Characteristics and selection of nest sites of the flexible cavity-nester, the European robin *Erithacus rubecula*, in the temperate primeval forest (Białowieża National Park, Poland)

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Abstract
Despite its broad range and high abundance, nest sites of the European robin *Erithacus rubecula*, a small forest passerine, are rarely characterised, and most studies refer to human-transformed habitats. In this paper, we describe the species’ nest sites in the natural conditions of a primeval forest. We also investigate robin preferences to address nest site selection which can only be assessed if the availability of potential nest sites is known. We studied robins’ nest sites in Białowieża National Park, eastern Poland, on three study plots (~30 ha each) in 2016–2019. Among all nests found (n = 165), the majority (118, ~72%) were found in tree holes, followed by ground nests (25, ~15%) and root-soil plates (22, ~13%). When the availability of cavities and root-soil plates is accounted for, it appears that robins preferred tree holes over plates. Robins appeared to be weakly selective in respect to tree species, preferring hornbeam *Carpinus betulus*, small-leaved lime *Tilia cordata* and Norway spruce *Picea abies* over other trees. Since both cavities and root-soil plates are superabundant in the Białowieża Forest, but scarce or absent in the heavily transformed robin breeding habitats of Western Europe (parks, orchards, hedgerows or managed forests), ground-nesting may predominate there simply due to these choice limits. In summary, our results provide a basis for understanding how original nest-site choices that evolved in natural, unmodified habitats can change when a species adapts to human-transformed habitats.

Keywords: facultative cavity nesters, nest parameters, nest preference, primeval habitat, root-soil plates

Introduction
The European robin *Erithacus rubecula* is small (c. 19 g), widespread and one of the most numerous forest passerines in Europe and Western Asia (Glutz Von Blotzheim & Bauer 1988; Cramp & Perrins 1993; Hegemeijer & Blair 1997). Despite its wide range and high abundance, surprisingly little is known of its breeding biology (Lack 1946, 1948, 1965a; Harper 1985; Cramp & Perrins 1993; Prokofeva 2006; Lebedeva & Lomadze 2007; Knysh 2008; Zimin 2009; Baranovskiy & Ivanov 2017). A search in the Web of Science databases (www.webofscience.com) for terms such as “European robin” plus “nest” in “all fields” resulted in just 27 records for European robin, while the same search for other numerous and frequently studied cavity nesters resulted in 5–26× more records (blue tit *Cyanistes caeruleus* – 362, great tit *Parus major* – 717, pied flycatcher *Ficedula hypoleuca* – 411, collared flycatcher *Ficedula albicollis* – 139). In particular, few studies deal with robins’ natural nesting places (Prokofeva 2006; Knysh 2008; Zimin 2009; Baranovskiy & Ivanov 2017), and all of them come from Russia or Ukraine and are not available in English. Nearly half of the published works refer to the British population (*E. r. melophilus*), which inhabits mostly human-transformed environments. In contrast to continental, nominate *E. r. rubecula*, British robins are mostly sedentary and highly synanthropic (Lack 1946, 1948, 1965a; Harper
the still increases potential long-term. The paucity of research related to the European robin’s nest sites may be due to its highly secretive behaviour during its nest building phase and difficulties in finding its nests other than nest-boxes (Cramp & Perrins 1993; Lebedeva & Komadze 2007; Zimin 2009).

Robins show a prominent level of plasticity in nest site choice, both in forests and in anthropogenic environments (Cramp & Perrins 1993; Zimin 2009; Baranovskiy & Ivanov 2017). In Western Europe, where they occur in the vicinity of humans – in gardens, yards or midfield hedges – nests are most often located on the ground, under vegetation cover and in various structures such as nest boxes, postboxes, old buckets, shoes, cracks in buildings, under windowsills, in piles of stones, and even in a dead cat or human skull (Lack 1965a; Glutz Von Blotzheim & Bauer 1988; Schmidt 1990). In forest environments, they build nests across the full range of niches and heights, ranging from ground level to the tree crowns, including tree holes (Zimin 2009; Baranovskiy & Ivanov 2017). A striking feature of all robins’ nests is their perfect hiding (Zimin 2009).

Studies aiming to investigate nest site selection in natural conditions should be performed in unmodified environments (e.g. Lack 1965b; Tomiałojć et al. 1984, Wesołowski 2007a). Unfortunately, most of the data on robins’ nests comes from human-transformed environments, including forests with long-term intensive management. The range of potential nesting niches is strongly limited there, which affects the choice of breeding sites and increases both inter- and intra-specific competition (Bruns 1960; Newton 1998). In such environments it is hardly possible to discover the robins’ adaptations to the primeval forest conditions, where they evolved (e.g. Lack 1965a; Harper 1985; Prokofeva 2006; Knysz 2008). There are very few areas in lowland Europe where such unmodified conditions still exist. Perhaps the best known among them is the Białowieża Forest in eastern Poland, in particular its strictly protected area (Białowieża National Park, hereafter BNP) (Faliński 1968; Bobiec 2002), representing the last fragment of European primeval lowland temperate forest. This area provides a unique opportunity to study the ecology and behaviour of organisms under conditions that prevailed in European forests before their strong transformation by humans (Wesołowski 1983; Tomiałojć et al. 1984; Tomiałojć & Wesołowski 1990, 2005, Wesołowski 2007a).

