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## Nest-sites of hole-nesters in a primaeval temperate forest (Białowieża National Park, Poland)

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The study provides the first description of nest-site distribution of European hole-nesters breeding in natural holes in unmanaged stands. The data are mostly from two types of climax stands, *i.e.* oak-hornbeam and ash-alder. The species dealt with are: *Sturnus vulgaris*, *Sitta europaea*, *Ficedula albicollis*, *F. hypoleuca*, *Parus major*, *P. caeruleus*, *P. palustris*, *Dendrocopos major*, *D. medius*, *D. minor*. The following aspects of hole localization are described: tree species, height above the ground, entrance's exposure, tree trunk girth, hole origin (woodpecker-made or "natural"), tree fragment in which hole was located, state of tree fragment containing hole (live or dead), slope of supporting structure, shape of entrance. Though the species showed differentiation in the majority of variables analysed, their patterns of hole utilization still overlapped. The same holes were often used consecutively by different species. Species of similar body sizes exchanged holes most frequently. It is argued that interspecific competition for holes in primaeval forests though present, is less pronounced than in man-transformed, secondary woods.

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Места гнездования дуплогнездников в первичном лесу умеренного пояса (Беловежский национальный парк, Польша)

В работе впервые приведены описания мест гнездования европейских дуплогнездников в естественных дуплах девственного леса. Данные были собраны в основном в двух биотопах климаксового леса: грудов и пойменных лесов, и касаются мест гнездования следующих видов птиц: *Sturnus vulgaris*, *Sitta europaea*, *Ficedula albicollis*, *F. hypoleuca*, *Parus major*, *P. caeruleus*, *P. palustris*, *Dendrocopos major*, *D. medius*, *D. minor*. Обращалось внимание на следующие аспекты положения дупла: вид дерева, высота над землей, отношение летка к солнечному свету, окружность дерева, происхождение дупла (выдолблено дятлом или „естественное”), часть дерева, где находилось дупло, состояние этой части дерева (живая или мертвая), ее наклон, форма летка. Хотя отдельные виды птиц были дифференцированы с точки зрения большинства анализируемых параметров, однако, их требования в значительной степени покрывались. Одни и те же дупла часто использовались по очереди различными видами. Чаще всего это были виды со

сходными размерами тела. Высказывается предположение, что межвидовая конкуренция за дупло, хотя и существует, в первичном лесу выражена слабее чем в преобразованных человеком вторичных лесах.

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## INTRODUCTION

Though hole-nesting birds belong to the most intensively studied species, our knowledge of their biology is heavily biased – almost all studies were carried out on birds breeding in nest-boxes. Data on their biology originating from studies in natural holes are rather scanty (LUDESCHER 1973, NILSSON 1975, 1984a, 1984b, 1986, van BALEN *et al.* 1982) and only a few of these papers (LUDESCHER 1973, van BALEN *et al.* 1982, NILSSON 1984b) contain quantitative information on nest-site requirements of hole-nesters. All the above-mentioned studies in natural holes were done in managed woodlands, and it is not known to what extent and in which direction the situation found in such places differs from that occurring in the pristine conditions. This question has had to remain unanswered till now as there was no information available on the breeding of the hole-nesters in the primaeval habitats.

The aim of the present paper is to fill this gap by providing data on hole-nester's nest-site requirements in the last parts of a primaeval European lowland temperate forest preserved in the Białowieża National Park (Eastern Poland). Data on some aspects of woodpeckers nest-site requirements in the Park were already presented (WESOŁOWSKI & TOMIAŁOJĆ 1986), and this paper is devoted mostly to

the description of nest-site requirements of secondary hole-nesters; data on woodpeckers are presented only for those aspects of their nest-sites which had not been touched upon in the earlier paper.

#### STUDY AREA

The description of the study area follows mainly the accounts of FALIŃSKI (1968, 1977) and of TOMIAŁOJĆ *et al.* (1984). The Białowieża National Park (hereafter referred to as BNP) is in the centre of the Białowieża Forest (1250 sq. km), which is situated at the border between Central and Eastern Europe and within the zone of subcontinental climate. Bio-geographically it falls within the mixed-forest zone characterized by the presence of a significant amount of Norway spruce *Picea abies* in almost all local tree stands. The stands in the Białowieża Forest are composed of exceptionally high trees (by European standards). The maximum measurements for several tree species there are as follows (FALIŃSKI 1968, 1977, FALIŃSKI & HEREŹNIAK 1977):

– height (m): spruce – 55, pine *Pinus silvestris* 45, pedunculate oak *Quercus robur* – 43, lime *Tilia cordata* – 42, ash *Fraxinus excelsior* – 42, alder *Alnus glutinosa* – 40, continental maple *Acer platanoides* – 37, hornbeam *Carpinus betulus* – 30;

– girth at breast height (cm): spruce – 440, pine – 500, oak – 785, lime – 630, ash – 375, alder – 315, maple – 345, hornbeam – 315.

The whole area of the Park (47.5 sq km) has been strictly protected as a nature reserve since 1921, but even before that time its tree stands were not clear cut. No management, except in order to clear fallen logs from a few forest roads is allowed. The stands in the Park contain large quantities of decaying trees, snags, stumps, freshly uprooted trees and old decaying logs.

The climax forest communities of the BNP consist mainly of oak-hornbeam *Tilio-Carpinetum* stands, which occupy 44.4% of its total area, and of swampy ash-alder *Circaeo-Alnetum* and alder *Carici elongate-Alnetum* stands occupying together 21.6% of the Park, and mixed-coniferous forests *Querco-Piceetum*, *Pino-Quercetum*, *Peucedano-Pinetum* covering jointly 28.1%.

The oak-hornbeam stands are the most structurally diversified ones. They are composed of a dozen or more species of trees, being extremely diverse as regards the age and size of trees. Several stands as a whole are over 200 years old, with many trees 250-400 years old. Usually three layers in the canopy are distinguishable in this forest type: the upper canopy (30-45 m) of spirelike spruces and some big oaks; the main canopy (20-30 m) of old limes, oaks, some spruces, maples and hornbeams; the lower canopy (10-20 m) consists mainly of hornbeam, also lime and spruce trees.

In the oak-hornbeam habitat the amount of dead timber is at best a half of that in swampy stands.

Swampy deciduous stands are less stratified; there are only two canopy layers visible: the main canopy composed mostly of alder, spruce and ash; the lower canopy of younger individuals of the same three species of tree. The highest number of fallen logs is characteristic of this habitat type.

In coniferous stands the amount of dead timber (mainly broken stumps or logs) is rather moderate, the canopy is composed of two layers: the main canopy of spruce and pine with an admixture of birches *Betula* spp., and the lower canopy mainly of spruces intermixed with birches and oaks.

#### MATERIALS AND METHODS

There are 24 (25 if one includes partially hole-nesting *Erithacus rubecula*) breeding species of hole-nesting birds in the BNP (TOMIAŁOJC *et al.* 1984). This paper, however, deals only with seven species of secondary hole-nesting birds, i.e.:

- *Ficedula albicollis* (FA),
- *Ficedula hypoleuca* (FH),
- *Parus caeruleus* (PE),
- *Parus major* (PJ),
- *Parus palustris* (PL),
- *Sturnus vulgaris* (S),
- *Sitta europaea* (SE),

and three species of woodpeckers, i.e.:

- *Dendrocopos major* (DA),
- *Dendrocopos medius* (DE),
- *Dendrocopos minor* (DI).

These species will be frequently referred to in the text by their acronyms (shown above in parentheses).

The reason for the exclusion of the remaining species was usually the lack of sufficient data. In one case, however, that of *Certhia familiaris*, the species was excluded on the ground that it utilized holes of quite a different type (most often crevices under loose bark) than did all the other species.

Field data were collected in 1975–86 mainly in the course of breeding bird census work carried out in 1975–86 (TOMIAŁOJC *et al.* 1984, unpubl.). The bulk of data is from the census plots, but some holes found outside the plots, in other parts of the BNP, as well as in natural stands in the managed part of the Białowieża Forest are also included.

Holes were located from the ground. A hole was considered occupied only if birds carrying nesting material or food for young/incubating female were recorded entering into it. On the other hand, observations of males singing near the hole and pecking into it, as well as observations of males and females entering the hole during courtship displays were not classified as signs of hole occupancy.

In the first years of the study the following standard parameters were recorded for the occupied holes:

- tree species,
- estimated height above the ground,
- entrance's exposure.

Other types of information, like for example data on hole origin or state of tree decay were noted less consistently.

From 1980 on additional aspects of hole localization have been also consistently recorded. These were:

- tree trunk girth at breast height,
- origin of hole (woodpecker vs "natural"),
- tree fragment (trunk vs limb/branch),
- state of tree fragment in which the hole was situated (live vs dead),
- slope of structure in which the hole was located (vertical, from above or below of sloping trunk/limb),
- shape of entrance (rounded vs slit-like),
- presence of holes in bulges.

As a first step in the analysis the data were always checked for presence of inter-habitat differences. If the differences were significant then the data were elaborated for each habitat separately, if not, they were pooled and treated as a single sample.

The data were collected in all the above described habitats but, due to very low densities of hole-nesting birds in the coniferous stands (TOMIAŁOJC *et al.* 1984), the number of holes found in them — 37 — was too small to allow one to analyse data for this habitat separately.

All probabilities shown in the text refer to the chi square test.

RENKONEN's similarity index (*RE*), was calculated according to the following formula:

$$RE = \sum_{i=1}^N \min(PC1_i, PC2_i),$$

where  $PC1_i$  and  $PC2_i$  are percentages in the  $i$ -th class in the first and second species respectively, and  $N$  is the number of different classes.

## RESULTS

### Tree species utilized

Patterns of tree-species utilization by different hole-nesting species in the swampy stands overlapped to a large extent (RENKONEN's index values for the least similar species pair exceeded 73%). All the species in this habitat type bred mostly

in alders (Table 1). Though the proportion of holes in this tree-species varied between 52% in *Parus caeruleus* and 90% in *P. major*, none of the interspecific differences was significant. Also the woodpeckers, while breeding in this habitat, preferred to make their holes in the alder (WESOŁOWSKI & TOMIAŁOJC 1986).

