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Nest tree characteristics of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in boreal forest landscapes

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Tree cavities, and especially cavities made by woodpeckers, are important microhabitats in forest ecosystems. However, the properties of woodpecker nest trees and cavities are poorly known even in boreal areas where most tree cavities are made by woodpeckers. We studied the nest tree characteristics of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in a 170-km^2 forest-dominated area in southern Finland during 1987–2018. The data included 97 nest trees with 106 nest cavities in five deciduous tree species. During the study period, more than one nest cavity (2–3) was excavated in 7% of all cavity trees. Nests were found in three forest types, but the proportions of nest tree species differed between them. Birch (*Betula* spp.) was the most common nest tree species with 40% of nests. Nest trees were either dead (79%) or decaying (21%), and the majority (69%) had a broken top. The mean diameter at breast height (DBH) of a nest tree was 24.7 cm and the mean height of a cavity hole was 3.3 m; size and height were significantly positively correlated. The mean ratio of cavity height in relation to the respective nest tree height was 0.49, and did not depend on the nest tree condition. The results highlight the importance of dead and decaying deciduous trees as nest cavity sites for this small woodpecker species. Provision of suitable cavity trees during forest management is important to maintain breeding and cavity building opportunities for the Lesser Spotted Woodpecker in managed forests.

1. Introduction

Woodpeckers are considered as keystone species in forest ecosystems, especially in boreal forest landscapes where most tree cavities for hole-nesting birds are made by them (Aitken & Martin 2007, Cockle *et al*. 2011, Andersson *et al.* 2018). The properties of nest trees are important for the woodpeckers themselves, especially to ensure the excavation of strong and safe cavities, but also for a variety of other cavity-nesting animals, such as mammals, birds and invertebrates that use these cavities afterwards (Jones *et al.* 1994, Drever *et al.* 2008, Cockle *et al.* 2011). Woodpeckers are also proposed as indicator species of forest structural complexity and species diversity (Mikusiński *et al.* 2001, Roberge *et al.* 2008, Pakkala *et al.* 2014), and their cavity trees are important components of the nest webs (in the sense of Martin & Eadie 1999) in high-quality forest areas.

In this study, we investigated the nest tree characteristics of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in a boreal forest landscape dominated by managed, mature conifer forests.

The Lesser Spotted Woodpecker is a widespread Eurasian woodpecker species, and its nest tree characteristics vary within different parts of its distribution area (Dementiev & Gladkov 1966, Glutz von Blotzheim & Bauer 1980, Cramp 1985, Winkler & Christie 2002). In general, the species prefers forest types with a high proportion of deciduous trees (Wesołowski & Tomiałojć 1986, Wiktander *et al.* 1992, Olsson *et al.* 1992, Glue & Boswell 1994, Charman *et al.* 2010), although it also occurs in suburban habitats, such as gardens and parks (Dementiev & Gladkov 1966, Cramp 1985, Nilsson 1997, Charman *et al*. 2010).

However, the boreal forest areas suitable for the species differ from more southern European areas as they contain a smaller number of suitable deciduous tree species (e.g., Remm & Lõhmus 2011, Wesołowski & Martin 2018; see below). Because of its small body and beak size, the Lesser Spotted Woodpecker uses, on average, softer trees and tree parts with smaller diameter for its cavities compared with its relatives. Thus dead and decaying deciduous trees with dead parts are important for the species all over its distribution area (Glutz von Blotzheim & Bauer 1980, Cramp 1985, Glue & Boswell 1994, Höntsch 2001, Smith 2007, Smith & Charman 2012), although published information in regard to the nest tree characteristics is sporadic, especially in regard to boreal forests.

We explored and documented the main characteristics of the nest trees and their forest types using a large data set from southern Finland. We compared the nest tree properties of the Lesser Spotted Woodpecker between different forest types in our boreal study area, but also with the current knowledge of nest tree characteristics from other areas in Europe. Since the availability of potential deciduous nest cavity trees differs greatly between boreal and more southern forest areas (Remm & Lõhmus 2011, Wesołowski & Martin 2018), we emphasise that more detailed knowledge of the characteristics of nest trees and their spatial variation in different types of forests is especially important for forest management and conservation in boreal forest areas.

2. Material and methods

2.1. Study area

The study area (170 km^2) is located within the southern boreal vegetation zone in southern Finland (around 61°15’ N, 25°03’ E; see Pakkala *et al.* 2017). It is dominated by mature, mostly managed coniferous forests on mineral soils, but with a mixture of stands of different ages, and many small oligotrophic lakes. Habitats suitable for the Lesser Spotted Woodpecker are patchy within the study area. More fertile moist forests on mineral soils are found scattered within the area, especially around the few agricultural areas. Wet, mixed and deciduous tree-dominated peatland forests mostly exist around lakes, but also in areas flooded by the North American Beaver (*Castor canadensis*). Human settlements in the area are scarce. The aim of forest management in the study area is mostly for timber production, and the prevailing harvesting method is clear-cutting.

2.2. Lesser Spotted Woodpecker nest tree surveys

As part of an intensive population study of forest bird species, especially woodpeckers (described in detail in Pakkala 2012 and Pakkala *et al.* 2014, 2017), Lesser Spotted Woodpecker nests and nest trees were searched within the study area each year during the period 1987–2018. The annual census typically lasted from early April to the middle of July and included the mapping of woodpecker territories within the study area with simultaneous efforts to locate potential nesting sites by observing the behaviour of the woodpeckers, and by searching for nests during the breeding season. All surveys of the nest trees and cavities (see below) were carried out by author TP. The estimated total number of territory sites during the study period was 43 with a mean of about 15 annually occupied territories within the total study area (T. Pakkala, unpublished data). Based on annual territory occupancy rates and nesting success estimates (T. Pakkala, unpublished data), the data in this study cover ca. 20–30% of all nesting attempts within the study area.

2.3. Nest tree and cavity data

Definitions of nest trees and cavities
All the trees where nesting by the Lesser Spotted Woodpecker was observed during the study period were classified as nest trees. Hence, the dataset comprised only those cavities where the Lesser Spotted Woodpecker definitely reached the egg-laying phase at least. Cavities where nesting attempts were interrupted during excavation, although they would have contained a seemingly complete nest cavity, were not included in these data. The observed nest trees and cavities were then followed annually during the study period to check for possible reuse by the Lesser Spotted Woodpecker (see Pakkala *et al.* 2019).

