Nest tree characteristics of the old-growth specialist Three-toed Woodpecker *Picoides tridactylus*

Timo Pakkala*, Juha Tiainen, Markus Piha & Jari Kouki

T. Pakkala, University of Helsinki, Lammi Biological Station, FI-16900 Lammi, Finland.
* Corresponding author's e-mail: timo.pakkala@hotmail.fi
J. Tiainen, Natural Resources Research Institute Finland, P. O. Box 2, FI-00791 Helsinki, Finland
M. Piha, Finnish Museum of Natural History – LUOMUS, P. O. Box 17, FI-00014 University of Helsinki, Finland
J. Kouki, University of Eastern Finland, School of Forest Sciences, P. O. Box 111, FI-80101 Joensuu, Finland

The Three-toed Woodpecker *Picoides tridactylus* is a mature and old-growth forest specialist but how the species uses trees for nesting in its breeding sites and whether cavity trees are a critical habitat feature is poorly known. We studied the nest tree characteristics of the species in a 170-km^2 area in southern Finland during 1987–2016. The data included 538 nest trees of eight different species and 665 nest cavities in 86 territory areas. Norway spruce *Picea abies* was the predominant nest tree comprising 71% of all nest trees. Proportionally, deciduous nest trees were more common in moist forests on mineral soils and conifer nest trees more common in spruce swamps. The majority of nest trees (85%) were dead or decaying trees; higher numbers of dead deciduous nest trees were recorded than dead conifer trees. The mean diameter of a nest tree at diameter at breast height (DBH) was 29.4 cm and the mean height of a cavity hole was 5.1 m; size and height were significantly positively correlated. The proportion of deciduous nest trees was significantly higher (45%) in natural forests compared with other areas subjected to variable amounts of forest management, where the respective proportion was only 9–17%. In addition, cavity holes were significantly higher in natural forests than in managed ones. In general, the results highlight the substantial flexibility in nest tree use but also the importance of large dead and decaying trees (including deciduous trees) as nest cavity sites for the species. Spruce swamps can be considered as key nesting habitats in managed forest landscapes.

1. Introduction

The properties of nest trees are important for woodpeckers, especially to enable the excavation of strong and safe cavities. The characteristics of the nest trees selected by woodpeckers are, however, a combination of the woodpecker needs and nest tree properties, and they are restricted by the availability of suitable nest trees in the breeding areas (e.g., Pynnönen 1939, Short 1982, Winkler & Christie 2002, Cockle *et al.* 2011).

In this study, we investigated the nest tree characteristics of the Three-toed Woodpecker (*Picoides tridactylus*) in southern Finland in a landscape

dominated by managed, mature conifer forests. The Three-toed Woodpecker has a wide northern range distribution that largely corresponds with that of spruce (*Picea* spp.) and larch (*Larix* spp.) trees, and it prefers mature and mixed conifer forests (Dementiev & Gladkov 1966, Ruge 1997). Its diet throughout the year predominantly consists of insects, mainly conifer bark beetles (Coleoptera, Scolytidae) or longhorn beetle larvae (Coleoptera, Cerambycidae) (Dementiev & Gladkov 1966, Glutz von Blotzheim & Bauer 1980, Pechacek & Krištín 2004), and, as such, the species favours forests with a high proportion of recently dead or dying trees, including fallen logs (Hess 1983, Pechacek 1995, Bütler *et al.* 2004, Stachura-Skierczyńska *et al.* 2009, Kajtoch *et al.* 2013).

The habitat preferences of the Three-toed Woodpecker have been relatively widely studied in its European distribution area (e.g., Pakkala *et al.* 2002, Pechacek & d'Oleire-Oltmanns 2004, Wesołowski *et al.* 2005, Stachura-Skierczyńska *et al.* 2009). However, published information in regard to the nest tree characteristics of the species has been sporadic, especially concerning boreal forests; the main distribution area of the species (but see Pakkala *et al.* 2018a, 2018b). Thus, in this study, we attempt to fill this gap.

Firstly, we explored and documented the main characteristics of the nest trees and their growth sites using a large data set. Secondly, we broadened the study focus to the forest landscape level by investigating the amount and variation of nest tree characteristics between various types of forest areas supporting territories. In particular, we compared the nest tree properties of the Three-toed Woodpecker between natural and managed forest areas, which provide different breeding situations in dynamic forest environments. The results from our boreal study area were then compared with the current knowledge of nest tree characteristics from other areas of the Three-toed Woodpecker's range in Europe.

2. Material and methods

2.1. Study area

The study area is located within the southern boreal vegetation zone in southern Finland (around 61°15' N; 25°03' E; Fig.1). The study area (170 km^2) is dominated by mature, mostly managed coniferous forests on mineral soils, with a mixture of stands of different ages, some spruce swamps and pine bogs, and many small oligotrophic lakes. Human settlements in the area are scarce. The study area is also characterised by a small-scale topographic variation that has resulted in a mosaic of dry and moist forest habitats. The clear-cut logging of mature, fairly continuous forests increased in the area during the study period and was quite intensive, especially in privately-owned land areas.

2.2. Three-toed Woodpecker nest tree surveys

As part of an intensive population study of the species (described in detail in Pakkala *et al.* 2006, 2017), we searched for Three-toed Woodpecker nests (and nest trees) within the study area annually between 1987–2016. The annual census typically lasted from early April to the middle of July and included systematic mapping of territories within the study area before the breeding season with efforts to locate potential nesting sites by observing the behaviour of the woodpeckers, followed by searching for nests during the breeding season.

Within each territory site, nest searching continued with systematic mapping of all potential sites if the behaviour of the woodpeckers indicated nesting. However, most efforts were allocated to cavity excavation and nestling periods when the detectability of nests was better than during the egg-laying and incubation phases (when visits to nest sites were limited in order to avoid excess disturbance). Annual territory locations and their approximate borders were defined by information from observed locations and the movements of the woodpeckers, and by the presence of the nest sites. The centres of territory sites for the study period were defined by locations of annual territories.

The locations of nest trees were mapped and each nest tree was linked to an individual territory. Old nest trees and cavities were checked in each study year in order to obtain information about their possible reuse. Old nest trees were annually monitored from the first year of Three-toed Woodpecker nesting until the trees were unsuitable for nesting (e.g., tree fallen, broken, logged, nest
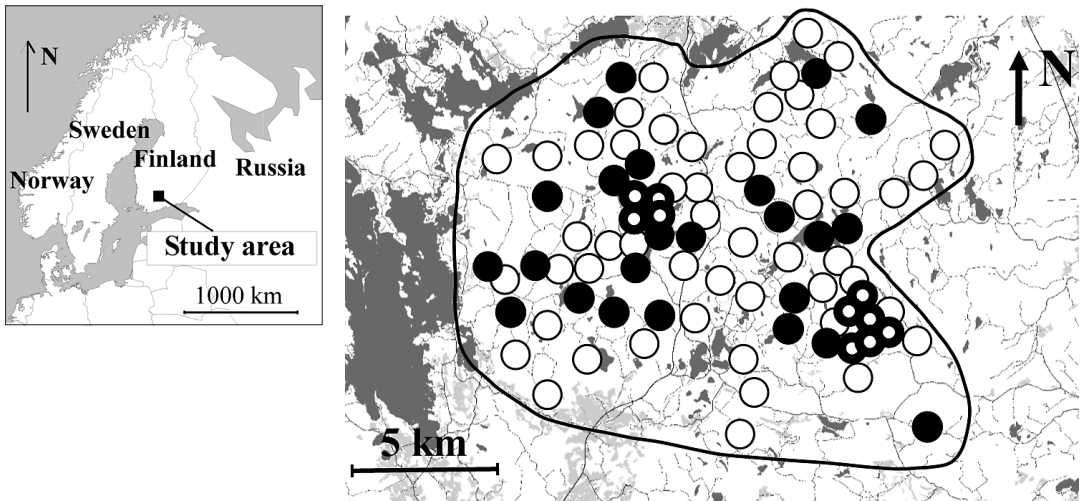
Fig. 1. Location of the study area in southern Finland (61°15' N; 25°03' E; left) and study area (encircled) with the locations of natural (bolded circle), managed core (filled circle) and other managed (normal circle) territory areas of the Three-toed Woodpecker in this study during the study period 1987–2016 (right). Areas of territory sites (*n* = 86) were first divided into two classes based on territory occupancy measures; core (*n* = 34) and other (*n* = 52) areas, and then core areas were divided into natural (*n* = 10) and managed (*n* = 24) core areas based on their forest management history. Lakes are represented by dark grey and agricultural areas by light grey shading. Roads are marked by thin black lines. Note that the map does not show the complete distribution or all territory areas of Three-toed Woodpecker, as only territories with observed active nestings were included in this study.

