Hole life: survival patterns and reuse of cavities made by the Lesser Spotted Woodpecker *Dendrocopos minor*

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Primary cavity-producers such as woodpeckers produce nest sites for several other cavity-nesting animals and, thus, are often considered to be keystone species. However, the persistence and occupancy rates of cavities are rarely known and as such the real importance of primary cavity-producers also remains unclear. Cavities of the Lesser Spotted Woodpecker *Dendrocopos minor* were monitored during their whole lifespan. The data include the annual availability and occupancy history of 106 cavities in a 170-km^2 area in southern Finland during 1987–2018. The median survival time of a cavity was six years, but there were differences between the various forest types (range six to eight years). The median time for cavity fall was six years, and five years for cavity damage. Six bird species used the old cavities for breeding, with the Pied Flycatcher *Ficedula hypoleuca* the dominant species accounting for 53% of all occupancies. The cavity reuse rate in the Lesser Spotted Woodpecker was 3.6%. The mean occupancy by secondary cavity-nesting birds in old cavities was 32%, with a range of 29–36% across the various forest types. There was a significant negative correlation between annual occupancy rates and the age of the cavity. The first two years of a cavity were found to be the most important for total occupancy and 90% of occupancies took place before the median age of the cavities. The expected mean number of lifespan occupancies by secondary cavity-nesters for a single cavity was 1.97. The results indicate that new, fresh cavities are continuously needed for the secondary cavity-nesters that use Lesser Spotted Woodpecker cavities in their territories.

Key words: Lesser Spotted Woodpecker, *Dendrocopos minor*, cavity, cavity survival, cavity damage, cavity fall, cavity occupancy, hole-nesting birds

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Woodpeckers are considered to be keystone species in their breeding environments, because they produce cavities that various cavity-nesting animals, such as mammals, birds and invertebrates use afterwards (Jones *et al.* 1994, Martin & Eadie 1999, Aitken & Martin 2007, Drever *et al.* 2008, Cockle *et al.* 2011). Studies assessing cavity numbers (see Remm & Lõhmus 2011, Andersson *et al.* 2018), species and occupancies of old cavities (e.g. van Balen *et al.* 1980, Carlson *et al.* 1998, Aitken *et al.* 2002, Aitken & Martin 2004, Bai *et al.* 2003, Günther & Hellmann 2005, Remm *et al.* 2006, Edworthy *et al.* 2017, Pakkala *et al.* 2018b), and the survival of cavity trees (Cockle *et al.* 2011, Wesołowski 2011, Edworthy *et al.* 2012, Edworthy & Martin 2014, Pakkala *et al.* 2018a) have been conducted at natural nest sites of hole-nesting birds in northern temperate and boreal forests, but detailed monitoring of the occupancy and survival of individual cavities throughout their lifespan has seldom been done. These types of studies are essential to evaluate the full ecological significance of primary cavity-producers for secondary cavity-inhabiting species. This information is also useful for forest management and for the identification of conservation options in a range of forest types, especially in boreal areas, where the majority of cavities for hole-nesting birds are made by woodpeckers rather than being naturally occurring hollows in trees (Aitken & Martin 2007, Cockle *et al.* 2011, Andersson *et al.* 2018).

We studied the persistence and reuse rates of cavities originally made by the Lesser Spotted Woodpecker *Dendrocopos minor*, which prefers deciduous-tree dominated or mixed forests with a good proportion of dead or decaying deciduous trees (Pynnönen 1939, Dementiev & Gladkov 1966, Cramp 1985, Wesołowski & Tomiałojc 1986, Olsson *et al.* 1992, Wiktander *et al.* 1992). In this study, we used a large data set from an area in southern Finland where cavities made by the Lesser Spotted Woodpecker were recorded annually and the subsequent use of the cavities monitored over their complete lifespan.

We focused on the following questions: (1) What are the annual survival patterns of Lesser Spotted Woodpecker cavities in different types of forests? (2) How do the occupancy patterns vary during the lifespan of the cavities? (3) What are the estimated total numbers of nesting attempts, including both the woodpecker and secondary species, during the lifespan of Lesser Spotted Woodpecker's cavities in different types of forests?