Nest tree and cavity characteristics
The species of all the detected nest trees was determined. At each nest tree location, the main forest type of the site was defined in the field, based on the classifications of Finnish forest and peatland types (Cajander 1949, Laine *et al*. 2012).

We used three classes to assess the condition of the nest tree (see also Pakkala *et al.* 2018c). 1) Healthy: generally a vital tree with no signs of decay. Small wounds or damages by external factors possible. 2) Decaying: the tree is alive, but signs of decay are visible, e.g., dead branches or defoliation detected. 3) Dead: the tree is not alive. The condition of nest trees was also divided into two additional classes: a) trees with a more or less intact crown, and b) trees with a broken top. At the tree level, the condition when the first cavity was made in the tree was used. At the cavity level, the first year of each cavity was applied to describe the condition of the nest tree.

The size of a nest tree was measured by defining its diameter at breast height (DBH, 1.3 m above the ground). Tree size at the time (i.e. year) when the first cavity was made was used in the analysis. The heights of nest trees and cavity holes < 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 then estimating the remaining height, with an accuracy of 0.2–0.5 m. Heights > 6.0 m were estimated by a standard stick method (West 2009) with an accuracy of 0.5 m; 2–3 repeated measurements of the same tree or cavity from different directions were done to decrease the error in measurements. All measurements were carried out by author TP.

2.4. Statistical methods

Forest type and condition of the nest tree between groups were compared with goodness-of-fit tests. The distribution of DBH and the height distribution of the cavity holes were leptokurtic and/or skewed in many of the tree species (the absolute values of the ratios of kurtosis and its standard error (SE), and the respective ratios of the skewness were > 2).

Therefore, median-based Kruskal–Wallis or Mann–Whitney tests were used in the comparisons between groups of DBH and height of the cavity holes between groups. In post hoc comparisons between pairs or subgroups after a significant result, either a Bonferroni-corrected level $p < 0.05$ in the comparisons of proportions (goodness-of-fit tests) or Dunn's test with Bonferroni correction (Kruskal–Wallis tests) was used. Spearman's rank correlation coefficient was used in testing the dependence between the DBH and height of the cavity holes. All statistical analyses were performed with IBM SPSS Statistics 23.

3. Results

3.1. Nest tree species and their forest types

A total of 97 nest trees of five different deciduous tree species, 106 nest cavities, and 110 nesting attempts were found during 1987–2018 (Table 1). Birch (*Betula* spp.) was the most abundant (35.5–40.2%) in terms of tree, cavity, and nesting attempt numbers, but grey alder (*Alnus incana*) (20.0–22.7%), black alder (*Alnus glutinosa*) (17.5–

Table 1. Nest tree species of the Lesser Spotted Woodpecker with the number and percentage (in parentheses) of trees, cavities, and nesting attempts (nestings).

Tree species	Trees	Cavities	Nestings
Birch (*Betula* spp.)	39 (40.2)	39 (36.8)	39 (35.5)
Aspen (*Populus tremula*)	17 (17.5)	19 (17.9)	21 (19.1)
Grey alder (*Alnus incana*)	22 (22.7)	22 (20.8)	22 (20.0)
Black alder (*Alnus glutinosa*)	17 (17.5)	24 (22.6)	26 (23.6)
Goat willow (*Salix caprea*)	2 (2.1)	2 (1.9)	2 (1.8)
Total	97 (100.0)	106 (100.0)	110 (100.0)

Table 2. Number and percentage (in parentheses) of Lesser Spotted Woodpecker nest trees in different forest types. The first row of each tree species shows the percentage of forest type for each cavity tree species (summing up to 100% for tree species over forest types). The second row shows the percentage of each cavity tree species of all tree species within the respective forest type (summing up to 100% within the forest type). The three forest types: MT = moist spruce dominated forests on mineral soil; OMT = moist mixed or deciduous tree-dominated forests on mineral soil; SWAMP = deciduous tree-dominated, mixed, or spruce-dominated swamp forests on peatland soil.

Nest tree species	MT	OMT	SWAMP
Birch (*Betula* spp.)	8 (20.5)	20 (51.3)	11 (28.2)
	(34.8)	(50.0)	(32.4)
Aspen (*Populus tremula*)	11 (64.7)	6 (35.3)	0 (0.0)
	(47.8)	(15.0)	(0.0)
Grey alder (*Alnus incana*)	2 (9.1)	8 (36.4)	12 (54.5)
	(8.7)	(20.0)	(35.3)
Black alder (*Alnus glutinosa*)	2 (11.8)	5 (29.4)	10 (58.8)
	(8.7)	(12.5)	(29.4)
Goat willow (*Salix caprea*)	0 (0.0)	1 (50.0)	1 (50.0)
	(0.0)	(1.0)	(1.0)
Total	23 (23.7)	40 (41.2)	34 (35.1)
	(100.0)	(100.0)	(100.0)

23.6%), and aspen (*Populus tremula*) (17.5–19.1%) were also common as nest trees. Two nesting attempts were observed in goat willow (*Salix caprea*). The Lesser Spotted Woodpeckers mainly used the trunk of the tree as the cavity excavation site, but in three cases (3.1% of all cavities) the cavity was in a large branch of the tree; all these cases occurred in birch trees.

Lesser Spotted Woodpeckers excavated more than one nest cavity in seven of the nest trees (7.2% of all nest trees) during the study period. These multicavity trees included five black alder and two aspen trees; in two of the trees three cavities, and in five of the trees two cavities were excavated in separate years. The Lesser Spotted Woodpecker used old cavities four times for nesting; these cases included two black alder and two aspen trees. Thus, the cavity reuse percentage was 3.6%; all observed cases were in cavities that were excavated in the preceding year.