To fill the gap in our knowledge on robins’ nesting places, in this paper we characterise nest sites of European robins breeding in natural conditions. Apart from fulfilling these descriptive purposes, we assess species nest site preferences for the first time in two main types of broad-leaved temperate forests in the BNP: ash–alder riverine and lime–hornbeam stands, differing in vegetation structure and the availability of various nesting niches. We discuss differences in patterns observed between these habitats and compare our results with other studies.

Materials and methods

Study area

The Białowieża Forest is located in north-eastern Poland on the Polish–Belarusian border (coordinates of the Białowieża village: 52°42′04″N, 23°52′00″E). It is situated in the transition zone between boreal and nemoral forests. The best-preserved parts of the Białowieża Forest have been under strict protection since 1921 within BNP. In 1992, it was inscribed on the United Nations Educational, Scientific and Cultural Organization World Heritage List (Jaroszewicz et al. 2019).

The unique, well-preserved stands of the strict reserve are a remnant of the vast forests that once covered most of Europe. Old-growth stands of BNP are highly diverse, in both species and structure, with superabundant dead wood (Faliński 1968; Falińska 1991; Wesołowski et al. 2006; Wesołowski 2012). The trees reach large sizes and ages (up to few hundred years). The tallest are Norway spruce Picea abies, which can reach 57 m in height, while the thickest are pedunculate oak Quercus robur, reaching up to 230 cm in diameter at breast height (DBH) (Falińska 1977; Falińska 1991). Other organisms are also present in a variety that is unique in Europe. Species communities and relations between them and the environment have been well preserved (Wesołowski 2012). Studies conducted on other bird species show that tree holes occur in excess in the strict BNP reserve (Walankiewicz 2002, Wesołowski 2007a, Wesołowski & Martin 2018). All of this makes the strict BNP reserve a unique place for studying avian nest site preferences as its forest stands are currently free from direct human activity.

Field methods

Study plots. The research was conducted from 2016 to 2019. Fieldwork was carried out during the species’ breeding season: from the third week of March to the end of June each year. Three sample plots, each about 30 ha, were designated within larger permanent census plots established in 1975 for
bird monitoring (Tomiałojć et al. 1984), with no or little human activity both in the forest stands and around them. One plot, designated plot K, was located in the ash–alder riverine forest Fraxino–Alnetum and bordered open, currently unmanaged tussocky meadows in the Narewka River valley at the edge of BNP. The two other plots comprised lime–hornbeam forest and were located either on the edge of the strict nature reserve (plot W, bordering meadows, partly mowed once a year) or ~3 km inside the forest (plot M). A detailed description of the plots can be consulted in e.g. Tomiałojć and Wesolowski (1996) or Wesolowski et al. (2015).

**Nest site characteristics.** Each year, from the earliest arriving birds, singing males and – later in the season – pairs were mapped on all three plots following a combined territory mapping approach (Tomiałojć 1980) every 2 days. Additionally, attempts to mist-net and colour-ring male robin were performed early in the season, and at the stage of nest building some 65% of males present were colour-ringed. Both these approaches were helpful in recognising the number of territories and delimiting their borders before the birds started nest building. Then, we searched for the robins’ nests exclusively by direct observation within the territories: by following adult, paired birds carrying building material or food to the chicks. Nests were found in 85% of the intensively searched territories on average (range 75–95%, depending on the plot and year), so the results are unlikely to be biased much, given that very few nests were missed. We classified a place as a nest site if a nest with at least one egg was found. After a nest was found, it was monitored at 5-day intervals until the young fledged or a nest loss occurred. During 2017 and 2018 all the nests were monitored with a camera-trap. Inspections of nests located up to 2.5 m above the ground were made with a flashlight and a mirror. A camera on an extension arm was used for the higher-placed nests in the tree holes. It was possible to check and monitor places up to approximately 10 m above the ground this way, and in a few higher locations the trees were climbed with spurs. Exact locations of all the nests were established using a Garmin 62s Global Positioning System.

Several measurements were recorded for each nest in a cavity: forest type (ash–alder vs lime–hornbeam forest), tree species, height of the nest location above the ground, tree condition (alive, dead or dying), tree tilt, DBH and cavity origin (woodpecker-made or other). After young fledged or a brood loss was recorded, the nest site was described with further measurements. The collected data differed for cavity and root-soil plates due to their different nature. The height and width along with the shape of the entrance of the hole were noted as well as the diameter of the tree under the hole. Hole types reflecting their origin were adopted after Wesolowski and Martin (2018), with five categories: round, scar, fissure, rot hollow and bulb. The holes were measured inside by their depth with the nest inside and the total depth (after removing the nest). Accessibility of a nest for predators was measured as the distance between the nest and the edge of the entrance (the so-called “danger distance”) (Wesolowski 2002).

