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Three-toed Woodpecker cavities in trees: A keystone structural feature in forests shows decadal persistence but only short-term benefit for secondary cavity-breeders

Timo Pakkala[a,b,*], Juha Tiainen[c], Markus Piha[d], Jari Kouki[b]

[a] University of Helsinki, Lammi Biological Station, FI-16900 Lammi, Finland
[b] University of Eastern Finland, School of Forest Sciences, P.O. Box 111, FI-80101 Joensuu, Finland
[c] Natural Resources Institute Finland, P.O. Box 2, FI-00791 Helsinki, Finland
[d] Finnish Museum of Natural History – LUOMUS, P.O. Box 17, FI-00014 University of Helsinki, Finland

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ABSTRACT

Primary cavity-producers like woodpeckers are often considered as keystone species, because they produce nest-sites also for several other cavity-nesting animals and, thus, maintain ecological webs of cavity-breeders. However, the detailed temporal dynamics of cavities and their lifetime occupancy rates and survival are not usually known which makes it difficult to assess the actual significance and full impact of primary cavity-breeders. In this study, we monitored cavities in a large forest landscape, covering the full lifetime of cavities. We focused on a mature and old-growth forest specialist cavity-breeder, the Three-toed Woodpecker *Picoides tridactylus*. The data include the annual occupancy history of 655 old cavities of the Three-toed Woodpecker in 86 territories in a 170-km^2 area in southern Finland during 1987–2017. The study area included both managed and natural forest types. The median survival time of a cavity was 10 years, but there were significant differences between forest area types with a range of 7–13 years. The occupancy in all cavities was 21.3%, and the cavities were available for secondary cavity-breeders each year. There was a significant negative correlation between the occupancy and the age of the cavity. The first five years of a cavity were important for the total occupancy, and 86% of occupancies took place before the median age of the cavities. In cavities older than 15 years the occupancy was only 7%. The pattern was similar in all types of forests. Our results show that cavities made by Three-toed Woodpeckers have rather long lifespan but also that their active use by other cavity-breeding species is restricted mostly to few years only. The result indicates that new, fresh cavities are needed continuously in a forest landscape, in order to maintain the role that Three-toed Woodpecker has as a keystone species.

1. Introduction

Woodpeckers are considered as keystone species in their breeding environments, because they produce cavities that various cavity-nesting animals like mammals, birds and invertebrates use afterwards (Jones et al., 1994; Martin and Eadie, 1999; Aitken and Martin, 2007; Drever et al., 2008; Cockle et al., 2011). Several studies about the numbers of various types of cavities (see Remm and Lõhmus, 2011; Andersson et al., 2017), species and occupancies of old cavities (e.g. van Balen et al., 1982; Carlson et al., 1998; Pulliainen and Saari 2002; Aitken et al., 2002, Aitken and Martin, 2004; Bai et al., 2003, Günther and Hellmann, 2005; Remm et al., 2006; Edworthy et al., 2017), and the survival of cavity trees (Cockle et al., 2011; Wesołowski 2011; Edworthy et al., 2012; Edworthy and Martin, 2014) have been conducted at natural nest sites of hole-nesting birds in northern temperate or boreal forests. However, detailed monitoring of occupancy and survival of individual cavities throughout their life-span is seldom done, and this makes it challenging to evaluate the ecological significance of primary cavity-producers for the secondary cavity-inhabiting species.

We studied the survival and reuse of cavities originally made by the Three-toed Woodpecker *Picoides tridactylus*, a mature and old-growth forest specialist, which is regarded as an indicator species of structural diversity and bird species richness of forest environments (Bütler et al., 2004; Roberge et al., 2008; Pakkala et al., 2014). In this study, we used an exceptionally large data set of cavities made by the Three-toed Woodpecker from southern Finland with annual information of the use of cavities during their lifetime.