The 97 nest trees were found in three main types of forests (Table 2). Forests on mineral soils included 1) moist spruce-dominated forests of *Myrtillus* type (MT; $n = 23$ (23.7% of nest trees)), and 2) the more fertile, moist mixed forests of *Oxalis-Myrtillus* type (OMT; $n = 40$ (41.2%)), in which we also included the less abundant class of moist and deciduous tree-dominated forests of the *Oxalis-Maianthemum* type. Forest peatlands included 3) deciduous tree-dominated, mixed, and

Table 3. Number and percentage (in parentheses) of nest tree species of the Lesser Spotted Woodpecker according to tree condition. The condition describes the situation when the first cavity is made in the tree. Live and healthy nest trees were not observed.

Tree species	Tree condition	
	Alive, decaying	Dead
Birch (*Betula* spp.)	6 (15.4)	33 (84.0)
Aspen (*Populus tremula*)	1 (5.9)	16 (94.1)
Grey alder (*Alnus incana*)	0 (0.0)	22 (100.0)
Black alder (*Alnus glutinosa*)	12 (70.6)	5 (29.4)
Goat willow (*Salix caprea*)	1 (50.0)	1 (50.0)
Total	20 (20.6)	77 (79.4)

spruce swamps (SWAMP; n = 34 (35.1%)) that were combined into a single class.

Different tree species were used in the various forest types (goodness-of-fit test: $\chi^2 = 29.3$, $p < 0.001$, $df = 8$). The difference was mainly due to proportionally higher numbers of aspen in spruce-dominated moist forests, and both alder species in the SWAMP forest type compared with other forest types (Bonferroni-corrected $p < 0.05$ for all pairwise differences, Table 2). Aspen was the most common nest tree (47.8%) in MT type, birch (50.0%) in OMT type, and grey alder (35.3%) in SWAMP type (Table 2).

3.2. Condition of the nest trees

The Lesser Spotted Woodpeckers selected only dead (79.4%) or decaying (20.6%) trees for their nests. The condition distributions of the nest tree species significantly differed from each other ($\chi^2 = 35.6$, $p < 0.001$, $df = 4$); the proportion of dead trees varied from 29.4% in black alder to 100% in grey alder (Table 3). Based on the Bonferroni-corrected level $p = 0.05$, the most important differences were the high proportions of decaying black alder and dead grey alder trees compared with the expected proportions (Table 3). The condition of the nest tree did not differ between the forest types ($\chi^2 = 1.07$, $p = 0.59$, $df = 2$).

The majority of nest trees, 69.0%, had a broken top at the time when the first cavity was excavated. This property significantly differed between the tree species ($\chi^2 = 39.8$, $p < 0.001$, $df = 4$). The difference was mostly caused by the significantly lower (Bonferroni-corrected level $p = 0.05$) proportion in black alder (5.9%), whereas all the other common tree species (birch, aspen, grey alder) had very similar numbers of broken tops (81.8–88.2%). The proportion of nest trees with a broken top did not differ significantly between the three forest types ($\chi^2 = 2.80$, $p = 0.25$, $df = 2$).

3.3. Size of the nest trees

The mean and median diameters of the nest tree (at DBH) were 24.7 cm and 24.0 cm, respectively (range 15.0–38.5 cm). The median DBH of individual nest tree species varied from 22.0 cm in aspen and grey alder to 28.5 cm in goat willow (Table 4), and the nest tree species can be divided into "large" (birch, black alder, goat willow) and "small" species (aspen, grey alder). The size of the nest tree (DBH) differed between the four main nest tree species (Kruskal–Wallis test: $H = 32.80$, p

Table 4. Number (N), mean, standard deviation (SD), median, minimum and maximum diameter at breast height (DBH) values (cm) of the Lesser Spotted Woodpecker nest trees in various nest tree species.

Tree species	*N*	Mean	*SD*	Median	Minimum	Maximum
Birch (*Betula* spp.)	39	26.3	4.85	25.5	18.5	38.5
Aspen (*Populus tremula*)	17	22.4	2.16	22.0	19.0	26.5
Grey alder (*Alnus incana*)	22	21.7	2.26	22.0	15.0	26.5
Black alder (*Alnus glutinosa*)	17	27.1	2.94	27.0	19.0	31.0
Goat willow (*Salix caprea*)	2	28.5	6.36	28.5	24.0	33.0
Total	97	24.7	4.30	24.0	15.0	38.50

Table 5. Number (*N*), mean, standard deviation (*SD*), median, minimum and maximum heights (m above the ground) of the Lesser Spotted Woodpecker cavity holes in various nest tree species.

Tree species	*N*	Mean	*SD*	Median	Minimum	Maximum
Birch (*Betula* spp.)	39	3.4	2.8	2.4	0.8	15.0
Aspen (*Populus tremula*)	19	2.3	0.5	2.2	1.3	3.5
Grey alder (*Alnus incana*)	22	2.2	0.9	2.0	1.0	4.5
Black alder (*Alnus glutinosa*)	24	4.8	2.0	4.5	1.0	12.0
Goat willow (*Salix caprea*)	2	4.4	2.3	4.4	2.8	6.0
Total	106	3.3	2.2	2.5	0.8	15.0

< 0.001, $df = 3$). All pairwise differences were significant (Dunn's test with Bonferroni correction: $p < 0.01$), except those between aspen and grey alder and between birch and black alder ($p > 0.10$).

The DBH did not differ between the various forest types (Kruskal–Wallis test: $H = 1.57$, $p = 0.46$, $df = 2$), but there was a significant difference according to tree condition type; dead trees (median DBH 23.0 cm) were significantly smaller than decaying (27.0 cm) trees (Mann–Whitney U-test: $U = 408.5$, $p < 0.001$, $n_1 = 77$, $n_2 = 20$). Nest trees with a broken top (median DBH 23.0 cm) were also significantly smaller than those with an intact crown (27.0 cm; Mann–Whitney U-test: $U = 218.0$, $p < 0.001$, $n_1 = 67$, $n_2 = 30$).

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 ($n = 24$) provides an approximate estimate for nest tree size at the height of the cavity. The mean of this diameter was 21.9 cm, median 21.5 cm, and the range was 15.0–31.0 cm.

3.4. Heights of cavity holes and nest trees

The mean and median heights of all cavity holes ($n = 106$) above the ground were 3.3 m and 2.5 m, respectively (range 0.8–15 m) (Table 5). The median heights of cavity holes between tree species varied from 2.0 m in grey alder to 4.5 m in black alder (Table 5). The median height of cavity holes significantly differed between the four most common tree species (Kruskal–Wallis test: $H = 30.2$, $p < 0.001$, $df = 3$). All pairwise differences between black alder and the other tree species were significant (Dunn's test with Bonferroni correction: $p < 0.001$), but all pairwise differences between the other tree species were insignificant ($p > 0.10$ in all cases).

