“Lifespan” of non-excavated holes in a primeval temperate forest: A 30 year study

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ABSTRACT

Numerous forest organisms rely on non-excavated tree-holes, which are often limited in managed European woods. Holes’ supply depends on formation rates and persistence times. I use 30 years of data from a primeval forest (strictly protected reserve, Białowieża National Park, Poland) to determine how long non-excavated holes persist, whether their persistence varies across forest types, tree species and conditions, or bird species using them. From 1979 to 2010, I followed the fate of 1794 holes, used by 14 non-excavator bird species. Almost half of them were destroyed during this time, most often (40%) due to tree fall or break off of the hole-bearing section, growing over injury (28%) or decay of walls (24%). Holes were retained for a median of 12 years, longer in deciduous habitats (11–13 years) than in coniferous forests (4.4–years). These differences were due to different sets of tree species used in different habitats. Lifespan of holes varied by tree species, ranging from 5 (Populus tremula) to 16.5 years (Quercus robur). Persistence was much lower for holes in dead (5 years) than in living (14 years) substrates. It increased with increasing tree size. Differences in persistence times of holes used by various bird species was mostly a by-product of them selecting trees of different qualities. Holes in large living trees, with relatively hard wood, persisted longest. Their retention should become a conservation priority. Current forestry policies should be modified, to assure that hole-bearing trees are retained, and trees in which replacement holes could be formed are maintained.

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1. Introduction

The formation and persistence of tree holes are key ecological processes that influence the abundance, diversity and conservatism of hole-dependent organisms (10–40% of bird and mammal species in forests, Cockle et al., 2011). Because most hole-users are non-excavators, i.e. they cannot excavate their own holes, their numbers can be limited by the availability of existing holes (e.g. birds, review in Newton, 1998). The shortage of holes can be especially pronounced in managed woods, where – due to forestry operations – a large proportion of trees are too young to contain any holes and larger, hole containing trees with signs of decay are often purposefully removed in forestry operations. Thus the presence of birds that can provide holes (excavators, e.g. woodpeckers) is often regarded as an indispensable requirement for the existence of the hole-dependent organisms and a top priority for the conservation of hole-nesting assemblages (Johnsson et al., 1990; Jones et al., 1994; Martin and Eadie, 1999; Mikusiński et al., 2001; Blanc and Walters, 2008; Drever et al., 2008). However, recent work revealed that woodpeckers appear to be the primary hole providers in North America but not on other continents (South America, Australasia or Eurasia) – Wesołowski (2007a), Cockle et al. (2011). Thus worldwide, most hole-using vertebrates are critically dependent on non-excavated holes, i.e. on holes “produced” by such processes as decay and damage. Therefore, if one wishes to preserve the whole assemblage of hole-users one has to assure that the non-excavated holes are available in an adequate supply and diversity. One has to guarantee, as well, that the processes “making” these types of holes are allowed to work at rates sufficient to produce an adequate supply of non-excavated holes.

It is difficult to study the role of these processes in Europe because the diversity of holes has been greatly reduced in managed European forests. Centuries of management have resulted in a reduced diversity of tree species, a shift in tree size towards smaller (younger) classes, and – due to sanitary felling – a reduction in availability of injured/decaying trees. In such conditions the array of substrates in which holes can be formed is highly restricted (Wesołowski, 2011).

Fortunately the role of the hole-forming processes can still be studied in the Białowieża National Park in eastern Poland, where the last fragments of primeval lowland temperate European forest persist. There, one can study processes which may have operated in European forests before their transformation by humans (Wesołowski, 1983; Tomiałojć et al., 1984; Tomiałojć and Wesołowski, 1990). In these conditions, free of direct human influence holes can form in diverse tree species, differing in their stature – from small young ones to large veteran trees – and condition, from live and healthy to dead and highly decayed (Wesołowski, 1989, 2007a). Here the “lifespan” of holes is not curtailed by management.
Therefore it is possible to measure their persistence times and to learn which factors affect their lifespan. Such benchmark data on hole retention times are necessary to inform policies to conserve the diverse suite of hole-dependent fauna (Sedgwick and Knopf, 1992; Wesołowski, 2007a; Cockle et al., 2011). Few data have been gathered on the lifespan of non-excavated holes (Sedgwick and Knopf, 1990, 1991; Remm et al., 2006; Nielsen et al., 2007; Cockle et al., 2011) including some preliminary results from the Białowieża National Park (Wesołowski, 2005; Cockle et al., 2011). They are mostly based on relatively short periods of observations, shorter than average persistence times of numerous holes in the studied systems.