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* Corresponding author at: University of Helsinki, Lammi Biological Station, FI-16900 Lammi, Finland.
E-mail addresses: timo.pakkala@hotmail.fi (T. Pakkala), juha.tiainen@luke.fi (J. Tiainen), markus.piha@helsinki.fi (M. Piha), jari.kouki@uef.fi (J. Kouki).
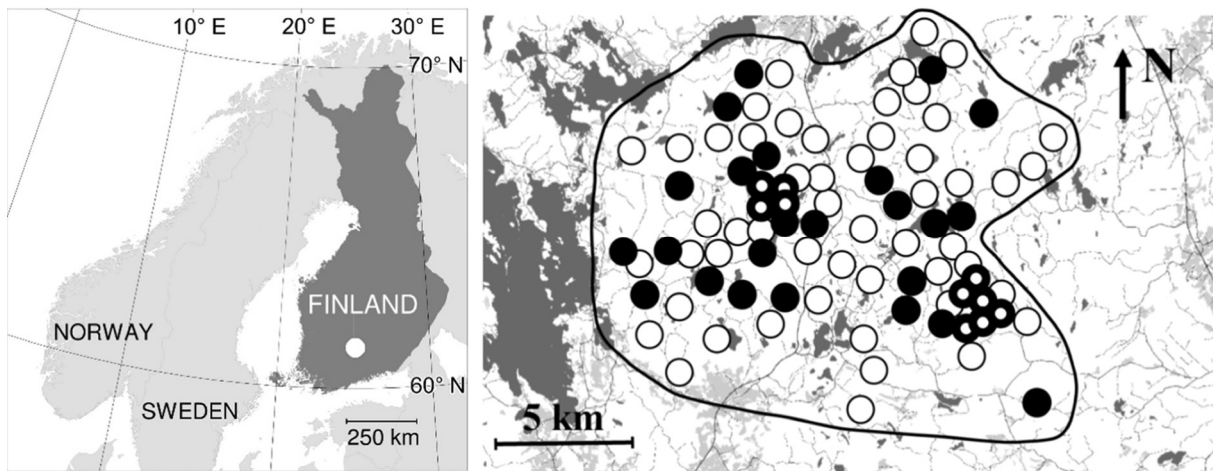
Fig. 1. Location of the study area (white dot) in southern Finland (61° 15′ N; 25° 03′ E; left) and study area (encircled) with the locations of natural (◉), managed core (●) and other managed (○) territory areas of the Three-toed Woodpecker in this study during the period 1987–2017 (right). Lakes are represented by dark grey and agricultural areas by light grey shading. Roads are marked by thin black lines.

We focused on the following questions:

(1) What are the survival patterns of Three-toed Woodpecker cavities in different kinds of forest areas?
(2) What is the occupancy of cavities originally made by Three-toed Woodpecker for forest bird species?
(3) How do the occupancy patterns vary during the complete lifetime of cavities?

Finally, we discuss the importance of survival and occupancy patterns (i) in relation to the current knowledge of the topic, (ii) and their implications for forest management and conservation.

2. Material and methods

2.1. Study area

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

2.2. Three-toed Woodpecker nest surveys

The Three-toed Woodpecker nests and nest trees were annually searched in the study area during 1987–2017 in connection with an intensive population study of the species (described in detail in Pakkala et al., 2006, 2017). Annual censuses lasted from early April to the middle of July. They included systematic mapping of territories before the breeding season with efforts to locate the most potential nesting sites by observing the behaviour of woodpeckers and searching of nests during the whole breeding season. Annual territory locations and their approximate borders were defined by information from woodpeckers and their nest sites. Locations of nest trees were mapped and the territory of each nest cavity was defined. All surveys were done by the author TP.

2.3. Nest cavity data

2.3.1. Definitions of nest cavities

All the cavities made by the Three-toed Woodpecker for nesting during the study period were classified as nest cavities. However, the data set comprised only those cases of cavities where the Three-toed Woodpecker most certainly reached at least the egg-laying phase, i.e. nesting attempts interrupted during excavation – although they would have contained a seemingly complete nest cavity – were not included in these data. The proportion of these cases was ca. 5% of all nesting attempts. We also included only cases where the complete annual reuse history (see below) of the cavity from the fresh cavity year was available during the study period.