METHODS

Study area

The study area measured 170 km^2 and is located within the southern boreal vegetation zone in southern Finland (around 61°15'N, 25°3'E; see Pakkala *et al.* 2017). It is dominated by mature, mostly managed coniferous forests on mineral soils, with a mixture of stands of different ages, and many small oligotrophic lakes. Habitats suitable for Lesser Spotted Woodpeckers are patchy within the study area. More fertile moist forests on mineral soil 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. Forest management in the study area is concentrated on timber production, and the prevailing harvesting method is clear-cutting. 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.

Lesser Spotted Woodpecker nest 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 were found within the study area each year during the period 1987–2018. The annual census typically lasted from early April to mid-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 cavities were carried out by the first author.

Nest cavity data

Nest cavities

All the cavities made by Lesser Spotted Woodpeckers for nesting during the study period were classified as nest cavities. However, the data set comprised only those cavities where the Lesser Spotted Woodpecker definitely reached at least the egg-laying phase, i.e. cavities where nesting attempts were interrupted during excavation, although they would have contained a seemingly complete nest cavity, were not included in these data. In addition, we only included cases where the complete annual reuse history (see below) of the cavity was available, starting from the year when the cavity was made.

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

The reuse of cavities

All nest cavities were monitored annually after the first year of Lesser Spotted Woodpecker nesting, until the cavities were no longer suitable for nesting (tree fallen, broken, logged, cavity damaged). Possible annual reuse (occupancy) of cavities by hole-nesting bird species was checked for during successive field visits in all territories by observations from the ground for up to 20–30 min per visit to confirm possible occupancy. The observations were made at such distances from the cavities that they did not disturb the behaviour of the cavity-breeding birds. The bird species using the cavity for breeding was recorded, although the occasional use of holes, e.g. for roosting, was not classified as a cavity occupancy. The visits were made 5–10 times per season at intervals of 1–7 days depending on the occupancy information of the cavity. If an occupancy in a cavity was not observed, it was nevertheless visited at least four additional times during the breeding season.

Possible uncertainties in estimations of survival and occupancy of cavities

All cavities in this study were actively initially used for nesting by Lesser Spotted Woodpeckers, therefore, the cavities were suitable for breeding for hole-nesting bird species. However, early damage in the first year of the cavity may have been underestimated, because several nests of the Lesser Spotted Woodpecker were not found until the nestlings were big and noisy. The probability of this type of damage is presumably quite low (see Wiktander *et al.* 2001), and thus this inaccuracy is likely to have a negligible effect on the overall cavity survival measures.

As the cavities were checked from the ground, there are potential errors associated with how the suitability of cavities and the occupancy of the cavities were measured (see Pakkala *et al.* 2018a,b). There may be an overestimation of suitable cavities, as part of the cavity could still be unsuitable, e.g. due to inside-cavity damage or other factors that cannot be detected from the ground. In addition, a proportion of true occupancies by hole-nesting bird species could have been missed in spite of efficient monitoring, which could result in an underestimation of the occupancy rates. Both types of errors tend to decrease the level of occupancies in all cavity age classes, but they should not affect the overall observed patterns of occupancy in our study. Occasional cases where a second breeding attempt occurred in the same cavity in the same year were not separately classified, and we were not able to control all possible second breeding attempts of birds in other cavities. The number of these cases was, however, small compared with total numbers and they have only negligible effects on general patterns. True survival rates may also be lower if the proportions of suitable cavities are overestimated, but this situation, together with possible greater occupancy rates, leads to similar or even steeper cumulative occupancy distributions and thus our main results should be robust (see also Pakkala *et al.* 2018a,b).

Age-class, cumulative and lifespan occupancies of cavities

In order to study and compare age-class and lifespan occupancies of cavities, we estimated the occupancy Occ_i in each age-class i during the lifespan of a cavity with the observed survival proportions q_i and occupancies o_i of each age class i of the cavities. Each age-class represented one year with a maximum of one nesting per year in a cavity (see below). This results in

$$Occ_i = o_i q_i.$$

To study the proportions of cavity occupancies during their lifespan, we estimated the cumulative occupancy $Occ_{cum,j}$ during the lifespan of a cavity to age-class j using the age-class occupancies Occ_i:

$$Occ_{cum,j} = \Sigma Occ_i, \text{ where } i = 1, ..., j.$$

If the oldest age-class of cavities is n, then, e.g. in a certain forest type, the total cumulative occupancy Occ_{tot} for a cavity during its lifespan is

$$Occ_{tot} = \Sigma Occ_i, \text{ where } i = 1, ..., n.$$

The value of Occ_{tot} equals (1) the expected total number of occupancies of secondary cavity-nesting birds during the lifespan of a cavity, and (2) the expected total annual numbers of occupied old cavities by secondary cavity-nesting birds per single territory of the Lesser Spotted Woodpecker, assuming that the territory is continuously occupied by the Lesser Spotted Woodpecker and a fresh cavity is produced every year (see Pakkala *et al.* 2018b).

