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SHORT COMMUNICATION

Disappearance rates of old nest material from tree cavities: An experimental study

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Abstract
Numerous forest organisms critically depend on availability of tree cavities. Some birds and rodents fill their cavities with bulky nests, which – if not removed – could accumulate and render cavities unusable, as recorded in nest-box studies. Data from earlier studies indicate that old nests can disappear from tree cavities so fast that practically no remnants are detectable the following spring. Rapid decomposition of nests in situ, augmented by physical removal of nest material by the cavity-users have been proposed as possible causative mechanisms. We tested these hypotheses in cavities used by tits (Parus major L., Poecile palustris L.) in the Białowieża National Park (E Poland). To mimic typical components of their nests – moss and mammalian hair – we inserted into cavities litter-bags filled with either cellulose or fleece of sheep. After 9.5 months of exposure a third of bags were missing from cavities, and 92–100% of cellulose and 84–98% of hair disappeared from the remaining ones. These results confirm that the rapid decomposition of the tit nests in cavities reinforced by material removed by vertebrates would suffice to “clean” the cavities between the consecutive seasons. To conclude, accumulation of litter in natural nests holes does not seem to affect nest hole availability.

Keywords: Bialowieza primaeval forest, cavity, decay, Great tit, Marsh tit, nest material.

Introduction
Tree cavities play a substantial role in forests as breeding or roosting places for a wide range of organisms (e.g. Newton 1998; Ranius & Jansson 2000; Parsons et al. 2003; Aitken & Martin 2004; Blanc & Walters 2008). Worldwide 10–40% of forest bird and mammal species are cavity-users (Cockle et al. 2011). However, most of these cavity-users are non-excavators, i.e. they cannot excavate their own cavities. Therefore, their numbers, distribution and diversity can be limited by the availability of existing holes (e.g. birds, review in Newton 1998).

The number of cavities in a forest depends primarily on cavity formation rates and cavity persistence, which vary widely across areas (Cocke et al. 2011; Wesołowski 2011, 2012). Some cavities are made unusable by the activities of cavity-dwelling vertebrates. Many cavity-users build bulky nests, most of which comprise plant (leaves, moss, flakes of bark) and animal material (wool, hairs, feathers) (Hansell 2000). Such nests fill much of cavity volume and, if they persisted, they could render cavity unusable for other users in the following season. This phenomenon is commonly observed in artificial cavities – nest boxes (Møller 1989). To prevent this, a common practice in nest-box “management” is to remove old nests from nest-boxes after the end of breeding season (Perrins 1979; Møller 1989; Lambrechts et al. 2010). On the other hand, the preliminary data from tree cavities, both excavated and non-excavated (Wesołowski 2000; Hebda & Mitrus 2011) indicate that old nests could disappear from tree cavities so quickly, that practically no remnants of old nests are detectable the following spring. It has been postulated (Wesołowski 2000; Hebda & Mitrus 2011) that the disappearance of old nest could be due to rapid decomposition of nests in situ, as well as physical removal (“cleaning”) of nest material by cavity-users. We used a long-term study of cavity-nesting species in primeval regions of the Białowieża National Park (E Poland) to test the...
hypothesis of rapid in situ decomposition of nest material in cavities. High abundances of tree cavities of different origin, and cavity-nesting birds and mammals occur in this rich deciduous old-growth oak-hornbeam (Tilio-Carpinetum) forest (Wesołowski 2007b). Dead wood in different stages of decay occurs in large quantities (Bobiec 2002), and diversity of macrofungi is very high (Kujawa 2009). Moreover, high rates of plant litter fall decomposition have been recorded in forests of this type (Dziadowiec 1987). These observations suggest that diverse assemblages of decomposing organisms (of both cellulose and lignin) commonly occur in these forests and that they are probably able to decompose these substrates both in tree cavities and outside them. Therefore, we expected high decomposition rates of old nest material.

We chose cavities used by tits for our experiment, because they built nests made of two, biochemically different types of materials, moss in the foundation (mostly cellulose), and wool and hair (mostly keratin) in the lining. Thus, to decompose such nests at least two groups of decomposers with quite different biochemical properties would be required (Van Veen & Kuikman 1990; Boddy 2001; Lynd et al. 2002). Plant parts (cellulose) in the soil are mostly decomposed by saprotrophic fungi (ascomycetes, basidiomycetes) and bacteria (Van Veen & Kuikman 1990; Boddy 2001). This type of substrate is so widely distributed in the wild, that within the basidiomycetes alone about 8500 species degrading ligno-cellulose complex are known (Lynch & Thorn 2006). Keratinolitic decomposers are less common in nature, as uncommon as is the patchy distribution of their substrate (Marchisio 2000). Although frequency of these decomposers in bird nests is relatively high, yet usually only single species of keratinolitic fungi and bacteria colonized individual nests (Hubálek et al. 1973; Goodenough & Stallwood 2010).