2.3.2. Monitoring the reuse of cavities

All nest cavities were annually monitored after the first year of Three-toed Woodpecker nesting until the cavities were not suitable for nesting (tree fallen, broken, logged, nest cavity damaged). The possible annual reuse (occupancy) of cavities by any hole-nesting bird species was checked during successive field visits in all territories by observations from the ground for up to 20–30 min in each 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 species. The bird species using the cavity for breeding was defined; occasional use of holes, e.g. for roosting, was not classified as a cavity occupancy. The visits were made 5–15 times per season with intervals of 1–7 days depending on the occupancy information of the cavity. If a confirmed nesting attempt in a cavity was not observed, it was visited at least four additional times during the breeding season.

2.4. Classification of forest area types

We divided the study area into various types to analyse the spatial variation in the nest cavity survival and reuse of old Three-toed Woodpecker's cavities. The division is based on two important ecological factors: (i) the occupancy of the Three-toed Woodpecker territories that indicates the structural complexity and quality of the forest landscape (Pakkala et al., 2002), and (ii) the intensity of forest management and naturalness of the forest area. We used a two-step classification. In the first step, all those territory sites where the Three-toed Woodpecker nestings were observed during the whole study period (31 years, $n = 86$ different territory sites) were classified as being either in core or other areas. The division was based on the occupancy rate of each territory. This rate was calculated as the proportion of years with

territorial behaviour or nesting during all census years (see Pakkala et al., 2017). The two classes based on occupancy rates were separated: (1) territories in core areas, 34 territores with occupancies > 90% (mean 0.98), and (2) territories in other areas, 52 territories with occupancies < 60% (mean 0.32). In the second step, the territory sites located in the core areas were divided into two classes, based on their forest management history: (i) natural and (ii) managed core areas. Natural areas included forests in their natural stage, without or with only slight management during the last 150 years (Tuominen, 1990; S. Tuominen, pers. comm.). Natural core areas included 10 territory sites in total. All other core areas (*n* = 24) were classified as managed core areas, with variable intensity of forestry activities during the last decades. We use the respective terms "natural core", "managed core", and "managed other" areas for the three types of forest areas (Fig. 1).

2.5. Cumulative lifetime occupancies of cavities

In order to study and compare the proportions of cavity occupancies during their lifetime, we estimated the cumulative occupancy *Cumocc_j* during the lifetime of a cavity to age-class *j* by the survival proportions q_i and occupancies o_i of each age class (*i*) of the cavities. Each age class represented one year with maximally one nesting per year in a cavity (see below).

$$Cumocc_j = \sum o_i q_i, \quad \text{where } i = 1,...,j. \tag{1}$$

If the oldest age-class of cavities is *n*, then, e.g. in a certain forest area, the total cumulative occupancy *Totocc* for a cavity during its lifetime is

$$Totocc = \sum o_i q_i, \quad \text{where } i = 1,...,n. \tag{2}$$

To compare cumulative occupancy distributions in cavities of different age in various areas, we use standardized estimates *Stcumocc_j* that are proportions of cumulative occupancy at an age class and total life-time occupancy of the cavities.

$$Stcumocc_j = Cumocc_j / Totocc. \tag{3}$$

2.6. Possible inaccuracies in estimations of survival and occupancy of cavities

In our study, all cavities were in the beginning actively used for nesting by Three-toed Woodpeckers hence indicating that the cavities were suitable for breeding for hole-nesting bird species. As the cavities were checked from the ground, there are possible errors in the measures of (i) the suitability of cavities, and (ii) the occupancy of cavities. In (i), there may primarily be an overestimation of suitable cavities because part of them could still be unsuitable e.g. due to inside-cavity damages, resin flow or other factors undetectable from the ground. Wesołowski (2001) detected an overestimation of 6–21% in suitable cavities when ground check results were compared with interior checks of mostly natural cavities in a temperate forest area in Poland. In (ii), part of true occupancies by hole-nesting bird species could have been missed in spite of efficient monitoring (see above) that can cause some underestimation of the occupancy proportions. Both types of errors tend to decrease the levels of occupancy in all cavity age classes, but they do not change the overall patterns of occupancy in our study. Occasional cases of second breeding in the same cavity in the same year were not separately classified, and we could not exactly control all possible second breeding attempts of birds in other cavities in the same year. The number of these cases was, however, very 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 values, leads to similar or even steeper cumulative occupancy distributions and thus our main results are not changed.