I analyse here 30 years of observations on non-excavated breeding holes of birds in the primeval forest, Białowieża National Park, to determine how long non-excavated holes persist, and whether their persistence varies across forest types, tree species and conditions, and bird species using them. I analyse as well, causes of hole “mortality” and how are they related to the factors mentioned above. Following patterns of longevity observed in woodpecker-made holes in the same forest (Wesołowski, 2011). I expected to find substantial differences among tree species (their structural resistance tends to vary), and declining persistence of holes with the deteriorating tree health (holes in living trees “survive” longer than holes in decayed wood). Additionally, as location of holes used by individual non-excavator species within trees and internal dimensions of their holes differ widely (e.g. Wesołowski, 1989, 2002, 2007a; Czeszczewik and Walankiewicz, 2003; Wesołowski and Rowiński, 2004; Walankiewicz et al., 2007), I anticipate that these differences could affect their “lifespan” as well. Finally I discuss implications of my findings for conservation, preservation of holes and hole-using organisms in forests.

2. Study area and methods

2.1. Study area

The Białowieża Forest complex is situated in the middle of the European plains, at the Polish–Belarusian border (co-ordinates of Białowieża village: 52°41’N and 23°52’E). The western part of the forest (613 km², ca. 45% of the area) belongs to Poland. The forest represents a remnant of the vast lowland forests that once covered large parts of temperate Europe. Its present unique features result from its considerable size and an exceptionally good state of preservation (Tomiałojć and Wesołowski, 1990; Wesołowski and Tomiałojć, 1995; Wesołowski, 2005, 2007a). The majority of the tree stands in the Polish part are now under management, but a 47.5 km² block of the best preserved primeval old-growth stands has been retained within the strictly protected part of Białowieża National Park (hereafter BNP).

The primeval stands preserved there are distinguishable by an array of features: they are multi-storey, mixed-species, and uneven-aged. They contain many legacy trees (the tallest Picea abies can reach 55 m, and several other species reach 42–45 m), and a large amount of dead timber and downed trees (20–25% of total wood volume. Bobiec, 2002). Most of the BNP area is covered by three types of old-growth stands:

(1) Oak–lime–hornbeam forest Tilio-Carpinetum, richest in tree species and structurally the most diverse, which covers the largest areas (44% of total acreage); mostly composed of Carpinus betulus, Tilia cordata, Quercus robur, P. abies and Acer platanoides. Other trees (Ulmus spp., Betula spp, Populus tremula) occur as an admixture.

(2) Riverine forests (Circaeo-Alnetum, Carici elongatae-Alnetum), swampy, open canopy deciduous forests (riverine stands and carrs), with abundant dead wood, made up mainly by alder Alnus glutinosa, ash Fraxinus excelsior and P. abies, with some admixture of Betula spp. (coverage 22%).

(3) Coniferous forest Piceetum–Pinetum, mixed coniferous forests, dominated by P. abies, Pinus sylvestris (coverage 28%); deciduous trees, Betula spp., some Q. robur and P. tremula form an admixture.

2.2. Field methods

The field work was mostly carried out within six, 25–54 ha, permanent plots (total area of ca. 260 ha) established in 1975–1976 (Tomiałojć et al., 1984). All the plots were situated in never managed old-growth stands of natural origin, well dispersed in space (distance between sites 1–6 km) – Fig. 1. Three were in oak–hornbeam forest (plots C, M and W), two (K and L) in riverine forest and a single large one in coniferous forest (N). Detailed descriptions of the vegetation composition in individual plots plus a map of their localisation in BNP are given in Tomiałojć et al. (1984), Tomiałojć and Wesołowski (1996), and Wesołowski et al. (2010).

Holes were located during standard bird census work (Tomiałojć et al., 1984; Wesołowski et al., 2010), as well as during shorter term, intensive, single species studies (references in Wesołowski, 2007b). Holes were located from the ground, by observing birds’ behaviour. To qualify as a hole, it had to be used for breeding by a bird. This was indicated by observations of birds bringing nest material, males bringing food to incubating females, parents entering hole with food (often accompanied by calls of nestlings), or young protruding from the entrance (Wesołowski, 1989, 2007b). Most holes were found at the building and nestling stages.

Holes were located on a field map, and bird species using it when found, tree species (genus), tree section (main trunk vs. limb), height of entrance from ground level (visually estimated for low holes, measured with a clinometer for holes higher than ca. 10 m), trunk girth at breast height and state of tree (live vs. dead) were noted. All signs of decay of the tree section with the hole (fungal conks, scars, bark-free patches) were recorded.