To compare occupancy distributions in cavities in various forest types, we used standardized proportional estimates $Occ_{pr,i}$ that are estimated proportions of cumulative occupancy at an age-class i and total lifespan occupancy of the cavities:

$$Occ_{pr,i} = Occ_{cum,i}/Occ_{tot}.$$

Statistical methods

Survival functions of cavities were estimated by the Kaplan-Meier method (Kaplan & Meier 1958). Incidents where nest cavities were lost (e.g. where the tree had fallen or was broken, or from cavity damage) were classified as 'events' in the first year that they were not available. If nest cavities were lost by logging, however, they were classified as 'censored' in the last year that they were available for any bird species. Nest cavities that still existed at the end of the study period were classified in a similar way to the logged cavities. Log-rank tests were used to compare the survival distributions of the different groups. Goodness-of-fit tests were used in the multiple comparisons of proportions. Correlations between cavity age and occupancy were tested with Spearman's rank-order correlation. The comparison in timing between cavity damage and tree fall was made by the Mann-Whitney U-test. All statistical analyses were performed with SPSS Statistics v. 23 (IBM).

RESULTS

Forest types and the survival of cavities

During this study, a total of 106 nest cavities of the Lesser Spotted Woodpecker were detected and monitored throughout their lifespans. They were found in three main types of forests. Forests on mineral soils included (1) moist spruce-dominated forests of *Myrtillus* type (MT; n = 24, 22.6% by number), and (2) the more fertile, moist mixed forests of *Oxalis-Myrtillus* type (OMT; n = 44, 41.5%), in which we also included the smaller class of moist and deciduous tree-dominated forests of the *Oxalis-Maianthemum* type. Forested peatlands included (3) both deciduous tree-dominated, mixed and spruce swamps (SWAMP; n = 38, 35.8%) that were combined to a single class.

Median survival time of the 106 cavities was 6 years with a 25–75% interval of 5–10 years (Table 1, Figure 1). The respective median cavity survival time estimates in the three forest types were 8 years for MT, 6 years for OMT and 6 years for SWAMP; the survival times did not differ significantly between the forest types (log-rank test: $\chi^2_2 = 0.104$, $P = 0.95$; Table 1).

There were 82 natural cavity losses during the study period, with 53 cases due to tree fall or breakage and 29 cases due to cavity damage. Five nest trees were logged during the study period. Thus, cavity damage accounted for 35.4% of the natural losses of cavities, with 35.0% loss in MT (n = 20), 37.1% in OMT (n = 35) and 33.3% in SWAMP (n = 27). The number of natural losses did not significantly differ between forest types (goodness-of-fit test: $\chi^2_2 = 0.98$, $P = 0.95$; Table 1). There was a significant difference between the median cavity age at tree fall (6 years) and cavity damage (5 years; $U_{53,29} = 415.5$, $P = 0.001$).

Occupancy of cavities by forest bird species

The occupancy of the 106 old Lesser Spotted Woodpecker cavities by forest bird species was 32.0% (n_{occ} = 216, n_{all} = 675) and varied between 28.6–35.8% in the three forest types (Table 2), although these proportions did not significantly differ from each other ($\chi^2_2 = 3.10$, $P = 0.21$). In total, six bird species, including the Lesser Spotted Woodpecker, used old cavities during the study period. The most common species were Pied Flycatcher *Ficedula hypoleuca* (52.8%, n = 114), Great Tit *Parus major* (24.5%, n = 53) and Blue Tit *Cyanistes caeruleus*