2.7. Statistical methods

Survival functions of cavities were estimated by the Kaplan-Meier method (Kaplan and Meier, 1958). The incidents where nest cavities were lost by the tree fallen or broken, or by cavity damage were classified as "events" in the first year they were no more available, but if nest cavities were lost by logging they were classified as "censored" in the last year they still were available for any bird species. Log-rank tests were used to compare the survival distributions of different groups. The occupancy distributions were compared with related samples Friedman's two-way analysis of variance of ranks. After a significant result, a Bonferroni-corrected level *p* < .05 in the multiple comparisons of proportions (goodness-of-fit tests) was used. Correlation between cavity age and occupancy was tested using Spearman's rank-order correlation. All statistical analyses were performed with IBM SPSS Statistics 23.

3. Results

3.1. The survival of cavities

The estimate for median survival time of the 655 cavities was 10 years with a 25–75% interval of 5–17 years (Table 1, Fig. 2a). The respective median cavity survival time estimates in the three areas were 11 years for natural (*n* = 143), 13 years for core managed (*n* = 322), and 7 years for other managed areas (*n* = 190). The areas significantly differed from each other (log-rank test: $\chi^2 = 44.1$, *p* < .001, *df* = 2; Table 1, Fig. 2b), and all pairwise differences were significant (natural vs. managed core: $\chi^2 = 6.1$, *p* = .013, managed core vs. other managed: $\chi^2 = 40.6$, *p* < .001; natural vs. other managed $\chi^2 = 13.1$, *p* < .001, *df* = 1 in all cases).

3.2. The occupancy of cavities

The occupancy of the 655 old Three-toed Woodpecker cavities was 21.3% ($n_{occ} = 1196$, $n_{all} = 5627$) varying between 20.7 and 23.2% in the three areas; these proportions did not significantly differ from each other (goodness-of-fit test: $\chi^2 = 2.99$, *p* = .22, *df* = 2). Altogether eight bird species, including the Three-toed Woodpecker, were detected to use old cavities during the study period. The most common species were the Pied Flycatcher *Ficedula hypoleuca* with 37.2% of cases (*n* = 445), the Great Tit *Parus major* with 25.7% (n = 307), and the Three-toed Woodpecker with 17.5% (*n* = 210). The Great Spotted Woodpecker *Dendrocopos major* with 9.4% (*n* = 112), and the Pygmy Owl *Glaucidium passerinum* with 8.0% (*n* = 96), were also regular users of old cavities, whereas three additional species were only occasional: the Blue Tit *Cyanistes caeruleus* with 1.3% (*n* = 16), the Redstart *Phoenicurus phoenicurus* and the Red-breasted Flycatcher *Ficedula parva* both with 0.4% (*n* = 5).

We observed a clear, nonlinear decrease in occupancy proportions as the cavities got older; the occupancy levels were 30–40% in cavities of the age of 1–3 years, ca. 20% in cavities of the age of 4–6 years, and then after 10 years the occupancy level was ca. 7–10% (Fig. 3a). This

Table 1
Total numbers, 75.0%, median (50%), and 25.0% estimates with respective SE for survival time of the Three-toed Woodpecker's cavities. The figures are presented for total and separately for the three areas. The Kaplan-Meier method was used.