Decomposition rates strongly depend on microclimate (i.e. humidity, temperature – Donnelly et al. 1990; Coûteaux et al. 1995; Kurka & Starr 1997; Kubartová et al. 2007), and microclimate of cavities is dependent on their dimensions (Sedgeley 2001; Wiebe 2001; Rhodes et al. 2009). Thus we tested decomposition rates in non-excavated cavities of two species: great tit Parus major L. and Marsh tit Poecile palustris L., which breed in the same habitat, built nests of the same type but use cavities of different dimensions (Wesołowski 1996; Maziarz & Wesołowski 2011). We expected, that these differences in cavity characteristics could affect microclimatic conditions, and, as a result, the decomposition rates.

Finally, to get some reference data on decomposition rates in the surrounding habitat we measured decomposition rates in ground litter in vicinity of the cavity trees. We selected this microhabitat as the decomposition processes in the litter have been intensively studied and are relatively well understood (e.g. Donnelly et al. 1990; Coûteaux et al. 1995; Lynd et al. 2002; Berg & Laskowski 2005).

Materials and Methods

The study was carried out in the least modified part of the Białowieża Forest (E Poland), strictly protected since 1921 within the Białowieża National Park (BNP, 47.5 km²). The forest represents a remnant of the vast lowland forests that once covered large parts of temperate Europe. It stands out from other European forests in respect of its considerable size and exceptionally good state of preservation (Tomiałojć & Wesołowski 1990, 2005). These old growth stands are distinguished by an array of features: they are multi-storey, mixed-species and uneven-aged (for detailed descriptions and photographs see Tomiałojć and Wesołowski 1990, 2005; Wesołowski 2007a).

Field work was carried out within three large (48–54 ha) structurally fairly similar sample plots (plots C, M and W – details presented in Wesołowski et al. 2010) in the oak–lime–hornbeam habitat. The old growth stands are composed mostly of Common hornbeam Carpinus betulus L., Small-leaved lime Tilia cordata Mill., Pedunculate oak Quercus robur L., Norway spruce Picea abies (L.) Karst. and Norway maple Acer platanoides L. A detailed description of the study plots is available in earlier papers (e.g. Tomiałojć et al. 1984; Tomiałojć & Wesołowski 2004; Wesołowski et al. 2010).

The Experimental Procedure

To measure the decomposition rates in cavities we used a standard method applied in the litter decomposition research, the litter-bag technique (e.g. Berg & Laskowski 2005). We made bags, c. 6 cm × 6 cm large, from a nylon net with mesh size about 1.5 mm. We filled them with either cellulose or fleece of sheep as they mimic typical components of tits nests – moss and mammals’ hair, respectively (Cramp & Perrins 1993; Glutz von Blotzheim & Bauer 1993; Hansell 2000). Both types of materials were dried to a constant mass (72 hours, 70°C), weighed to the nearest 0.001 g, and then sealed in litter-bags. A bag was stuffed with either 2.2 (±5%) g dry cellulose (12 laboratory filter papers made from cellulose, Eurochem BGD company, diameter 55 mm, specific mass: 80 g/m²), or
with 0.5 (±5%) g of dry sheep fleece. Each bag was provided with a uniquely numbered marker (a 2 cm piece of plastic Dymo® tape, with the embossed number).

After the tits in the study areas had finished breeding in 2010, we inserted into all the cavities from which the young had fledged, accessible from a ladder (up to 6 m above the ground), sets of two bags, one with cellulose and one with fleece. We placed the bags into 20 Great tits and 24 Marsh tits cavities. All tree cavities used by the tits were non-excavated, situated in the living, deciduous (common hornbeam: 27, small-leaved lime: 17) trees. However, in comparison with Great tit, the Marsh tit cavities were shallower, smaller and situated lower above the ground (Table I). These differences could have influenced the action of decomposers. The nest cavities were not cleaned and if possible the bags were buried within the nest material. Additionally, we placed the same set of bags in the litter, ca. 5 cm deep, about 2 m from each nest tree, alternatively south or north from it. To prevent displacement by larger animals, the bags in the litter were tied on nylon thread to small wooden pegs stuck into the ground.

