Nest sites, nest depredation, and productivity of avian broods in a primeval temperate forest: do the generalisations hold?

Tomasz Wesolowski and Ludwik Tomialojć


Data on nest success and brood productivity of three ground-nesting, three canopy-nesting and four hole-nesting (non-excavator) passerines were gathered in a primeval lowland temperate forest (Białowieża National Park, E Poland). Natural holes were superabundant and the birds had to cope with a heavy pressure of a diverse assemblage of nest predators. We tested whether in such conditions nesting in holes is more productive, and whether nesting on the ground is most risky, as expected from some earlier generalisations. The nesting success varied significantly across the nest types. As predicted, the success of hole-nesters (51–74%) and their brood productivity were the highest. Contrary to expectations, the ground-nesters (27–40%) did not breed less successfully than the canopy-nesters (22–33%). Nest predators, responsible for 64–94% of nest losses in individual species, were the major cause of the differences among nest types. The Białowieża results confirm the long-held view that holes tend to be the safest breeding places, but lend no support for the idea that nesting on the ground is more dangerous than in tree crowns.

There are some, long established, generalisations on the relationships between type of nest site, nesting success and brood productivity in birds. It is generally accepted that the relative breeding success of hole-nesting birds is higher than that of open-nesting species, and that this difference is to large extent caused by varying nest predation rates (reviews by Lack 1954, Nice 1957, Ricklefs 1969, Payevski 1985). Additionally, it is proposed that nests of open-nesters, situated above the ground (in shrubs and bushes), are less often destroyed than nests on the ground (Ricklefs 1969, Slagsvold 1982). Overall, an increasing safety gradient of nest sites, from the most endangered ground nests, through open nests in shrubs/trees to the safest nests in tree-holes, seems to exist in forest birds.

Nilsson (1986) questioned these findings. He stressed that the majority of the breeding success data on hole-nesting birds had been gathered using nest boxes, where rates of predation and partial nest losses were often lower than in natural holes. This could produce a spurious relationship between high brood productivity and hole nesting. He compared the breeding success of six European species in natural holes and showed that the proportion of eggs laid that give rise to fledglings was about the same as in a set of ten open-nesting species. However, the patterns of nest failure differed between...
the two groups. Similarly to the earlier studies, the proportion of complete nest losses was lower in the hole-nesters, but the partial loss in their successful broods was much higher than in the open-nesters. Thus, in natural holes, lower complete losses appeared to be balanced by higher partial losses.

Martin (1993, 1995) challenged the idea that predation rates were greater on the ground-nesting than on the off-ground-nesting birds. His analysis showed, that among the North American forest open-nesters, predation was actually the lowest on ground nests (31%), intermediate on canopy nests (36%) and the highest on shrub nests (48%). He also demonstrated (Martin and Li 1992, Martin 1995) that the hole-nesters did not form a homogenous group, and that predation on nests of excavator species (11%) was much lower that on the nests of non-excavators (31%). Nests of the former group were the safest, as predicted, but nests of the latter group were no safer than the open nests on the ground. Only when the pooled data on hole-nesters were contrasted with the combined data on the open-nesters did holes emerge as a safer nest type.

The findings of Nilsson and Martin appear to undermine the validity of the earlier generalisations, yet their impact has still to be evaluated. These results could imply that there are no general rules, and that even in a single habitat type, within a single climatic zone, no stable relationships between nest types, predation risk and brood productivity exist. This would invalidate any attempts to relate nest types used by a species with features of its breeding behaviour, demography or life-history traits. On the other hand, their results could just constitute special cases (local exceptions to the general rules) that introduce some noise to the data and make detection of the underlying patterns more difficult, but that do not refute the existence of causal relationships between nest types and brood productivity. With the data at hand it is impossible to answer which of these two possibilities fits the reality better.