Area	Number	75% (years)	SE	Median (years)	SE	25% (years)	SE
Natural	143	6.0	0.67	11.0	1.1	16.0	0.83
Managed core	322	6.0	0.55	13.0	0.89	25.0	–
Managed other	190	5.0	0.36	7.0	0.32	10.0	0.44
Total	655	5.0	0.26	10.0	0.51	17.0	1.1
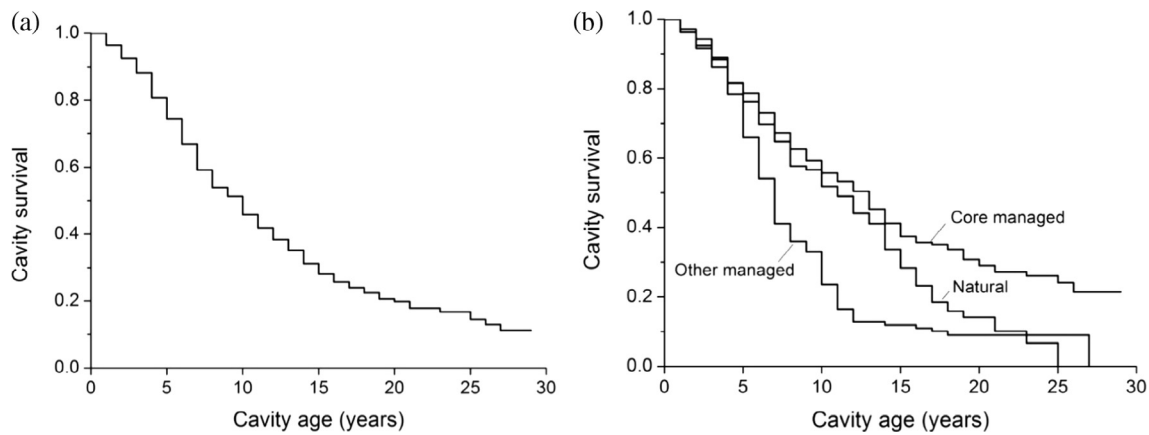
Fig. 2. The survival functions of the Three-toed Woodpecker's nest cavities. (a) All cavities (*n* = 655, *Md* = 10 years); (b) cavities in the three areas (natural: *n* = 143; *Md* = 11 years; managed core: *n* = 322, *Md* = 13 years; managed other: *n* = 190, *Md* = 7 years). The Kaplan-Meier method was used.

negative correlation between the age of the cavity and the respective age-class occupancy was highly significant (Spearman's rank correlation, all cavities: $r_s = -0.857$, $p < .001$, $df = 27$; Fig. 3). Within the three areas, the correlation patterns were similar (natural: $r_s = -0.859$, $df = 23$; managed core: $r_s = -0.756$, $df = 27$; other managed areas: $r_s = -0.837$, $df = 25$; $p < .001$ in all cases; Fig. 3a). The occupancy distributions did not differ from each other (related samples Friedman's two-way analysis of variance of ranks: $F = 4.85$, $df = 2$, $p = .88$).

When we cumulatively sum up the pairwise products of survival and occupancy proportions of cavities in each age-class (see Eq. (3)), 67% of all occupancies were restricted to cavities that were at most five years, and 86% to cavities 10 years of age or younger, respectively (Fig. 3b). The respective proportions of the three areas were 67% and 88% for natural, 62% and 83% for core managed, and 81% and 96% for other managed areas. The total proportion of all cavities older than 15 years was 10% and their occupancy was 7% (Fig. 3).

4. Discussion

We found quite a striking pattern in the occupancies of forest bird species in old Three-toed Woodpecker's cavities. Even two thirds of all occupancies during the lifetime of cavities took place during the first five years after the excavation, and 86% during the first half of the lifetime of cavities. The occupancy patterns were quite similar in various forest areas that significantly differed in their cavity survival times. Long-term studies of cavity survival (e.g. Meyer and Meyer, 2001;

Cockle et al., 2011; Wesołowski, 2011; Blanc and Martin, 2012; Edworthy et al., 2012; Edworthy and Martin, 2013, 2014) have pointed out the absolute survival times, survival risks, and factors connected to the aging of cavities in various environments. These matters are essential to understand the general dynamics of cavity amounts and their availability, but we think that studies concentrating on the occupancy "profiles" of various types of cavities or cavities of different primary excavators are needed to complete the picture and give information about the important ecological scales in cavity occupancy.