cavity damaged). All surveys and measurements of the nest trees (see below) were carried out by the first author.

2.3. Nest tree data

2.3.1. Definitions of nest trees

All the trees where nesting of the Three-toed Woodpecker was observed during the study period were classified as nest trees. The final data set only included trees, cavities or nests where the Three-toed Woodpecker had reached at least the egg-laying phase. Nesting attempts interrupted during excavation, even if they included a seemingly complete nest cavity, were not included in these data.

In nine of the trees, an old cavity of the Great Spotted Woodpecker *Dendrocopos major* was used, and in four nest trees, nest-boxes instead of a cavity were used. These cases were not included in the set of "original" nest trees, cavities and nests of the Three-toed Woodpecker. In addition, where old cavities of the Great Spotted Woodpecker

were used in two nest trees, cavities of the Three-toed Woodpecker were also present in the same trees. These two trees were classified as original nest trees of the Three-toed Woodpecker, although the two old cavities used by Three-toed Woodpecker and the nestings in them were not included in the respective numbers of original Three-toed Woodpecker's cavities or nestings.

2.3.2. Nest tree species and the forest type

The tree species of all the detected nest trees was defined. Based on the classifications of Finnish forest and peatland types (Cajander 1949, Laine *et al.* 2012) the main forest type of their growth site was determined in the field. The proportions of forest types in the territory sites were calculated using land cover and forest classification data (Vuorela 1997), digital topographic maps of the area made by the National Land Survey of Finland, aerial photographs and extensive field information from the study area (see Pakkala *et al.* 2014). The forest types were determined within a 500-m radius from the centre of each territory site.

2.3.3. Condition of nest trees

We used three classes to assess the condition of the nest tree. (1) Healthy: generally a vital tree with no signs of decay; small wounds or damages by external factors possible. (2) Decaying: tree alive, but signs of decay clearly visible, e.g., dead branches, defoliation or needle loss detected. (3) Dead: tree not alive. At the tree level, the condition of the first cavity made in the tree was used, and at the cavity level the respective condition of the first year of each cavity was applied to describe the condition of the nest tree.

2.3.4. Size of nest trees and height of cavity holes

The size of a nest tree was measured by defining its diameter at breast height (DBH, 1.3 m above the ground). The girth of the tree was measured with a flexible measuring tape, and the diameter of the tree was then calculated by dividing the girth value by π (a rounded value of 3.1416 was used). Tree size in the year when the first cavity was made was used in the analysis.

The heights of cavity holes below 4.0 m were measured either with a rigid measuring tape, a telescopic pole or a long stick of known length with an accuracy of 0.1 m. Heights between 4.0 m and 6.0 m were estimated by measuring the 4.0 m level and estimating the remaining height, with an accuracy of 0.2–0.5 m. Heights over 6.0 m were estimated by the standard stick method (West 2009) with an accuracy of 0.5 m; usually two to three repeated measures of the same cavity from different directions were undertaken to decrease the error in measurements. All measurements were carried out by the first author.

2.3.5. Classification of forest areas

We divided the study area into various classes to analyse the variation in properties of Three-toed Woodpecker's nest trees and cavities. The division is based on two important ecological factors: (i) occupancy of the Three-toed Woodpecker territories that indicates the structural complexity and quality of the forest landscape (Pakkala *et al*. 2002); and (ii) the intensity of forest management and naturalness of the forest area. We used a two-step classification. In the first step, all territory sites where Three-toed Woodpecker nesting was observed during the whole study period (30 years, $n = 86$ different territory sites) were classified as

being either in core or other areas. The division was based on the occupancy rate of each territory. This rate was calculated as the proportion of years with territorial behaviour or nesting during all census years (see Pakkala et al. 2017).

Two classes based on occupancy rates were separated: (1) territories in core areas; 34 territories with occupancies > 90% (mean 0.98) and (2) territories in other areas; 52 territories with occupancies < 60% (mean 0.33). In the second step, the territory sites located in the core areas were divided into two classes, based on their forest management history: (i) natural and (ii) managed core areas. Natural areas included forests in their natural stage, either without or with only minimal management during the last 150 years (Tuominen 1990; S. Tuominen, pers. comm.). Natural core areas included 10 territory sites in total. All other core areas ($n = 24$) were classified as managed core areas, with a variable intensity of forestry activities during the last decades. We use the respective terms "natural core", "managed core", and "managed other" areas for the three classes of forest areas (Fig. 1).

2.4. Statistical methods

Forest type and condition of the nest tree between groups were compared by goodness-of-fit tests. The distributions of DBH and the height of the cavity holes were leptokurtic with positive skewness (the ratios of the standard error (SE) of the kurtosis and the kurtosis, and the respective ratios of the skewness were > 2) in most of the tree species. Therefore, median-based Kruskal-Wallis tests were used in comparisons of DBH and height of the cavity holes between groups. In multiple comparisons between pairs or subgroups after a significant result, either a Bonferroni-corrected level $p < 0.05$ in comparisons of proportions (goodness-of-fit tests) or a Dunn's test with Bonferroni correction (Kruskal-Wallis tests) was used. All statistical analyses were performed with IBM SPSS Statistics 23.

3. Results

3.1. Nest tree species and their forest types

A total of 538 nest trees of eight different species, three coniferous and five deciduous trees, were

Table 1. The nest tree species of the Three-toed Woodpecker and the percentages and numbers (in parentheses) of trees, cavities, and nesting attempts (nestings) in all nest trees (all) and original Three-toed Woodpecker's nest trees (ttw). The respective combined numbers are presented separately for coniferous and deciduous tree species.