Here we test all the above-proposed relationships between nest sites, predation rates and brood productivity using data on ten species of small to moderate-sized birds collected in the last fragments of primeval lowland forests of temperate Europe (Białowieża National Park, Poland). This site is unique because organisms live there under conditions that existed in European forests before their transformation by humans (Wesolowski 1983, Tomiałojć et al. 1984, Tomiałojć and Wesolowski 1990). Three features of this forest are the most important in the context of this study: 1) the presence of an entire (except brown bear Ursus arctos) assemblage of predators that use diverse detection and attack techniques to destroy small birds’ nests (Tomiałojć et al. 1984, Tomiałojć and Wesolowski 1990, Jędrzejewska and Jędrzejewski 1999) guarantees that the recorded nest predation rates are not biased by the absence of some crucial predators, 2) the existence of a full spectrum of superabundant natural holes in old-growth primeval stands. This enables hole-nesters to choose their preferred hole types (Walankiewicz 1991, Wesolowski 1989, 1996, 2002, Wesolowski and Rowiński 2004) and assures that the recorded nest loss rates and brood reduction frequencies among hole-nesters are not biased due to the frequent use of low quality holes, and 3) the retention of a diversified structure of primeval tree-stands with very heterogeneous structure of the ground (numerous uprooted trees and decaying logs) and canopy layers (Faliński 1986, Bobiec 1995, Bobiec et al. 2000). This offers the birds a whole array of nesting microhabitats in which to conceal nests. Therefore, the nest loss rates should not be inflated by habitat simplification and shortage of hiding places.

**Study area and methods**

The Bialowieża Forest complex is situated at the Polish-Belarussian border. Its western part (613 km², ca 45% of the area) lies inside 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 Wesolowski 1990, Wesolowski and Tomiałojć 1995). The majority of the tree stands in the Polish part are now under management, but a block of the best preserved primeval old-growth stands has been strictly protected within the Bialowieża National Park (hereafter BNP). The primeval stands preserved in BNP are distinguishable by an array of features: they are multi-storey, mixed-species, uneven-aged, contain many oversized trees (the tallest Norway spruce Picea abies can reach 55 m, and several other species reach 42–45 m), and a large amount of dead timber and uprooted trees. Detailed descriptions and photographs are given in Tomiałojć et al. (1984) and in Tomiałojć and Wesolowski (1990). Field data were gathered in the strictly protected part, mostly in upland oak-lime-hornbeam stands composed mostly of hornbeam Carpinus betulus, lime Tilia cordata, pedunculate oak Quercus robur, spruce and continental maple Acer platanoides. For all species but collared flycatcher Ficedula albicollis, data were also collected in swampy riverine forest, made up mainly by alder Alnus glutinosa, ash Fraxinus excelsior and spruce.

This is a review of papers (+some unpubl. data) concerning ten species of passerines studied during four to 13 seasons spread over 1976–2002 (see references in Table 1). Field procedures and methods of data analysis used in studies of individual species are described in detail in the appropriate papers. Here, only common features of the study design, relevant for the topic of this paper are summarised. All the studies were aimed at
Table 1. Nest type and nesting success, share of predation in total nest loss, daily mortality rates, productivity of broods of passerines in the Bialowieża National Park. For definitions of variables, see “Methods”.

<table>
<thead>
<tr>
<th>Species by nest location and type</th>
<th>N years/nests</th>
<th>Nest success (%)</th>
<th>Proportion of total nest loss due to predation (%)</th>
<th>Daily mortality rate of nests (%)/length of nesting cycle (days)</th>
<th>Productivity (%)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground, domed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Phylloscopus collybita</em> Chiffchaff&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5/169</td>
<td>44</td>
<td>26–51</td>
<td>78&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.35/35</td>
<td>40 Piotrowska and Wesolowski (1989)</td>
</tr>
<tr>
<td><em>Troglodytes troglodytes</em> Wren&lt;sup&gt;c&lt;/sup&gt;</td>
<td>4/101</td>
<td>40</td>
<td>12–50</td>
<td>91</td>
<td>2.35/39</td>
<td>37 Wesolowski (1983)</td>
</tr>
<tr>
<td>Canopy, open</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Turdus merula</em> Blackbird</td>
<td>6/245</td>
<td>33</td>
<td>21–42</td>
<td>95</td>
<td>3.58/31</td>
<td>29 Tomiało (1994)</td>
</tr>
<tr>
<td><em>Turdus philomelos</em> Song thrush</td>
<td>5/405</td>
<td>28</td>
<td>26–34</td>
<td>87</td>
<td>4.11/31</td>
<td>26 Tomiało (unpubl. data)</td>
</tr>
<tr>
<td><em>Coccothraustes coccothraustes</em> Hawfinch</td>
<td>6/263</td>
<td>22</td>
<td>10–31</td>
<td>?&lt;sup&gt;d&lt;/sup&gt;</td>
<td>5.22/29</td>
<td>&lt;22&lt;sup&gt;e&lt;/sup&gt; Tomiało (1997)</td>
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<td>Hole, non-excavator</td>
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</tr>
</tbody>
</table>
| *Ficedula hypoleuca* Pied flycatcher    | 6/100         | 51               | 25–85                                             | 90                                                            | 1.87/36          | 46 Czeszczewik (2004),
| *Sitta europaea* European nuthatch      | 7/356         | 73               | 60–78                                             | 64<sup>e</sup>                                                | 0.75/42          | 59 Wesolowski and Stawarczyk (1991),
|                                         |               |                  |                                                   |                                                               |                  | Wesolowski (2001),
|                                         |               |                  |                                                   |                                                               |                  | Wesolowski and Rowiński (2004)            |