The description of the root-soil plates was different. Their maximum height and width were measured, and the tree species was noted. A five-grade decomposition scale was used to assess the degree of log decomposition (Brown 1974). To describe the potential suitability of the root-soil plate for birds, the presence of roots, soil and vegetation was assessed according to three more scales: root decay level (RDL) = 0 (0–25%), 2 (51–75%), 3 (76–100%), 4 (present but covered by soil); soil coverage degree (SCD) = 0 (old compacted soil), 1 (<5%), 2 (<25%), 3 (<50%), 4 (<75%), 5 (>75%); plant cover degree (PCD) = 0 (0–25%), 1 (26–50%), 2 (51–75%), 3 (76–100%). Due to the large variety in form and the absence of any regular concealment boundaries, it was impossible to record additional information on ground nests.

**Statistics.** One could reasonably assume that most traits of nest sites can be described by a normal distribution. However, since there were frequent outliers in the data, we simply describe them as they are to provide basic descriptive statistics. Where necessary, non-parametric methods (e.g. the bootstrap; Efron & Tibshirani 1998) not requiring assumptions in respect to underlying distributions were used to compare means. The general additive mixed models (GAMMs) used to estimate the mean number of holes for a given tree species in each DBH class included counts as a response, treated as having a Poisson distribution; these are described below.

**Nest site selection.** We assessed nest site and tree species preferences of robins using Ivlev’s electivity index (Ivlev 1961). This method characterises the degree of selection (or electivity), given the proportions of objects present (available) to those actually used according to the equation

\[
EI = \frac{r_i - p_i}{r_i + p_i},
\]

where \(r_i\) is the relative abundance (i.e. proportion among all present) of objects of a given type available
and \( p_i \) is the proportion of objects used (among all used). The index has a straightforward interpretation: it takes values from the \([-1, 1]\) range, with negative values indicating avoidance, positive indicating preference and zero indicating no selectivity (i.e. the use of a resource is proportional to its availability). In our case, \( r_i \)'s were relative abundances of tree holes and root-soil plates present on the plots, while \( p_i \)'s were proportions of robins’ nests in each nest site type. In the case of tree holes and selectivity for tree species (all plots combined), \( r_i \)'s were estimates of the tree holes in each tree species, and \( p_i \)'s reflected the proportions of nests in a given tree species. With nest sites, only selectivity for cavities and root-soil plates could be assessed, despite robins also having nested on the ground (it is impossible to assess the relative abundance of the ground, so ground nests were excluded from this analysis). Root-soil plates were fully censused and mapped in 2019 across all plots, totalling 1878, 266 and 413 plates at K, M and W plots, respectively, so that there is no uncertainty associated with these numbers. However, the number of cavities had to be estimated with survey sampling methods. We estimated the number of available tree holes in three steps: first, we estimated the number of trees of the eight most common species on each of the three plots for each of the 11 DBH (size) classes (see \textit{Estimation of tree abundance} below). The mean number of holes per tree of a given species and for a given DBH class was estimated separately with a GAMM, using data from the Kapusta (2019) survey (see \textit{Estimation of cavity numbers per tree} below). The total abundance of tree holes on a given plot (or across the plots in each tree species in a given DBH class) potentially available to birds is, then, the product of the number of trees from each species-and-diameter combination on that plot times the number of cavities per tree in a given species-and-diameter combination. Both the number of trees of a given species in a given DBH class and the number of tree holes in that species-and-diameter class are estimates and have associated uncertainty measures. We addressed uncertainty in both these estimates with a resampling (bootstrap) technique (Efron & Tibshirani 1998) to obtain distributions of desired quantities and to fully propagate both sources of uncertainty into Ivlev’s electivity index \((EI)\). Therefore, our EI estimates became distributions as well, which allowed us to estimate and report any uncertainty associated with the index itself. Calculation of EI’s was performed with the selectapref package (Jason 2020), built into a self-written loop over bootstrap resamples to estimate variation, in R 3.6.3 (R Core Team 2019).