4.1. The survival patterns of cavities

There were significant differences in the median survival times of the cavities between areas indicating spatial variation in the forest landscape, but probably also in the cavity tree properties which, however, were not investigated in this study. The median survival times of cavities were longer in the core territories (11 and 13 years) than in the non-core ones (7 years). The median survival time in natural areas, representing a sort of "original" environment of the Three-toed Woodpecker in southern Finland, was 11 years. This was significantly greater than in a primeval temperate forest in Poland, the only other known survival study of cavities of the species, where the median survival time was only 5 years with quartiles of 3 and 8 years (n = 38; Wesołowski, 2011). In Poland, the survival times of Three-toed Woodpecker's cavities were similar to those of other woodpecker species that also use mostly dead or decaying trees, namely the Lesser
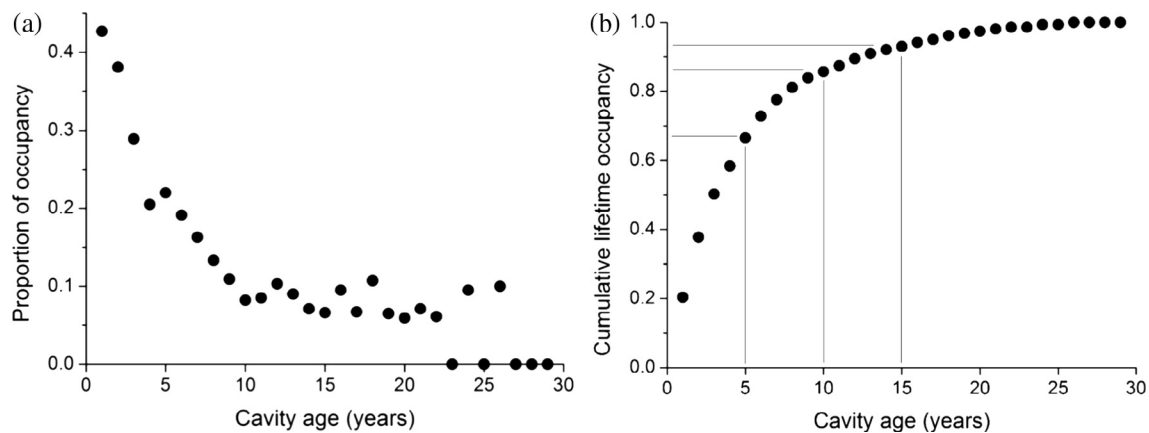
Fig. 3. (a) The occupancy of all Three-toed Woodpecker's old cavities at different age. The occupancy decreases to the level of 7–10% at the median survival age of the cavities (10 years). (b) The cumulative proportion of the lifetime occupancy of old Three-toed Woodpecker's cavities. The pairwise products of survival and occupancy proportions of cavities in each age-class are cumulatively summed up. Note that 67% of all occupancies take place during the first five years, and 86% before the median age of the cavities. The total proportion of all cavities older than 15 years was 10% and their occupancy was only 7%.

Spotted Woodpecker *Dendrocopos minor*, and White-backed Woodpecker *D. leucotos*. The median cavity survival times of the Great Spotted Woodpecker and Black Woodpecker *Dryocopus martius* were significantly longer, 9 and 18 years, respectively (Wesołowski, 2011). Long survival times of the cavities of the latter two species were observed also in Germany, where 70% of the cavities of Great Spotted Woodpecker in living Sessile Oaks *Quercus petraea* after 20 years (Günther and Hellmann, 2005), and 94% of the cavities of Black Woodpecker in living Common Beeches *Fagus sylvatica* after 24 years (Meyer and Meyer, 2001) were still usable.