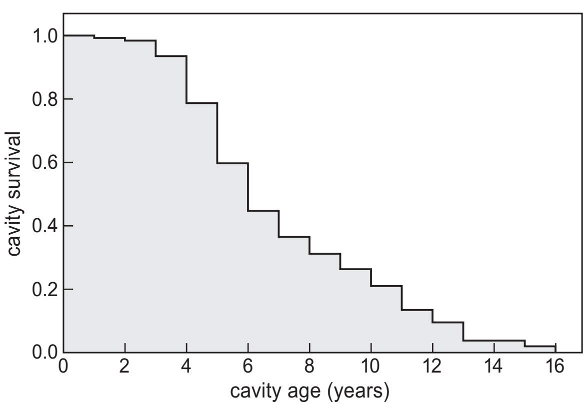

Figure 1. The survival function of the nest cavities of the Lesser Spotted Woodpecker (n = 106, Median = 6 years). Estimates are based on the Kaplan-Meier method.

Table 1. Survival time of the cavities of the Lesser Spotted Woodpecker, showing total number, 75%, median (50%) and 25% estimates with standard error (SE) in different 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). Estimates are based on the Kaplan-Meier method.

Area	Number	75% (years)	SE	Median (years)	SE	25% (years)	SE
MT	24	5.0	0.68	8.0	1.42	10.0	0.77
OMT	44	5.0	0.26	6.0	0.34	8.0	0.74
SWAMP	38	4.0	0.48	6.0	0.87	11.0	0.84
Total	106	5.0	0.28	6.0	0.43	10.0	0.80

Table 2. Bird species that occupied old cavities of the Lesser Spotted Woodpecker in relation to the forest type of the nest cavity location (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). For each species, and for each of the three forest types, the number of occupancies is presented.

Bird species	Forest type			Total
	MT	OMT	SWAMP	
Lesser Spotted Woodpecker *Dendrocopos minor*	1	3	–	4
Wryneck *Jynx torquilla*	2	3	–	5
Great Tit *Parus major*	15	18	20	53
Coal Tit *Periparus ater*	1	–	–	1
Blue Tit *Cyanistes caeruleus*	8	22	9	39
Pied Flycatcher *Ficedula hypoleuca*	21	51	42	114
Total number of occupancies	48	97	71	216
Occupancy (%)	28.6	35.8	30.1	32.0
Number of cases	168	271	236	675

(18.1%, $n = 39$). The other three species were only occasional users of old cavities: Wryneck *Jynx torquilla* (2.3%, $n = 5$), Lesser Spotted Woodpecker (1.9%, $n = 4$) and Coal Tit *Periparus ater* (0.5%, $n = 1$; Table 2). The occupancy distributions of the six species did not differ from each other between the forest types ($\chi^2_{10} = 14.5$, $P = 0.15$). Cavity reuse in the Lesser Spotted Woodpecker was 3.6% (four reuse cases out of 110 nesting attempts; Table 2).

We observed a strong, nonlinear decrease in occupancy proportions as the cavities became older: occupancy levels were 50–60% in cavities of age-class 1–2 years, 25–30% in cavities of age-class 3–5 years, c. 10% in cavities of age-class 6–11 years, and after 11 years cavities were practically unoccupied (Figure 2A). This negative correlation between the age of a cavity with the respective age-class occupancy was highly significant (Spearman's rank correlation, all cavities: $r_s = –0.882$, $df = 14$, $P < 0.001$). Within the three forest types, the correlation patterns were similar (MT: $r_s = –0.902$, $df = 11$; OMT: $r_s = –0.861$, $df = 14$; SWAMP: $r_s = –0.812$, $df = 11$; $P < 0.001$ in all cases).

If survival of cavities is taken into account, we estimate that 55% of all occupancies in old cavities took place during the first two years, and over 90% before the median age of the cavity (6 years; Figure 2B).