The median height of the cavity holes did not significantly differ among the forest types (Kruskal–Wallis test: $H = 1.88$, $p = 0.39$, $df = 2$). However, there was a significant difference in the height of cavity holes between the tree condition types; cavity holes in dead nest trees (median height 2.2 m) were significantly lower than those in decaying nest trees (4.7 m; Mann–Whitney U-test: $U = 210.5$, $p < 0.001$, $n_1 = 80$, $n_2 = 26$). Cavities in nest trees with broken top were also significantly lower (median height 2.0 m) compared to nest trees with intact crowns (4.5 m; Mann–Whitney U-test: $U = 325.5$, $p < 0.001$, $n_1 = 69$, $n_2 = 37$).

There was a significant positive correlation between DBH and the height of cavity holes in all nest trees (Spearman's correlation: $r_s = 0.71$, $p < 0.001$, $df = 104$); this general pattern was similar in the four most common tree species although significant only in two of them (birch: $r_s = 0.80$, $p < 0.001$, $df = 37$; aspen: $r_s = 0.29$, $p = 0.22$, $df = 17$; grey alder: $r_s = 0.73$, $p < 0.001$, $df = 20$; black alder: $r_s = 0.17$, $p = 0.42$, $df = 22$).

The mean and median heights of all nest trees ($n = 97$) were 6.8 m and 6.0 m, respectively (range 2–18 m). Nest trees with intact crowns were significantly higher (median 10.0 m) than nest trees with broken tops (4.5m; Mann–Whitney U-test: $U = 107.0$, $p < 0.001$, $n_1 = 30$, $n_2 = 67$). The mean and median relative heights (height of the cavity hole/height of the nest tree) of all cavities were 0.49 and 0.48, respectively (range 0.08–0.86). The median relative heights of cavities did not differ between cavities in dead (median 0.49) and decaying trees (0.48; Mann–Whitney U-test: U = 1133.0, p = 0.49, n_1 = 80, n_2 = 26) or between cavities in trees with broken top (median 0.50) and those with intact crowns (0.45; Mann–Whitney U-test: U = 1509.5, p = 0.12, n_1 = 69, n_2 = 37).

4. Discussion

4.1. Nest tree species and their habitat types

We detected four common and one occasional nest tree species in our study, and we found that the proportions of tree species used by the Lesser Spotted Woodpecker clearly depended on forest type. Alder was the dominant species in peatland forests (65%), and aspen and birch were dominant in moist forests on mineral soil (65–82% of nest trees). Our results were consistent with earlier Finnish studies: Pynnönen (1939) observed that birch was the most common nest tree (47%) of 18 nest trees in a study area in eastern Finland with forests mostly on mineral soil, and Hurme (1972) observed that 78% of 18 nests were found in alder trees in a study area dominated by riparian forests in SW Finland. In another study from SW Finland (Karlin 1979) where the data were collected over a relatively large area, the most common trees (n=38) were birch (37%), alder (34%) and aspen (29%). These three studies from Finland contained a total of 74 nest trees of four different species, namely birch, aspen, black alder and grey alder, which were also the four most common nest trees recorded in our study.

The composition of nest trees in our study was quite similar to other studies from northern Europe. In three Norwegian studies, Hågvar *et al.* (1990; number of nest trees = 50) detected nest cavities in aspen (40%), birch (34%), and alder species (26%); Stenberg (1996; n = 11), in aspen (82%) and grey alder (18%); and Lislevand *et al.* (2009; n = 167) found that aspen and birch comprised 70% of all nest trees. In a study in boreal western Russia, Fetisov (2017b; n = 26) reported that alders (73%) were the dominant nest tree species group.

In more southern European areas where the Lesser Spotted Woodpecker also uses suburban habitats, such as gardens and parks (Glutz von Blotzheim & Bauer 1980, Cramp 1985), the number of observed nest tree species is usually larger than in boreal areas. For example, in local studies in Germany and UK, between nine and twelve nest tree species were detected (Höntsch 2001, Wirthmüller 2006, Charman *et al*. 2012). In general, more nest tree species are also detected in regional or national studies where the dataset tends to be large, e.g., a total of twelve species were recorded (127 and 167 nest trees, respectively) in both UK and Norway (Glue & Boswell 1994, Lislevand *et al.* 2009). In a review study, Fetisov (2017a) similarly listed 20 different nest tree species used by the Lesser Spotted Woodpecker in Russia.

Lesser Spotted Woodpeckers predominantly select deciduous tree species for nesting, but coniferous tree species, such as Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and firs (*Abies* spp.) are also occasionally used (Haftorn 1971, Glutz von Blotzheim & Bauer 1980, Lislevand *et al.* 2009, Fetisov 2017a). In addition, nest-boxes may be used for nesting (e.g., Kivirikko 1926, Hortling 1929, Svärdson & Durango 1950, Haftorn 1971, Glutz von Blotzheim & Bauer 1980, Glue & Boswell 1994), but these cases are most probably very rare.

4.2. Selection of nest trees

In northern Europe, the nest cavities are most often situated in the trunk of the tree, and only occasionally in branches (e.g., this study, Pynnönen 1939, Hurme 1972, Hågvar *et al.* 1990, Stenberg 1996, Wiktander 1998). This may be linked to the structural differences of the nest trees. In northern Europe, nest cavities are often in snags with broken tops (69% in this study; 67% in Hurme 1972; 76% in Karlin 1979; 81% in Hågvar *et al.* 1990; 73% in Stenberg 1996), and in trees without large branches, but in more southern European areas, various deciduous tree species have suitably large decaying or dead branches as the cavity excavation site. Besides birch, alders and aspen, which are also used in boreal forests, branched trees such as oaks (*Quercus* spp.), willows (*Salix* spp.), ashes (*Fraxinus* spp.), hornbeams (*Carpinus* spp.), beeches (*Fagus* spp.), elms (*Ulmus* spp.), and various fruit trees (e.g., *Prunus* spp., *Malus* spp.) are available as cavity trees in temperate areas (see references below). For example, 39–56% of nest cavities in UK (Glue & Boswell 1994, Charman *et al.* 2012), 25–28% in Poland (Wesołowski 1989, Kosiński & Kempa 2007) and 45–81% in Germany (Höntsch 2001, Wirthmüller 2006) were situated in branches.