There are no published long-term data of woodpecker cavity survival from boreal forest areas of northern Europe. However, based on the information of nest trees of different woodpecker species in boreal forests (e.g. Pynnönen, 1939; Pouttu, 1985; Hågvar et al., 1990; Johnsson, 1993; Rolstad et al., 1995; Stenberg, 1996; Rolstad, et al., 2000; T. Pakkala, unpublished), we can expect substantially longer survival times for Great Spotted and Black Woodpecker cavities compared with those of the Three-toed Woodpecker, because the former two species use bigger, harder, and healthier trees for their nest cavities. Besides the spatial variation of cavity survival observed within our study area, there may be geographical variation within the boreal area that has effects on survival times of the cavities. E.g., in our study area in southern Finland, the Norway spruce *Picea abies* was the dominant nest tree with the proportion of 70.1% (T. Pakkala, unpublished), but in northern Finland the Scots pine *Pinus sylvestris* constituted 60.4% of observed nest trees, and the proportion of the Norway spruce was only 31.2% (Saari et al., 1998). The Norway spruce nest trees of the Three-toed Woodpecker are usually infected by heart rot, and they have greater risks to fall than the Scots pines (T. Pakkala, unpublished; Lännenpää et al., 2008; Wesołowski, 2011).

4.2. The cavity occupancy patterns

The cavity occupancy in our study area was 21.3% with only small variation (20.7–23.0%) between different forest areas. In other studies, the occupancies of hole-nesting bird species in Eurasian boreal and temperate areas were quite variable. Small occupancy values were detected e.g. in northern Finland: 3.3% (boreal, mostly woodpecker cavities, Pulliainen and Saari, 2002), in Mongolia: 5.2% (boreal, mostly natural cavities, Bai et al., 2003), and in south central Sweden: 5–10% (hemiboreal, mostly natural cavities, Carlson et al., 1998). Larger occupancy values were observed e.g. in Wales: 21% (temperate, mostly natural cavities, Edington and Edington, 1972), in Poland: 36–52% (temperate, mostly natural cavities, Wesołowski, 2011), and in the Netherlands: 54–93% (temperate, mostly natural cavities, van Balen et al., 1982). The environment type affects the cavity occupancy, as shown for the Black Woodpecker's (central Sweden, Johnsson et al., 1993) and Great Spotted Woodpecker's (northern Japan, Kotaka and Matsuoka, 2002) old cavities. In Black Woodpecker cavities the occupancies of hole-nesting birds were 48–61% in forests around agricultural areas and 20% in more continuous forest areas, and in Great Spotted Woodpecker cavities 69% in urban, and 17% in suburban forest areas. Part of the variation in observed occupancy proportions between the studies is most probably connected to variable efficiencies and methods that were applied to define the suitability of cavities (see Ouellet-Lapointe et al., 2012), but we think that the different magnitudes of occupation give a reliable overall view of the patterns.

We detected a significant, nonlinear decrease in the occupancy proportions as the cavities got older; the occupancy levels were 30–40% in cavities of the age of 1–3 years, then decreased and finally after 10 years stabilized to the level of ca. 7–10%. The patterns were relatively similar in all different forest areas, which indicates a common cause of decrease in the quality of cavities with age. The general decrease in cavity occupancy over time is usually expected because e.g. physical suitability, safety, and both temperature and humidity regulation abilities of cavities diminish (Wiebe, 2001, Günther and

Hellmann, 2005; Edworthy et al., 2012; Maziarz and Wesołowski, 2013; Edworthy and Martin, 2014).