Table 1. Percentage distribution of breeding attempts of secondary hole-nesting birds among different tree species in the ash-alder habitat

Tabela 1. Rozkład procentowy częstości wykorzystania różnych gatunków drzew przez dziuplaki wtórne w lasach łągowych

Bird species Gatunek ptaka	Tree species – Gatunek drzewa									N (= 100%)
	<i>Acer platanoides</i>	<i>Alnus glutinosa</i>	<i>Betula</i> spp.	<i>Fraxinus excelsior</i>	<i>Picea excelsa</i>	<i>Populus tremula</i>	<i>Quercus robur</i>	<i>Tilia cordata</i>	<i>Ulmus</i> spp.	
<i>F. albicollis</i>	–	69.2	–	24.6	3.0	–	–	1.5	1.5	65
<i>F. hypoleuca</i>	–	61.1	5.6	27.8	–	–	–	–	5.6	18
<i>P. caeruleus</i>	–	52.4	–	47.6	–	–	–	–	–	21
<i>P. major</i>	–	90.0	–	10.0	–	–	–	–	–	10
<i>P. palustris</i>	–	57.8	–	42.7	–	–	–	–	–	19
<i>S. vulgaris</i>	–	63.2	–	34.4	2.4	–	–	–	–	125
<i>S. europaea</i>	0.3	66.2	–	25.3	3.9	2.6	1.0	–	0.6	308

Tree-species utilized in the oak-hornbeam stands were almost totally different from those utilized in the former habitat (*cf* Tables 1 and 2,  $p < 0.001$  for each species). Moreover, in the oak-hornbeam forest there was a much higher differentiation of tree-species utilization patterns of different species than in the swampy forest (Tables 2 and 3). The major differentiating factor was the proportion of holes in hornbeams. *Ficedula albicollis* showed the strongest attachment to this tree-species. It possessed over 85% of its holes in this tree-species (Table 2). Also *F. hypoleuca* and all the tits bred most often in hornbeams. Two species, however, namely *Sturnus vulgaris* and *Sitta europaea* bred in this tree-species significantly less often, in fewer than 20% of cases (Table 2).

There were other interspecific differences as well. If one compared the frequency of utilization of various tree-species by all hole-nesting birds jointly with their usage by each species separately (Table 2) then it would appear that maples were overutilized by *Sitta europaea* ( $p < 0.001$ ), mountain ash *Sorbus aucuparia* was utilized almost exclusively by *Parus palustris* ( $p < 0.001$ ) and oaks and aspens *Populus tremula* were utilized out of proportion by *Sturnus vulgaris* ( $p < 0.001$ ).

A comparison of interspecific overlaps in tree-species utilization patterns showed (Table 3, Fig. 1) that the tits and flycatchers overlapped to a large extent (RENKONEN'S index values  $> 72\%$ , Table 3), and formed a separate group in the

Table 2. Percentage distribution of secondary hole-nesting birds breeding attempts among different tree-species in the oak-hornbeam habitat. Data on woodpeckers – cf WESOŁOWSKI & TOMIAŁOJC (1986)  
Significant differences (for nesting in hornbeam vs nesting in other tree-species): S – any other species but SE and SE – any other species but S –  $p < 0.001$ ; FA – PL –  $p < 0.001$ ; FA – PJ –  $p < 0.05$ ; FA – PE –  $p < 0.02$

Tabela 2. Rozkład procentowy częstości wykorzystywania różnych gatunków drzew przez dziuplaki wtórne w grądach. Dane o dzięciołach – patrz WESOŁOWSKI i TOMIAŁOJC (1986)

Istotne różnice (dla porównania: gnieźdzenie na grabie – gnieźdzenie na innych gatunkach drzew): S – jakikolwiek inny gatunek poza SE i SE jakikolwiek inny gatunek oprócz S –  $p < 0,001$ ; FA – PL –  $p < 0,001$ ; FA – PJ –  $p < 0,05$ ; FA – PE –  $p < 0,02$

Bird species Gatunek ptaka	Tree species – Gatunek drzewa										N (= 100%)	
	<i>Acer platanoides</i>	<i>Betula</i> spp.	<i>Carpinus betulus</i>	<i>Corylus avellana</i>	<i>Fraxinus excelsior</i>	<i>Picea excelsa</i>	<i>Populus tremula</i>	<i>Quercus robur</i>	<i>Sorbus aucuparia</i>	<i>Tilia cordata</i>		<i>Ulmus</i> spp.
<i>F. albicollis</i>	5.9	0.4	85.1	0.4	0.8	0.4	0.8	1.2	1.6	3.5	–	255
<i>F. hypoleuca</i>	12.5	–	68.8	–	–	–	12.5	–	–	6.2	–	16
<i>P. caeruleus</i>	7.4	–	72.8	–	3.7	–	6.2	2.5	–	7.4	–	81
<i>P. major</i>	22.2	–	66.7	–	–	–	7.4	–	–	3.7	–	27
<i>P. palustris</i>	7.5	–	61.2	2.2	1.1	1.1	–	–	11.8	15.0	–	93
<i>S. europaea</i>	32.2	7.2	14.5	–	7.2	9.9	9.3	3.3	–	13.8	2.6	152
<i>S. vulgaris</i>	12.6	1.0	17.5	–	1.9	2.9	20.4	31.1	–	12.6	–	103

Table 3. Percentage overlaps (RENKONEN's index) of tree species utilization by secondary hole-nesting birds in the oak-hornbeam habitat

Tabela 3. Procentowe pokrywanie się (wskaźnik RENKONENA) wykorzystywania różnych gatunków drzew przez dziuplaki wtórne w grądach

FA	FH	PE	PJ	PL	S	SE	
x	79.0	85.0	76.9	73.8	30.5	27.5	FA
	x	88.6	90.3	74.9	48.7	42.5	FH
		x	84.0	77.1	42.9	41.7	PE
			x	72.4	41.2	47.8	PJ
				x	39.8	38.0	PL
					x	58.1	S
						x	SE

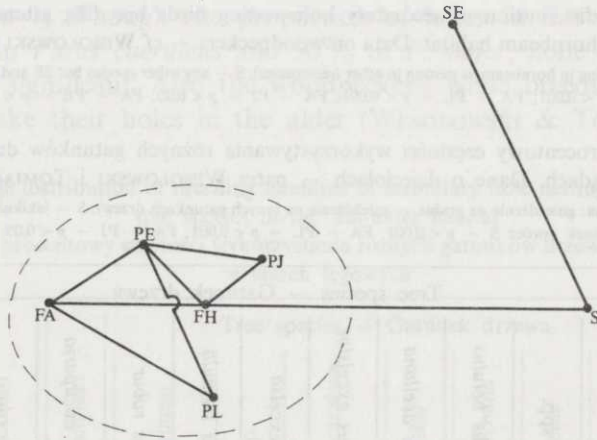


Fig. 1. Similarities of tree-species utilization by secondary hole-nesting birds in the oak-hornbeam habitat

The points denote the bird species studied, the distances between them reflect the differences between patterns of tree-species utilization by bird species. The species which situate over a half of their holes in hornbeams are surrounded with dashed line

Ryc. 1. Podobieństwo wykorzystywania różnych gatunków drzew do gnieźdzenia przez dziuplaki wtórne w grądach

Punktami oznaczono badane gatunki; odległości między punktami odzwierciedlają wielkość różnic międzygatunkowych w wykorzystywaniu poszczególnych gatunków drzew do gnieźdzenia. Przerywaną linią obwiedziono gatunki, które w ponad połowie przypadków gnieździły się w grądach

diagram (Fig. 1). *Sturnus vulgaris* and *Sitta europaea* on the other hand differed from all of them and occupied separate positions in Figure 1.

Because of the lack of quantitative data a direct comparison of tree-species utilization by the secondary hole-nesting birds and availability of different tree-species in the Forest is impossible. Yet in some cases the differences were so obvious that they should be mentioned here. Namely, though the spruce constitutes a quarter or more of all trees in both types of stands (TOMIAŁOJĆ *et al.* 1984) it is clearly avoided by all the species (Tables 1 and 2). Alders and hornbeams, on the contrary, are preferred. The alder accounts for only a quarter up to a half of the trees in swampy habitat, yet the majority of holes in this habitat type are situated in it (Table 1). Similarly, the hornbeam constitutes about a half of the trees in the oak-hornbeam forest but five of the seven species locate the majority of their holes in it (Table 2).

#### Height above ground

Holes were situated between 0.3 m (*Parus major*) and 31 m (*Sturnus vulgaris*). Their distribution in relation to height varied between the habitats (Table 4, Figs 2-4). In the majority of species the birds nested higher in the swampy stands than in the oak-hornbeam ones. This difference was most pronounced in *Parus palus-*



Table 4. Height distribution of nesting attempts by the secondary hole-nesting birds in relation to habitat

Habitat codes: AA – ash-alder, OH – oak-hornbeam. Data on woodpeckers cf WESOŁOWSKI & TOMIAŁOJC (1986)  
 Significant difference. Between-habitat comparisons: FA –  $p < 0.001$ , PE –  $p < 0.02$ , PL –  $p < 0.001$ , SE –  $p < 0.001$ . Within-habitat comparisons – ash-alder stands: S – any other species but SE –  $p < 0.05$ , SE – any other species but S and PL –  $p < 0.05$ , PJ – any other species but FH –  $p < 0.02$ ; oak-hornbeam stands: S – any other species and PL – any other species –  $p < 0.01$ , SE – any other species –  $p < 0.05$ , FA – PE –  $p < 0.01$

Tabela 4. Rozkład wysokości miejsc gnieźdzenia dziuplaków wtórnych w zależności od siedliska