Tree species	Trees, all	Trees, ttw	Cavities all	Cavities, ttw	Nestings, all	Nestings, ttw
Norway spruce (*Picea abies*)	70.1 (377)	71.8 (377)	71.7 (477)	73.4 (477)	73.3 (635)	74.7 (635)
Scots pine (*Pinus sylvestris*)	8.4 (45)	7.6 (40)	8.9 (59)	8.0 (52)	8.8 (76)	8.1 (69)
Siberian larch (*Larix sibirica*)	0.2 (1)	0.2 (1)	0.2 (1)	0.2 (1)	0.1 (1)	0.1 (1)
Aspen (*Populus tremula*)	15.8 (85)	16.0 (84)	14.6 (97)	14.8 (96)	14.0 (121)	14.1 (120)
Silver birch (*Betula pendula*)	3.0 (16)	2.7 (14)	2.4 (16)	2.2 (14)	1.8 (16)	1.6 (14)
Grey alder (*Alnus incana*)	1.5 (8)	1.5 (8)	1.2 (8)	1.2 (8)	0.9 (8)	0.9 (8)
Black alder (*Alnus glutinosa*)	0.2 (1)	0.2 (1)	0.3 (2)	0.3 (2)	0.3 (3)	0.4 (3)
Rowan (*Sorbus aucuparia*)	0.2 (1)	–	0.2 (1)	–	0.1 (1)	–
Nest box (*Nidus ligneus*)	0.7 (4)	–	0.6 (4)	–	0.6 (5)	–
In coniferous trees	78.6 (423)	79.6 (418)	80.8 (537)	81.5 (530)	82.2 (712)	82.9 (705)
In deciduous trees	20.6 (111)	20.4 (107)	18.6 (124)	18.5 (120)	17.2 (149)	17.1 (145)
Total	100.0 (538)	100.0 (525)	100.0 (665)	100.0 (650)	100.0 (866)	100.0 (850)

found in the study (Table 1), of which 525 of seven species were original nest trees of the Three-toed Woodpecker. Norway spruce *Picea abies* was predominant (70.1–74.7%) in the tree, cavity, and nesting attempt numbers. Aspen *Populus tremula* (14.0–16.0%) and Scots pine *Pinus sylvestris* (7.6–8.4%) were relatively abundant as nest trees, but the proportions were less than 3.0% for all other tree species (Table 1). The respective proportions of all conifer tree species were between 78.6–82.9%, and those of deciduous trees between 17.1–20.6%; five nesting attempts were observed in four nest-boxes.

Four main types of forests were associated with the sites of nest trees. Forests on mineral soil included (i) moist spruce-dominated forests (*Myrtillus* and *Oxalis-Myrtillus* types) and (ii) dry pine-dominated forests (*Vaccinium* and *Calluna* types). Forest peatlands included (iii) spruce swamps and (iv) pine bogs in which the smaller group type of pine dominated swamps was included.

The highest proportion (58.7%) of the original nest trees was found in moist forests on mineral soil (Table 2), which was also the most common (66.0%) forest type among the territory sites. Spruce swamps were favoured in relation to their area (14.2%); 46.4% of Norway spruce and 35.6% of all nest trees were located in spruce swamps. When the proportions of the four forest types were compared with their expected proportions, the difference was highly significant (goodness-of-fit test: $\chi^2 = 228.8$, $p < 0.001$, $df = 3$).

Individual tree species had specific forest type profiles, and the sites of coniferous and deciduous nest trees also significantly differed from each other (goodness-of-fit test: $\chi^2 = 57.05$, $p < 0.001$, $df = 3$). The difference was mainly due to proportionally higher amounts of deciduous nest trees in moist forest areas and smaller amounts in spruce swamps, and the opposite trend for coniferous tree species (Bonferroni-corrected $p < 0.05$ for both pairwise differences, Table 2).

Within the main forest types, 16 nest trees were situated in swamp and bog areas flooded by the Canadian beaver *Castor canadensis*, six nest trees were located in new prescribed burning areas of moist forests, and three nest trees were observed as single trees in clear-cut areas of moist forest, although less than 60 meters from the edge of the nearest mature forest.

3.2. Condition of the nest trees

The Three-toed Woodpeckers mostly selected dead (54.1%) or decaying (32.3%) trees for their nests (Table 3). The proportion of dead trees varied from 48.5% in Norway spruce to 100% in silver birch *Betula pendula*. Healthy trees ranged be-

Table 2. The percentage and number (in parentheses) of Three-toed Woodpecker nest trees in different forest types. Moist forests represented MT (*Myrtillus* type) and OMT (*Oxalis-Myrtillus* type), and dry forests VT (*Vaccinium* type) and CT (*Calluna* type) types of forests on mineral soil; spruce swamps and pine bogs represent forest mire types. The proportions of forest types (last row) represent their area in the territory sites. Only original Three-toed Woodpecker's nest trees are included.

Nest tree species	Forest type			
	Moist forest	Dry forest	Spruce swamp	Pine bog
Norway spruce (*Picea abies*)	51.7 (195)	0.5 (2)	46.4 (175)	1.3 (5)
Scots pine (*Pinus sylvestris*)	37.5 (15)	12.5 (5)	10.0 (4)	40.0 (16)
Siberian larch (*Larix sibirica*)	100 (1)	–	–	–
Aspen (*Populus tremula*)	97.6 (82)	–	2.4 (2)	–
Silver birch (*Betula pendula*)	57.1 (8)	–	28.6 (4)	14.3 (2)
Grey alder (*Alnus incana*)	87.5 (7)	–	12.5 (1)	–
Black alder (*Alnus glutinosa*)	–	–	100 (1)	–
All coniferous trees (*n* = 418)	50.5 (211)	1.7 (7)	42.8 (179)	5.0 (21)
All deciduous trees (*n* = 107)	90.7 (97)	–	7.5 (8)	1.9 (2)
Total (*n* = 525)	58.7 (308)	1.3 (7)	35.6 (187)	4.4 (23)
Total percentage of forest type in territory sites	66.0	11.8	14.2	8.0

tween 0–27.5% across the different species, and were only represented by the three most common nest tree species; Norway spruce (14.6%), aspen (7.1%) and Scots pine (27.5%) (Table 3). The coniferous and deciduous nest trees differed significantly in their condition (goodness-of-fit test: $\chi^2 = 14.1, p = 0.001, df = 2$, Fig. 2). In pairwise comparisons with the Bonferroni-corrected $p = 0.05$, the proportion of healthy trees was higher in conifers than deciduous trees. The opposite was the case with dead trees, whereas proportions in decaying trees did not differ from the expected.

The condition distributions of the four most common nest trees; Norway spruce, aspen, Scots pine and silver birch, differed significantly from each other ($\chi^2 = 34.6, p < 0.001, df = 6$). Based on the Bonferroni-corrected level $p = 0.05$, the most important differences were the high proportions of healthy Scots pine and dead silver birch trees, and the more stable condition distribution of Norway spruce compared with the expected proportions (Table 3). The condition of the nest tree did not depend on the forest type ($\chi^2 = 9.84, p = 0.13, df = 6$).

3.3. Size of the nest trees

The mean size of the nest tree (at DBH) was 29.4 cm (median value 28.5 cm, range 18.5–54.0 cm). The mean DBH of individual nest tree species var-
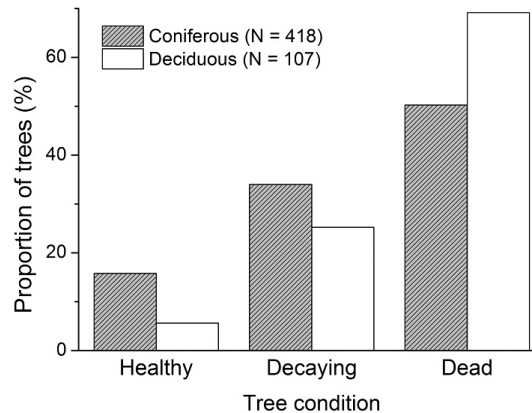

Fig. 2. Condition of the Three-toed Woodpecker's nest trees. Proportions in the three condition classes are presented for both coniferous and deciduous trees.

ied from 23.9 cm in grey alder *Alnus incana* to 30.5 cm in Siberian larch *Larix sibirica*.