All nest cavities in our study were in dead (79%) or decaying (21%) trees, as also reported in other Finnish studies (89% dead or decaying in Pynnönen 1939; 94% dead in Hurme 1972; 76% dead in Karlin 1979). Moreover, the vast majority of nest cavities in other European studies were in dead or decaying trees; e.g., 96–100% in Norway (Hågvar *et al.* 1990, Stenberg 1996, Lislevand *et al.* 2009), 98% in Poland (Wesołowski 2011), 75% in UK (Glue & Boswell 1994) and 94% in Spain (Camprodon *et al.* 2015). The cavities in decaying or otherwise healthy trees were most often found in the dead parts of the trunk or branch as evident in our study. Similarly, Smith (2007) in UK observed that 88% of nest sites in living trees were located in the dead parts, and Charman *et al.* (2012) found that although the branch was dead in all cases of branch nesting, in 73% of these cases the tree itself was alive. In Germany, Höntsch (2001) observed that 63% of nest trees were relative healthy, but 95% of the nest cavities were in dead or decaying parts of the trees.

The preference of the Lesser Spotted and other woodpecker species to use dead or decaying trees for nesting is commonly explained by the optimal hardness of the tree: cavity excavation is relatively easy because of the soft interior, but the outer layer of the tree is rigid enough to provide sufficient protection (e.g., Short 1979, Jackson & Jackson 2004, Losin *et al*. 2006, Blanc & Martin 2012, Pakkala *et al.* 2018). In the case of the Lesser Spotted Woodpecker, availability of nest trees with suitable conditions are more limited compared to its larger relatives, because it is a small species with a short and slender bill, and thus has a weak excavation capability (see Hågvar *et al.* 1990, Glue & Boswell 1994, Höntsch 2001).

4.3. Size of nest trees and height of cavities

We found a mean DBH of 24.7 cm for nest trees, but grey alder and aspen were smaller than the other three tree species. Dead nest trees were also smaller than decaying trees, and nest trees with broken tops were smaller than those with intact crowns. In different European studies, the mean nest tree diameter varied considerably depending both on the location of the study area and the nest tree species availability: 28.7–32.2 cm in Norway (Hågvar *et al.* 1990, Stenberg 1996); 19.9–38.0 cm in UK (Glue & Boswell 1994, Charman *et al.* 2012), 19.3 cm in Germany (Höntsch 2001); 47.8 cm in Poland (Kosiński & Kempa 2007), and 21.8 cm in Spain (Camprodon *et al.* 2015).

However, in studies where the nest tree diameter of several (3–7) woodpecker species were compared within the same areas, the nest trees of the Lesser Spotted Woodpecker were the smallest, although in Norwegian studies they were similar in size to the nest trees of the Three-toed Woodpecker (*Picoides tridactylus*) (Pynnönen 1939, Hågvar *et al.* 1990, Glue & Boswell 1994, Stenberg 1996, Kosiński & Kempa 2007, Fetisov 2017b). The nest trees of the Three-toed Woodpecker in our study area were larger (mean diameter 29.4 cm; Pakkala *et al.* 2018) than those of the Lesser Spotted Woodpecker, although the size difference was small (median diameter values of the Three-toed Woodpecker and Lesser Spotted Woodpecker nest trees were 26 cm and 24 cm, respectively) if only deciduous tree species were compared. The Three-toed Woodpecker is a considerably larger species than the Lesser Spotted Woodpecker, and it also has larger nest cavities (Pynnönen 1939, Glutz von Blotzheim & Bauer 1980). Thus, in relation to its size, the Lesser Spotted Woodpecker uses rather large nest trees in northern Europe (see also Fetisov 2017b).

If we examine the mean diameters of nest trees at the height of cavity opening, our results are similar to previous studies: 21.9 cm in our study; 19.7 cm in Finland (Pynnönen 1939); and 21.1 cm (Hågvar *et al.* 1990) and 22 cm (Stenberg 1996) in Norway. In western Russia, the respective values were 16–18 cm (Malchevsky & Pukinsky 1983), 22 cm (Ivanchev 2005) and 15.2 cm (Fetisov 2017b). Pynnönen (1939) measured the inside of six nest cavities; the mean diameter at the cavity opening was 9.5 cm, and the transverse diameter was 7.6 cm. These values can be compared with the observed minimum diameters of the nest trees from literature: 7.5 cm (Fetisov 2017b), 9.5 cm (Höntsch 2001), 10 cm (Blagosklonov 1968, Glue

& Boswell 1994), 12 cm (Hågvar *et al.* 1990, Stenberg 1996, Ivanchev 2005), 12.5 cm (Pynnönen 1939), 13 cm (Camprodon *et al.* 2015) and 15 cm (this study). However, the mean diameter values were considerably greater than these minimum values, which indicate that the nest cavity walls of the Lesser Spotted Woodpecker are usually quite thick and thus ensure additional protection against outside factors, such as wind, extreme temperatures and nest predation.

We observed a mean height of 3.3 m for cavity holes, although the range (0.8–15 m) and variation in the means of tree species (2.2–4.8 m) were relatively large, with the lowest mean values in grey alder and aspen, and the highest observed in black alder. The cavities were also located at a lower level in dead trees compared to decaying trees, and were lower in trees with broken tops than those with intact crowns. In other studies in Finland, a mean height of 3.2 m (range 1–5.8 m) was reported by Pynnönen (1939), 5.1 m (range 2–10 m) by Hurme (1972) and 2.8 m by Karlin (1979).