AA – łęg, OH – grąd. Dane o dziuplach – patrz WESOŁOWSKI & TOMIAŁOJC (1986)  
 Istotne różnice. Porównania między siedliskami: FA –  $p < 0.001$ , PE –  $p < 0.02$ , PL –  $p < 0.001$ , SE –  $p < 0.001$ . Porównania w obrębie siedlisk – łęgi: S – z każdym innym gatunkiem poza SE –  $p < 0.05$ , SE – z każdym innym gatunkiem poza S i PL –  $p < 0.01$ , PJ – z każdym innym gatunkiem poza FH –  $p < 0.02$ ; grądy: S – z każdym innym gatunkiem i PL – z każdym innym gatunkiem –  $p < 0.01$ , SE – z każdym innym gatunkiem –  $p < 0.05$ , FA – PE –  $p < 0.01$

Species Gatunek	Habitat Siedlisko	Height class Klasa wysokości			$\Sigma$	$\bar{x}$ (m)
		< 5	> 5–10	> 10 m		
<i>F. albicollis</i>	AA	9	20	34	63	12.0
	OH	86	120	40	246	7.5
<i>F. hypoleuca</i>	AA	5	8	5	18	9.4
	OH	7	6	3	16	6.3
<i>P. caeruleus</i>	AA	2	11	8	21	11.1
	OH	34	21	26	81	8.3
<i>P. major</i>	AA	8	0	2	10	5.2
	OH	10	9	8	27	8.7
<i>P. palustris</i>	AA	3	7	10	20	10.8
	OH	61	25	4	90	4.2
<i>S. vulgaris</i>	AA	7	83	203	293	14.2
	OH	3	25	62	90	14.3
<i>S. europaea</i>	AA	4	27	94	125	14.8
	OH	23	50	81	154	12.1

*tr*is, which on average bred twice as high in the ash-alder forest as in the oak-hornbeam one (Table 4, Fig. 3). Two species, however, did not fit this pattern, i.e. *Sturnus vulgaris*, which bred at similar heights in both the habitats (Table 4, Fig. 4) and *Parus major*, which, as the only species, bred lower (though the difference was not significant) in the ash-alder stands (Table 4, Fig. 3).

Apart from the inter-habitat differences there were also consistent interspecific differences: *Sturnus vulgaris* and *Sitta europaea* nested significantly higher than the other species (Table 4).

*Parus caeruleus*, *Ficedula albicollis* and *F. hypoleuca* nested at intermediate heights while *Parus major* and *P. palustris* behaved differently depending on the habitat. In the ash-alder stands *P. major* nested significantly lower than all the other species except *Ficedula hypoleuca*, but in the oak-hornbeam habitat it nested higher, at similar heights to flycatchers and *Parus caeruleus*. The distribution pattern of *P. palustris* was just the opposite, it was similar to that of flycatchers and *P. caeruleus* in the ash-alder stands, but it was very different in the oak-

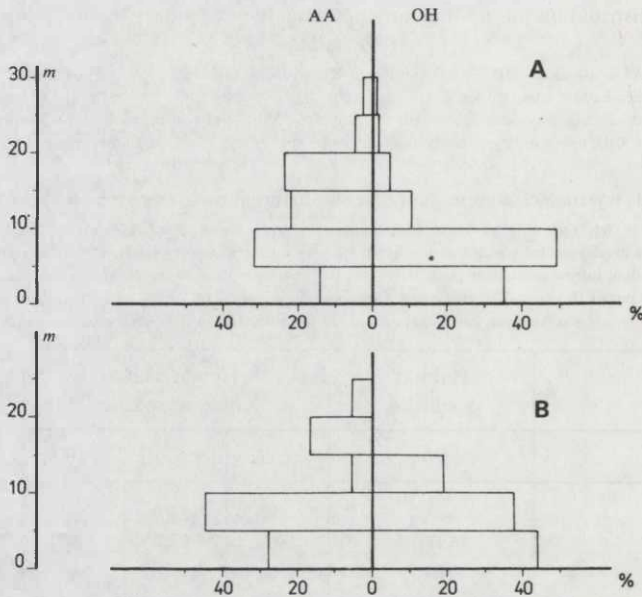


Fig. 2. Percentage distribution of nesting heights of *Ficedula albicollis* – A and *Ficedula hypoleuca* – B in ash-alder stands (AA) and oak-hornbeam stands (OH)

Sample sizes as in Table 4

Ryc. 2. Rozkład procentowy wysokości miejsc gnieźdzenia mucholówki białoszyjej – A i mucholówki żałobnej – B w łęgach (AA) i grądach (OH)

Wielkości prób jak w tabeli 4

hornbeam ones. In the latter habitat *P. palustris* bred significantly lower than any other species (Table 4).

A comparison of interspecific overlaps in height distribution patterns in the two habitats (Table 5, Figs 5, 6) reveals interesting differences. In the ash-alder stands all the species but *Parus major* form a group situated at the right-hand part of the diagram (Fig. 5). In the oak-hornbeam stands, on the other hand, the majority of species are grouped in the left-hand part of the diagram (Fig. 6). In other words – in the oak-hornbeam stands the hole-nesting birds bred mostly at low to moderate heights, while in the ash-alder stands the birds bred mostly at moderate to upper heights.

#### Entrance's exposure

Though the exposures, when recorded in the field, have been counted among eight compass directions, the data are presented here only in relation to four main compass directions. This results from the fact that a preliminary checking for

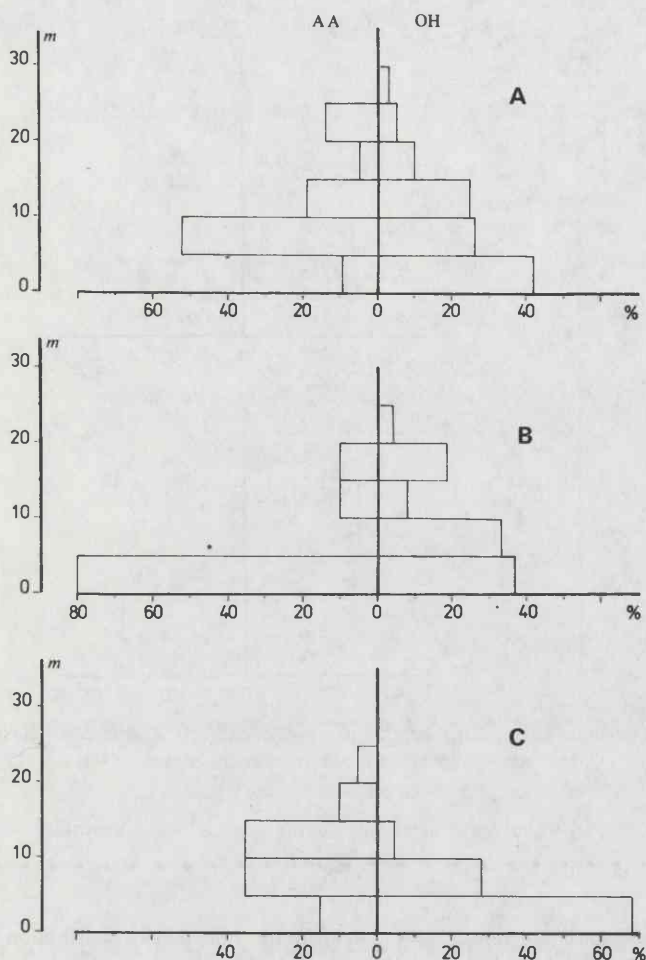


Fig. 3. Percentage distribution of nesting heights of *Parus caeruleus* – A, *Parus major* – B and *Parus palustris* – C in ash-alder stands (AA) and oak-hornbeam stands (OH)

Sample sizes as in Table 4

Ryc. 3. Rozkład procentowy wysokości miejsc gnieźdzenia modraszki – A, bogatki – B i sikory ubogiej – C w łęgach (AA) i grądach (OH)

Wielkości prób jak w tabeli 4

consistency of data has revealed that holes exposed to the main compass directions (N, E, S, W) were much more frequent (63,5% of 1135 cases) than holes exposed to the intermediate directions (NE, NW, SW, SE). This constituted a highly significant deviation from the expected fifty-fifty ratio. Such a result suggested the existence of a systematic error in data collection, due to the holes being too frequently classified as being exposed to the main compass directions.

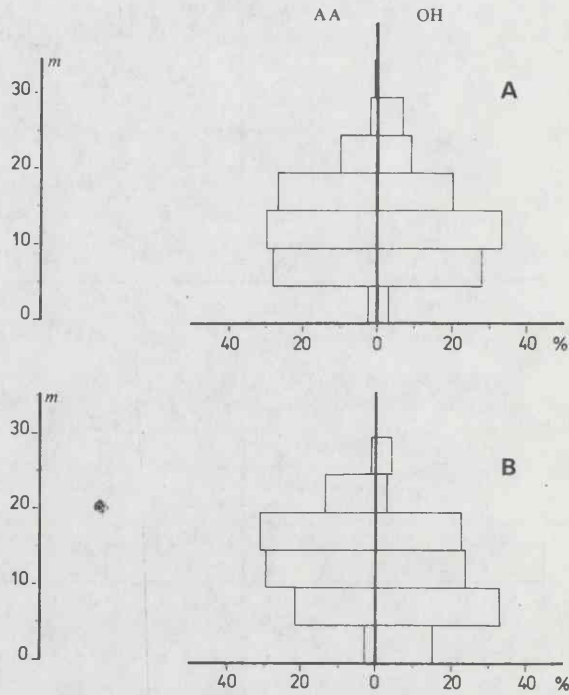


Fig. 4. Percentage distribution of nesting heights of *Sturnus vulgaris* A, and *Sitta europaea* – B in ash-alder stands (AA) and oak-hornbeam stands (OH)

Sample sizes as in Table 4

Ryc. 4. Rozkład procentowy wysokości miejsc gnieźdzenia szpaka – A i kowalika – B w łęgach (AA) i grądach (OH)

Wielkości prób jak w tabeli 4

Table 5. Percentage overlaps (RENKONEN's index) in the hole-height distribution of the secondary hole-nesting birds in ash-alder stands (A) and in oak-hornbeam stands (B)

Tabela 5. Procentowe pokrywanie się (wskaźnik RENKONENA) wysokości miejsc gnieźdzenia u dziuplaków wtórnych w łęgach (A) i w grądach (B)