\textit{Estimation of tree abundance.} To obtain the number of trees on a plot, we used data from a survey-sampling of trees, performed in our study plots in 1999 (plot K), 2015 (plot W) and 2015–2016 (plot M). Censuses were performed on squares within the \(50 \times 50\) m grid, chosen at random and covering the whole square area (0.25 ha) (Walankiewicz et al. 2007; Stański et al. 2021). At plot K, 32 squares were sampled this way (total area surveyed 8 out of 33.5 ha) totalling 5000 individual trees, while the respective numbers at W and M were 24 and 16 squares (6 and 4 ha surveyed, out of 35 and 30 ha, respectively), totalling 5632 and 2847 individual trees, respectively. Within each square, all trees with DBH \( \geq 1\) cm were counted and their DBH values measured, providing data on species and age composition of the tree stands at the time of survey. Original, continuous DBH values were then simplified into 11 classes (1–10, 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, 81–90, 91–100 and \(\geq101\) cm). We used bootstrapping and resampled the datasets from each plot 1000 times to obtain distributions of abundance of trees of a given species and in a given DBH class on a given plot, from which medians, interquartile ranges and 95% intervals were extracted as summary statistics. Although we bootstrapped the complete datasets (i.e. including trees too thin to bear holes suitable for robins), only trees with DBH \( \geq 13\) cm (the smallest diameter of a tree with a robin’s nest in a tree hole) were considered in further calculations.

\textit{Estimation of cavity numbers per tree.} Kapusta (2019) surveyed cavity abundance at 45 points (each 0.05 ha) on three sample plots on BNP, where all trees with DBH \( \geq 10\) cm and/or 130 cm height were measured and searched for cavities. In total, 107 cavities were found in 84 trees, with the minimal size limits for a cavity to be considered available for small, passerine cavity nesters set at 7 cm bottom diameter (sufficient to fit the nest of a small bird) and a 2.5 cm entrance width. These criteria fit the smallest-size cavities occupied by robins as found in our study (minimal entrance diameter 2.3 cm, minimal inside/bottom diameter 5.0 cm), which means that occasionally robins are able to occupy cavities even smaller than those classified by Kapusta (2019) as “available to birds”. In turn, the possible number of cavities being available for robins may be a bit higher than found by Kapusta (2019), since some of the smallest ones might have been omitted, but this difference is unlikely to be large and we are unable to correct it in any way. We used these data to estimate the number of cavities per tree.
with Poisson GAMM, including tree species as a fixed factor (with eight levels), tree diameter expressed as the number (1–11) as described above and modelled with a smooth function, and a plot random effect (see Table S1). We again used non-parametric bootstrapping (1000 resamples) of the original dataset and fitted GAMM to each resample. The predicted numbers of cavities per tree in a given DBH class were obtained with the predict function from the models fitted to each resample. Medians, along with 95% confidence intervals, were then extracted from the distribution of predicted values (Figure S1).

Estimation of total number of cavities. Distributions of the number of trees of a given species–diameter combination and the number of cavities per tree were multiplied to obtain the final quantity: the expected distribution of the total number of cavities on a plot or in a given tree species. EI was also used to assess preferences for the seven most common tree species, using the above-described approach (Tables S2–S4).

Results

Nest types

Three types of robin’s nests were recognised in BNP: ground nests, cavity nests and root-soil plate nests. Cavities were the most numerous nest type found in lime–hornbeam habitat (plots M and W), and the second most numerous in the ash–alder plot (K) (Figure 1). The majority of robins’ nests in root-soil plates were found in ash–alder forest, while they were less numerous in lime–hornbeam. Ground nests were the least represented nest type in both forest types. Differences in nest-type proportions between the two habitats were significant ($\chi^2 = 66.09$, df = 2, $P < .001$).

Ground nests

Due to both the difficulties in characterising ground nests by measurements and their small number ($n = 22$), we only characterised these nests descriptively. Five types of ground nests could be recognised. The first ($n = 2$) type that could be distinguished were the ones built in clumps of grass and fern. These were very well-hidden nests, invisible to human eyes from a distance of 2 m. In this case, robins utilised the space between grass stalks and fallen grass leaves (Figure 2(a)). “Hazel nest” was the second ($n = 5$) type of ground nest – these nests often had no top cover and were tightly fitted, low over the ground, between hazel trunks. All such nests were built low at the base of trunks (Figure 2(b)). Also, five ground nests were found in root crowns of several tree species. Nests of this type were usually located within a root crown, close to or just under the main trunk overhang and more or less hidden (Figure 2(c)). The most numerous ground nest type ($n = 6$) was the “rotten stump” nest, localised under the overhang of highly decomposed deadwood, most often in the form of a stump (Figure 2(d)). Finally, the last type was found integrated into the litter under fallen branches. In these nests ($n = 5$), the branch formed a cover and roof for the nest (Figure 2(e)).

Nests in tree holes

The majority of robins’ nests were found in non-excavated cavities, mostly in living trees (Table I). Robin cavity nests were found in 11 tree species. The greatest number of cavity nests were situated in hornbeams in lime–hornbeam habitats and in alders in ash–alder forest – these tree species predominate in their respective habitats, suggesting that robins are opportunistic and may simply occupy cavities in the most abundant trees (Figure 3). However, when the availability of cavities in a particular tree species is considered, it appears that there are clear preferences for Norway spruce, hornbeam and lime, all with positive Ivlev’s electivity indices, while no avoidance is evident (Table II). This might, however, be due to extremely small sample sizes in some cases resulting in wide uncertainty around our EI estimates.