From 1979 to 2010 all holes were marked when found, and checked (through binoculars) from the ground every spring thereafter, to determine whether they were still useable. A hole was treated as no longer useable when it was either mechanically damaged (tree/trunk with hole broke or fell down, hole walls collapsed, Wesołowski, 2001) or when the entrance diameter was reduced below the smallest size accessible by any bird (18 mm) due to injury growing over (Wesołowski, 1995). The cause of hole failure was recorded. Observations of c 3% of holes had to be discontinued because they could not be relocated (the mark had disappeared) or the tree section with the hole ceased to be visible from the ground.

2.3. Data classification

Before the analysis, the field data were divided into classes. The condition of the substrate (tree section with the hole) was classified as ‘dead’ (irrespective of the phase of decay, from freshly broken, to completely rotten); ‘decaying’ (hole placed in a section of living tree showing signs of decay/heart rot, see above), or ‘living’ (living healthy tree, no signs of wood decay of section with hole). The causes of failure were classified as ‘breaking off’ when the tree fell or section supporting the hole broke away; ‘decay’ when some of the hole walls disappeared due to rotting; ‘vertebrate’ if parts of

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the cavity walls were forcefully removed (pecked or torn away); or 'grown over', when the entrance was constricted by growing tissue of the tree.

2.4. Statistical analyses

The persistence of a hole (hole lifespan, in years) was calculated from the year the hole was found until the year it was no longer useable or the observations were censored. The holes were added to the study in a staggered fashion and many of them were still useable in the final year of observations (2010). To account for data with such structure, Kaplan–Meier survival estimates were used to calculate how long holes persisted. This type of test is best suited for dealing with such right-censored data and it is widely used in biology and medicine (Kaplan and Meier, 1958; StatSoft, 2010).

Each hole, when used one or multiple times (Wesołowski, 2006) by one or multiple species was included in the analysis only once. The hole persistence time was measured from the first year of recorded use and the species using it that year was taken as its user. However, when several holes were found in the same tree, each hole was treated as an independent case. This because the holes were found in different years, in different tree sections, they often used by different bird species when found, or – even if used by the same species – by different individuals. Moreover the ‘health’ of a tree often deteriorated with time.

Fig. 1. Distribution of major habitat types and census plots (K, L, W, C, M, N) in the strictly protected part of BNP.
3. Results

3.1. Persistence of holes

A total of 1794 holes, used by 14 non-excavator bird species, was followed from 1979 to 2010, about half of which (49.6%) were destroyed during the study period. The holes were followed for up to 30 years, but their lifespan could be longer, as two of holes found in 1979 and eight of 25 holes recorded in 1980 were still present at the end of observation period. In contrast, 11 holes were already destroyed in the same season in which they had been found. Overall, the median persistence time was 12 years, and half of the holes (25–75% quartile) “survived” for 5–24 years.

Holes in coniferous forest persisted for less time than those in deciduous forest (median 4.4 and 11–13 years, respectively). The middle 25–75% of the holes in coniferous forest persisted 2–7.5 years, while those in deciduous habitats persisted 5–26 years (Fig. 2). The habitats differed qualitatively in sets of tree species used by hole-nesters, the majority of holes in each habitat type were located in non-overlapping sets of the dominant tree species (Table 1). The lifespan of holes strongly depended on the tree species; median persistence times ranged 5 (P. tremula) to 16.5 years (Q. robur, Fig. 3). Thus, the ‘habitat’ and ‘tree species’ variables were very strongly correlated.

The lifespan of holes strongly depended on the condition of substrate in which the hole had been situated. Holes in dead wood (n = 198, median = 5, 25–75% quartile = 2.6–8 years) persisted only about one third of those in the living sections of trees (n = 1553, median = 14 years, 25–75% quartile = 7–25.8 years); Kaplan–Meier survival functions, Cox F test, F = 3.18, p < 0.0001. Holes in ‘decaying’ wood were very infrequent (n = 56, 3.1% of all). Moreover, the persistence time of holes in ‘decaying’ wood (median = 9 years) did not differ significantly from that of holes in the living trees (Cox’s F-test, F = 1.09, p = 0.36). Therefore, holes in “decaying wood” have been included into the “living” category in all further analyses. Proportion of holes in dead wood varied strongly across tree species, from 4% in T. cordata to almost 91% in P. sylvestris (Table 2). However, the observed interspecific variation in the hole lifespan across tree species, was only weakly related to the share of holes in dead wood (cf. Table 2 and Fig. 3, rs = −0.45, P < 0.12). Girth at breast height, and height of holes above the ground varied significantly across tree species (Table 3). At the interspecific level, the persistence of holes increased significantly with the median girth (rs = 0.64, P = 0.017) but not significantly with the median height (rs = 0.43, P = 0.145), even though the two variables were tightly correlated (rs = 0.92, P = 0.0001). Holes in trunks (n = 1404) persisted slightly shorter (median = 12, 25–75% = 5–24 years) than holes in limbs (n = 194, median = 13, 25–75% = 7–22 years). The difference approached significance (Gehan’s Wilcoxon test, Z = −1.82, P = 0.067).