The DBH of coniferous nest trees (median 28.75 cm) was significantly larger than that of deciduous trees (median 26.0 cm, Mann-Whitney U-test: $U = 14158.5, p < 0.001, n_1 = 418, n_2 = 107$). In a comparison of DBH of the five most abundant nest trees (Fig. 3), there was a significant difference in the nest tree size (Kruskal-Wallis test: $H = 44.05, p < 0.001, df = 4$). Two significant differences were detected in pairwise comparisons

Table 3. Percentage and number of nest tree species (in parentheses) of the Three-toed Woodpecker according to tree condition. The condition describes the situation when the first cavity is made in the tree. Only original Three-toed Woodpecker's nest trees are included.

Nest tree species	Tree condition		
	Alive, healthy	Alive, decaying	Dead
Norway spruce (*Picea abies*)	14.6 (55)	36.9 (139)	48.5 (183)
Scots pine (*Pinus sylvestris*)	27.5 (11)	7.5 (3)	65.0 (26)
Siberian larch (*Larix sibirica*)	–	–	100 (1)
Aspen (*Populus tremula*)	7.1 (6)	29.8 (25)	63.1 (53)
Silver birch (*Betula pendula*)	–	–	100 (14)
Grey alder (*Alnus incana*)	–	25.0 (2)	75.0 (6)
Black alder (*Alnus glutinosa*)	–	–	100 (1)
Total (*n* = 525)	13.7 (*n* =72)	32.3 (*n* = 169)	54.1 (*n* = 284)

Table 4. The numbers (N), mean, standard deviation (SD), median, minimum and maximum heights (m above the ground) of the Three-toed Woodpecker cavity holes in various nest tree species. The respective numbers are also presented for all coniferous and deciduous trees. Only original Three-toed Woodpecker's nest cavities are included.

Tree species	N	Mean	SD	Median	Minimum	Maximum
Norway spruce (*Picea abies*)	477	5.2	3.71	4.5	0.6	21.0
Scots pine (*Pinus sylvestris*)	52	5.9	3.85	4.8	1.0	14.0
Siberian larch (*Larix sibirica*)	1	2.7	–	2.7	2.7	2.7
Aspen (*Populus tremula*)	96	4.2	2.18	4.0	0.9	11.0
Silver birch (*Betula pendula*)	14	4.5	5.59	3.1	2.4	14.0
Grey alder (*Alnus incana*)	8	2.3	0.59	2.3	1.2	3.2
Black alder (*Alnus glutinosa*)	2	5.0	1.41	5.0	4.0	6.0
Coniferous trees	530	5.3	3.72	4.5	0.6	21.0
Deciduous trees	120	4.1	2.31	3.5	0.9	14.0
Total	650	5.1	3.53	4.0	0.6	21.0

(Dunn's test with Bonferroni correction): Norway spruce vs. grey alder: $t = 3.49$, $p = 0.005$; Norway spruce vs. aspen: $t = 5.81$, $p < 0.001$; Norway spruce was larger in both cases. No other pairwise differences were significant.

The DBH did not differ between the various forest types (Kruskal-Wallis test: $H = 3.23$, $p = 0.36$, $df = 3$), but there was a significant difference in DBH in tree condition types ($H = 52.3$, $p < 0.001$, $df = 2$). Dead nest trees (median DBH 27.0 cm) were significantly smaller than decaying (30.0 cm) or healthy trees (30.0 cm; Dunn's test with Bonferroni correction: healthy vs. dead: $t = 5.67$, $p < 0.001$; decaying vs. dead: $t = 5.87$, $p < 0.001$; healthy vs. decaying: $t = 1.26$, $p = 0.21$).

3.4. Heights of cavity holes

The mean and median heights of all cavity holes ($n = 650$) above the ground were 5.1 m and 4.0 m, respectively (range 0.6–21 m) (Table 4). There was a rather large variation in the mean heights between tree species; 2.3 m in grey alder to 5.9 m in Scots pine (Table 4). Cavity holes appeared to be higher in coniferous (median 4.5 m) than in deciduous trees (3.5 m), but the difference was not significant (Mann-Whitney U-test: $U = 28513$, $p = 0.08$). There were no significant differences in the median heights of the cavity holes in the five most common nest tree species (Kruskal-Wallis test: $H = 8.89$, $p = 0.064$, $df = 4$, Table 4).
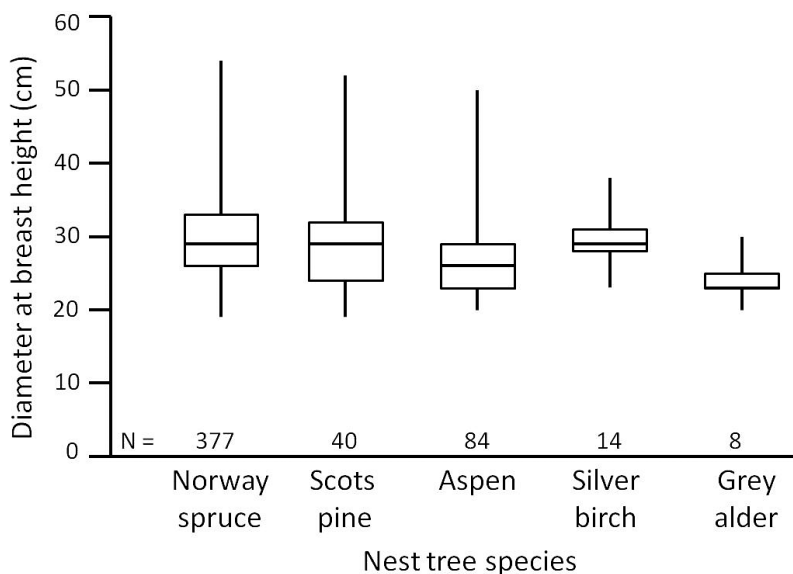
Fig. 3. Size (diameter at breast height, DBH; cm) of the five most common nest tree species. Median values with 25 and 75% percentiles presented in boxes and the range (min, max) in whiskers.

The median height of the cavity holes did not differ significantly among the forest types (goodness-of-fit test: $\chi^2 = 5.74$, $p = 0.13$, $df = 3$). However, there were significant differences in the height of cavity holes between the various tree condition types (Kruskal-Wallis test: $H = 100.1$, $p < 0.001$, $df = 2$; Fig. 4). The median height in healthy trees was 7.0 m, in decaying trees 5.0 m, and significantly smaller in dead trees (2.5 m) (Dunn's test with Bonferroni correction: healthy vs. dead: $t = 7.80$, $p < 0.001$; decaying vs. dead: $t = 8.24$, $p < 0.001$; healthy vs. decaying: $t = 1.99$, $p = 0.14$).

There was a significant positive correlation between DBH and the height of cavity holes in all nest trees (Spearman's correlation: $r_s = 0.59$, $p < 0.001$, $df = 648$); this pattern was similar in the three most common tree species (Norway spruce: $r_s = 0.58$, $p < 0.001$, $df = 475$; aspen: $r_s = 0.41$, $p < 0.001$, $df = 94$; Scots pine: $r_s = 0.86$, $p < 0.001$, $df = 50$).