In BNP, robins occupied cavities highly variable in size, in respect to both the entrance and the inside. The smallest diameters of the entrance ranged from 2.3 to 17.0 cm (median 5.0 cm), whereas the greatest diameters varied from 5.0 to 73.0 cm (median 14.0 cm) (Table III).

The most common hole entrance shape found during this research was a slit hole, with a narrow and tall entrance. Robins also built their nests in rot holes with irregular shape, probably mostly created
by fungi in the wood decay process. A marginally lower share of robin nests were round holes, and these included mainly old woodpecker holes or perfectly round non-excavated cavities. Other types of cavity entrance shapes constituted less than 10% of the total: knotholes (where a branch was detached in a living tree, Wesolowski & Martin 2018) and crack holes – an opened scar after frost created a scratch and chimney – i.e. the top of a broken tree. Entrance

![Figure 2. Different kinds of ground nest of European robin in BNP (n = 22). Arrows indicate the exact location of the nest: (a) nest in the clump of fern, (b) hazel type, (c) nest under the root crown, (d) rotten stamp type, (e) nest under the fallen branch.](image)

| Cavity type       | n   | %  |
|-------------------|-----|----|
| Excavation        |     |    |
| Non-excavated     | 111 | 90.2|
| Excavated         | 12  | 9.8 |
| Status            |     |    |
| Live              | 102 | 65.0|
| Dead              | 55  | 35.0|

![Figure 3. Location of European robins’ nests in different tree species in ash–alder and oak–hornbeam habitats.](image)
Table II. Robin’s nest site selection as measured with Ivlev’s electivity indices for the eight tree species, the most common in the studied plots (data combined for all three plots), in which 94% of all robin’s nests in cavities were found (n = 132). Availability (total) and nest numbers (used) are given. Totals represent the median estimated number of cavities (25–75% interquartile range in parentheses) in all trees of a given species with DBH ≥13 cm and age structure considered (see Methods). EI is the Ivlev electivity index, while P preferred is the probability that EI is positive (i.e. the proportion of estimates >0). No nests were found in oaks, so the EI is −1 by default (complete avoidance).

| Tree species                  | Cavities |          |          |          |          |
|-------------------------------|----------|----------|----------|----------|----------|
|                               | Total    | Used     | EI       | P preferred |
| Pendunculate oak *Quercus robur* | 131      | 0        | −1       | 0         |
| (79–188)                      |          |          |          |           |
| Hornbeam *Carpinus betulus*    | 2620     | 90       | 0.10     | 0.942     |
| (2328–3054)                   |          |          |          |           |
| European ash *Fraxinus excelsior* | 163      | 3        | −0.04    | 0.315     |
| (82–262)                      |          |          |          |           |
| Norway maple *Acer platanoides* | 285      | 2        | −0.59    | 0         |
| (236–348)                     |          |          |          |           |
| Small-leaved lime *Tilia cordata* | 400      | 15       | 0.14     | 0.878     |
| (338–472)                     |          |          |          |           |
| Black alder *Alnus glutinosa*  | 418      | 9        | −0.15    | 0.372     |
| (243–646)                     |          |          |          |           |
| Norway spruce *Picea abies*    | 87       | 4        | 0.27     | 0.870     |
| (58–119)                      |          |          |          |           |
| Elm *Ulmus sp.*               | 155      | 1        | −0.23    | 0.301     |
| (14–249)                      |          |          |          |           |

Table III. Characteristics of the European robin cavity nests in Białowieża National Park in 2016–2019.

| Variable             | n  | Mean  | SD  | 25%  | 75%  | CV  |
|----------------------|----|-------|-----|------|------|-----|
| Entrance             |    |       |     |      |      |     |
| Smallest diameter (cm) | 90 | 5.7   | 2.5 | 4.0  | 7.0  | 43.9 |
| Greatest diameter (cm) | 85 | 21.3  | 17.2| 10.0 | 26.0 | 80.8 |
| Area (cm²)           | 82 | 128.3 | 202.6| 10.8 | 127.2| 157.9|
| Hole                 |    |       |     |      |      |     |
| Smallest diameter (cm) | 90 | 10.9  | 3.0 | 9.0  | 13.0 | 27.5 |
| Greatest diameter (cm) | 90 | 14.3  | 4.7 | 11.1 | 16.0 | 32.9 |
| Area (cm²)           | 87 | 131.8 | 78.2| 31.4 | 151.3| 59.3 |
| Volume (cm³)         | 87 | 2100.9| 2261.1| 157.0| 2593.9| 107.6|
| Nest distance from entrance (cm) | 87 | 8.5 | 7.3 | 3.5 | 12.5 | 85.9 |
| Danger distance (cm)  | 88 | 12.8  | 8.0 | 8.0  | 17.0 | 62.5 |
| Depth (cm)           | 70 | 16.6  | 9.9 | 10.0 | 21.0 | 59.6 |
| Tree                 |    |       |     |      |      |     |
| DBH (cm)             | 77 | 40.5  | 13.5| 31.8 | 47.4 | 33.3 |
| Diameter under the hole (cm) | 96 | 38.4 | 12.6| 30.2 | 45.2 | 32.9 |

sizes (height and breadth) were clearly associated with hole origin (Figures 4–6).