All the bags were distributed between 16 June and 20 June 2010. The following spring, on April 3–5, the bags were removed and transported to a laboratory. They were opened in the laboratory, and their contents were carefully cleaned (of sand, roots, fauna and other foreign materials) by hand-using brush and tweezers. The remaining material was dried up (72 hours, 70°C), then weighed to the nearest 0.001 g. The material dry mass loss was calculated separately for each bag according to the following formula:

\[ L = \frac{(M1 - M2)}{M1} \times 100\% \]

where \( L \) is material dry mass loss (in%); \( M1 \) is the initial dry mass of material; \( M2 \) is the dry mass of the remaining material.

All data-sets were tested for normal distribution using the Shapiro–Wilk test. Our data-sets did not have a normal distribution, thus to compare decomposition rates in two groups we used the Mann–Whitney \( U \)-test. When multiple tests were performed, we corrected the \( \alpha \)-values according to the Bonferroni approach (Sokal & Rohlf 1995). We used Fisher’s exact test to determine if there were differences in frequency of litter bags loss between cavities used by Blue and Great tits. All statistical analyses followed formulae in STATISTICA 6.1. (StatSoft Inc. 2004).

### Results

The bags were exposed to the action of decomposers for about 9.5 months, after which we found no visible remnants of old nests while inspecting the cavities during the spring removal of the bags.

Due to disappearance of whole bags from the cavities (see below), the decomposition rates could be assessed only in about two-thirds of cases. Decomposition rates did not differ significantly between the species either for cellulose (Mann–Whitney \( U \)-test, \( U = 73.0, \alpha = 0.44 \)) or for fleece (\( U = 62.0, \alpha = 0.19 \)). In all instances almost all material disappeared during 9.5 months of exposure (Table II). Therefore,

### Table I. Dimensions of non-excavated Great and Marsh tits cavities used in the experiment in the Bialowieża National Park in 2010–2011.

<table>
<thead>
<tr>
<th>Species (number of cavities)</th>
<th>Height above the ground [m]</th>
<th>Least entrance diameter [cm]</th>
<th>Distance from entrance to the nest [cm]</th>
<th>Bottom area [cm²]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great tit (20)</td>
<td>4 (3–6)</td>
<td>2.5 (2.5–3.5)</td>
<td>18.5 (16–23)</td>
<td>200 (147–243)</td>
</tr>
<tr>
<td>Marsh tit (24)</td>
<td>1.6 (1.2–5.0)</td>
<td>2.5 (2.0–3.0)</td>
<td>14 (12.5–17)</td>
<td>78 (50–92)</td>
</tr>
<tr>
<td>Mann–Whitney ( U )-test: Z</td>
<td>−2.73</td>
<td>1.01</td>
<td>2.52</td>
<td>−5.15</td>
</tr>
<tr>
<td>( p )</td>
<td>0.006</td>
<td>0.307</td>
<td>0.011</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Note: The median values shown; in parentheses are 25–75% quartiles.

### Table II. Decomposition rates of cellulose or fleece in litter-bags in the Bialowieża National Park in 2010–2011 in relation to the cavity type and the type of the substrate.

<table>
<thead>
<tr>
<th>Cavity type (initial size)</th>
<th>No. of bags recovered in the spring</th>
<th>Median (25–75% quartiles) mass loss (%)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cellulose</td>
<td>Fleece</td>
<td>Cellulose</td>
</tr>
<tr>
<td>Great tit cavity (20)</td>
<td>9</td>
<td>9</td>
<td>84 (65–91)</td>
</tr>
<tr>
<td>Marsh tit cavity (24)</td>
<td>20</td>
<td>20</td>
<td>95 (61–100)</td>
</tr>
<tr>
<td>Litter (45)</td>
<td>34</td>
<td>32</td>
<td>98 (95–100)</td>
</tr>
</tbody>
</table>

Note: Loss mass after 9.5 months of exposure.
decomposers appeared the most important factor responsible for cleaning of holes. As the data from tree holes used by Marsh tit and Great tit did not differ, we pooled them and compared them with the ground litter samples. In tree cavities fleece decomposed to a much larger extent than in the litter (Table II, \( U = 79.0, p < 0.0001 \)) but the opposite pattern was found for cellulose (Table II, \( U = 332.5, p = 0.023 \)).