There were consistent differences in persistence of holes used by individual bird species (Fig. 4), median persistence times ranged from 5 (Lophophanes cristaus, Periparus ater) to 19 years (Sitta europaea). Proportion of holes in dead wood ranged from below 10% in the majority of species, through 15–18% in the Ficedula flycatchers and P. ater, to 81% in L. cristatus. However, the interspecific variation in the holes’ lifespan (Fig. 4) was only weakly related to this factor (rs = −0.44, P < 0.23). Girth at breast height, and height of holes above the ground varied significantly among holes used

![Fig. 2. Persistence of non-excavated holes (Kaplan–Meier survival functions) in relation to forest type in BNP: oak–hornbeam (n = 1491), riverine (n = 272) and coniferous (n = 31). Holes in coniferous habitat persisted shorter than the holes in deciduous habitats (χ² = 28.1, df = 2, P < 0.001). Holes in riverine forest persisted shorter than in the oak–hornbeam habitat (Cox–Mantel test = 2.19; p = 0.029).](image)

![Fig. 3. Persistence of non-excavated holes (Kaplan–Meier survival functions) in relation to tree species in BNP. Sample size: 15 (Ulmus) – 348 (Carpinus) holes. Median (black dots), 25–75% (boxes) and minimum (whiskers) values of lifespan are shown. Calculation of the 75% value for Carpinus was impossible due to too manyensored observations. The persistence of holes varied significantly across tree species (χ² = 50.0, df = 9, P < 0.00005).](image)

### Table 1

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Habitat</th>
<th>Riverine</th>
<th>Oak–hornbeam</th>
<th>Coniferous</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Deciduous</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alnus glutinosa</td>
<td></td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td></td>
<td>0.4</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td></td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Coniferous</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Picea abies</td>
<td></td>
<td>0.7</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Pinus sylvestris</td>
<td></td>
<td>0.0</td>
<td>35.5</td>
<td>0.0</td>
</tr>
<tr>
<td><em>N</em> holes:</td>
<td></td>
<td>211</td>
<td>1490</td>
<td>31</td>
</tr>
</tbody>
</table>

*Table 1* Distribution (%) of non-excavated holes across tree species in relation to habitat in BNP. Habitats differed significantly in the sets of trees used (Kruskal–Wallis ANOVA, H = 310.4, P < 0.0005; P < 0.0005 for any pair-wise comparison).
The persistence of holes varied significantly across tree species (ANOVA, \( H = 7.5, p < 0.006 \)). Tree species differed significantly in the distribution of causes of failure (\( \chi^2 \) test, \( df = 3 \); Almus, Carpinus, Tilia, \( p < 0.0001 \); Acer \( P < 0.0001 \); other species combined \( P < 0.0001 \)).

<table>
<thead>
<tr>
<th>Tree species</th>
<th>N holes</th>
<th>% Dead wood</th>
<th>N failed</th>
<th>Cause of failure (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Breaking off</td>
</tr>
<tr>
<td>Almus glutinosus</td>
<td>138</td>
<td>11.6</td>
<td>82</td>
<td>45.1</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>150</td>
<td>8.0</td>
<td>95</td>
<td>57.9</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td>900</td>
<td>10.8</td>
<td>384</td>
<td>34.9</td>
</tr>
<tr>
<td>Tilia cordata</td>
<td>348</td>
<td>3.7</td>
<td>181</td>
<td>26.0</td>
</tr>
<tr>
<td>Acer platanoides</td>
<td>118</td>
<td>7.6</td>
<td>53</td>
<td>58.5</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>22</td>
<td>22.7</td>
<td>9</td>
<td>33.1</td>
</tr>
<tr>
<td>Ulmus spp.</td>
<td>18</td>
<td>22.2</td>
<td>11</td>
<td>63.6</td>
</tr>
<tr>
<td>Sorbus aucuparia</td>
<td>12</td>
<td>8.3</td>
<td>11</td>
<td>72.7</td>
</tr>
<tr>
<td>Corylus avellana</td>
<td>8</td>
<td>37.5</td>
<td>7</td>
<td>14.3</td>
</tr>
<tr>
<td>Populus tremula</td>
<td>17</td>
<td>29.4</td>
<td>16</td>
<td>81.3</td>
</tr>
<tr>
<td>Betula sp.</td>
<td>26</td>
<td>53.8</td>
<td>7</td>
<td>0.0</td>
</tr>
<tr>
<td>Picea abies</td>
<td>16</td>
<td>43.8</td>
<td>10</td>
<td>80.0</td>
</tr>
<tr>
<td>Pinus sylvestris</td>
<td>11</td>
<td>90.9</td>
<td>9</td>
<td>22.2</td>
</tr>
<tr>
<td>Total</td>
<td>1787</td>
<td>11.0</td>
<td>876</td>
<td>39.6</td>
</tr>
</tbody>
</table>