<sup>a</sup>As a rule chiffchaffs build their nests slightly above the ground, but they remain accessible to every ground-bound predator.

<sup>b</sup>94% if desertion is included.

<sup>c</sup>Wrens actually breed low above the ground, mostly in soil covered upturned roots of fallen trees or in logs laying on the ground.

<sup>d</sup>Probably the majority of nest depredated, but it has been impossible to ascertain the cause of failure in many inaccessible nests (in outer parts of tree crowns, high above the ground).

<sup>e</sup>Frequently observed premature fledging resulted in some brood reduction, but due to inaccessibility of numerous nests, quantifying the amount of partial loss has been impossible. The value shown indicates only the effect of the total nest loss.

<sup>f</sup>79% if desertion is included.

<sup>g</sup>86% if desertion is included.
gathering unbiased data on nesting success and nest predation rates of the local populations. To achieve this, the data were collected within permanent study plots. Data on all species were gathered in the same plots, but the total area covered depended on the species abundance (larger in the less numerous species). Intensive nest searches aimed at finding all nests were carried out in the same areas every spring, but due to varying numbers of birds breeding there, the number of nests actually found differed among seasons. With few exceptions (see below) nests were found at early stages of the nesting cycle (building, egg laying), and were followed (mostly from a distance) from the onset of laying till their destruction or fledging of young. As complete nest histories were available, no need to apply the Mayfield estimates existed, and the nest success was expressed as a percentage of nests from which at least one young had fledged. In species, in which a substantial fraction of nests was found at later stages of the nesting cycle (wood warbler \textit{Phylloscopus sibilatrix}, chiffchaff \textit{Phylloscopus collybita}) – to avoid bias – different subsets of nests were used to calculate nest survival at the egg and nestling stages. So estimated values were later combined to produce the overall nest success (Wesołowski 1985, Piotrowska and Wesołowski 1989).

For each species, data on nest success in different years, mean share of predators in nest destruction, and nest productivity were extracted from the original sources. The variables were defined as follows: 1) nest success: percentage of nesting attempts (=nests in which egg-laying commenced) that successfully fledged at least one young, expressed as the overall success (calculated from pooled data from all seasons/habitats), as well as the range (extreme values from individual seasons/habitats), 2) total nest loss: 100% – nest success, 3) importance of predation: percentage of the total nest loss caused by predation, 4) nest productivity: percentage of eggs laid that produced fledglings, this measure includes simultaneously effects of the total nest loss and of partial brood failures in successful nests, 5) partial nest loss; percentage of eggs laid in successful nests which failed to produce fledglings, calculated as the difference between nest productivity and nest success, 6) length of nesting cycle: time necessary to rear a brood (number of days between onset of laying and fledging), the values for individual species were extracted from the respective volumes of the “Handbuch der Vögel Mitteleuropas” (Glutz von Blotzheim and Bauer 1985–1997), and 7) daily nest mortality rate (m): calculated following the formula given by Ricklefs (1969): \( m = -(\log P)/t \), where \( P \) is the proportion of surviving nests (nest success), and \( t \) is the length of nesting cycle (days).

To omit problems with non-normality of the data distribution, the non-parametric statistical tests were used, and all probability values shown in the text are two tailed.