In other European studies, the mean cavity height was consistent with the Finnish results; 3.4–4.2 m in Norway (Hågvar *et al.* 1990, Stenberg 1996) and 2–5.4 m in western Russia (Malchevsky & Pukinsky 1983, Nikolaev 1998, Klimov *et al.* 2004, Ivanchev 2005, Fetisov 2017b), but was larger in western Europe (5.3–9.4 m; Glue & Boswell 1994, Höntsch 2001, Wirthmüller 2006, Charman *et al*. 2012, Camprodon *et al.* 2015), and very large in Poland (11.1–12 m; Wesołowski & Tomiałojć 1986, Kosiński & Kempa 2007). The observed cavity height was generally dependent on the size of the nest tree (see above), although the range of cavity height was wide; 0.4 m to > 25 m (Glutz von Blotzheim & Bauer 1980 and the above-mentioned studies).

Mean relative height of nest cavities was approximately 0.5 in various studies (0.49 in this study; 0.52 in Hågvar *et al.* 1990; 0.59 in Pynnönen 1939; 0.61 in Kosiński & Kempa 2007), but larger mean values (0.63–0.84) were also detected (see Hurme 1972, Glue & Boswell 1994, Stenberg 1996, Charman *et al.* 2012, Camprodon *et al.* 2015). In relation to other woodpecker species studied within the same area, both the absolute and relative cavity heights of the Lesser Spotted Woodpecker considerably varied between different European studies (Wesołowski & Tomiałojć 1986, Hågvar *et al.* 1990, Glue & Boswell 1994, Stenberg 1996, Kosiński & Kempa 2007). In our study area, the mean height of all nest cavities of the Three-toed Woodpecker was larger (5.1 m) (Pakkala *et al.* 2018) than that of the Lesser Spotted Woodpecker (3.3 m), but the respective value of Three-toed Woodpecker's cavities in deciduous nest trees was only 4.1 m. The higher variation in cavity height in more southern European areas compared with northern areas is probably a combination of the larger morphological and size varieties of suitable nest tree species (see above), thus offering more options for the Lesser Spotted Woodpecker at different heights.

4.4. Nest tree and cavity reuse

We observed that ca. 7% of nest trees were used for nesting in several years, and nest tree reuse has also been reported in other studies (e.g., 5.5% in Pynnönen 1939; 16.7% in Hurme 1972; 18.2% in Stenberg 1996; 3.9% in Wirthmüller 2006). However, the comparability of tree reuse values depends on the number of study years, and, especially, how often older nest trees have been systematically monitored.

We found that the Lesser Spotted Woodpecker reused its old cavities in four cases (3.6% of all nesting attempts). Lislevand *et al.* (2009) reported two similar cases (1.2%), and, as in our study, they were detected in cavities that were excavated in the preceding year, which seems to be the most common reuse pattern in boreal woodpecker species (see Pakkala *et al.* 2017). However, in intensive population studies of the species (e.g., Wiktander 1998, Höntsch 2001, Wirthmüller 2006), cavity reuse was not detected, which indicates that it is a relatively rare phenomenon compared with other European woodpecker species (see Wiebe *et al*. 2006, 2007, Pakkala *et al.* 2017). While this was not the focus of our study here, we think that the most probable causes for the low reuse rate are simultaneously (i) low quality of the old cavities indicated by their short persistence times (Wesołowski 2011, Pakkala *et al.* 2019), (ii) the avoidance of competing for old cavities with other cavity reusers (Hurme 1972, Wiebe 2003, Wiebe *et al.* 2007, Camprodon *et al.* 2015, Pakkala *et al.* 2017, 2019), and (iii) the avoidance of nest predation (see Martin 1993, Wiebe *et al.* 2007), especially indicated in areas with a high proportion of cavities located underneath relatively thin branches (e.g., Glue & Boswell 1994, Höntsch 2001, Wirthmüller 2006).

4.5. Nest trees in forest environments

Nest trees of the Lesser Spotted Woodpecker are located within breeding territories, which are large for a species of this size (see Wiktander *et al.* 2001). In studies with radio-tracked birds, the estimated mean home-range size was ca. 350 ha in early spring, ca. 100 ha in late spring preceding nesting, and 43 ha during the nesting season in southern Sweden (Wiktander *et al.* 2001), and 209 ha in early spring and 37 ha during the nesting season in Germany (Höntsch 1996). The relatively small home range during nesting has been explained by high energy requirements during this period, when woodpeckers predominantly use the most profitable habitats (e.g., Pynnönen 1939, Höntsch 1996, Wiktander *et al.* 2001, Rossmanith *et al*. 2007). Thus, the nest trees should often be located in or near the central parts of breeding territories, and they then indicate the most important forest sites for the Lesser Spotted Woodpecker.

It is often difficult to estimate whether the availability of suitable nest trees is a limiting factor in the territory areas of the Lesser Spotted Woodpecker. However, as dead and decaying deciduous trees are used for nesting, and a new nest cavity is excavated almost every year (although the same nest trees can be used in several years), continuous availability of suitable nest trees is essential in the breeding sites of the Lesser Spotted Woodpecker (see also Höntsch 2001, Wiktander *et al.* 2001, Smith 2007). In managed Finnish forests (and also in our study area), large diameter dead deciduous trees are rare compared to natural boreal forests (e.g., Nilsson *et al.* 2002; Kouki *et al.* 2004; Vaillancourt *et al.* 2008). Maintaining the availability of suitable or preferred types of trees during forest management and the conservation of key habitats of the species are therefore important for the favourable development of breeding populations. Since the Lesser Spotted Woodpecker prefers deciduous trees, this recommendation is particularly relevant for forest habitats where deciduous trees prevail.

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Millaisia ovat pikkutikan pesäpuut boreaalisessa metsämaisemassa?

Puiden onkalot, erityisesti tikkojen kovertamat pesäkolot ovat tärkeitä pienelinympäristöjä metsäekosysteemeissä. Tikkojen pesäpuiden ja kolojen ominaisuudet ovat kuitenkin huonosti tunnettuja jopa pohjoisilla havumetsäalueilla, missä ne muodostavat pääosan puiden onkaloista. Tutkimme pikkutikan pesäpuiden ominaisuuksia 170 km^2:n suuruisella alueella Evolla Etelä-Suomessa vuosina 1987–2018. Aineisto käsitti 97 pesäpuuta ja niissä 106 pesäkoloa. Pesäpuulajeista neljä oli yleisiä (koivu, haapa, harmaaleppä ja tervaleppä) ja yksi satunnainen (raita).