Table 2
Proportion (%) of non-excavated holes in dead wood and causes of holes' failure (%) in relation to tree species in BNP. Proportion of holes in dead wood differed significantly across tree species (Kruskal–Wallis ANOVA, \( H = 64.6, p = 0.0005 \)).

![Fig. 4. Persistence of non-excavated holes (Kaplan-Meier survival functions) in BNP in relation to bird species using them in the year of finding. Number of holes: Lophophanes cristatus = 16, Periparus ater = 26, Poecile palustris = 496, Parus major = 151, Cyanistes caeruleus = 218, Ficedula hypoleuca = 38, Ficedula albicollis = 583. Sturnus vulgaris = 78. Sitta europaea = 173. Median (black dots). 25–75% (boxes) and minimum (whiskers) values of lifespan are shown. Calculation of the 75% values for F. albicollis and S. europaea is impossible due to too many censored observations. The persistence of holes varied significantly across tree species (\( \chi^2 = 82.3, df = 8, P < 0.00005 \)).](image)

3.2. Holes' failure

Most often (40%) losses were because the tree fell or the section with the hole broke off. Injury growing over and decay of walls were responsible for 28% and 24% of failures, respectively. Destruction by woodpeckers or mammals caused only 8% of losses (Table 2). Breaking off (66.5%), followed by decay of walls (26.7%) were the most common causes of disappearance of holes in dead wood. Holes in living substrate failed mostly due to, injury growing over (34.5%), breaking off (33.5%) and decay of walls (24%). Interspecific differences in proportion of holes in dead wood partially accounted for the observed variation in causes of failure across tree species.
Holes, mostly in ing out by woodpeckers, already in the season of finding. Some holes lost due to other factors (medians = 6–7, 25–75% quartile = 2–8 years) than above the ground (not independent, the holes in larger trees tended to be higher (Table 2).

Table 4
Time to failure, girth at breast height of hole-trees and height of non-excavated holes above the ground in relation to bird species using them in the year of finding in BNP. Birds are arranged according to increasing persistence times of their holes. The persistence of holes (Kruskal–Wallis ANOVA, H = 67.7, p < 0.0005) and height (H = 219.9, p < 0.0005) varied significantly across the users.

<table>
<thead>
<tr>
<th>Species</th>
<th>Persistence (years)</th>
<th>Girth (cm)</th>
<th>Height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median 25% 75%</td>
<td>Median 25% 75%</td>
<td>Median 25% 75%</td>
</tr>
<tr>
<td>Periparus ater (n = 16)</td>
<td>1.8  1.2  5.5</td>
<td>116     88  152</td>
<td>3.0  2.0  5.0</td>
</tr>
<tr>
<td>Poecile palustris (n = 281)</td>
<td>4.0  1.9  7.0</td>
<td>100     65  135</td>
<td>5.0  3.0  10.0</td>
</tr>
<tr>
<td>Parus major (n = 42)</td>
<td>4.0  2.0  6.0</td>
<td>149     125  175</td>
<td>7.5  3.0  11.0</td>
</tr>
<tr>
<td>Cymistes caeruleus (n = 89)</td>
<td>5.0  1.7  12.0</td>
<td>134     105  169</td>
<td>5.0  3.0  11.0</td>
</tr>
<tr>
<td>Ficedula hypoleuca (n = 22)</td>
<td>5.8  4.0  11.0</td>
<td>135     112  160</td>
<td>6.5  4.0  11.0</td>
</tr>
<tr>
<td>Ficedula albicollis (n = 289)</td>
<td>6.0  3.5  9.0</td>
<td>140     108  170</td>
<td>6.0  3.0  10.0</td>
</tr>
<tr>
<td>Lophophanes cristatus (n = 15)</td>
<td>10.0 4.0 16.0</td>
<td>118     89  174</td>
<td>3.0  1.0  6.0</td>
</tr>
<tr>
<td>Sturnus vulgaris (n = 43)</td>
<td>15.0 12.0 18.0</td>
<td>200     150  270</td>
<td>11.0 7.0 20.0</td>
</tr>
<tr>
<td>Sitta europaea (n = 86)</td>
<td>15.5 12.0 19.0</td>
<td>223     165  285</td>
<td>10.0 6.0 14.0</td>
</tr>
</tbody>
</table>

Results of regression analysis based on Cox’s proportional hazard model, with persistence probabilities as the dependent variable, and tree species, tree condition, girth at breast height and bird species as independent variables. Significant differences are bolded.