During spring inspections about a third of the bags were missing in the cavities. This happened more frequently in the cavities used by Great tits (Table II, Fisher exact test, \( p = 0.0017 \)). In six of the cavities rodent nests establishes after the initiation of the experiment (Yellow-necked mouse Apodemus flavicollis Melchior or Bank vole Myodes glareolus Schreber). Both bags remained in one cavity only the cellulose bags in three cavities and two of them contained no bags. In addition, in six cavities the netting of one or both bags was damaged, probably by small rodents. These samples were not included in calculations of mass loss or decay rate.

**Discussion**

We recorded very high decomposition rates in tree cavities, almost all of cellulose and fleece disappeared during 9.5 months of exposure, independent of tits species originally using it. This, despite the fact that the small mesh size of the bags prevented access of larger invertebrates, known to be important agents speeding up the litter decomposition (Zhang et al. 2001; Salminen et al. 2010). Thus, the results of the experiment confirm our expectation that “rapid decomposition of nests in situ” is the cause for the disappearance of old nests, and this process alone would be sufficient, to “clean” cavities containing the “tit-type” nests material between the consecutive seasons (Wesołowski 2000; Hebda & Mitrus 2011). However, these data were collected in a rich deciduous forest, in a single type of cavity (non-excavated, in living trees), and, as a result, might not reflect general patterns. Supplementary studies in habitats with poorer assemblages of decomposers (e.g. coniferous forests), in other types of cavities (woodpecker-made, in dead wood) or of nests made of harder materials would be necessary to test their generality.

We detected frequent removal of the experimental bags by larger animals. However, the bags were larger structures than nest material, so it remains unknown whether nest material would be removed more often than fragments of old nests. Woodpeckers are known to remove objects from their roosting cavities (Mazgajski 2002). However, entrances of the experimental holes were too narrow to permit access of the larger species of all woodpeckers (except Lesser spotted woodpecker Dendrocopos minor) in our study. As one bag was found in a rodent nest, we suspect that the bags were removed by cavity-using rodents, mainly by yellow-necked mouse and bank vole, two most numerous species in the forest (Pucek et al. 1993).

We found much higher decomposition rates of hair in cavities in BNP (over 90%) than Hebda and Mitrus (2011) in a managed oak–hornbeam forest in SW Poland (56%). This difference could be at least partially due to the shorter time of the bags’ exposure in the latter study (7 vs 9.5 months). The bags were not exposed to decomposers during the summer months (Hebda & Mitrus 2011), when decomposition rates and fungal biomass reach the highest level (Kubartová et al. 2007). The difference could be also partially due to differences in decomposers richness, presumably higher in the primeval, and reduced, in the managed forest.

 Decomposition rates in soils depend strongly on decomposers diversity and their biomass (Mikola & Setälä 1998; Boddy 2001; Setälä & McLean 2004). Therefore, the fast disappearance rates of the bag contents in our experiment indicate that the tree cavities constituted a favorable microhabitat for decomposers, especially, from the keratinolitic group. Conditions for decomposition process in the cavities could be actually better than in the litter. Cavities in living trees are well insulated from cold (i.e. McComb & Noble 1981; Rhodes et al. 2009). Hence, their interiors probably freeze later than the litter on the ground, what probably allows for longer periods of decomposers activity. The decomposer activity in the litter often decrease substantially during periods of drought (Donnelly et al. 1990; Boddy 2001). This limiting factor plays no role in cavities in living trees, as their interiors remain constantly humid (i.e. McComb & Noble 1981; Rhodes et al. 2009).

Whereas, the presence of diverse assemblages of cellulose digesting organisms in the cavities is understandable (their walls are made of wood), the high presence of keratinolitic organisms is less obvious – hair and feathers are not the usual component of cavity interiors. In contrast to cellulose which is very widespread in forest, keratin is rather uncommon with most probably a very patchy distribution. Therefore, tits nests in cavities could constitute high quality “hot-spots” for keratin decomposers. It seems that the cavity-breeding birds themselves could serve as dispersal agents of decomposing organisms. Both cellulolitic and keratinolitic organisms are known to occur on birds feathers and were found in nests in nest-boxes (Pugh 1965; Hubalek et al. 1973; Burtt & Ichida 1999). It is also possible
that decomposing organisms could be already present on hairs and wool brought by the birds as the lining material. In conclusion, we have experimentally demonstrated that activity of decomposers in combination with the removal of nest material by mammals and birds could prevent accumulation of old nest material (moss, hair, fleece) in cavities. Thus, such cavities would be accessible for cavity-dependent organisms in subsequent seasons, and temporary removal of cavities from the cavity-web (Martin et al. 2004) by accumulation of old nests would be of less relevance.

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