We did not measure or estimate the nest tree sizes at the height of the cavity holes. However, as DBH is measured at a height of 1.3 m above the ground, the selection of nest trees with cavities at heights of 0.8–1.8 m ($n = 98$) provides a rough estimate for the nest tree size at the height of the cavity. The respective mean diameter was 26.2 cm, median 25.5 cm, and the range was from 19.0 to 52.0 cm. There was no significant difference in the size between the tree species (Kruskal-Wallis test:
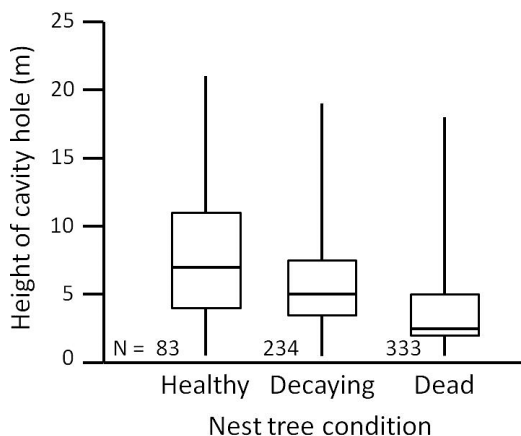

Fig. 4. Height of cavity hole (m) in the nest trees with variable condition. Median values with 25 and 75% percentiles presented in boxes and the range (min, max) in whiskers.

$H = 5.14$, $p = 0.16$, $df = 3$); of which 87% were Norway spruce.

3.5. Nest tree characteristics in forest areas

There was quite a large variation in the properties of nest trees between the various forest area classes. The proportions of coniferous and deciduous nest tree species differed significantly between the classes (goodness-of-fit test: $\chi^2 = 58.2$, $p < 0.001$, $df = 2$). The proportion of deciduous

Table 5. Properties of Three-toed Woodpecker's nest trees and cavity holes in various forest areas.

	Natural areas	Managed core ares	Other managed areas	All
Number of territories	10	24	52	86
Number of nest trees	110	237	178	525
Number of cavities	144	317	189	650
Percentage of deciduous nest trees	45.5	17.3	9.0	20.4
Percentage of nest trees in spruce swamps	33.6	30.4	43.8	35.6
Percentage of dead nest trees	51.8	54.9	54.5	54.1
Median DBH of nest tree, cm	28.0	28.5	28.5	28.5
Median height of cavity hole, m	5.5	4.0	3.5	4.0

nest trees was 45.5% in natural, 17.3% in the managed core areas, and only 9.0% in other managed areas (Table 5). Based on the Bonferroni-corrected level $p = 0.05$, there were significant deviations from the overall proportions of coniferous (79.6%) and deciduous (20.4%) nest trees in the natural and other managed class areas, but not in the managed core areas. Moreover, the proportions of the five most common nest tree species differed significantly between the area classes ($\chi^2 = 74.5, p < 0.001, df = 8$). This pattern was caused by significant (Bonferroni-corrected level $p = 0.05$) differences in the proportions of aspen and Norway spruce in the areas (natural: aspen 40.9%, Norway spruce 50.9%; managed core: aspen 13.6%, Norway spruce 73.3%; other areas: aspen: 4.0%, Norway spruce 83.6%). No significant differences were connected to the other three species; Scots pine, silver birch, and grey alder.

The proportions of the forest types differed significantly within each area class (goodness-of-fit test; natural: $\chi^2 = 36.1$, managed core: $\chi^2 = 62.3$, other areas: $\chi^2 = 138.8, p < 0.001, df = 3$ in all cases). In all three areas, the proportion of spruce swamp forest growth sites was larger and the proportions of other types were smaller than expected. The proportion of spruce swamps was quite constant (14.0–14.9%) in territory sites of different area classes, but the proportion of spruce swamp forest growth sites was significantly (Bonferroni-corrected level $p = 0.05$) larger in other managed areas (43.8%) compared with natural (33.6%) and managed core areas (30.4%) that did not differ from each other ($\chi^2 = 8.25, p = 0.016, df = 3$, Table 5). The condition of the nest trees did not differ between the areas ($\chi^2 = 3.54, p = 0.47, df = 4$), as shown in the rather constant proportions of dead

nest trees in the areas; 51.8–54.9% (Table 5).

The DBH of nest trees did not differ between the area classes (Kruskal-Wallis test: $H = 2.73, p = 0.25, df = 2$, Table 5), but there was a significant difference in the height of cavity holes (Kruskal-Wallis test: $H = 18.5, p < 0.001, df = 2$). The cavity holes were higher in the natural class (median 5.5 m) than in the managed core (4.0 m) or other managed areas (3.5 m; pairwise comparisons, Dunn's test with Bonferroni correction: natural vs. managed: $t = 3.65, p = 0.001$; natural vs. other: $t = 4.06, p < 0.001$; managed vs. other: $t = 0.89, p = 1.0$, Table 5).

4. Discussion

The Three-toed Woodpecker is a species of the taiga forest, which, in addition to the dominance of coniferous trees, is characterised by a spatial mosaic of dry, moist and wet habitats that also include various forest peatlands (Syrjänen *et al.* 1994, Shorohova *et al.* 2009). In our study area, this pattern of coniferous-dominated forest on mineral land and spruce swamps was detected at the sites with nest trees. The nest trees, especially Norway spruce, were located in spruce swamps significantly more often than expected on the basis of their total area thereby indicating their importance as nest sites for the Three-toed Woodpecker. The proportion of nest trees in spruce swamps was highest in the territories of other managed areas with low occupancy rates. Mature spruce swamps that typically include large trees and dead trees can be considered as key nesting habitats in areas with intensive forest management. Although boreal spruce swamps have been intensively drained to

increase their timber production (e.g., Hökkä *et al.* 2002, Kaakinen *et al.* 2012,), some areas are left unmanaged as harvesting may be uneconomical or difficult (Päivänen & Hånell 2012, Vanhatalo *et al.* 2015). If intensive forestry operations threaten spruce swamps, the Three-toed Woodpecker may find it difficult to establish even short-term territories in managed forest landscapes.

We observed a significant difference in the proportion of deciduous nest trees in natural and managed areas; deciduous tree use was several times more common in natural areas compared with managed areas. The result indicates the differences in forest structure between areas with long natural succession and forest management areas, but it also highlights the nest tree selection patterns of the Three-toed Woodpecker: if suitable deciduous trees are available, they are used almost as often as coniferous trees even in forest areas dominated by conifers.

We consider that one of the key factors in nest tree selection of the Three-toed Woodpecker, as also observed in several other woodpecker species, is a suitable tree structure with a soft interior and hard outer layer (e.g., Short 1979, Stenberg 1996, Blanc & Martin 2012). This structure permits efficient cavity excavation and provides protection for the cavity. Various saproxylic fungi have a major role in modifying the tree substrate for woodpeckers (e.g., Jackson & Jackson 2004, Zahner *et al.* 2012).

4.1. The nest tree species

We detected quite a large number of nest tree species (total eight), and the species was also observed to use nest-boxes for breeding. In contrast, 1–4 nest tree species were typically found in other Three-toed woodpecker studies (von Haartman *et al.* 1963–72, Haftorn 1971, Ruge 1974, Wesołowski & Tomiałojć 1986, Hågvar *et al.* 1990, Stenberg 1996, Saari *et al.* 1998, Pechacek 2001, Wesołowski 2011). The large data set in this study (538 nest trees) was an order of magnitude larger than the above-mentioned studies (13–48 nest trees each); the large sample size alone has an effect on the high numbers of nest tree species noted in our study. In fact, we detected only four abundant nest tree species: Norway spruce, aspen,

Scots pine, and silver birch, whilst the other tree species were only occasionally used.

As discussed above, the species composition of nest trees varies geographically and is dependent on local conditions. In our study area in southern Finland, Norway spruce was the dominant nest tree (70.1%), although in northern Finland, Scots pine constituted 60.4% of observed nest trees ($n = 48$), and the proportion of Norway spruce was only 31.2% (Saari *et al.* 1998). Similar variation in preferences for nest trees was detected in Norwegian studies: in Haftorn's (1971) data ($n = 37$) the most common nest trees were Scots pine and aspen, both with 29.7% of nest trees. Hågvar *et al.* (1990) reported that Norway spruce was the most common nest tree in southern Norway (69.2%, $n = 13$), whereas Stenberg (1996) found that all Three-toed Woodpeckers nested in aspen in western Norway ($n = 15$).