Variable Beta SE t Wald test P
Tree condition −0.97 0.09 −10.48 109.8 0.00000
Girth 0.00 0.00 −4.87 23.7 0.00000
Tree species 0.05 0.01 4.27 18.3 0.00002
Bird species 0.01 0.01 0.88 0.8 0.38
Model $\chi^2 = 150.3, df = 4, P < 0.000005$

(H (Table 2). Holes in T. cordata were most often lost due to injury growing over (44%). This process was also responsible for inactiva- tion and hole-making processes, holes in living parts of trees (Wesołowski, 2001, 2007a), could grow over in a couple of months as well. Overall, the time to failure of holes destroyed by different means differed significantly. The holes destroyed by vertebrates persisted shorter (median = 4, 25–75% quartile = 2–8 years) than holes lost due to other factors (medians = 6–7, 25–75% quartiles = (34–11 years; Kaplan–Meier survival functions, $\chi^2 = 14.5, df = 3, P = 0.0023$).

Overall, holes in larger trees (girth at breast height, n = 869, $r_c = 0.21, P < 0.0001$) and those situated higher above the ground (n = 889, $r_c = 0.23, P < 0.0001$) persisted longer. This relationship between tree size and hole height and their persistence time hold as well, when holes destroyed by different factors were analysed separately ($r_c = 0.20–0.36, P < 0.002$, girth of holes lost by decay of walls $r_c = 0.13, P = 0.07$). The “girth” and “height” variables were not independent, the holes in larger trees tended to be higher above the ground ($r_c = 0.60, P < 0.0001$).

4. Discussion

The observations reported here were gathered over 30 years, in a set of well spaced study areas, covering all major forest habitats. Therefore, they are most probably representative of the situation that existed in pristine lowland woods of temperate Europe (Wesołowski, 2007b). It should be stressed, though, that all values of non-excavated holes “lifespan” presented here are conservative estimates. The estimates refer to the minimum number of years a hole persisted. This, because the year the hole first became suitable is unknown. As there is an excess of holes in BNP, and many of them remain unused for a long time (Wesołowski, 2001, 2007a), a hole could have existed long time, before it was detected being used by a hole-nesting bird.

The median lifespan on non-excavated holes in BNP amounted to 12 years (value of 13 years reported in Cockle et al., 2011 was based on a smaller sample of holes, with known outcome, observed over a shorter period). Both estimates are substantially longer than the persistence of 7 years for woodpecker-made holes in BNP (Wesołowski, 2011). In comparison with data from other areas (Table 6), holes in BNP were rather short lived. This conclusion has to remain tentative, though, as the longest reported lifespans are based on extrapolations from periods of observations shorter than estimated persistence times.

Persistence time of the non-excavated holes (but not of the woodpecker-made ones, Wesołowski, unpubl.) tended to increase with tree size in BNP. The same found Lindenmayer and Wood (2010) in non-excavated holes in mountain ashes Eucalyptus regnans in Australia and Edworthy et al. (in press) in woodpecker holes in trembling aspens Populus tremuloides in Canada. It remains unknown how generally this relationship holds. However, if it would appear widespread, this would make holes in large trees more valuable resource, on which conservation efforts should be focused. The more so, if larger trees harbour larger hole sizes, large enough for the non-excavator species requiring larger holes (like e.g. S. europaea, internal diameter of its holes amounts to 20 cm on average; Wesołowski and Rowiński, 2004), whereas smaller trees could harbour only smaller holes, suitable for a subset of species, such as P. palustris or Ficedula albicollis, requiring holes with only 9–10 cm cross-section (Wesołowski, 1996; Walankiewicz et al., 2007). Therefore, other things being equal, larger trees with holes of are of higher conservation value.