Most studies with information on the occupancy of cavities during several years are restricted to compare occupancy or reuse of cavities mostly in two or three successive years without knowledge of the exact age of the cavity (e.g. van Balen et al., 1982; Sedgwick, 1997; Meyer and Meyer, 2001; Aitken et al., 2002; Aitken and Martin, 2004; Remm et al., 2006). However, Edworthy et al. (2017) studied the occupancy of secondary users in various types of cavities during a 21-year period. They found that cavity occupancy was highest one year post-excavation (53%), declined to 40% after two years, remained at 33% between 3 and 16 years of age, and finally increased to 50% during 17–20 years after excavation. Different cavity types and secondary users had various preferences to cavity age. Günther and Hellmann (2005) studied the occupancies by forest bird species in old *Dendrocopos* woodpecker cavities of varying age during a 20-year period. They found a clear decrease in occupancy during their study period. There are few studies where the occupancy by hole-nesting bird species was investigated in the same cavities during several years directly after the excavation year. Kotaka and Matsuoka (2002) followed the occupancies of hole-nesting bird species in old Great Spotted Woodpecker's cavities during the first four years after the excavation, and they found that in urban areas, 86% of 1 year-old and 57% of 2–4 year-old cavities were occupied, while the respective occupancies were 25 and 13% in suburban areas. Mazgajski (2007) studied the use of old Great Spotted Woodpecker's cavities by the Starling *Sturnus vulgaris* during five years after the cavity excavation, and he detected a significant, linear decrease in occupancy from the level of 76% in the first year cavities to ca. 30% in the fifth year. In all of the last studies, the physical deterioration of the cavity and the accumulation of old nest material were estimated as the main reasons for decreased occupancies (Kotaka and Matsuoka, 2002; Günther and Hellmann, 2005; Mazgajski, 2007).

4.3. Combining survival and occupancy: cavity occupancy profiles over time are important for management and conservation

The cumulative lifetime cavity occupancy, where cavity occupancies are weighted by the survival proportions of cavities in each age-class, gives a cavity occupancy profile for old Three-toed Woodpecker's cavities. As the occupancy distribution was decreasing, we get an even more uneven pattern when cavity survival is included: two thirds of all occupancies were on average restricted to relatively new cavities of the age of five years or younger. The median survival time of cavities was ten years, but 86% of all occupancies took place already during the first half of a cavity's lifetime. Concerning the hole-nesting bird species that use Three-toed Woodpecker's old cavities, a constant production of new cavities would then be essential for them. As many territories are not continuously occupied by the Three-toed Woodpecker, and the species also reuses old cavities for breeding (Pakkala et al., 2017), the numbers of relatively new cavities and availability for other species considerably vary between its territories.

The Three-toed Woodpecker is a part of the guild of primary excavators in boreal forests, where most cavities for hole-nesting birds are made by woodpeckers (Aitken and Martin, 2007; Cockle et al., 2011; Andersson et al., 2017). It should be useful to get respective occupancy profile information about other woodpecker species' cavities, especially concerning the Great Spotted and Black Woodpecker that are the most common Eurasian boreal woodpecker species (Dementiev and Gladkov, 1966; Glutz von Blotzheim and Bauer, 1980; Cramp, 1985; Winkler and Christie, 2002), and thus the most important producers of cavities in these areas. The Great Spotted and Black Woodpecker are considered as strong excavators, but they probably select the suitable nest trees and cavity sites in trees with harder outer layers and softer interior parts (Meyer and Meyer, 2001; Zahner et al., 2012; Hebda et al., 2017). In general, woodpecker species seem to have species-specific decay selection profiles for cavity excavation in relation to the suitable nest tree stages (Blanc and Martin, 2012).

5. Conclusions

Woodpeckers are often regarded as keystone species as providers of nesting cavities for a number of hole-nesting birds. Three-toed Woodpecker cavities showed long-term persistence but only short-term benefit for secondary cavity-breeders. The survival of cavities was higher in less managed forest areas, but there were no differences in occupancy between variously managed forests. To conclude, our results highlight the importance and availability of relatively new cavities for cavity-nesting forest bird species, but comparative studies concerning other woodpecker species are needed to evaluate the relevant time scales of the cavity use which would be important for the conservation and management of forest environments. Although it is important for cavity-nesting species to save existing cavity trees, especially those with several cavities and thus obvious long-term use, we think that the most useful strategy in the long run is to ensure a continuum of such living trees that are suitable for the woodpeckers' cavity trees in managed forest areas.

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