\textbf{Results}

Data on breeding performance of ten passerine species, three ground-nesters, three canopy-nesters and four secondary hole-nesters (non-excavators) are available from BNP (Table 1). Their nesting success varied extensively across years, in the majority of species, two- to three-fold differences between the extreme values were found (Table 1). The inter-year differences notwithstanding, there are clear interspecific differences (Table 1).

The nesting success of passerines at BNP varied significantly across the nest types (Kruskal-Wallis ANOVA: \( H_{2,10} = 7.04, P = 0.03 \)). The success of hole-nesters (51–74\%) was significantly higher than that of the ground-nesters (27–40\%), but the success of the latter was not significantly higher than that of the canopy-nesters (22–33\%, Dunn Multiple Comparisons test: \( Q = 2.54, P < 0.05 \) and \( Q = 1.1, P > 0.5 \), respectively, Table 1).

The differences between the nest types were almost totally due to predation, which accounted for 64–95\% of the total nest loss (Table 1). The second most important cause of nest loss among birds at BNP, brood desertion, is frequently a consequence of an unsuccessful predator’s attack or of a parent bird being killed by a predator. Therefore, it seems justified to treat desertion, at least to a large extent, as an indirect effect of predators, and to include it into a broadly understood predation impact. Such a predator impact would account for nearly all total nest losses (Table 1). Hence, the differences in the nesting success across the nest types at BNP resulted almost entirely from the differences in their susceptibility to predation.

The length of the breeding cycle differed across species, they needed 29 (hawfinch \textit{Coccothraustes coccothraustes}) to 42 days (nuthatch \textit{Sitta europaea}) to rear a brood, which could have influenced the results. The daily nest mortality rates allow for a more direct comparison of risk. The daily loss rates differed almost sevenfold, from 0.75\% in nuthatch and marsh tit \textit{Parus palustris}, to 5.22\% in hawfinch (Table 1). They varied significantly across the nest types (Kruskal-Wallis ANOVA: \( H_{2,10} = 7.13, P = 0.03 \)), in a fashion opposite to the nest success. The daily loss of hole nests (0.75–1.87\%) was significantly lower than that of the ground-nests (2.35–4.22\%), but the loss of the latter was not significantly lower than that of the canopy-nests (3.58–5.22\%, Dunn Multiple Comparisons test: \( Q = 2.54, P < 0.05 \) and \( Q = 1.1, P > 0.5 \), respectively, Table 1).

The partial nest losses, were significantly higher in hole-nesters than in open-nesters (5–14 and < 5\% respectively, Mann Whitney test: \( Z = -2.56, P = 0.01 \), yet the productivity of hole-nesters’ broods (41–56\%) was the highest. Like for the nest success, the productiv-
ity in the ground-nesters (25–40%) was intermediate, and in the canopy-nesters it was the lowest (< 22–29%). Overall, the productivity differed significantly across nest types (Kruskal-Wallis ANOVA: $H_{2,10} = 7.0$, $P = 0.03$).

Discussion

Nesting success of individual species at BNP could vary substantially among years. This clearly demonstrates that using results of one-two year studies for making generalisations on relationships between nest sites, nest types and predation rates is unwarranted, and would frequently result in mistaken conclusions. For this purpose it would be ideal to have long-term data sets, collected in the same areas, simultaneously for all species, but it is unfortunately not the case. The individual species were studied at BNP for 4–13 seasons and the study years only partially overlapped. Moreover, studies on ground nesters were carried out in the 1970s whereas data on hole nesters were gathered mostly in the 1990s. This could potentially affect the results. However, there are some lines of evidence indicating that it has not been probably the case: 1) the data on longest studied marsh tits and collared flycatchers (references in Table 1) show that their nesting success did not exhibit any long-term trends, the very “bad” and very “good” seasons were well interspersed, 2) the long-term data on numbers of predators spanning the whole study period (Wesolowski and Tomiałojć 1997, Jędrzejewska and Jędrzejewski 1999, Walankiewicz 2002) demonstrate the presence of wide year-to-year fluctuations but no long-term declining trends, and 3) differences in nest success between the groups remain when data from the same seasons (1987–1999: nuthatch and marsh tits vs. song thrush Turdus philomelos and blackbird Turdus merula; 1990s: hawfinch vs. all hole nesters) are compared. Thus, the results analysed here cover probably a substantial part of the inter-year variation in nest success, and might be treated as representative for the local habitat conditions.