The lifespan of holes strongly depended on tree health in BNP. Holes in dead wood persisted almost three times shorter than those in the living sections of trees, even though they were not lost due to the entrance growing over. This suggests that the most important feature deciding upon the hole’s lifespan is the mechanical strength of a hole tree (its fragment with hole). This relationship was repeatedly found in studies carried out in different regions, both on non-excavated and woodpecker-made holes (Remm et al., 2006; Nielsen et al., 2007; Lindenmayer and Wood, 2010; Cockle et al., 2011; Edworthy et al., in press; Wesołowski, 2011). Although this is not invariably true (woodpecker-made holes in mostly dead Pinus sylvestris persisted in BNP for over 22 years; Wesołowski, 2011), one can tentatively generalise this relationship and propose that, independent of the geographical position and hole-making processes, holes in living parts of trees would persist longest, while holes in dead wood would be shorter “lived”.

Apart from tree health, the persistence of non-excavated holes in BNP strongly depended on the tree species, the differences in lifespan were over threefold. This variation could be partially due
4.1. Conservation ramifications

namely they demonstrate that no single solution to retain both ing them and substrate softness and not so much on the tree activated holes was contingent upon the woodpecker species excavated and size but not to the bird species using it. The lifespan of excavated holes (Wesołowski, 2007a; Cockle et al., 2011). Therefore, persistence of non-excavated holes was related to the tree species dead shows some similarities – expected lifespan of both types of holes – lasted longest. It could be that walls made of hard sapwood were mechanically more resistant to breaks, than in the softer sapwood. Holes in harder wood were also less easily grown over (see below). There could be as well differences in extent to which heart-trot fungi weakened the endurance of different tree species, but nothing appears to be known on this problem.

Falling of trees or limbs appears to be the most important cause of hole loss in BNP both for non-excavated (this study) and woodpecker-made holes (Wesołowski, 2011). This was also true in other areas (Sedgwick and Knopf, 1990; Nielsen et al., 2007; Lindenmayer and Wood, 2010; Edworthy et al., in press). Thus, wind emerges as the most influential hole destructive agent. As the frequency and strength can differ vastly among sites, it is to be expected that the hole persistence could vary widely, even in floristically and structurally similar forests. Within a site, differences in mechanical resistance of individual tree species (see above) would probably be the most important differentiating factor. Injury growing over was as important as breaking off in living trees, and in living T. cordata, it was the most frequent cause of hole loss. Although birds could slow down the process of entrance sealing by removing callus wood growing along of the entrance edges (Wesołowski, 1995, 2011), they were apparently not efficient enough to fully prevent it. The low proportion of hole loss due to their destruction by vertebrates (mostly woodpeckers) underlies the importance of strong walls made of living sapwood as an antipredator defence (Stenberg, 1996; Wesołowski, 2002; Paciık et al., 2009; Tozer et al., 2009).

Comparison of persistence patterns of non-excavated holes and those excavated by woodpeckers (Wesołowski, 2011) in BNP shows some similarities – expected lifespan of both types of holes declines with deteriorating wood condition, holes in decayed wood generally persist for less time (but see woodpecker-made holes in dead P. sylvestris). They also bring several important differences. The persistence of non-excavated holes was related to the tree species and size but not to the bird species using it. The lifespan of exca-vated holes was contingent upon the woodpecker species excavating them and substrate softness and not so much on the tree species or size. These differences have practical consequences, namely they demonstrate that no single solution to retain both types of holes in a forest would work, one would have to propose a range of measures geared at preserving different types of holes.

4.1. Conservation ramifications

As a substantial proportion of forest organisms depends on tree holes (e.g. Gibbons and Lindenmayer, 2002; Cockle et al., 2011) and – in many parts of the world – they primarily rely on non-exca-vated holes (Wesołowski, 2007a; Cockle et al., 2011). Therefore, preservation of adequate diversity and numbers of the non-exca-vated holes is of fundamental importance if we are to preserve biological diversity of forests. How can this be achieved?

The number of holes in a forest depends not only on their life-span (the current study) but, perhaps even to a larger extent, on rates of their production. One can envisage that depending on variation in abiotic (moisture, winds, temperatures) and biotic (floristic composition, combination of wood decaying agents) factors the rates of holes’ production would differ substantially across areas. Others things being equal, formation of holes by wood decay would be probably much slower than their excavation (it can accomplished in only 2–3 weeks in some woodpeckers, Wesołowski, unpubl.), but to the best of my knowledge there is not a single paper measuring the actual hole formation rates. There is an urgent need to fill this knowledge gap. Carrying out field studies on this subject should be strongly recommended.

Despite our inadequate understanding some conservation pro-posals can be made. The most appropriate course of action would differ depending on wood assignment, whether the forest area is mostly devoted to timber production or allocated to nature conser-vation. Unless, there is a critically endangered hole-nester in need of immediate direct intervention (provision of artificial holes) the best recommendation for protected areas, such as nature reserves and national parks, in which timber production is not a goal, would be “no management”. This would allow fungi and other natural processes to produce holes unabated. This “hands off” approach requires no financial investments, no human work, so it could be immediately implemented anywhere. This would require changing very deeply ingrained human conviction, apparently shared also by many conservationists, that acting (managing) is something positive, far better than non-acting, than non-interfering with processes. This mind set seems to constitute the major obstacle in implementation of process-oriented conservation of forests (Wesołowski, 2005).