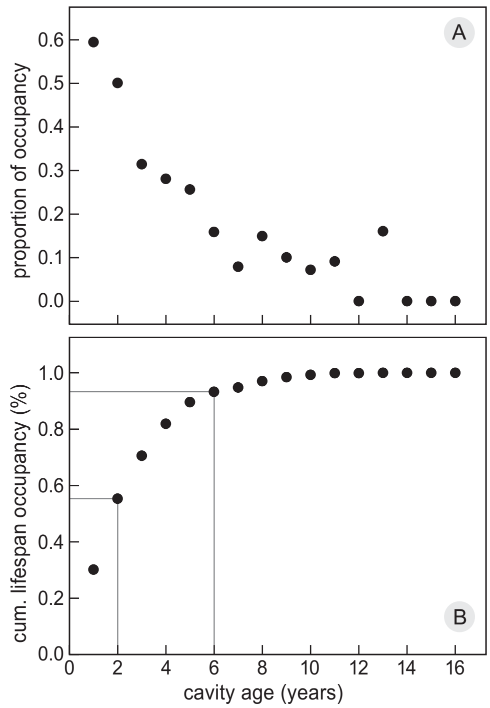

Figure 2. (A) Observed occupancies of old cavities of the Lesser Spotted Woodpecker at different ages (years). The occupancy rapidly decreases to 10% after the median survival age of the cavities (6 years), and cavities are unoccupied in the oldest age-classes. (B) Estimated cumulative lifespan occupancy percentage at different ages of old cavities. The thin grey lines show that 55% of all occupancies in old cavities took place during the first two years, and over 90% before the median survival age of the cavities.

Total number of nesting attempts in cavities

The total number of nesting attempts during the lifespan of a single nest cavity after the initial use by the Lesser Spotted Woodpecker (Occ_{tot}) was 1.97 for all cavities, 1.94 for MT, 2.14 for OMT and 1.84 for SWAMP. These values are also equal to the annual number of occupied old Lesser Spotted Woodpecker cavities per single territory if a new cavity is produced continuously every year.

DISCUSSION

Based on detailed, cavity-level and full lifespan monitoring, we found that cavities made by the Lesser Spotted Woodpecker have a rather long lifespan in boreal forests, but also that their reuse was quite limited, both in terms of number of species that used them as well as in times they were reused. These findings were generally similar to the respective patterns of the Three-toed Woodpecker *Picoides tridactylus* within the same study area (Pakkala *et al.* 2018a,b). The occupancy patterns in Lesser Spotted Woodpecker's cavities were quite similar across the various forest types and were also comparable to the survival time of the cavities. Long-term studies of woodpecker cavity survival (e.g. Meyer & Meyer 2001, Cockle *et al.* 2011, Wesołowski 2011, Blanc & Martin 2012, Edworthy *et al.* 2012, Edworthy & Martin 2013, 2014) have reported absolute survival times and described the risks and factors connected to the aging of cavities in various environments. However, studies that concentrate on the annual occupancy 'profiles' of various types of cavities or on the cavities of different primary excavator species are also needed to provide critical information of important ecological scales in cavity occupancy (see Pakkala *et al.* 2018a,b).

Survival patterns of cavities

The median survival times of the cavities within the various forest types were quite similar and varied between six and eight years. The median survival time of all cavities in this study (6 years: quartiles 5 and 10 years) was higher than the value reported for the Białowieża primeval temperate forest in Poland (4 years: quartiles 2 and 8 years); the only other known survival study of cavities of the Lesser Spotted Woodpecker (n = 54; Wesołowski 2011). In Poland, the survival times were similar to those of other woodpecker species that also use mostly dead or decaying trees, namely the Three-toed Woodpecker and White-backed Woodpecker *Dendrocopos leucotos*. The median cavity survival times of the Great Spotted Woodpecker *D. major* and the Black Woodpecker *Dryocopus martius* were significantly longer, at 9 and 18 years, respectively (Wesołowski 2011); long cavity survival times for these two species were also observed in other central European studies (Meyer & Meyer 2001, Günther & Hellmann 2005, see Pakkala *et al.* 2018a).

The median survival time of the Three-toed Woodpecker's cavities in our study area was longer (10 years) than that of the Lesser Spotted Woodpecker, although there were significant differences between forest types (range 7–13 years; Pakkala *et al.* 2018a). Although not studied here, the difference can be partly explained by the nest tree characteristics: Three-toed Woodpeckers mostly use coniferous trees with long survival times (Pakkala *et al.* 2018c, Pakkala unpubl. data), whereas Lesser Spotted Woodpeckers use only deciduous trees (Pakkala unpubl. data). In addition, cavity damage was higher (35.4%) in the old cavities of the Lesser Spotted Woodpecker compared to the cavities of the Three-toed Woodpecker in our study area (18%; Pakkala unpubl. data) and with all woodpecker cavities in Poland (19.8%; Wesołowski 2011). As cavity damage events always happen before the tree falls, a high percentage of cavity damage leads to a decrease in the total survival time of cavities. We do not have detailed data for all the various causes of cavity damage, although the Great Spotted Woodpecker often damage existing cavities in our study area.