The hole-nesters were the most successful and the most productive species group, despite their higher partial loss rates compared to those in the open nesters. Therefore, the results do not support the Nilsson’s (1986) idea of balancing selection pressures—the slightly higher partial losses in the hole-nesters were not enough to compensate for their much lower complete losses. All the BNP data pertain to breeding in natural holes. Hence, the higher success of the hole-nesters at BNP could not be explained away as a nest box bias either (studies in nest boxes tend to produce inflated success values; reviews in Nilsson 1986, Purcell et al. 1997, Mitrus 2003). Similarly, the results could not be due to admixture of excavators, which tend to be more successful breeders (Martin and Li 1992, Martin 1995), as all the species studied at BNP were non-excavators. Thus, the higher nest success of the hole-nesters seems to be a genuine phenomenon, the result of lower rates of nest predation. These results fully support the “classical” view, that nesting in holes is safer than in other places, and justify asking “why more birds do not nest in holes” (Lack 1954, Nice 1957). The lack of difference between nesting success of non-excavators and open nesters found in some studies (Nilsson 1986, Martin 1993, 1995) may rather have resulted from unusually high nesting success of open nesters and not from poor performance of the hole-nesters (see below). The latter group reproduced equally well as birds at BNP.

Contrary to expectations, the ground-nesting birds at BNP were not the least successful group, if anything, they tended to reproduce more successfully than the canopy-breeders. It is difficult to tell, though, whether nesting was equally risky in both strata, as apart from being situated in separate layers, the nests differed in two important respects: 1) nests on the ground were domed, whereas the canopy-ones were of open-cup type, and predators could see their content from above. This is not due to biased sampling, but reflects a real biological difference between birds using these two layers at BNP: all ground breeders there, except blackcaps Sylvia atricapilla nesting low above the ground, build domed nests or hide their nests under branches or tussocks, whereas all crown nesters, except the quite sparsely breeding long-tailed tits Aegithalos caudatus, build open-cup nests (Tomiałojć et al. 1984, Tomiałojć and Wesolowski 1990). As domed nests tend to be more successful than the open ones (Lack 1954, Nice 1957), the differences in the nest success could rather be due to differences in nest-types than due to differences in position among vegetation layers. However, nest success of long-tailed tits in Poland (c. 25%, Wesolowski and Czuchra 2000) was no higher than the success of canopy nesters at BNP, and 2) canopy nests were both much larger (i.e. possibly easier to be found) and more profitable (a predator would have to eat contents of about ten chiffchaff nests to get an energetical equivalent of robbing a single blackbird nest). The results of Willson and Gende (2000) from an Alaskan forest underline this possibility, they found no differences in predation rates among vegetation strata, but larger nests (thrush-sized) were more often depredated than the small (warbler-sized) ones.

Whatever, the cause though, the BNP data give no support to the idea that the forest floor constitutes the most dangerous place to breed in the forest. The results from other temperate/subboreal forests lend no support to this notion either. Nests on the ground were either more successful (Martin 1993, 1995) than the canopy
ones or there was no difference between the layers (Yanes and Suárez 1995, Willson and Gende 2000). In all these areas the predation rates on the ground nests were much lower (up to 50% lower) than at the BNP. It is difficult to understand this relative immunity to predation of ground-nesters outside the BNP. In places such as high mountains in Arizona (Martin 1993) or in Alaska (Willson and Gende 2000), this could be due to impoverishment of the predator fauna under severe climatic conditions, but otherwise the reasons remain obscure.

In conclusion, hole-nests in temperate/subboreal forests are really safer, even in areas such as the BNP, characterised by high predation pressure. On the other hand, there is no support for the idea that nesting on the ground is more dangerous than the open nests in tree crowns. Therefore, it does not seem justified to use the “safer nest site” arguments to explain the variation in breeding behaviour and life-history of non-hole nesters using different vegetation strata. However, a long established tradition to use the security of nesting places in interpreting biological traits of hole-nesters (Lack 1954, Nice 1957, von Haartman 1957) remains valid.

References


Walankiewicz, W. 1991. Do secondary-cavity nesting birds suffer more from competition for cavities or from predation in a primeval deciduous forest? – Natural Areas J. 11: 203—212.


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