In timber managed woods a compromise between economical goals and conservation objectives would have to be achieved. It is not going to be easy, though. Persistence time of non-excavated holes tended to increase with tree size in BNP and in several other areas (see above). Thus, holes in large trees would be more valu-able resource, on which conservation efforts should be focused. Unfortunately large live trees are, at the same time, most valuable from timber production point of view. As these two objectives are incompatible, there is no easy way to solve this conflict. Political decisions allowing for retention of large living trees with holes at a cost of extracted amount of timber volume would have to be made. Governments and nature conservation administrators should require forest owners and managers to conserve a sufficient supply of large old trees for wildlife (Cockle et al., 2011). However, this would not suffice. To ensure a long-term supply of these trees, special wildlife tree policies focused on maintaining a range of tree types in which diverse holes could be formed in the future should be implemented (Gibbons and Lindenmayer, 2002; Cockle et al., 2011).

Restoration of non-excavated hole supply in the relatively young tree stands, prevailing over most of Europe, would not be easy task. For a hole to form, a tree has first to reach sufficient diameter to accommodate it. T. cordata was the only tree species

Table 6

Median persistence time of non-excavated holes in different regions of the world.

<table>
<thead>
<tr>
<th>Area</th>
<th>N study years</th>
<th>Persistence (years)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Białowieża NP</td>
<td>30</td>
<td>12</td>
<td>This study</td>
</tr>
<tr>
<td>Estonia</td>
<td>5</td>
<td>18</td>
<td>Remm et al. (2006)</td>
</tr>
<tr>
<td>Canada, British Columbia</td>
<td>15</td>
<td>14</td>
<td>Cockle et al. (2011)</td>
</tr>
<tr>
<td>USA, Illinois</td>
<td>10</td>
<td>14</td>
<td>Aix sponsa holes, Nielsen et al. (2007)</td>
</tr>
<tr>
<td>USA, Colorado</td>
<td>5</td>
<td>6</td>
<td>Sedwick and Knopf (1990, 1991)</td>
</tr>
<tr>
<td>Argentina, Missiones</td>
<td>7</td>
<td>25</td>
<td>Cockle et al. (2011)</td>
</tr>
<tr>
<td>Australia</td>
<td>7</td>
<td>11-23</td>
<td>Cacatuidae holes, Gibbons and Lindenmayer (2002)</td>
</tr>
</tbody>
</table>

* Calculated from data provided in the paper.
in BNP, in which non-excavated holes were commonly present already in thin trees. Judging from their diameter at breast height, such hole trees were at least 70–80 years old (Koop, 1989). Despite the holes in thin T. cordata were relatively short-lived and harboured holes suitable only for smaller hole-nester species, they could nevertheless provide first non-excavated holes in forest patches, in which none had existed before. As this species is widespread in deciduous and mixed forest zones in Europe and can grow on a variety of soils, it seems worthwhile to suggest addition of T. cordata to managed woods as a standard forestry procedure, geared at providing more non-excavated holes in forests.

Holes were found in other tree species in BNP, in larger individuals, which – inferring from their size – could be ca. 130 (F. excelsior, Szymura et al., 2010), ca. 200 years (Q. robur, A. Bobiec, pers. comm.), or over 200 (C. betulus; Koop, 1989) years old. These figures correspond well with the data from Eucalyptus forests of Australia, where “hollows suitable for vertebrate fauna do not typically appear until trees are at least 120 years old. Hollows for larger species may not appear until trees are at least 220 years old” (Gibbons and Lindenmayer, 2002). The same was found in Tasmanian Eucalyptus obliqua forest. The holes started to appear there only in trees which were 100–140 years old and 100 cm diameter (Koch et al., 2008). Also in Atlantic sub tropical forests in Argentina, where trees <60 cm DBH contained hardly any non-excavated holes, the holes were more regular in trees >100 cm DBH (Cockle et al., 2010). Therefore, replacement of such trees would be very difficult, if a sufficient number of old trees with some decay had not been retained in the system.

Summing up, in order to preserve an adequate supply of the non-excavated holes it is necessary to modify current conservation/management policies to assure that (1) most of the existing hole trees are retained in the forestry operations and (2) allowance is made for maintaining a range of tree types, in which additional replacement holes could be formed.

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