European robins occupied cavities located between 0.1 and 16 m above the ground. The majority of robins’ nests in cavities (71% of all nest types) were located low, up to 2 m above the ground (Figure 7).

Root-soil plate nests

European robins’ nests in root-soil plates were well hidden among clods of soil and tangled roots. Root-soil plates chosen by robins to build nests strongly varied in size: lengths ranged from 60.0 to 670.0 cm (median 245.0 cm), whereas heights ranged from 42.0 to 370.0 cm (median 130.0 cm). Nests in root-soil plates were almost always located in recesses – i.e. places resembling a tree hole. However, birds were able to construct an “entrance tunnel” with rotten leaves and moss, creating a cavity-like structure. There were only few cases (n = 4) where robins built semi-open nests in plates (unlike cavities). The dimensions of root-soil plate nests differed from those of nests in cavities (Table IV). The mean entrance area was larger in cavities, but the danger distance was ~5 cm greater in comparison to root-soil plate nests (Tables III and IV).
Nest site preference

There was a significant difference in the frequency of hole-nesting vs root-nesting robins between habitats. In the two lime–hornbeam plots (M and W), 0 of 25 and 2 of 59 nests (0% and ~3.5%), respectively, were on root-soil plates, while the remaining pairs nested in tree holes. At the K plot (riverine), 19 nests were on root-soil plates (~45%) and 23 in cavities. These numbers did not follow the available number of either nest site type, suggesting significant nest site selection: in riverine forest robins preferred cavities (Ivlev’s index of 0.24 indicates their more intense use than expected given their availability in the forest) and avoided roots (Ivlev’s index −0.13; used less frequently than expected given
Table IV. Characteristics of robin’s nests in root-soil plates in the BNP.

| Variable                        | n  | Mean | SD  | 25% | 75% |
|---------------------------------|----|------|-----|-----|-----|
| Entrance                        |    |      |     |     |     |
| Smallest diameter (cm)          | 14 | 9.7  | 3.9 | 8.0 | 9.9 |
| Greatest diameter (cm)          | 14 | 11.0 | 2.6 | 9.3 | 13.0|
| Area (cm²)                      | 14 | 110.5| 60.9| 74.6| 125.4|
| Nest distance from entrance (cm)| 18 | 5.6  | 4.5 | 3.0 | 7.5 |
| Danger distance (cm)            | 15 | 7.9  | 3.6 | 7.3 | 10.0|
| Root-Soil Plate                 |    |      |     |     |     |
| Width (cm)                      | 18 | 250.9| 165.7| 130.0| 279.0|
| Height (cm)                     | 18 | 167.7| 107.1| 92.5 | 214.3|

Table V. Robin’s nest site selection measured as Ivlev’s electivity indices for the two nest site types (cavities vs root-soil plates) at the three plots. For both nest site types, availability (total) and nest numbers (used) are given. Totals for roots come from a complete census, are estimates for cavities (see Methods) which include all trees with DBH ≥13 cm (95% confidence intervals in parentheses). EI – Ivlev’s electivity index. No nests were found in roots at M so the EI equals −1 by default (complete avoidance).

| Plot | Cavities | Root-soil plates |
|------|----------|------------------|
|      | Total    | Used  | EI     | Total | Used | EI    |
| K    | 1082     | 23    | 0.24   | 1878  | 19   | −0.13 |
|      | (555−1941)|      | (0.13; 0.36) |       |
| M    | 1334     | 35    | 0.55   | 266   | 0    | −1    |
|      | (1006−1849)|      | (0.53; 0.56) |       |
| W    | 1954     | 57    | 0.51   | 413   | 2    | −0.80 |
|      | (1381−2894)|      | (0.49; 0.52) |       |

availability), but both these trends were rather weak. In lime–hornbeam forests (M and W) these patterns were much stronger: roots were strongly avoided (Ivlev’s indices of −1 and −0.80; either not used at all or used much less frequently than expected given their availability), while cavities were moderately preferred (Ivlev’s indices of 0.55 and 0.51) (Table V; Figure 8).