Tutkimusvuosien aikana 7 %:in puista koverrettiin useampi kuin yksi (2 tai 3) kolo. Pesiä löytyi kolmentyyppisistä metsistä (mustikkatyyppi, käenkaali-mustikkatyyppi, korpi). Pesäpuiden lajisuhteet vaihtelivat metsätyyppien kesken. Koivu oli koko aineistossa (40 % pesäpuista) ja käenkaali-mustikkatyypillä yleisin, mutta haapa oli yleisin mustikkatyypillä ja tervaleppä korvissa. Pesäpuut olivat joko kuolleita (79 %) tai lahoavia (21 %), ja suurimmalla osalla (69 %) oli katkennut latva. Muilla puulajeilla valtaosa pesäpuista oli kuolleita, mutta tervalepällä vain 29 %.

Pesäpuiden rinnankorkeusläpimitta oli keskimäärin 24,7 cm ja kolon lentoaukon korkeus maanpinnasta keskimäärin 3,3 m; läpimitta ja korkeus korreloivat positiivisesti keskenään. Havaitut pesäpuiden ominaisuudet korostavat sitä, että metsissä tulisi säästää sekä pökkelöitä että kuolevia puita, ja lisäksi huolehtia myös tulevasta lahopuujatkumosta, jotta tikoille olisi tarjolla sopivia kolopuita.

References

Aitken K. E. H. & Martin K. 2007: The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada. — J. Ornithol. 148: 425–434.

Andersson J., Gómez E. D., Michon S. & Roberge J.-M. 2018: Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. — Scand. J. For. Res. 33: 233–244.

Blagosklonov, K. N. 1968: Gnezdovyye derev'ya dyatlov v razlichnykh tipakh lesa [The nest trees of woodpeckers in various types of forests]. — Ornitologija 9: 95–102. (in Russian)

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.

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

Camprodon, J., Faus, J., Salvanyà, P., Soler-Zurita, J. & Romero, J. L. 2015: Suitability for poplar plantations for a cavity nesting specialist, the Lesser Spotted Woodpecker *Dendrocopos minor*, in the Mediterranean mosaic landscape. — Acta Ornithol. 50: 157–169.

Charman, E. C., Smith, K. W., Gruar, D. J., Dodd, S. & Grice, P. V. 2010: Characteristics of woods used recently and historically by Lesser Spotted Woodpeckers *Dendrocopos minor* in England. — Ibis 152: 543–555.

Charman, E. C., Smith, K. W., Dodd, S., Gruar, D. J. & Dillon, I. A. 2012: Pre-breeding foraging and nest site habitat selection by Lesser Spotted Woodpeckers *Dendrocopos minor* in mature woodland blocks in England. — Ornis Fennica 89: 182–196.

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.

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.

Drever, M. C., Aitken, K. E. H., Norris, A. R. & Martin, K. 2008: Woodpeckers as reliable indicators of bird richness, forest health, and harvest. — Biol. Cons. 141: 624–634.

Fetisov, S. A. 2017a: O gnezdovykh duplakh i evolyutsii gnezdostroyeniya u dyatlov Picidae: Rol' fautnogo drevostoya i derev'yev s "myagkoy" drevesinoy dlya gnezdovaniya dyatlov [The nest cavities and the evolution of nesting in Picidae: the role of injured and softwood trees for nesting]. — Russian Journal of Ornithology 26(1499): 3867–3901. (in Russian)

Fetisov, S. A. 2017b: O gnezdovykh duplakh i evolyutsii gnezdostroyeniya u dyatlov Picidae: kharakteristiki razmeshcheniya gnezdovykh dupel na derev'yakh [The nest cavities and the evolution of nesting in Picidae: characteristics of the location of cavities]. — Russian Journal of Ornithology 26(1527): 4835–4856. (in Russian)

Glue, D. E. & Boswell, T. 1994: Comparative nesting ecology of the three British breeding woodpeckers. — Brit. Birds 87: 253–269.

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

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.

Höntsch, K. 1996: Radiotelemetrische Untersuchungen zur Raum-Zeit-Nutzung des Kleinspechts *Picoides minor*. — Diplomarbeit, Technische Hochschule Darmstadt, Darmstadt. (in German)

Höntsch, K. 2001: Brut- und Schlafhöhlen des Kleinspechts *Picoides minor*. — Abh. Ber. Mus. Heineanum 5: 107–120. (in German with English summary)

Hortling, I. 1929: Ornitologisk handbok. — J. Simelii arvingar, Helsingfors. (in Swedish)

Hurme, T. 1975: Pikkutikan *Dendrocopos minor* soitimesta ja pesimisbiologiasta. — Lintumies 10: 77–83. (in Finnish with German summary)

Ivanchev, V. P. 2005: Malyi pestryi diatel *Dendrocopos minor* (Linnaeus, 1758) (Lesser spotted woodpecker *Dendrocopos minor* (Linnaeus, 1758)). – In: Butev, V. T., Zubkov, N. I., Ivanchev, V. P., Koblik, E. A., Kovshar, A. F., Kotiukov, J. V., Liuleeva, D. S., Nazarov, J. N., Nechaev, V. A., Priklonsky, S. G., Pukinsky, J. B., Rustamov, A. K., Sorokin, A. G. & Fridman, V. S., Ptitsy Rossii i sopredel'nykh regionov: Sovoobraznye, Kozodoeobraznye, Strizheobraznye, Raksheobraznye, Udodoobraznye, Diatloobraznye [Birds of Russia and adjacent regions. Volume 6: Strigiformes, Caprimulgiformes, Apodiformes, Coraciiformes, Upupiformes, Piciformes], pp. 401–412. Tovarishchestvo nauchnykh izdanii KMK. (in Russian)

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

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

Karlin, A. 1979: Pikkutikka. — Ukuli 10: 42–51. (in Finnish)

Klimov, S. M., Zemlianukhin, A. I. & Melnikov, M. V. 2004: Ptitsy basseina Verkhnego Dona: Piciformes [The birds of the Upper Don basin: Piciformes]. — Russian Journal of Ornithology 13 (251): 75–85. (in Russian)

Kivirikko, K. E. 1926: Suomen Linnut, ensimmäinen osa. — WSOY, Porvoo. (in Finnish)

Kosiński, Z. & Kempa, M. 2007: Density, distribution and nest-sites of woodpeckers Picidae, in a managed forest of western Poland. — Pol. J. Ecol. 55: 519–522.

