moilanen, J., Mäkelä, H. & Peräsaari, J. 1998. Kunnittaiset metsävaratiedot 1990–94. *Metsätieteen aikakauskirja – Folia Forestalia* 4B/1998: 619–839. (In Finnish).

Total of 33 references