Differences in locations and altitudes, and small sample sizes may have effects on the results; Haftorns's (1971) data were based in more northern and higher regions than the other two Norwegian studies (Hågvar *et al.* 1990, Stenberg 1996). In the Białowieża forest area in Poland, the most common nest trees were Norway spruce (62%), and Scots pine (27%) ($n = 38$, Wesołowski 2011). Ruge (1974) gathered nest tree information from Switzerland: in mostly mountainous areas all nests were in coniferous trees, of which Norway spruce was the most common (71.4%) ($n = 35$). In southern Germany, Pechacek (2001) reported Norway spruce as the dominant nest tree species with 92.3% in 13 territories.

4.2. The selection of nest trees

The Three-toed Woodpecker, like many other woodpecker species, is known to excavate several unfinished cavities each spring before the actual nesting cavity is made ready (Blume 1968, Ruge 1974, Cramp 1985, Pechacek & d'Oleire-Oltmanns 2004, Zahner *et al.* 2012, Pakkala *et al.* 2017). Furthermore, old unfinished cavities can be completed for nesting even several years after they were started (Blume 1968, Ivanchev 1997, Rolstad *et al.* 2000, Meyer & Meyer 2001, Matsuoka 2010). The suitability of a nest tree, especially its hardness, is also commonly tested by excavating

several small "trial" holes in different parts of the tree (Blume 1968, Matsuoka 2008, 2010, Lorenz *et al.* 2015). By this "monitoring" of the potential nest trees within their territories, the Three-toed Woodpecker, as with other woodpecker species, can select suitable tree individuals and locations for their nest site.

The preference of the Three-toed and other woodpecker species for dead or decaying trees for nesting is usually explained by the optimal hardness of the tree: the cavity excavation is not too difficult because of the soft interior, but the outer layer of the tree is rigid and provides sufficient protection (e.g., Short 1979, Jackson & Jackson 2004, Losin *et al.* 2006, Blanc & Martin 2012). Saproxylic fungi and micro-organisms can modify the structure of trees suitable for woodpecker cavities (Kilham 1971, Conner *et al.* 1976, Hart & Hart 2001, Jackson & Jackson 2004, Zahner *et al.* 2012), and the various butt and heart rots that are common in Norway spruce (e.g., Hallaksela 1984, Mattila & Nuutinen 2007) are especially advantageous for the Three-toed Woodpecker.

Heart rot caused by several species of fungi, advances upwards from the basal area in the core of the tree, and can commonly reach heights of 6–10 m or more (e.g., Arhipova *et al.* 2011). The bark and outermost core layers usually remain intact thereby providing hard walls for the cavity. Heart rot is not always visible and it is probable that a proportion of the nest trees classified as healthy in our study were infected. Similar types of fungal modification are common in deciduous nest tree species of the Three-toed Woodpecker (Manion 1991, Kärki 1999, Mattila & Nuutinen 2007).

We detected that 86.3% of nests were in dead or decaying trees, and the proportion was higher in deciduous trees (94.4%) than in conifers (84.2%). Our results are consistent with earlier nest tree information (Glutz von Blotzheim & Bauer 1980, Cramp 1985). The patterns observed in other studies were similar to our study or, in some cases, more pronounced: in northern Finland 93.2% of nests in conifer trees ($n = 44$, Saari *et al.* 1998), and all nests both in southern ($n = 13$, Hågvar *et al.* 1990) and in western Norway ($n = 15$, Stenberg 1996) were in dead or decaying trees; in Poland the proportion was 97.3% ($n = 38$, Wesołowski 2011); while in southern Germany, Pechacek (2001) detected that only 46.2% of nest cavities in 13 territo-

ries were in dead trees, although he also recorded the frequency of heart rot in living nest trees.

We observed a mean DBH of 29.4 cm for nest trees; coniferous trees were larger than deciduous, and healthy or decaying trees were larger than dead ones. In Norway, Hågvar *et al.* (1990) found a mean DBH of 31.3 cm (at 0.5 m height, $n = 11$) for nest trees that were mostly dead or decaying Norway spruce (87%), and Stenberg (1996) reported a DBH of 28.7 cm in nest trees that were either dead or decaying aspens ($n = 15$, see above). These measures are very near to the mean DBH values reported for Norway spruce in our study (31.0 cm), although the aspen trees in our study were smaller (27.0 cm) than in Norway. In southern Germany, the nest trees were larger than in our study area; mean DBH was 36.8 cm in 13 territories (Pechacek 2001).

4.3. Implications of the cavity height

The Three-toed Woodpecker's nesting cavities are commonly found to be lower than those of its relatives (Cramp 1985, Wesołowski & Tomiałojć 1986, Hågvar *et al.* 1990, Stenberg 1996). The mean height of the cavity hole was 5.1 m in our study, and there was a strong clustering in the heights of 2–7 m, although the range was large (0.6–21 m). The cavities were also lower in dead and decaying trees than in healthy ones. Although cavity height was positively correlated with the size of the nest tree, we think that the condition of the tree, i.e., suitable structure, is the main reason for the low cavity heights of the Three-toed Woodpecker in northern Europe. The observed height distribution patterns match well with the respective patterns of heart rot in Norway spruce. One reason for the presence of cavities at lower heights may be explained by the use of snags with broken tops. The cavities were somewhat lower in deciduous trees compared with conifers, which may indicate reduced availability of suitably high deciduous trees, especially aspen in the managed parts of our study area.

In northern Finland, the mean cavity height was 5.6 m (range 1–11 m) ($n = 48$, Saari *et al.* 1998). In Norwegian studies the mean cavity height was 4.0 m (range 1–9 m) ($n = 32$, Haftorn 1971), 2.0 m ($n = 11$, Hågvar *et al.* 1990), and 4.2

m ($n = 15$, Stenberg 1996), while in the Białowieża forest in Poland, the mean cavity height was much higher; 10.5 m ($n = 17$), but was still the lowest of the five studied woodpecker species (Wesołowski & Tomiałojć 1986). In Switzerland, the mean cavity height was 5.5 m (range 1–15 m) ($n = 33$, Ruge 1974), and in southern Germany 3.7 m (range 1.3–10.5 m) (Pechacek 2001).

Our estimates of the size (diameter) of the nest tree at cavity height were 26.2 cm (mean) and 25.5 cm (median; $n = 98$). These were somewhat smaller than in Hågvar *et al.* (1990; mean 28.1 cm, $n = 10$) but larger than Stenberg (1996) (mean 22.9, median 22 cm, $n = 15$), which were the only other studies (to the best of our knowledge) where this characteristic was measured. The difference in size compared with the latter study may be caused by the nest tree species; our estimates and the values reported by Hågvar *et al.* (1990) were based mostly on the size of Norway spruce, whereas the nest trees in Stenberg (1996) were all aspens that were even smaller than the aspens in our study (see above).

4.4 Nest trees in dynamic forest environments

Over its large range, the Three-toed Woodpecker is adjusted to disturbance dynamics that create suitable spatially and temporally variable breeding areas modified by wind, fire, snow damage and flooding (e.g., Shorohova *et al.* 2009, Kuuluvainen & Aakala 2011). During most of the year, the Three-toed Woodpeckers feed predominantly on conifer bark beetles that are found in dead and dying spruce trees (Hogstad 1970, Fayt 1999, Pechacek & Kristin 2004).