Kouki, J., Arnold, K. & Martikainen, P. 2004: Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. — Journal for Nature Conservation 12: 41–52.

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

Lislevand, T., Myklebust, M., Rangbru, B., Rudolfsen, G. & Aarvak, T. 2009: Dvergspetten *Dendrocopos minor* i Norge. — NOF rapport 4-2009. (in Norwegian with English summary)

Losin, N., Floyd, C. H., Schiweitzer, 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.

Malchevsky, A. S. & Pukinsky, J. B. 1983: Ptitsy Leningradskoi oblasti i sopredel'nykh territorii: Istoriia, biologiia, okhrana [Birds of the Leningrad region and adjacent territories: History, biology, protection] 1. — Leningradskogo universiteta, Leningrad, 480 pp. (in Russian)

Martin, T. E. 1993: Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? — Am. Nat. 142: 937–946.

Martin, K. & Eadie, J. M. 1999: Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. — For. Ecol. Manage. 115: 243–257.

Mikusiński, G., Gromadzki, M. & Chylarecki, P. 2001: Woodpeckers as indicators of forest bird diversity. — Cons. Biol.15: 208–217.

Nikolaev, V. I. 1998: Ptitsy bolotnykh landshaftov natsional'nogo parka "Zavidovo' i Verkhnevolzh'ia [Birds of marsh landscapes of Zavidovo National Park and Upper Volga]. — Tver, 215 pp. (in Russian)

Nilsson, S. G. 1997: Lesser Spotted Woodpecker *Dendrocopos minor*. — In: Hagemeijer, E. J. M. & Blair, M. J. (eds.), The EBCC Atlas of European breeding birds: their distribution and abundance, pp. 456–457. — T. & A. D. Poyser, London.

Nilsson, S. G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J. M., Linder, P., Ljungberg, H., Mikusiński, G. & Ranius, T. 2002: Densities of large living and dead trees in old-growth temperate and boreal forests. — Forest Ecology and Management 161: 189–204.

Olsson, O., Nilsson, I. N., Nilsson, S. G., Pettersson, B., Stagen, A. & Wiktander, U. 1992: Habitat preferences of the Lesser Spotted Woodpecker *Dendrocopos minor*. — Ornis Fennica 69: 119–125.

Pakkala, T. 2012: Spatial ecology of breeding birds in forest landscapes: an indicator species approach. — Diss. Forestales 151.

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. 2018: Nest tree characteristics of the old-growth specialist Three-toed Woodpecker *Picoides tridactylus*. — Ornis Fennica 95: 89–102.

Pakkala, T., Tiainen, J., Piha, M. & Kouki, J. 2019: Hole life: survival patterns and reuse of cavities made by the Lesser Spotted Woodpecker *Dendrocopos minor*. — Ardea 107: 173–181.

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

Remm, J. & Lõhmus, A. 2011: Tree cavities in forests – The broad distribution pattern of a keystone structure for biodiversity. — For. Ecol. Manage. 262: 579–585.

Roberge, J.-M., Angelstam, P. & Villard, M.-A. 2008: Specialized woodpeckers and naturalness in hemiboreal forests deriving quantitative targets for conservation planning. — Biol. Cons. 141: 997–1012.

Rossmanith, E., Höntsch, K. & Blaum, N. 2007: Reproductive success and nestling diet in the Lesser Spotted Woodpecker (*Picoides minor*): the early bird gets the caterpillar. — J. Ornithol. 148: 323–332.

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

Smith, K. W. 2007: The utilization of dead wood resources by woodpeckers in Britain. — Ibis 149: 183–192.

Smith, K. W. & Charman, E. C. 2012: The ecology and conservation of the Lesser Spotted Woodpecker. — British Birds 105: 294–307.

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

Svärdson, G. & Durango, S. (eds.) 1950: Svenska djur. Fåglarna. — P. A. Norstedt & Söners Förlag, Stockholm. (in Swedish)

Vaillancourt, M.-A., Drapeau, P., Gauthier, S. & Robert, M. 2008: Availability of standing trees for large cavity-nesting birds in the eastern boreal forest of Quèbec, Canada. — Forest Ecology and Management 255: 2272–2285.

Wesołowski, T. 1989: Nest-sites of hole-nesters in a primaeval temperate forest (Białowieża National Park, Poland). — Acta Ornithol. 25: 321–351.

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., & Martin, K. 2018: Tree holes and hole-nesting birds in European and North American Forests. — In: Mikusiński, G., Roberge, J.-M., & Fuller, R. J. (eds.), Ecology and conservation of forest birds. Cambridge University Press, Cambridge, UK, pp. 79–134.

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

Wiebe, K. L. 2003: Delayed timing as a strategy to avoid nest-site competition: testing a model using data from starlings and flickers. — Oikos 100: 291–298.

Wiebe, K. L., Koenig, W. D. & Martin, K. 2006: Evolution of clutch size in cavity-excavating birds: the nest site limitation hypothesis revisited. — Am. Nat. 167: 343–353.

Wiebe, K. L., Koenig, W. D. & Martin, K. 2007: Costs and benefits of nest reuse versus excavation in cavity-nesting birds. — Ann. Zool. Fennici 44: 209–217.

Wiktander, U. 1998: Reproduction and survival in the Lesser Spotted Woodpecker – effects of life history, mating system and age. — PhD thesis, Lund University, Lund, Sweden.

Wiktander, U., Nilsson, I. N., Nilsson, S. G., Olsson, O., Pettersson B. & Stagen A. 1992: Occurrence of the Lesser Spotted Woodpecker *Dendrocopos minor* in relation to area of deciduous forest. — Ornis Fennica 63: 113–118.

Wiktander, U., Olsson, O. & Nilsson, S. G. 2001: Seasonal variation in home-range size, and habitat area requirement of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in southern Sweden. — Biol. Cons. 100: 387–395.

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.

Wirthmüller, R. 2006: Beobachtungen zur Brutbiologie und zum Verhalten des Kleinspechts *Dryobates minor*. — Charadrius 42: 110–119. (in German with English summary)