Discussion

Robins are often classified as a nest site opportunist or ground nester (Cramp & Perrins 1993; Prokofeva 2006; Knysh 2008) or a facultative cavity-nester (Wesołowski 2007a, Wesołowski & Martin 2018; Zawadzka 2018). Our results suggest that this species prefers to nest in cavities, rather than in other places imitating holes. The results suggest a specific category for this species: “flexible cavity nester”, since robins facultatively build nests in other places, but the most preferred nesting places are still cavities (Figure 8). Our studies in Białowieża Forest also indicate that this species is extremely timid in the breeding season. A female robin may put nest material in a different place to mislead an intruder if she is feeling observed, or she could drop nest material from her bill and, for example, start foraging. Sometimes this species can build a nest in just a few hours (Lack 1965a; Glutz Von Blotzheim & Bauer 1988), which makes search much more difficult as there is less time to follow birds carrying nest material.

Ground nests

Among the three types of robins’ nests, the most difficult to characterise were ground ones due to their wide variety (Figure 2). Results similar to these presented in our study from Białowieża NP were obtained by Zimin (2009) in Karelia (taiga zone, NW Russia), Prokofeva (2006) in the St. Petersburg region (NW Russia), Knysh (2008) in a forest-steppe zone (E Ukraine) and Baranovskiy and Ivanov (2017) in Riazan region in suburban, managed forests and a city area (central European Russia). Apart from nests similar to ground nest types as found in the Białowieża NP (a variety of rotten stumps, clumps of plants, root crowns and nests among roots and branches, under litter or old leaves) these authors also describe ground nests as follows: nests in walls of steep and low slopes, in small dimples and under fallen trunks. Contrary to our study, in many regions the most numerous robins’ nest type was ground nests (Figure 9). This may be a result of low availability of tree holes, as in the Russian Karelia taiga forest (Zimin 2009), in managed forest in the Russian Leningrad Region (Prokofeva 2006) or Sumy Ukraine region (Knysh
and in anthropogenic habitats in Switzerland (Glutz Von Blotzheim & Bauer 1988). Low availability of suitable tree holes could also affect European robin nest site choice in Great Britain, where studies were carried out mostly in university gardens and hedges (Lack 1965a). Zimin (2009) stresses the problem with searching tree-hole nests: finding ground nests is much easier than finding nests high in the trees.

*Importance of root-soil plates*

The root-soil plate robins’ nests in Białowieża NP were most often found in ash–alder habitats. In spite of such results, cavities were still the most preferred nest site in both habitats (ash–alder and oak–lime–hornbeam forest). Nests were situated mostly in the low, ground part of the root plate, but also on the side, and in the turfy back of the root plate. Robins nesting in such places have also been reported from Karelia (Zimin 2009), Riazan region (Baranovskiy & Ivanov 2017) and SE Poland (Zabłocie reserve – oak–hornbeam forest) (Wojton & Pitucha 2020). In taiga, root-soil plates seem to play a significant role as a nesting place for robins (26% of all nests), perhaps because tree holes are much less abundant, but still, plates were the least used nesting location (Zimin 2009) (Figure 9). Root-soil plates in Riazan region were used by robins as nesting places only in 1.1% of cases (Baranovskiy & Ivanov 2017). In robins of SE Poland, 2.1% out of over 180 searched root-soil plates were occupied. Few studies have addressed the importance of root-soil plates as nesting places for birds, especially for the wren Troglodytes troglodytes, which builds its nests most often.
in these structures (Wesołowski 1983; Tomiałojć & Wesołowski 2005; Czeszczewik & Walankiewicz 2016; Wojton & Pitucha 2020). Our study shows for the first time that robins choose root-soil plates for nesting, particularly where these are superabundant, but they are used less frequently than would be expected given their availability.

Robins as a cavity nester

Indisputably, in both studied habitats, the most preferred nest location for European robin in the Białowieża NP were tree holes. Białowieża Forest offers a vast variety of available tree holes (e.g. Tomiałojć & Wesołowski 2004; Wesołowski 2011, 2012; Walankiewicz et al. 2007). The long-term monitoring studies of cavity fates by Wesołowski (2007a, 2007b) leaves little doubt that competition might be missing as an important mechanism here. There are many more cavities than cavity-nesters in Białowieża Forest, and the former are extremely variable. The birds do not compete for cavities in this forest. In contrast to most managed forests, conditions in Białowieża are strikingly different – so much so that mechanisms widely recognised as limiting may not act here.

The preference is therefore expected, since cavities are most likely the safest breeding place in the forest (Wesołowski & Tomiałojć 2005; Wesołowski & Martin 2018). Nests of European robin in the Białowieża NP were mostly located in slit tree-holes (cavities with a long vertical diameter and a short horizontal diameter). Similarly to our results, other authors have identified many nest-cavity types like those presented in our study (Zimin 2009; Baranovskiy & Ivanov 2017).