(A)

FA	FH	PE	PJ	PL	S	SE	
x	73.1	69.8	34.3	83.0	83.5	76.4	FA
	x	69.9	43.4	70.6	58.6	52.7	FH
		x	24.3	73.3	64.7	62.2	PE
			x	35.0	22.4	23.2	PJ
				x	75.4	69.4	PL
					x	91.6	S
						x	SE

(B)

FA	FH	PE	PJ	PL	S	SE	
x	82.7	77.3	81.5	67.2	47.5	63.8	FA
	x	82.7	77.7	76.0	49.9	66.2	FH
		x	83.9	72.3	61.3	70.6	PE
			x	69.2	60.7	75.9	PJ
				x	35.5	47.1	PL
					x	87.0	S
						x	SE

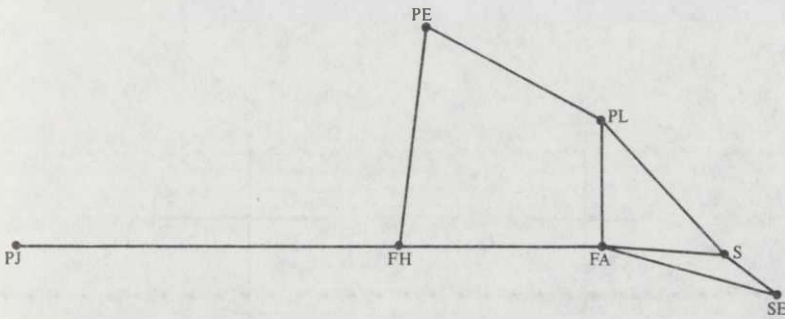


Fig. 5 Similarities of height distribution of secondary hole-nesters holes in the ash-alder stands

Explanations as in Fig. 1

Ryc. 5. Podobieństwa rozkładu wysokości umieszczenia dziupli różnych gatunków dziuplaków wtórnych w łęgach

Objaśnienia jak na ryc. 1

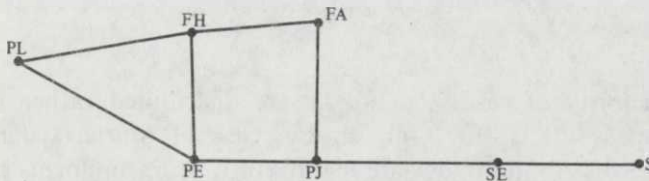


Fig. 6. Similarities of height distribution of secondary hole-nesters holes in the oak-hornbeam stands

Explanations as in Fig. 1

Ryc. 6. Podobieństwa rozkładu wysokości umieszczenia dziupli różnych gatunków dziuplaków wtórnych w grądach

Objaśnienia jak na ryc. 1

To find a way out of this problem, it was decided to pool the data and analyse them broken down only into four main categories. To achieve this the samples of holes with intermediate exposures were halved and added to the samples from the two neighbouring main directions. Only after such transformations were the data used for further analyses.

As samples from the two habitats did not differ significantly, they were pooled and are presented in Figures 7 and 8 in a comprehensive form. As can be seen in

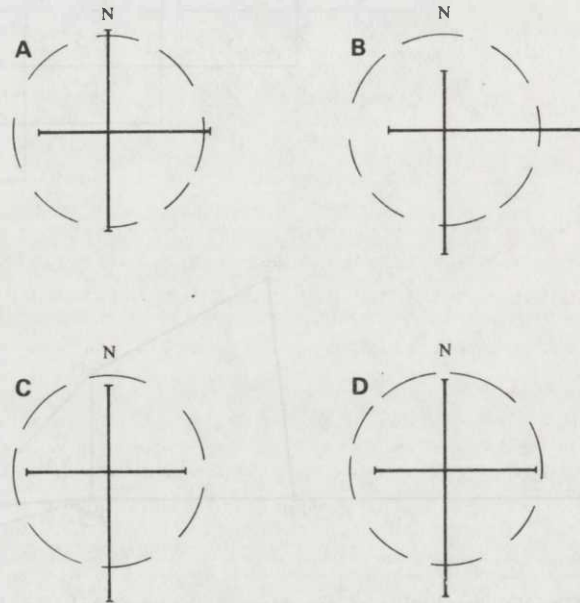


Fig. 7. Percentage distribution of hole-entrance exposures in *Ficedula albicollis* – A ( $N = 288$ ), *Ficedula hypoleuca* – B ( $N = 34$ ), *Sturnus vulgaris* – C ( $N = 331$ ), and *Sitta europaea* – D ( $N = 257$ )

Patterns of hole-entrance exposures in *Sturnus vulgaris* ( $p < 0.001$ ) and *Sitta europaea* ( $p < 0.01$ ) differed significantly from uniform

Rys. 7 Rozkład procentowy ekspozycji otworów dziupli u muchołówki białoszyjnej – A, muchołówki żałobnej – B, szpaka – C, i kowalika – D

U szpaka ( $p < 0.001$ ) i kowalika ( $p < 0.01$ ) rozkład ekspozycji otworów dziupli różnił się istotnie od równomiernego

them, in the majority of cases the holes were distributed rather uniformly with respect to compass directions. Only in the case of *Sturnus vulgaris* and *Sitta europaea* did the distributions deviate significantly from uniform. In both species South-oriented holes were more frequent than expected.

Due to this relative uniformity, the interspecific overlaps were quite high. Even in the least similar species pair the value of RENKONEN'S index still amounted to 83%.

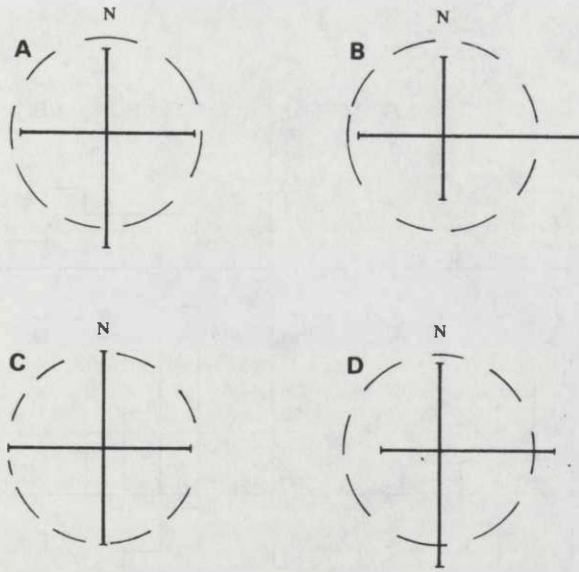


Fig. 8. Percentage distribution of hole-entrance exposures in *Parus caeruleus* – A ( $N = 96$ ), *Parus major* – B ( $N = 31$ ), *Parus palustris* – C ( $N = 98$ ) and *Dendrocopos minor* – D ( $N = 26$ )

Patterns of hole-entrance exposures in neither species differed significantly from uniform

Ryc. 8. Rozkład procentowy ekspozycji otworów dziupli u modraszki – A, bogatki – B, sikory ubogiej – C i dzięciołka – D

Rozkład ekspozycji otworów dziupli u żadnego gatunku nie odbiegał istotnie od rozkładu równomiernego

### Hole-tree trunk girth at breast height

The girth of trees in which the holes were found varied between 36 cm (*Parus palustris*) and 5.2 m (*Dendrocopos medius*). With the exception of *Parus palustris* and *Sitta europaea* (Table 6) it did not differ significantly between the habitats.

Table 6. Distribution of hole-tree girths in relation to habitat

AA – ash-alder stands, OH – oak-hornbeam stands. *Sitta europaea* bred significantly more often in trees with girth > 1.5 m in the ash-alder stands ( $p < 0.05$ ) while the opposite was true of *Parus palustris* ( $p < 0.02$ )

Tabela 6. Częstość wykorzystywania do gnieźdzenia drzew o różnych obwodach w zależności od siedliska

AA – łęgi, OH – grądy. Kowalik istotnie częściej gnieździł się w drzewach o obwodzie większym niż 1,5 m w łęgach niż w grądach ( $p < 0,05$ ), podczas gdy u sikory ubogiej stwierdzono sytuację odwrotną ( $p < 0,02$ )

Species Gatunek	Habitat Siedlisko	Girth – Obwód			$\Sigma$
		< 1	1–1.5	> 1.5 m	
<i>P. palustris</i>	AA	4	2	5	11
	OH	25	20	5	50
<i>S. europaea</i>	AA	3	24	59	86
	OH	3	17	57	107