Thus, if enough suitable spruce trees exist for feeding and for territory establishment, a nest tree can also probably be found in and around feeding areas. However, our results suggest that leaving deciduous, and dead and dying trees in forests is important for the Three-toed Woodpecker. As the quality of trees for breeding varies considerably within a forest stand, good nest trees are critical for the Three-toed Woodpecker as indicated by the high proportion of nesting attempts in the same trees over long periods in long-term territories in our study area (Pakkala *et al.* 2017).

Pohjantikan pesimäympäristö ja pesäpuiden valinta

Pohjantikka on vanhojen havupuuvaltaisten metsien laji, jonka pesäpaikan ja pesäpuun valintaa on tutkittu vähän erityisesti pohjoisella havumetsävyöhykkeellä. Pohjantikan on havaittu vaativan ravintonsa turvaamiseksi reviirillään suhteellisen paljon kuollutta tai huonokuntoista puuta, mutta sopivien kolopuiden merkitystä elinympäristössä ei juuri tunneta.

Tutkimme vuosina 1987–2016 pohjantikan pesäpuiden ominaisuuksia 170 km²:n suuruisella alueella Evolla Etelä-Suomessa. Aineisto käsittää 538 pesäpuuta (kahdeksan eri puulajia) ja 665 pesäkoloa 86 reviirillä. Tärkein pesäpuulaji oli kuusi (71 % kaikista pesäpuista). Lehtipuut olivat tuoreilla kankailla pesäpuina yleisempiä kuin korvissa, missä taas havupuut olivat yleisempiä kuin kankailla. Suurin osa pesistä (85 %) oli kuolleissa tai lahovikaisissa puissa; kuolleiden osuus oli suurempi lehti- kuin havupuilla.

Pesäpuiden keskimääräinen läpimitta 1.3 metrin korkeudella oli 29.4 cm ja pesäkolojen keskikorkeus 5.1 m. Puun läpimitta ja pesän korkeus korreloivat positiivisesti. Lehtipuiden osuus pesäpuista oli luonnontilaisissa metsissä suurempi (45 %) kuin eriasteisesti hoidetuissa talousmetsissä (9–17 %). Pesäkolot olivat myös merkittävästi korkeammalla luonnonmetsissä kuin talousmetsissä. Kaiken kaikkiaan tulokset osoittavat melkoista joustavuutta pesäpuun valinnassa, mutta myös suurten kuolleiden ja lahovikaisten puiden, niin havu- kuin lehtipuidenkin, merkitystä pohjantikan pesäpaikkoina. Etenkin talousmetsämaisemissa kuusivaltaiset korvet ovat tärkeitä pesimisympäristöjä.

References

Arhipova, N., Gaitnieks, T., Donis, J., Stenlid, J. & Vasaitis, R. 2011: Butt rot incidence, causal fungi, and related loss in *Picea abies* stands of Latvia. — Can. J. For. Res. 41: 2337–2345.

Blanc, L. A. & Martin, K. 2012: Identifying suitable woodpecker nest trees using decay selection profiles in trembling aspen *(Populus tremuloides)*. — For. Ecol. Manage. 286: 192–202.

Blume, D. 1968: Die Buntspechte (Gattung *Dendrocopos*). — A. Ziemsen Verlag, Wittenberg, Lutherstadt (In German with English summary)

Bütler, R., Angelstam, P., Ekelund, P. & Schlaepfer, R. 2004: Dead wood threshold values for the Three-toed Woodpecker presence in boreal and sub-Alpine forest. — Biol. Cons. 119: 305–318.

Cajander, A. K. 1949: Forest types and their significance. — Acta For. Fenn. 56: 1–71.

Cockle, K. L., Martin, K. & Wesołowski, T. 2011: Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. — Front. Ecol. Environ. 9: 377–382.

Conner, R. N., Miller, O. K. & Adkisson, C. S. 1976: Woodpecker dependence on trees infected by fungal heart rots. — Wilson Bull. 88: 575–581.

Cramp, S. (ed.). 1985: Handbook of the birds of Europe, the Middle East and North Africa. Vol. 4. — Oxford Univ. Press, Oxford.

Dementiev, G. P. & Gladkov, N. A. (eds.) 1966: Birds of the Soviet Union Vol. 1. — Israel Progr. for Scientific Translations, Jerusalem.

Fayt, P. 1999: Available insect prey in bark patches selected by the Three-toed Woodpecker *Picoides tridactylus* prior to reproduction. — Ornis Fennica 76: 135–140.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1980: Handbuch der Vögel Mitteleuropas. Vol 9. — Akademische Verlagsgesellschaft, Frankfurt a.M. (In German)

von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin. — Otava, Keuruu. (In Finnish)

Haftorn, S. 1971: Norges fugler. — Universitetsforlaget, Oslo. (In Norwegian)

Hågvar, S, Hågvar, G. & Mønness, E. 1990: Nest site selection in Norwegian woodpeckers. — Holarctic Ecol. 13: 156–165.

Hallaksela, A.-M. 1984: Causal agents of butt-rot in Norway spruce in southern Finland. — Silva Fennica 18: 237–243.

Hart, J. H. & Hart, D. L. 2001: Heartrot fungi's role in creating Picid nesting sites in living aspen. — USDA Forest Service Proceedings RMRS-P 18: 207–213.

Hess, R. 1983: Verbreitung, Siedlungsdichte und Habitat des Dreizehenspechtes *Picoides tridactylus* im Kanton Schwyz. — Orn. Beob. 80: 153–182. (In German with English summary)

Hogstad, O. 1970: On the ecology of the Three-toed Woodpecker *Picoides tridactylus* (L.) outside the breeding season. — Nytt. Mag. Zool. 18: 221–227.

Hökkä, H., Kaunisto, S., Korhonen, K. T., Päivänen, J., Reinikainen, A. & Tomppo, E. 2002: Suomen suometsät 1951–1994. — Metsätieteen aikakauskirja 2A/2002: 201–357. (In Finnish).

Jackson, J. A. & Jackson, B. J. S. 2004: Ecological relationships between fungi and woodpecker cavity sites. — Condor 106: 37–49.

Kaakinen, E., Kokko, A. & Aapala, K. 2012: Assessment of threatened mire habitats in Finland. — In: Lindholm, T. & Heikkilä, R. (eds.), Mires from pole to pole, pp. 181–195. Finnish Environment 38/2012, Finnish Environment Institute, Helsinki.

Kajtoch, Ł., Figarski, T. & Pełka, J. 2013: The role of forest structural elements in determining the occurrence of two specialist woodpecker species in the Carpathians, Poland. — Ornis Fennica 90: 23–40.

Kärki, T. 1999: Prediction of the value of grey alder (*Alnus incana*) logs based on external quality. — Silva Fennica 33: 13–23.

Kilham, L. 1971: Reproductive behavior of Yellow-bellied Sapsuckers I. Preference for nesting in *Fomes*-infected aspens and nest hole interrelations with flying squirrels, raccoons, and other animals. — Wilson Bull. 83: 159–171.

Kuuluvainen, T. & Aakala, T. 2001: Natural forest dynamics in boreal Fennoscandia: a review and classification. — Silva Fennica 45: 823–841.

Laine, J., Vasander, H., Hotanen, J.-P., Nousiainen, H., Saarinen, M. & Penttilä, T. 2012: Suotyypit ja turvekankaat — opas kasvupaikkojen tunnistamiseen. — Metsäkustannus, Hämeenlinna. (In Finnish)

Lorenz, T. J., Vierling, K. T., Johnson, T. R. & Fisher, P. C. 2015: The role of wood hardness in limiting nest site selection in avian cavity excavators. — Ecol. Appl. 25: 1016–1033.