The only studies reporting a substantial proportion of robins’ nests in cavities were found in the Riazan region, Russia (~65%, Baranovskiy & Ivanov 2017, compared to ~72% in the Białowieża NP, this study). Those authors emphasise the importance of cavities as nesting places for robins in that area. All other studies from continental Europe reported much lower percentages (1–30%) of all nests in cavities (Figure 10), which may simply stem from their unavailability as a result of forest management. There are no published data on measurements of cavities occupied by robins, and the only information we could find was reported in collective studies (Glutz Von Blotzheim & Bauer 1988; Cramp & Perrins 1993).

Cavity nesters have evolved many ways to minimise predation risk. For example, nuthatches Sitta europaea choose voluminous cavities, which makes it harder for a predator to reach for chicks, and they cover the entrance with clay and mud to reduce its size (Wesołowski & Rowiński 2004; Rowiński 2013). Titmice Paridae and flycatchers Muscicapidae choose narrow cavities with a relatively small entrance; predators have more difficulty accessing such holes (Wesołowski 2002; Czeszczewik & Walankiewicz 2003; Maziarz 2012; Wesołowski & Rowiński 2012; Maziarz et al. 2015) (Figure 10). Titmice evolved hissing behaviour (Löhr 1964; Rowiński 2013; Zub et al. 2017), which is helpful in deterring predators, as it is difficult for tit mice to escape from deep hollows when threatened (Adamik & Král 2008). The relatively large entrance size, short entrance–nest distance and “danger distance” in cavities chosen by robins (Figure 7) could reflect yet another antipredator strategy: birds can easily escape such cavities when attacked, by sacrificing the brood instead of their own life. In addition, robins are a species with good night vision (Bolshakov & Rezyji 1998), so they have a non-zero chance to escape when attacked during the night, in comparison to birds with poor night vision such as titmice (Cramp & Perrins 1993). This might be important as the vast majority of avian broods in the Białowieża NP are predated at night (Rowiński 1993).

**Figure 10.** Cavity dimensions occupied by European robin in comparison to other cavity-nest species in BNP (ER – Erithacus rubecula; PP – Poecile palustris; SE – Sitta europaea; FH – Ficedula hypoleuca; FA – Ficedula albicollis; PM – Parus major; PE – Cyanistes caeruleus) (Wesołowski 1996, Czeszczewik & Walankiewicz 2003; Wesołowski & Rowiński 2004, 2012; Walankiewicz et al. 2007; Maziarz 2012). Medians shown (cm).
2013). Interestingly, another species known as a facultative cavity nester, also studied in the Bialowieża NP, shows similar tendencies: the blackbird *Turdus merula* (Czeszczewik & Walankiewicz 2016). Despite being well known for nesting in forks of branches, near tree trunks or in concavities, ~50% of its nests were located in tree-holes or in decaying snags in the Bialowieża NP (Tomiałojć 1993).

In the primeval forest of the Bialowieża NP, a vast number of bird species avoid cavities in dead wood, most likely due to prominent levels of predation (Wesołowski 2007a, Maziarz et al. 2015; Wesołowski & Martin 2018). The robin case seems to confirm this, with over 60% of nests located in living trees (Table I). Dead wood is softer, and it is much easier for predators to reach the brood (Christman & Dhandt 1997; Walankiewicz 2002; Rowiński 2013). Similarly, tree holes excavated by woodpeckers are also more vulnerable to attacks by predators (woodpeckers themselves visit old tree-holes and rob nests found there), and thus are less frequently occupied by small, passerine non-excavators (Bai et al. 2005, Remm et al. 2006; Wesołowski 2007a, Walankiewicz et al. 2007; Maziarz 2012; Rowiński 2013), including the European robin: ~90.2% of nests in cavities were in non-excavated cavities (Table I).

**Nest height**

European robin nest cavities were found in the Bialowieża NP mostly within 0.1–2 m above the ground, but a single robin’s nest was placed as high as 16 m above the ground. Authors from other regions found robins’ nests mostly at lower heights: up to 2 m in the Caucasus region (Lebedeva & Lomadze 2007), up to ~4 m in St. Petersburg (Prokofeva 2006) and Riazan regions (Baranovskiy & Ivanov 2017), and up to 8 m in Karelia (Zimin 2009). Zimin (2009) found robins’ nests also down to 6 cm below the ground, but 93% of nests were located up to 1 m above the ground level. Zimin (2009) indicates that there is no nest philopatry among this species. Nest choice is believed to be dictated by conditions of habitat and other circumstances. The same marked birds could occupy a ground nest in the first brood and a cavity in the second one (Zimin 2009). Data obtained in the BNP seems to confirm such facts – seven out of 10 birds changed their nest type during the second brood in the season.

**Conclusions**

Our results indicate that robins are not nest site opportunists under natural conditions: they appear to be moderately to highly selective in respect to nest sites. This selectivity seems to be of variable magnitude in different forest types, but with evident preference for cavities and the avoidance of root-soil plates. Therefore, the frequency of use of particular nest sites in mostly human-transformed habitats in Western Europe might not reflect robins’ true preferences.

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