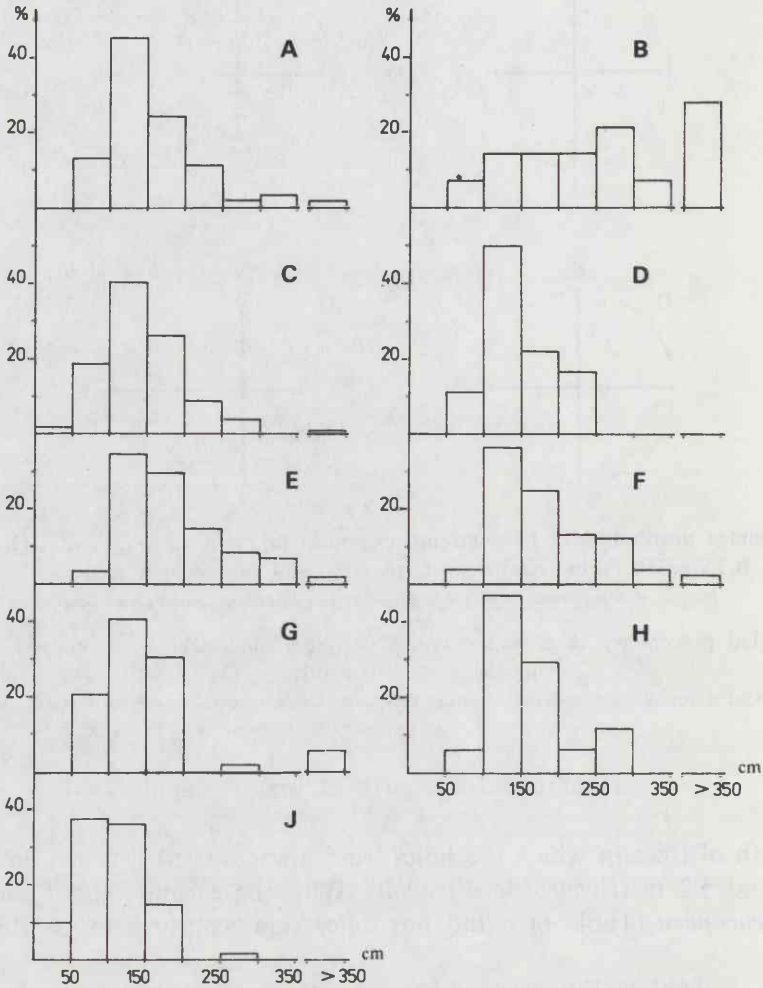


Fig. 9. Percentage distribution of breast-height girths of trees used for breeding by different species of hole-nesters A – *Dendrocopos major* ( $N = 62$ ), B – *Dendrocopos medius* ( $N = 14$ ), C – *Ficedula albicollis* ( $N = 127$ ), D – *Ficedula hypoleuca* ( $N = 18$ ), E – *Sturnus vulgaris* ( $N = 139$ ), F – *Sitta europaea* ( $N = 194$ ), G – *Parus caeruleus* ( $N = 49$ ), H – *Parus major* ( $N = 17$ ), J – *Parus palustris* ( $N = 61$ )

Significance level (for 3 classes: < 1 m, 1–1.5 m, > 1.5 m): PL – any other species  $p < 0.05$ ; S – DA, FA or PE –  $p < 0.01$ , SE – DA, FA or PE –  $p < 0.02$

Rys. 9. Rozkład procentowy obwodów drzew, w których gnieździły się różne gatunki dziuplaków A – dzięcioł duży, B – dzięcioł średni, C – mucholówka białoszyja, D – mucholówka żałobna, E – szpak, F – kowalik, G – modraszka, H – bogatka, J – sikora uboga

Istotność różnic (dla 3 klas: < 1 m, 1–1,5 m, > 1,5 m): PL z każdym innym gatunkiem –  $p < 0,05$ ; S z DA, FA lub PE –  $p < 0,01$ ; SE z DA, FA lub PE –  $p < 0,02$



Table 7. Percentage overlaps (RENKONEN's index) in nesting-tree girth distribution in the hole-nesting birds

Tabela 7. Procentowe pokrywanie się (wskaźnik RENKONENA) obwodów drzew, w których gnieździły się różne gatunki dziuplaków

DA	DE	FA	FH	PE	PJ	PL	S	SE	
x	53.4	88.4	89.8	81.1	82.8	65.4	80.0	82.6	DA
	x	49.1	50.0	43.8	52.2	37.3	64.4	65.8	DE
		x	82.2	87.8	81.9	72.9	77.5	79.4	FA
			x	74.1	81.1	62.0	74.7	76.3	FH
				x	78.1	72.9	71.7	70.6	PE
					x	58.4	82.0	83.7	PJ
						x	54.5	56.6	PL
							x	91.8	S
								x	SE

*Parus palustris* nested in the thinnest trees, almost half of its holes were in trees with girth  $\leq 1$  m (Fig. 9), and average tree-girth in this species was only 109 cm. Only two other species, *P. caeruleus* and *Ficedula albicollis* to a larger extent used such thin trees. They chose about 20% of their holes in them. The other species hardly ever bred in such small trees (Fig. 9).

Though for all species but *Dendrocopos medius* the most often utilized girth class was  $> 1-1.5$  m, three species located the majority of their holes in large ( $> 1.5$  m girth) trees. These were *Sturnus vulgaris*, *Sitta europaea* and *Dendrocopos medius*, which situated respectively, about 62, 60 and 79% of their holes in such places. The average tree girth was about 190 cm in *Sturnus vulgaris* and *Sitta europaea* and 287 cm in *Dendrocopos medius*.

A comparison of interspecific overlaps in utilization patterns revealed that all the species but *Dendrocopos medius* and *Parus palustris* had large, exceeding 70% values of overlap (Table 7). *P. palustris* and *Dendrocopos medius* stood out from the rest due to the utilization of very thin trees by the former and very big ones by the latter.

#### Origin of holes

There were significant differences in the extent to which various species of secondary hole-nesting birds utilized woodpecker-made holes. All the species of tits nested almost exclusively in "natural" holes, while 56% of *Sturnus vulgaris* nests

were in the woodpecker-made holes (Table 8). Other species were intermediate in this respect. The difference between the frequency of usage of woodpecker holes by *Ficedula albicollis* (26<sup>0</sup>/<sub>0</sub>) and *F. hypoleuca* (47.4<sup>0</sup>/<sub>0</sub>) –  $0.1 > p > 0.05$  was almost significant.

Table 8. Origin of holes used by different species of secondary hole-nesters

„Natural” – means holes formed by breaking branches, cracking, rotting etc.

Significance level: S – any other species but FA –  $p < 0.001$ ; SE – PL or PE –  $p < 0.001$ ; PL – FH or FA and PE – FH or FA –  $p < 0.001$ ; PJ – FH –  $p < 0.05$

Tabela 8. Pochodzenie dziupli, w których gnieździły się różne gatunki, dziuplaków wtórnych

„Naturalne” – oznacza dziuple powstałe w wyniku oblamywania gałęzi, pękania pni, butwienia itp.

Istotność różnic: S – z każdym innym gatunkiem poza FA –  $p < 0.001$ ; SE – PL lub PE –  $p < 0.001$ ; PL – FH lub FA i PE – FH lub FA –  $p < 0.001$ ; PJ – FH –  $p < 0.05$

Species Gatunek	Hole-origin – Pochodzenie dziupli				Total Łącznie
	„Natural” „Naturalna”		Woodpecker-made Dzięciola		
	N	(%)	N	(%)	
<i>F. albicollis</i>	107	(73.8)	38	(26.2)	145
<i>F. hypoleuca</i>	10	(52.6)	9	(47.4)	19
<i>P. caeruleus</i>	57	(96.6)	2	(3.4)	59
<i>P. major</i>	15	(88.2)	2	(11.8)	17
<i>P. palustris</i>	64	(98.5)	1	(1.5)	65
<i>S. vulgaris</i>	67	(43.8)	86	(56.2)	153
<i>S. europaea</i>	129	(65.4)	68	(34.5)	197

Only *Sitta europaea* showed significant inter-habitat differences. In ash-alder stands it placed 32.8<sup>0</sup>/<sub>0</sub> ( $N = 85$ ) of its nests in the woodpecker holes, while in oak-hornbeam stands, the woodpecker holes constituted 41.4<sup>0</sup>/<sub>0</sub> ( $N = 111$ ) –  $p < 0.02$ .

#### Slope of supporting structures

There was no significant inter-habitat difference in this aspect of hole localization. In all but one species the holes in vertical trunks/limbs constituted over 80<sup>0</sup>/<sub>0</sub> of the sample. Only *Dendrocopos medius* differed from this picture. It made one third of its holes from the underside of leaning structures (Table 9). Due to the relative uniformity of utilization patterns, the between-species overlaps were very high. If one excluded *D. medius*, then the RENKONEN's index values for the other pair-wise comparisons always exceeded 82<sup>0</sup>/<sub>0</sub>.

The leaning angle of the supporting structure did not necessarily correspond with the opening orientation angle. Though it was impossible, for an observer on the ground, to measure precisely any deviations of hole entrances from the

horizontal plane, there are some observations demonstrating that the entrances of holes situated in vertical structures did in some cases face upwards ( $N = 51$ ). The birds had to enter such holes from above. If one transferred these upward facing holes from the "vertical" to the "upperside" category in Table 9, then it would

Table 9. Situation of holes of different hole-nesting species in relation to the tree/trunk leaning

Significant differences (for comparison: vertical – others): DE – DA, PL or SE –  $p < 0.05$

Tabela 9. Położenie dziupli różnych gatunków dziuplaków w zależności od nachylenia pni/konarów

Istotne różnice (dla porównania: pion – inne): DE – DA, PL lub SE –  $p < 0,05$

Species Gatunek	Number of holes in – Liczba dziupli w						Total Łącznie
	leaning structures – pochyłych strukturach				vertical structures pionowych strukturach		
	underside od spodu		upperside od góry				
	N	(%)	N	(%)	N	(%)	
<i>D. major</i>	6	(9.1)	–	–	60	(90.9)	66
<i>D. medius</i>	5	(33.3)	–	–	10	(66.7)	15
<i>D. minor</i>	–	–	–	–	7	(100)	7
<i>F. albicollis</i>	12	(8.7)	4	(2.9)	122	(88.4)	138
<i>F. hypoleuca</i>	2	(10.0)	2	(10.0)	16	(80.0)	20
<i>P. caeruleus</i>	2	(3.5)	7	(12.1)	49	(84.5)	58
<i>P. major</i>	–	–	3	(17.6)	14	(82.4)	17
<i>P. palustris</i>	2	(3.2)	4	(6.3)	57	(90.5)	63
<i>S. vulgaris</i>	13	(8.7)	10	(6.7)	127	(84.7)	150
<i>S. europaea</i>	10	(5.1)	11	(5.6)	174	(89.2)	195
Total Łącznie	52	(7.1)	41	(5.6)	636	(87.2)	729

appear that the proportion of upward facing entrances was 12.6% in the total sample. None of the woodpecker holes faced upwards (significantly less than expected,  $p < 0.001$ ). In *Sturnus vulgaris* and *Ficedula albicollis* such holes constituted 8–10%, in *Sitta europaea* = 16.9%, 20.7% in *Parus caeruleus*, 23.5% in *P. major* and 23.8% (significantly more than expected –  $p < 0.05$ ) in *P. palustris*.