Cavity occupancy patterns

Cavity occupancy in our study area was 32% with relatively small variation (28.6–35.8%) between the different forest types. In other studies, the occupancies of cavity-nesting bird species in natural and woodpecker-made cavities in Eurasian boreal and temperate areas are quite variable (range 3–93%; see review in Pakkala *et al.* 2018a). The occupancies of the Three-toed Woodpecker's cavities within our study area were lower than those of the Lesser Spotted Woodpecker; the value for all cavities was 21.3% and varied between 20.7–23.2% in the three forest types studied (Pakkala *et al.* 2018a). The higher occupancy levels observed in the Lesser Spotted Woodpecker's cavities may be because they are preferred by secondary cavity-nesters and/or may be due to the higher densities of these species in Lesser Spotted Woodpecker territories compared to Three-toed Woodpecker territories (see below).

We detected a significant, nonlinear decrease in the occupancy levels as the cavities aged: occupancy levels were 50–60% in cavities of age-class 1–2 years, then rapidly decreased and stabilized at 0–15% after 6 years. The general occupancy patterns were relatively similar to those observed in old cavities of the Three-toed Woodpecker within the same study area (Pakkala *et al.* 2018a). The occupancy patterns in old cavities of the Lesser Spotted and Three-toed Woodpecker were also similar across the different forest types, which would suggest a common cause of decreased quality in the cavities as they age. The general decrease in cavity occupancy by secondary cavity-nesting birds over time (review in Pakkala *et al.* 2018a) is usually expected as physical suitability and the temperature and humidity regulatory capacity of the cavities diminish with age (Wiebe 2001, Hilton *et al.* 2004, Günther & Hellmann 2005, Edworthy *et al.* 2012, Maziarz & Wesołowski 2013, Edworthy & Martin 2014).

Bird species assemblage using old cavities of the Lesser Spotted Woodpecker

The bird species assemblage that uses the old cavities of the Lesser Spotted Woodpecker reflects both the size of the nest entrance and cavity, and the forest types associated with the nest trees. The diameter of the cavity entrance of the Lesser Spotted Woodpecker is the smallest of all European woodpeckers, only 3–3.5 cm, and the cavity size is small (Glutz von Blotzheim & Bauer 1980, Cramp 1985, Glue & Boswell 1994), which prevents or decreases the opportunities for larger cavity-nesting bird species, such as Starling *Sturnus vulgaris*, Pygmy Owl *Glaucidium passerinum* and other woodpecker species, to use these cavities. The forests around the cavity sites were dominated by deciduous trees, often representing fertile forest types that were relatively rare in our study area, which is dominated by coniferous forests. The three most abundant secondary cavity-nesting bird species that were observed to nest in the old cavities of the Lesser Spotted Woodpecker were Pied Flycatcher, Great Tit and Blue Tit, which comprised over 95% of all observed nesting attempts in those old cavities. These three species are small in body size and occur at high densities in the nesting habitats of the Lesser Spotted Woodpecker within our study area (Pakkala unpubl. data).

We are not aware of any other study where the use of old cavities of the Lesser Spotted Woodpecker was annually investigated throughout the lifespan of each cavity, and so the most relevant comparison here is the respective use of old Three-toed Woodpecker cavities within the same study area (Pakkala *et al.* 2018b). Pied Flycatchers were the dominant secondary cavity-nesters both in Lesser Spotted cavities (55% of all nesting attempts) and in old cavities of the Three-toed Woodpecker (37.2%). In comparison, the respective percentages for Great Tits were 24.5% and 25.7%, while Blue Tits were much more abundant in old cavities of the Lesser Spotted Woodpecker (18% of all nesting attempts) compared with only occasional nesting attempts in old cavities of the Three-toed Woodpecker (1.3%). All other secondary cavity-nesting bird species only used the old cavities of Lesser Spotted Woodpeckers (three occasional species) or those of Three-toed Woodpeckers (two occasional species plus Three-toed Woodpecker (17.5%), Great Spotted Woodpecker (9.4%) and Pygmy Owl (8%); see Pakkala *et al.* 2018b).