Losin, N., Floyd, C. H., Schweitzer, T. E. & Keller, S. J. 2006: Relationship between aspen heartwood rot and the location of cavity excavation by a primary cavity-nester, the Red-naped Sapsucker. — Condor 108: 706–710.

Manion, P. D. 1991: Tree disease concepts. 2nd ed. — Prentice-Hall, Englewood Cliffs, New Jersey.

Matsuoka, S. 2008: Wood hardness in nest trees of the great spotted woodpecker *Dendrocopos major*. — Ornithological Science 7: 59–66.

Matsuoka, S. 2010: Great Spotted Woodpeckers *Dendrocopos major* detect variation in wood hardness before excavating nest holes. — Ornithological Science 9: 67–74.

Mattila, U. & Nuutinen, T. 2007: Assessing the incidence of butt rot in Norway spruce in southern Finland. — Silva Fennica 41: 29–43.

Meyer, W. & Meyer, B. 2001: Construction and use of Black Woodpecker holes in Thuringia, Germany. — Abh. Ber. Mus. Heineanum 5: 121–131. (In German with English summary)

Päivänen, J. & Hånell, B. 2012: Peatland ecology and fore-

stry — a sound approach. — University of Helsinki, Department of Forest Sciences, Helsinki.

Pakkala, T., Hanski, I. & Tomppo, E. 2002: Spatial ecology of the three-toed woodpecker in managed forest landscapes. — Silva Fennica 36: 279–288.

Pakkala, T., Kouki, J. & Tiainen, J. 2006: Top predator and interference competition modify the existence, abundance and breeding success of a declining specialist species in a structurally complex environment. — Ann. Zool. Fennici 43: 137–164.

Pakkala, T., Lindén, A., Tiainen, J., Tomppo, E. & Kouki, J. 2014: Indicators of forest biodiversity: which bird species predict high breeding bird assemblage diversity in boreal forests at multiple spatial scales? — Ann. Zool. Fennici 51: 457–476.

Pakkala, T., Tiainen, J. & Kouki, J. 2017: The importance of nesting cavity and tree reuse of the Three-toed Woodpecker Picoides tridactylus in dynamic forest landscapes. — Ann. Zool. Fennici 54:154–175.

Pakkala, T., Tiainen, J., Piha, M. & Kouki, J. 2018a: Three-toed Woodpecker cavities in trees: a keystone structural feature in forests shows decadal persistence but only short-term benefit for secondary cavity-breeders. — Forest Ecology and Management 413:70–75. https://doi.org/10.1016/j.foreco.2018.01.043

Pakkala, T., Tiainen, J., Piha, M. & Kouki, J. 2018b: How important are nest cavities made by the Three-toed Woodpecker Picoides tridactylus for cavity-nesting forest bird species? — Acta Ornithologica 53: 69–79. DOI 10.3161/00016454AO2018.53.1.007

Pechacek, P. 1995: Spechte (Picidae) im Nationalpark Berchtesgaden. — Forschungsbericht 31: 1–183. Nationalpark Berchtesgaden, Germany. (In German with English summary)

Pechacek, P. 2001: Tree selection for roosting and nesting in the Three-toed Woodpecker, and possible consequences for forest management practices. — In: Field, R., Warren, R. J., Okarma, H & Sievert, P. R. (eds.), Wildlife, land, and people: priorities for the 21st century, Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, pp. 15–18.

Pechacek, P. & Krištín, A. 2004: Comparative diets of adult and young Three-toed Woodpeckers in a European alpine community. — J. Wildl. Manage. 68: 683–693.

Pechacek, P. & d'Oleire-Oltmanns, W. 2004: Habitat use of the Three-toed Woodpecker in central Europe during the breeding period. — Biol. Cons. 116: 333–341.

Pynnönen, A. 1939: Beiträge zur Kenntnis der Biologie finnischer Spechte. I. — Ann. Zool. Soc. Zool.-Bot. Fenn. "Vanamo" 7: 1–171. (In German)

Rolstad, J., Rolstad, E. & Sæteren, Ø. 2000: Black Woodpecker nest sites: characteristics, selection, and reproductive success. — J. Wildl. Manage. 64: 1053–1066.

Ruge, K. 1974: Zur Biologie des Dreizehenspechtes Picoides tridactylus. 4. Brutbiologische und brutökologishe Daten aus der Schweiz. — Orn. Beob. 71: 303–311. (In German with English summary)

Ruge, K. 1997: Three-toed Woodpecker Picoides tridactylus. — In: Hagemeijer, E. J. M. & Blair, M. J. (eds.), The EBCC Atlas of European breeding birds: their distribution and abundance, pp. 458–459. T. & A. D. Poyser, London.

Saari, L., Pulliainen, E. & Hietajärvi, T. 1998: Itä-Lapin linnut. — Oulun yliopistopaino, Oulu (in Finnish).

Shorohova, E., Kuuluvainen, T., Kangur, A. & Jõgiste, K. 2009: Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. — Ann. For. Sci. 66: 1–20.

Short, L. L. 1979: Burdens of the picid hole-excavating habit. — Wilson Bull. 91: 16–28.

Short, L. L. 1982: Woodpeckers of the world. — DMNH Monograph Series No. 4.

Stachura-Skierczyńska, K., Tumiel, T. & Skierczyński, M. 2009: Habitat prediction model for the three-toed woodpecker and its implications for the conservation of biologically valuable forests. — For. Ecol. Manage. 258: 697–703.

Stenberg, I. 1996: Nest site selection of six woodpecker species. — Fauna norv. Ser. C. Cinclus 19: 21–38.

Syrjänen, K., Kalliola, R., Puolasmaa, A. & Mattson, J. 1994: Landscape structure and forest dynamics in subcontinental Russian European taiga. — Ann. Zool. Fenn. 31: 19–34.

Tuominen, S. 1990: Kotisten aarniometsän metsähistoria ja puustorakennetyypit. — M. Sc. Thesis, University of Helsinki. (In Finnish)

Vanhatalo, K., Väisänen, P., Joensuu, S., Sved, J., Koistinen, A. & Äijälä, O. (eds.) 2015: Metsänhoidon suositukset suometsien hoitoon, työopas. — Tapion julkaisuja. (In Finnish)

Vuorela, A. 1997: Satellite image based land cover and forest classification of Finland. — Reports of the Finnish Geodetic Institute 97: 42–52.

Wesołowski, T. 2011: "Lifespan" of woodpecker-made holes in a primeval temperate forest: a 30 year study. — For. Ecol. Manage. 262: 1846–1852.

Wesołowski, T. & Tomiałojć, L. 1986: The breeding ecology of woodpeckers in a temperate primaeval forest — a preliminary data. — Acta Ornithol. 22: 1–22.

Wesołowski, T., Czeszczewik, D. & Rowiński, P. 2005: Effect of forest management on three-toed woodpecker Picoides tridactylus in Białowieża Forest (NE Poland) — conservation implications. — Acta Ornithol. 40: 53–60.

West, P. W. 2009: Tree and forest measurement. 2nd ed. — Springer, Berlin Heidelberg.

Winkler, H. & Christie, D. A. 2002: Family Picidae (Woodpeckers). — In: del Hoyo, J., Elliott, A. & Sargatal, J. (eds.), Handbook of the Birds of the World. Vol. 7. Jacamars to Woodpeckers. Lynx Editions, Barcelona, pp. 296–555.

Zahner, V., Sikora, L. & Pasinelli, G. 2012: Heart rot as a key factor for cavity tree selection in the Black Woodpecker. — For. Ecol. Manage. 271: 98–103.