CONNOR (1975) suggested that one of the gains achieved by woodpeckers nesting from the underside of leaning trunks was protection against rain water entering the holes. However, holes in vertical structures placed just under fungal conks are similarly protected. Thus, it seems reasonable to consider such holes ( $N = 26$ ) together with the sample of "underside" holes from Table 9. This operation, however, did not change substantially the pattern visible in the Table. Only in *Dendrocopos major* did the frequency of the "underside" holes more than double and amount to 22.7%.

## Tree fragment

The two habitats did not differ significantly in this respect, so the data were pooled for the analysis. In all the species the majority of holes were in trunks (Table 10). The percentage of holes situated in limbs/branches varied, however,

Table 10. Localization of holes of different species in relation to tree fragment

Significance level: DE – any other species but PJ –  $p < 0.05$ ; FA – S or SE –  $p < 0.05$ ; PL – S or SE –  $p < 0.02$ 

Tabela 10. Umieszczenie dziupli różnych gatunków w zależności od fragmentu drzewa

Istotność różnic: DE – z każdym innym gatunkiem poza PJ –  $p < 0,05$ ; FA – S lub SE –  $p < 0,05$ ; PL – S lub SE –  $p < 0,02$ 

Species Gatunek	Tree fragment – Fragment drzewa				Total Łącznie
	Trunk – Pień		Limbs & branches Konary i gałęzie		
	N	%	N	%	
<i>D. major</i>	56	83.6	11	16.4	67
<i>D. medius</i>	9	52.9	8	47.0	17
<i>D. minor</i>	5	71.4	2	28.6	7
<i>F. albicollis</i>	122	87.1	18	12.9	140
<i>F. hypoleuca</i>	18	90.0	2	10.0	20
<i>P. caeruleus</i>	51	86.4	8	13.6	59
<i>P. major</i>	14	82.4	3	17.6	17
<i>P. palustris</i>	59	92.2	5	7.8	64
<i>S. vulgaris</i>	117	78.0	33	22.0	150
<i>S. europaea</i>	154	78.6	42	21.4	196

among the species. At one extreme was *Parus palustris* with only 7.8% of holes in limbs/branches, at another extreme was *Dendrocopos medius* which situated 47% of its holes in such places. The latter species differed significantly from almost any other species (Table 10). The species tendency to nest in limbs/branches roughly corresponds to their tendency to high nesting (cf Tables 4 and 10). The lowest breeding species utilized the limbs to the least extent, while high breeding *Sturnus vulgaris* and *Sitta europaea* utilized them to the largest extent.

Interspecific overlaps of utilization patterns were quite high. In all pair-wise comparisons of secondary hole-nesters and *Dendrocopos major*, the overlaps exceeded 85%. Only *D. medius* and *D. minor* were less similar. Their overlaps with other species ranged from 60 to 80%.

## Tree state

The proportion of holes in dead trees did not differ between the habitats, thus the data were analysed jointly (Table 11). All species of the tits bred almost exclusively in living trees – only 0.9–9.6% of their holes were in dead wood. *Sitta*

Table 11. Occurrence of holes of different species in live and dead wood

Apart from holes situated in snags, holes located in dead limbs & branches of living trees are included into the latter category. Significance level: DI – any other species –  $p < 0.05$ ; DE – any other species –  $p < 0.05$ ; S – any other species but DA –  $p < 0.05$ ; FA – any other species but DA or FH –  $p < 0.001$ ; FH – any species of tits or SE –  $p < 0.01$ ; DA – any species of tits or SE –  $p < 0.01$

Tabela 11. Występowanie dziupli różnych gatunków w żywych i martwych drzewach

Do kategorii „martwe” zaliczono także dziuple znajdujące się w martwych konarach i gałęziach, poza tym żywych, drzew. Istotność różnic: DI – z każdym innym gatunkiem –  $p < 0.05$ ; DE – z każdym innym gatunkiem –  $p < 0.05$ ; S – z każdym innym gatunkiem poza DA –  $p < 0.05$ ; FA – z każdym innym gatunkiem poza DA lub FH –  $p < 0.001$ ; FH – z każdym gatunkiem sikor lub SE –  $p < 0.01$ ; DA – z każdym gatunkiem sikor lub SE –  $p < 0.01$

Species Gatunek	State of tree – Stan drzewa				Total Łącznie
	Living – Żywe		Dead – Martwe		
	N	%	N	%	
<i>D. major</i>	44	65.7	23	34.3	67
<i>D. medius</i>	4	21.1	15	78.9	19
<i>D. minor</i>	–	–	9	100.0	9
<i>F. albicollis</i>	83	55.3	67	44.7	150
<i>F. hypoleuca</i>	10	52.6	9	47.4	19
<i>P. caeruleus</i>	47	90.4	5	9.6	52
<i>P. major</i>	16	100.0	–	–	16
<i>P. palustris</i>	58	93.5	4	6.5	62
<i>S. vulgaris</i>	116	74.4	40	25.6	156
<i>S. europaea</i>	169	84.5	31	15.5	200

*europaea*, *Sturnus vulgaris* and *Dendrocopos major* utilized dead wood to a larger extent, placing in it 15.5, 25.6, and 34.3% of their holes, respectively. The flycatchers used dead wood still more, in almost 50% of their nesting attempts. *Dendrocopos medius* and *D. minor* may be called the “dead wood specialists”. They excavated over 75% of their holes in such dead timber. The majority of the above-described differences were statistically significant (Table 11).

Interspecific overlaps in utilization patterns were rather diversified (Table 12), RENKONEN'S index values ranged from no overlap (PJ-DI) to over 95% (PE-PL).

### Shape of entrance

Hole openings were usually round to oval, but about 20% of all nestings took place in holes with slit-like entrances (Table 13). There were statistically significant interspecific differences in frequency of use of such holes. The tits used them out of proportion, but *Sturnus vulgaris* and *Sitta europaea* almost totally avoided them.

### Nesting in bulges

A characteristic feature of numerous holes was their localization not inside trunks/limbs but inside conical or dome-shaped protuberances – bulges formed on tree surfaces. Such holes constituted about 28% of all those found (Table 13).

Table 12. Percentage overlaps (RENKONEN's index) of dead and living wood utilization by various species of hole-nesting birds

Tabela 12. Procentowe pokrywanie się (wskaźniki RENKONENA) wykorzystywania martwych i żywych drzew przez różne gatunki dziuplaków

DA	DE	DI	FA	FH	PE	PJ	PL	S	SE	
x	55.4	34.3	89.6	86.9	75.3	65.7	72.2	91.3	81.2	DA
	x	78.9	65.8	68.5	30.7	21.1	27.6	46.7	36.6	DE
		x	44.7	47.4	9.6	0.0	6.5	25.6	15.5	DI
			x	97.3	64.9	55.3	61.8	80.9	70.8	FA
				x	62.2	52.6	59.1	78.2	68.1	FH
					x	90.4	96.9	84.0	94.1	PE
						x	93.5	74.4	84.5	PJ
							x	80.9	91.0	PL
								x	89.9	S
									x	SE

Table 13. Utilization of holes in bulges and holes with slit-like entrances by different species of secondary hole-nesting birds

Significance level. Nesting in bulges: FA - PE, S, or SE -  $p < 0.05$ ; FH - SE -  $p < 0.05$ ; PL - S -  $p < 0.02$ ; PL - SE -  $p < 0.001$ . Nesting in holes with slit-like entrances: S - any other species -  $p < 0.01$ ; SE - any other species -  $p < 0.05$ ; PL - FA -  $p < 0.001$ . PL - FH -  $p < 0.01$

Tabela 13. Wykorzystanie dziupli w naroślach i dziupli z otworami w kształcie szczeliny przez różne gatunki dziuplaków wtórnych

Istotność różnic. Gnieźdzenie w naroślach: FA - PE, SE lub S -  $p < 0.05$ ; FH - SE -  $p < 0.05$ ; PL - S -  $p < 0.02$ ; PL - SE -  $p < 0.001$ . Gnieźdzenie w dziuplach ze szczelinowatym otworem: S - z każdym innym gatunkiem -  $p < 0.01$ ; SE - z każdym innym gatunkiem -  $p < 0.05$ ; PL - FA -  $p < 0.001$ ; PL - FH -  $p < 0.01$

Species Gatunek	N (= 100%)	In bulges W naroślach		Slit-like entrance Szczelinowaty otwór	
		N	%	N	%
<i>F. albicollis</i>	156	20	12.8	48	30.8
<i>F. hypoleuca</i>	20	3	15.0	4	25.0
<i>P. caeruleus</i>	59	16	27.1	26	44.1
<i>P. major</i>	17	5	29.4	7	41.2
<i>P. palustris</i>	67	12	17.9	38	56.7
<i>S. vulgaris</i>	162	54	33.3	—	—
<i>S. europaea</i>	204	84	41.2	11	5.4
Total Łącznie	685	194	28.3	134	19.6

The species differed significantly in their tendency to breed in such holes. The flycatchers avoided breeding in them, while over 33% of *Sturnus vulgaris* and 41% of *Sitta europaea* nesting attempts were in bulges (Table 13).

### Constancy of hole occupation

So far in this paper several aspects of hole-nesting species nest-sites were described and their use by individual species compared. It was assumed that if utilization patterns of two species overlapped to a large extent, they could potentially use the same holes. Another approach to this problem is to compare utilization of the same hole in consecutive breeding attempts. In this way one can directly demonstrate that different species do use identical holes. The results of such comparisons are shown in Table 14.