The role of Lesser Spotted Woodpecker and other woodpecker species as cavity producers in boreal forests

Over half of all nesting attempts in the old cavities of the Lesser Spotted Woodpecker were restricted to relatively young cavities of 1–2 years of age, and over 90% of them occurred during the first half of the lifespan of the cavities. The expected total number of nesting attempts in a single old cavity during its lifespan was around two, with only a slight variation between the different forest types. This value is also equal to the annual number of occupied old cavities of the Lesser Spotted Woodpecker per single territory (provided a new cavity is produced continuously every year). A similar type of cavity occupancy profile was also observed in the old cavities of Three-toed Woodpeckers within the same study area (Pakkala *et al.* 2018a,b), which may indicate a common pattern whereby cavities are mostly excavated in dead or decaying trees (Pakkala *et al.* 2018c, Pakkala unpubl. data) with poor temperature and humidity regulatory capacities (see above). If older cavities are rarely occupied, then those cavity-nesting bird species that use the old cavities of Lesser Spotted and Three-toed Woodpeckers would constantly need new cavities to be produced for them.

In an earlier study, we reported that while the Three-toed Woodpecker was important for some cavity-nesting bird species, mainly in natural and lightly managed forests, its impact as a cavity producer was generally small (Pakkala *et al.* 2018b). As the Lesser Spotted Woodpecker is a relatively rare woodpecker species with a cavity occupancy profile type similar to the Three-toed Woodpecker, we consider that the use of its old cavities for cavity-nesting bird species in the boreal forest ecosystem is not significant. However, in certain special habitats, e.g. in riparian forests and in fertile forests around agricultural areas, old cavities may have a local importance for cavity-nesting birds in boreal forest areas.

It has been suggested that in boreal forest areas most cavities for hole-nesting birds are made by woodpeckers (Aitken & Martin 2007, Cockle *et al.* 2011, Andersson *et al.* 2018). However, to fully understand the role that cavities made by woodpeckers have, requires detailed and repeated surveys on the reuse patterns and longevity of the cavities. Based on our results, secondary cavity-nesters seem to prefer rather new cavities, as the reuse of older cavities declines rapidly as cavities become older. This suggests that the occupancy of a cavity by secondary users is not directly related to its persistence. The observed pattern emphasizes the need for regular and annual production of new cavities to meet the needs of secondary cavity-users. To facilitate this, it seems essential to better understand the role of different woodpecker species and host trees in the provision of cavities.

To be a true forest keystone species, a woodpecker species should also be able to produce cavities in a wide range of forest types, since secondary users occur in various forest habitats. Thus, in Eurasian boreal areas, the Great Spotted Woodpecker and Black Woodpecker are good candidates for such keystone species: they are the most common woodpecker species (Dementiev & Gladkov 1966, Glutz von Blotzheim & Bauer 1980, Cramp 1985), and thus probably the most important producers of cavities in these areas.

Finally, there is a need to address the maintenance of cavities in managed forests. To enhance cavity availability and survival in managed forests, existing cavities should be maintained and the possibilities for new cavities should be supported. Cavities are lost through tree falls, which can be partly compensated by avoiding the logging of existing cavity trees whenever possible. Moreover, by leaving large, decaying trees, which are generally preferred by most woodpecker species (see Winkler & Christie 2002), we can ensure a continuum of suitable cavity trees in the future that will benefit both the common and more specialized woodpecker species and their secondary cavity-nesters.

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REFERENCES

Aitken K.E.H. & Martin K. 2004. Nest cavity availability and selection in aspen-conifer groves in a grassland landscape. Can. J. For. Res. 34: 2099–2109.

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.

Aitken K.E.H., Wiebe K.L. & Martin K. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119: 391–402.

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.

Bai M.-L., Wichmann F. & Mühlenberg M. 2003. The abundance of tree holes and utilization by hole-nesting birds in a primeval boreal forest of Mongolia. Acta Orn. 38: 95–102.

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.

Carlson A., Sandström U. & Olsson K. 1998. Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. Ardea 86: 109–119.

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.

Edworthy A.B. & Martin K. 2013. Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. J. Wildl. Manage. 77: 770–776.

Edworthy A.B. & Martin K. 2014. Long-term dynamics of the characteristics of tree cavities used for nesting by vertebrates. For. Ecol. Manage. 334: 122–128.