It is easily seen from the Table that the woodpeckers hardly ever re-used their own holes, and that the secondary hole-nesters often bred in holes utilized previously by their own species. If we exclude *Ficedula hypoleuca* and *Parus major* (due to small samples), then the constancy of occupation by the secondary hole-nesting species varied from 43.8% in *Ficedula albicollis* to 66.7% in *Sitta europaea*. Nevertheless there was also ample evidence of interchange of holes utilization. Holes made by larger woodpeckers were almost exclusively used by *Sturnus vulgaris* and *Sitta europaea*, while those made by smaller *Dendrocopos minor*

Table 14. Constancy and change of occupation of the same holes in consecutive breeding attempts  
Constancy percentages calculated for the totals of columns and rows

Tabela 14. Stałość i zmienność użytkowania tych samych dziupli w kolejnych lęgach  
Dla obliczenia stałości użyto zsumowanych danych z odpowiednich kolumn i wierszy

First species Pierwszy gat.	Second breeding species – Drugi gniazdujący gatunek									
	DA	DE	DI	FA	FH	PE	PJ	PL	S	SE
<i>D. major</i>	1	—	—	—	—	—	1	—	14	10
<i>D. medius</i>	—	—	—	—	—	—	—	—	3	1
<i>D. minor</i>	—	—	—	1	1	—	—	—	—	—
<i>F. albicollis</i>	—	—	—	21	2	2	—	1	1	4
<i>F. hypoleuca</i>	—	—	—	—	1	—	—	1	—	—
<i>P. caeruleus</i>	—	—	—	2	—	17	2	2	—	1
<i>P. major</i>	—	—	—	1	—	—	2	—	—	1
<i>P. palustris</i>	—	—	—	3	—	2	—	13	—	—
<i>S. vulgaris</i>	—	—	—	3	—	—	—	—	68	6
<i>S. europaea</i>	—	—	—	7	2	—	3	—	10	90
Total Łącznie	26	4	2	48	7	28	10	22	105	135
Constancy (%) Stałość (%)	3.8	—	—	43.8	14.3	60.7	20.0	59.0	64.8	66.7

were good for the flycatchers. *Ficedula albicollis* took intermediate position. It could use holes of larger (*Sturnus vulgaris*, *Sitta europaea*) and smaller (the tits) species alike. Likewise, its holes were used by both the larger and the smaller species. The tits utilized mostly other tit holes and those of flycatchers, rarely *S. europaea* holes, and no case of occupation of *Sturnus vulgaris* hole by them was found.

This variation in frequency of hole interchange by different species corresponded roughly to size differences between the species; the greater the difference between two species sizes the less frequently they interchanged holes.

#### DISCUSSION

The proportion of holes found varied among species. If one compared the data on the numbers of various species within the BNP census plots (TOMIAŁOJĆ *et al.* 1984) with the number of their holes found (*cf.* Table 4), then it would appear that in some species, like *Sturnus vulgaris*, *Sitta europaea* or *Parus palustris*, much higher proportion of holes were found than in others. *P. major* was the species in which the smallest fraction of holes was discovered. It is difficult to assess possible biases introduced to the results by this uneven detectability. It seems that, if anything, the data on heights above the ground could be affected most, as low nests could be much easier to find than the higher ones.

Surprisingly enough it is quite difficult to find in the literature data on a variable even so easy to record as tree-species utilized by different species of secondary hole-nesters. A typical example of what one can usually find in the literature can be the monograph, otherwise very detailed, of British tits by PERRINS (1979). He writes about *Parus major* nest-sites "The nest-site itself is very varied. Since this species is larger than the other tits, it needs a larger hole. As with the blue tit a wide variety of nesting sites have been described ... (here follows a description of various bizzare nest-sites)... ..This species is the one which, of all the tits, most readily accept nesting boxes..." Thus, possibilities for comparisons with the results of others are rather limited.

Data from Holland (van BALEN *et al.* 1982), southern Sweden (NILSSON 1984b) and Czechoslovakia (HUDEC 1983) demonstrate that tree-species utilized there by various species of secondary hole-nesters are different from those used in the BNP. The patterns of tree-species utilization differ among them as well. This, along with the finding that birds breeding in two types of habitats in the same Forest (*cf.* p. 326) use almost completely non-overlapping sets of tree-species, allows one to conclude that tree-species does not appear to be an important factor influencing nest-site selection in this group of birds. It seems rather that the birds would settle in trees of very different species as long as they were providing them with holes of demanded qualities.

Non-random compass orientations of hole entrances occurred only in *Sturnus*



*vulgaris* and *Sitta europaea*. It is not known, however, if these birds really chose southward facing holes or, like *Sialia sialis* (PINKOWSKI 1976), they settled randomly in respect to compass directions, and their "preference" was only a by-product of higher availability of south-oriented holes. Two lines of evidence speak in favour of the latter possibility. Firstly – in the Dutch study (van BALEN *et al.* 1982) it was found that though *Parus major* and *Sturnus vulgaris* hole orientations were non-random in relation to compass directions, they were random with respect to availability of differently oriented holes. Secondly, it was shown (WESOŁOWSKI & TOMIAŁOJC 1986) that *Dendrocopos major* and *D. medius* preferred to make their holes from the south. Since *Sturnus vulgaris* and *Sitta europaea* used woodpecker-made holes to a large extent (*cf* Tables 8 and 14), higher availability of south-oriented woodpecker holes could explain the pattern observed in them.

In comparison with data from England (EDINGTON & EDINGTON 1972), Holland (van BALEN *et al.* 1982), southern Sweden (NILSSON 1984b), Primore – Soviet Far East (POLIVANOV 1981) and FRG – only *Parus palustris* (LUDESCHER 1973) the secondary hole-nesters in the BNP nested two-four times higher. The average nesting heights of different species in the above-mentioned areas ranged 1.1–5.2 m, whereas in the BNP they varied between 4.2 (*P. palustris* in the oak-hornbeam stands) and 14.3 m (*Sturnus vulgaris* in the ash-alder stands. Similarly, woodpeckers in this Forest nested much higher then elsewhere (WESOŁOWSKI & TOMIAŁOJC 1986).

A partial explanation of this phenomenon could be the unusual stature of tree stands in the BNP (*cf* p.326). Even if holes in all the areas compared were available at the same places relative to total tree heights, *e.g.* in the upper third of trunks, occurrence of much higher trees in the BNP would result in higher location (when measured in absolute units) of holes there.

Another explanation of these differences, not inconsistent with the former one, can be the hypothesis put forward by NILSSON (1984b). He found that nesting losses due to predation in *Sturnus vulgaris*, *Parus caeruleus* and *P. palustris* were height dependent. They were decreasing with increasing hole heights above the ground. Thus, as an anti-predator tactic, the birds should prefer to nest high. This was confirmed in choice experiments with nest boxes in *Sturnus vulgaris* (VERHEIJEN 1969, COLEMAN 1974) *Parus caeruleus* and *Sitta europaea* (LÖHRL 1970) but not in *P. major*. The latter species did not show any clear-cut height preferences (LÖHRL 1970).

As predation rates on ground nests in the BNP were higher than elsewhere (WESOŁOWSKI 1983, 1985, PIOTROWSKA & WESOŁOWSKI 1989), they could be also higher in the hole-nesters. Thus, it seems reasonable to suppose that the higher nesting of hole-nesters in the BNP was, at least to some extent, the result of their attempt to avoid stronger than elsewhere predation.

Predator avoidance, however, could not account for the inter-habitat differences in the BNP, for the higher breeding of the majority of species in the ash-alder stands (*cf* Table 4). As nesting losses of ground nesting birds in this habitat were

lower or equal to those in the oak-hornbeam stands (WESOŁOWSKI 1983, 1985, PIOTROWSKA & WESOŁOWSKI 1989), one would expect a lower, not higher, breeding there if the antipredator explanation worked. It seems rather that hole distribution could differ between the two habitats, that there were fewer low holes in the ash-alder stands.

If one compared the rank order of different species according to their nesting heights among the same set of areas as above, then it would appear that to a large extent it was the same as that in the BNP. *Sturnus vulgaris* and *Sitta europaea* usually were nesting the highest, *Parus caeruleus* followed them and *P. major*, *P. palustris* and *Ficedula hypoleuca* belonged most often to the lowest nesting group. Such a stability of species arrangement suggests that both the relative distribution of different hole types and species preferences remain roughly the same among different areas.

The girth of trees used by different species did not vary much (cf Fig. 9). The frequency distribution of girth sizes was normal in most species, with median values falling between 1 and 1.5 m. Such a pattern most probably reflected the pattern of hole availability in differently sized trees. In thin (young) trees the number of holes should be lower than in the older ones (it takes some years for a hole to form) and, additionally to this, the existing holes could be too small to be useful (cf also van BALEN *et al.* 1982). The lower frequency of holes in thicker trees, on the other hand, reflected the diminishing, with the increasing girth, proportion of such trees in tree stands.

*Parus palustris* differed from the above described standard. In the oak-hornbeam stands, but not in the ash-alder ones, it used trees with quite small girths (cf Fig. 9). This coincided with its nesting low in this habitat type (cf Table 4). It is tempting to explain this phenomenon in the way NILSSON (1984b) did: as a subordinate species *P. palustris* attempts to avoid interference competition with other tits by nesting in places not attractive to the latter (holes in thin trees, low above the ground). However there are some problems with accepting this explanation. Densities of would-be competitors (*P. caeruleus* and *P. major*) — jointly 5–6 p/10 ha (TOMIAŁOJC *et al.* 1984) in the ash-alder stands were not lower than those in the oak-hornbeam stands, but *P. palustris* did not nest low in thin trees in the former habitat. On the contrary, it bred at the same heights and in trees not thinner than the majority of other species (cf Tables 4 and 6). However, one cannot exclude that this distribution was forced, that *P. palustris* could not breed in the preferred places in the ash-alder stands due to their relative scarcity there (cf p. 330).

*Dendrocopos medius* deviated from the most frequent distribution of girth sizes in the opposite direction to that followed by *Parus palustris*. *Dendrocopos medius* used to breed in large trees (cf Fig. 9), frequently in big oaks (WESOŁOWSKI & TOMIAŁOJC 1986). This species was unique in other respects as well. It was the second highest nesting species (cf Table 4, WESOŁOWSKI & TOMIAŁOJC 1986), making almost half of its holes in limbs (other species placed in limbs below 30%)

of nests — cf Table 10), and situating a substantial proportion of its holes on the underside of leaning limbs. This habit was very rare in other species (cf Table 9). In nesting from the underside of limbs *D. medius* resembles several North American woodpecker species, which habitually peck their holes from below leaning structures (KILHAM 1971, CONNER 1975, STAUFFER & BEST 1982).

It was found that the entrance diameter of holes could be an important factor influencing their occupation by the secondary hole nesters. As a rule larger species accepted holes with bigger openings than did the smaller ones (van BALEN *et al.* 1982, NILSSON 1984b, LÖHRL 1985). These body size dependent preferences could be responsible for interspecific variation in the utilization of woodpecker-made holes found in the BNP. The majority of such holes there were pecked by the two commonest species, *i.e.* *Dendrocopos medius* and *D. major* (WESOŁOWSKI & TOMIAŁOJC 1986), which produce holes with an entrance diameter of 34 and 45 mm, respectively (GLUTZ 1980). Such a size of openings fits well the requirements of the two largest species (*Sturnus vulgaris*, *Sitta europaea* — van BALEN *et al.* 1982, NILSSON 1984b) but is too large for the smaller ones. In accordance with this, *Sturnus vulgaris* and *Sitta europaea* utilized woodpecker-made holes to a large extent, while the tits accepted them very infrequently (cf Table 8).

Interspecific differences in frequency in of breeding in holes with slit-like entrances in the BNP seems also to be best explained in terms of body size related variation in acceptable entrance diameters. In this case, though, slits that are rather narrow would allow only the smaller species to enter. The data at hand (cf Table 13) are in full accord with this explanation. The larger the species, the less often it bred in holes with slit-like openings.

Differences among woodpecker species with regard to the extent to which they made their holes in living trees seem to be body size related as well. Two smaller species (*Dendrocopos minor*, *D. medius*) most often placed their holes in dead, softened by decay, timber, while the reverse was true in the case of larger and stronger *D. major* (cf Table 11). Among secondary hole-nesters, however, both the largest and smallest species bred mostly in living trees, while the two medium sized flycatchers used holes in snags to the largest extent. The reasons for this differentiation are obscure. Perhaps they reflect some other, not measured in this study, features of nest-sites as, for example, microclimate, internal dimensions of holes, or microhabitat structure in the vicinity of holes.

Numerous cases of utilization of the same holes by different species consecutively (cf Table 14), as well as the occurrence of interspecific fights over holes (TOMIAŁOJC *et al.* 1984) demonstrate that interspecific interactions could play some role in creating the pattern of hole utilization found in the BNP. The interspecific competition, however, could be relatively less important in this primaeval forest than in managed secondary woods where studies were carried out elsewhere (van BALEN *et al.* 1982, NILSSON 1984b). This suggestion stems from the fact that the numbers of secondary hole-nesters in the BNP in relation to the number of available holes seem to be far lower there than in the other areas. Though it was

impossible to estimate the number of holes in the BNP directly, it seems reasonable to assume that the number was at least of the same order of magnitude as in other deciduous stands in Europe (50–170 holes/10 ha — KNEITZ 1961, LUDESCHER 1973, EDINGTON & EDINGTON 1972, van BALEN *et al.* 1982). A comparison of these figures with densities of hole nesting birds: up to 23 pairs/10 ha in the forest interior and up to 38 pairs/10 ha at the forest edge (TOMIAŁOJC *et al.* 1984) reveals that the densities of hole nesters were much below the number of holes. The existence of an excess of holes is further demonstrated by numerous cases in which the holes remained unutilized, or they were utilized only in some years, with breaks (sometimes of several years) in between (WESOŁOWSKI unpubl.).

Moreover, competition for holes with *Sturnus vulgaris*, which was the superior competitor in the other areas, was much reduced in the BNP, because of limited distribution of this species. *S. vulgaris* bred there mostly in a narrow belt along forest margins (TOMIAŁOJC *et al.* 1984). Hence, it could interfere with the breeding of only a negligible minority of other species pairs, and could not be responsible for creating the patterns of hole utilization found in the species.

From what has been said above it follows that the hole distribution pattern found in *Sitta europaea* in the BNP could not result from interspecific competition, as *Sturnus vulgaris* was the only other species which could constitute serious challenge to it.

Interspecific competition could be more important in shaping hole utilization patterns of the tits and flycatchers. Potentially the flycatchers could mostly be influenced, as their requirements overlapped those of the greatest number of species, both larger and smaller. Moreover, as they commenced breeding later than the other hole nesting species (WESOŁOWSKI unpubl.), they had either to accept holes left unused by the earlier breeding species or attempt to conquer the already occupied ones. It is impossible to say, however, whether the distribution of flycatcher holes was really more affected by interspecific competition than that of the other species. To solve this question it would be necessary to gather additional information on species-specific preferences, on behavioural interactions between species, and/or perform manipulation experiments.

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[Miejsca gnieźdzenia dziuplaków w pierwotnym lesie strefy umiarkowanej (Białowieski Park Narodowy)]

W pracy analizowane są dane o miejscach gnieźdzenia siedmiu gatunków dziuplaków wtórnych (tzn. gatunków korzystających z gotowych dziupli): szpaka, kowalika, muchówki białoszyjej, muchołówki żałobnej, modraszki, bogatki i sikory ubogiej oraz trzech gatunków dzięciołów: dużego, średniego i dzięciołka. Objasnienia skrótów nazw gatunkowych używanych w tabelach podano na str. 324.

Dane zbierano w latach 1975–86. Początkowo zapisywano tylko w jakim gatunku drzewa umieszczona była dziupla, jak wysoko nad ziemią się znajdowała i jaka była jej ekspozycja. Od roku 1980 notowano dodatkowo pierśnicę drzewa, pochodzenie dziupli (dzięcioła czy „naturalna”), w jakim fragmencie drzewa znajdowała się dziupla, stan tego fragmentu (żywy czy martwy), jego nachylenie, kształt otworu dziupli oraz to czy dziupla znajdowała się w rozszerzeniu pnia (bulwie).

Przeważająca większość danych pochodzi z lasów grądowych i łęgowych. W łęgach wszystkie gatunki ptaków gnieździły się głównie w olchach (tab. 1), natomiast zestaw gatunków drzew, w których ptaki gniazdowały w grądach był bogaty (tab. 2), a między zestawami wykorzystywanymi przez poszczególne gatunki ptaków występowały tu duże różnice (tab. 3, ryc. 1). Obie muchołówki i wszystkie sikory gnieździły się w grądzie głównie w grabach, natomiast szpaki i kowaliki unikały tego gatunku drzewa, zakładając w nim poniżej 20% gniazd.

Dziuple znajdowano na wysokości 0,3–31 m nad ziemią. Wysokość gnieźdzenia zależała od siedliska: w grądach większość gatunków gnieździła się niżej niż w łęgach (tab. 4 i 5, ryc. 2–6). W obu siedliskach najwyżej gniazdującymi gatunkami były szpak i kowalik, natomiast najniżej gniazdowały bogatka (w łęgach) i sikora uboga (w grądach).

Otwory wylotowe dziupli większości gatunków były skierowane dość równomiernie w różne strony świata (ryc. 7 i 8), a tylko u szpaka i kowalika przeważały dziuple o otworach skierowanych na południe.

Dziuple znajdowały się na drzewach o obwodzie od 36 do 520 cm. Sikora uboga gnieździła się w drzewach najcieńszych; wiele jej dziupli znajdowało się w drzewach o obwodzie mniejszym niż 1 m (tab. 6, ryc. 9). Inne gatunki gnieździły się w tak cienkich drzewach znacznie rzadziej. Najwięcej dziupli znajdowało się w drzewach o obwodzie 1–1,5 m. Trzy gatunki: kowalik, szpak i dzięcioł średni lokowały jednak większość swoich dziupli w drzewach grubszych, o obwodzie przekraczającym 1,5 m.

Sikory gnieździły się prawie wyłącznie w dziuplach „naturalnych”, natomiast szpaki w prawie połowie przypadków korzystały z dziupli po dzięciołach (tab. 8).

U prawie wszystkich gatunków ponad 80% dziupli znajdowało się w pionowych fragmentach drzew (tab. 9). Jedynie dzięcioły średnie wykuwały około jednej

trzeciej dziupli w pochylonych odcinkach drzew, przy czym otwór dziupli umieszczony był od spodu. Gatunek ten różnił się również od innych tym, że wiele (prawie połowę) dziupli wykuwał w konarach, podczas gdy pozostałe gatunki wykorzystywały przede wszystkim dziuple znajdujące się w pniach (tab. 10).

Sikory unikały gnieźdzenia w martwych drzewach, muchołówki zakładały w nich ok. 50% gniazd. Najczęściej w martwych drzewach gnieździły się dzięcioł średni i dzięciołek (tab. 11).

Otwory dziupli miały zwykle kształt zbliżony do koła lub owalu, w ok. 20% przypadków były to jednak wąskie, długie szczeliny (tab. 12). Dziuple z tego typu otworem były najczęściej zajmowane przez sikory.

Dziuple w bulwach stanowiły około 20% całości (tab. 13). Najczęściej zajmowały je szpaki i kowaliki.

Jeśli dziupla była użytkowana wielokrotnie, to w ok. 60% przypadków kolejnym gospodarzem dziupli zajmowanej uprzednio przez szpaka, kowalika, modraszkę czy sikorę ubogą był osobnik tego samego gatunku (tab. 14). W przypadku, gdy kolejnym użytkownikiem był inny gatunek, był to zwykle ptak o zbliżonych rozmiarach ciała.

Porównanie danych białowieskich z danymi z innych obszarów wykazuje, że gatunki drzew używanych najczęściej do gnieźdzenia w Białowieży są inne niż w innych obszarach oraz że w BPN ptaki gnieździły się znacznie wyżej niż gdzie indziej. To ostatnie może wynikać z nadzwyczajnej wysokości drzewostanów białowieskich.

Duża część zróżnicowania sposobów gniazdowania poszczególnych gatunków ptaków wydaje się być pochodną różnic rozmiarów ich ciała. W przypadku muchołówek i sikor pewien wpływ może wywierać również konkurencja międzygatunkowa, jednakże ze względu na niskie zagęszczenia tych grup ptaków w BPN, wpływ tego czynnika może być tu mniejszy niż w lasach zagospodarowanych.