Edworthy A.B., Wiebe K.L. & Martin K. 2012. Survival analysis of a critical resource for cavity-nesting communities: patterns of tree cavity longevity. Ecol. Appl. 22: 1733–1742.

Edworthy A.B., Trzcincki M.K., Cockle K., Wiebe K.L. & Martin K. 2017. Tree cavity occupancy by nesting vertebrates across cavity age. J. Wildl. Manage. 82: 639–648.

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. (In German)

Günther E. & Hellmann M. 2005. Development and new tenants of holes of spotted woodpeckers (*Dendrocopos*) in the "Swift-forest" in the Harz Mountains (Sachsen-Anhalt). Results of twenty years investigations of the use of natural tree holes. Orn. Jber. Mus. Heineanum 23: 103–122. (In German with English summary)

Hilton G.M., Hansell M.H., Ruxton G.D., Reid J.M. & Monaghan P. 2004. Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. Auk 121: 777–787.

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

Kaplan E.L. & Meier P. 1958. Nonparametric estimation from incomplete observations. J. Amer. Stat. Ass. 53: 457–485.

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

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.

Maziarz M. & Wesołowski T. 2013. Microclimate of tree cavities used by great tits (*Parus major*) in a primeval forest. Avian Biol. Res. 6: 47–56.

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

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. 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. For. Ecol. Manage. 413: 70–75.

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 Orn. 53: 69–79.

Pakkala T., Tiainen J., Piha M. & Kouki J. 2018c. Nest tree characteristics of the old-growth specialist Three-toed Woodpecker *Picoides tridactylus*. Ornis Fennica 95: 89–102.

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.
Remm J., Lõhmus A. & Remm K. 2006. Tree cavities in riverine forests: What determines their occurrence and use by hole-nesting passerines? For. Ecol. Manage. 221: 267–277.
van Balen J.H., Booy C.J.H., van Francker J.A. & Osieck E.R. 1982. Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest sites. Ardea 70: 1–24.
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 – preliminary data. Acta Orn. 22: 1–21.
Wiebe K.L. 2001. Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? Auk 118: 412–421.
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. Annual and seasonal reproductive trends in the Lesser Spotted Woodpecker *Dendrocopos minor*. Ibis 143: 72–82.
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.

SAMENVATTING

Spechten en andere holenbroeders die zelf holtes in bomen hakken (primaire holenbroeders) leveren nestlocaties voor verschillende andere holenbroeders (secundaire holenbroeders) op en worden daarom vaak beschouwd als soorten die een sleutelrol in het systeem spelen. De mate van hergebruik en de bezettingsgraad van nestholtes zijn zelden onderzocht, waardoor het werkelijke belang van primaire holenbroeders onduidelijk blijft. In dit onderzoek zijn nestholtes van Kleine Bonte Spechten *Dendrocopos minor* gedurende hun hele bestaan gevolgd. De gegevens omvatten de jaarlijkse beschikbaarheid en bezettingsgeschiedenis van 106 nestholtes in een gebied van 170 km^2 in Zuid-Finland gedurende 1987–2018. De mediane bestaanstijd van een nestholte was zes jaar, maar er waren verschillen tussen de verschillende bostypen (range zes tot acht jaar). De mediane tijd tot verval van de holtes was zes jaar en voor schade aan de holtes vijf jaar. Zes vogelsoorten gebruikten de oude holtes om later in te broeden, met de Bonte Vliegenvanger *Ficedula hypoleuca* als dominante soort (met 53% van alle nestholtebezettingen). Hergebruik van de nestholtes door Kleine Bonte Spechten bedroeg 3,6% van alle broedpogingen. De gemiddelde bezetting van oude nestholtes door secundaire holenbroeders was 32% (variërend van 29% tot 36% in de verschillende bostypen). Er was een significant negatief verband tussen de jaarlijkse bezettingsgraad en de leeftijd van de nestholte. In de eerste twee bestaansjaren van een nestholte werden ze het meest gebruikt; 90% van de bezetting vond plaats voor de mediane leeftijd (6 jaar) van de holtes. Het verwachte gemiddelde aantal bezettingen gedurende de bestaansduur van een nestholte door secundaire holenbroeders was 1,97 per nestholte. De resultaten geven aan dat er voortdurend nieuwe holtes nodig zijn voor secundaire holtebroeders die gebruikmaken van nesten van Kleine Bonte Spechten in hun territorium.

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