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The breeding ecology of woodpeckers in a temperate primaeval forest — preliminary data

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The study was carried out in the Białowieża National Park (E Poland) in 1975–84. Habitat distribution, densities, fluctuation in numbers, nest-sites and timing of breeding of *Dendrocopos leucotos*, *D. major*, *D. medius*, *D. minor*, *Dryocopus martius* and *Picoides tridactylus* are described.

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Экология размножения дятлов в первичном лесу умеренной зоны — предварительные данные

Наблюдения были проведены в Беловежском национальном парке (Восточная Польша) в 1975–84 годах. Проанализировали размещение по биотопам, плотность, изменения численности, места гнездования и время гнездования следующих видов: *Dendrocopus leucotos*, *D. major*, *D. medius*, *D. minor*, *Dryocopus martius* и *Picoides tridactylus*.

INTRODUCTION

In many parts of Europe woodpeckers, especially *Dendrocopos leucotos*, *D. medius* or *Picoides tridactylus*, are rare and vanishing species (Tomiałojć 1972, Ahlén *et al.* 1978, Schubert 1978, Glutz and Bauer 1980, Müller 1982).

Hence, there is an urgent need to study their biology in detail in the hope of finding some sound protective measures which, in turn, might improve their long lasting survival. However, in order to evaluate properly data collected in areas of population decline it should be possible to confront them with data collected in other places, where conditions still remain relatively unchanged.

Since 1975 a team consisting of two of us and of W. Walankiewicz has had the opportunity to study birds in such a place, in primaeval forests preserved in the Białowieża National Park (hereafter called BNP) in Eastern Poland. This forest is especially rich in woodpeckers, as all European species except *Dendrocopos syriacus* breed there (Tomiałojć *et al.* 1984, unpubl.). This paper deals, however, only with six species inhabiting the forest interior, namely *Dendrocopos major*, *D. medius*, *D. minor*, *D. leucotos*, *Dryocopus martius* and *Picoides tridactylus*. Three other species living along the forest edges (*Jynx torquilla*, *Picus canus*, *P. viridis*) have not been frequent enough in our study areas to make an analysis possible.

As Białowieża studies have been mainly focused on the whole bird community analysis (Tomiałojć *et al.* 1977, 1984) and not just on woodpeckers, the data presented here deal only with some aspects of breeding ecology of woodpeckers in the BNP, i.e. those aspects for which it was possible to gather data by means of our standard field procedures. Though incomplete, the data are worth presenting, as they can add to the present knowledge of habitat requirements and nesting ecology of woodpeckers.

STUDY AREA

The description of the study area is following mainly the accounts of Faliński (1968, 1977) and Tomiałojć *et al.* (1977, 1984).

The Białowieża National Park is in the centre of the Białowieża Forest (1250 km^2), which is situated at the border between Central and Eastern Europe and within the zone of sub-continental climate: mean July temperature = 17.6°C, mean January temperature = −4.3°C, mean period of snow-cover = 92 days, mean yearly rainfall = 624 mm. Biogeographically, 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 exceptionally high for European standards.

The whole area of the Park (47.5 km^2) has been strictly protected as a nature reserve since 1921, but even before its tree stands were not 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 dead standing trees, stumps, freshly uprooted trees and old decaying logs.

The climax forest communities of the Białowieża National Park 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 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 *Quercus robur*; the main canopy (20–30 m) of old lime trees *Tilia cordata*, oaks, some spruces, maples *Acer platanoides* and hornbeams *Carpinus betulus*; the lower canopy (10–20 m) consists mainly of hornbeam, also lime and spruce trees.

In this 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 upper canopy composed mainly of alder *Alnus glutinosa*, spruce and ash *Fraxinus excelsior*; the lower canopy of younger individuals of the same three species of tree. The highest number of fallen logs is characteristics of this type of habitat.

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

MATERIAL AND METHODS

Data on woodpeckers distribution and abundance were collected in the course of census work carried out during the 1975–83 breeding seasons (Tomiałojć *et al.* 1984 and unpubl.). Our study plots, 24–33 ha, were chosen in three main types of climax forest stands in the BNP. The total area censused ranged from 187.5 ha (1980–83) to 358.1 ha (1977). In order to reduce the potential overestimation of densities of scarce birds like woodpeckers, our several basic plots (sub-plots) were located in pairs adjoining each other. In this way some of our plots became quite big, *e.g.* 48, 50.1 and 54 ha in oak-hornbeam forest, 25–33 ha in riverine ash-alder stands, and 32 and 50 ha in coniferous ones. Additionally one big plot of 98 ha covering all three habitats was studied for a gradient analysis of bird distribution (unpubl.).

Censuses were carried out with the application of the "combined mapping technique". The method is fully described elsewhere (Tomiałojć 1980, Tomiałojć *et al.* 1984). Here only a brief summary of field procedures is presented. Some points especially important in woodpecker censusing are given the prominence. Each plot was checked every 8–10 days during the breeding season (10 April–25 June). Census-taker walked slowly (about 2.5 hr/10 ha) through

the plot putting on its plan all the records of birds and paying special attention to simultaneous records of territorially behaving birds. In *Dendrocopos medius* the "mewing" call and in other woodpecker species "drumming" or other

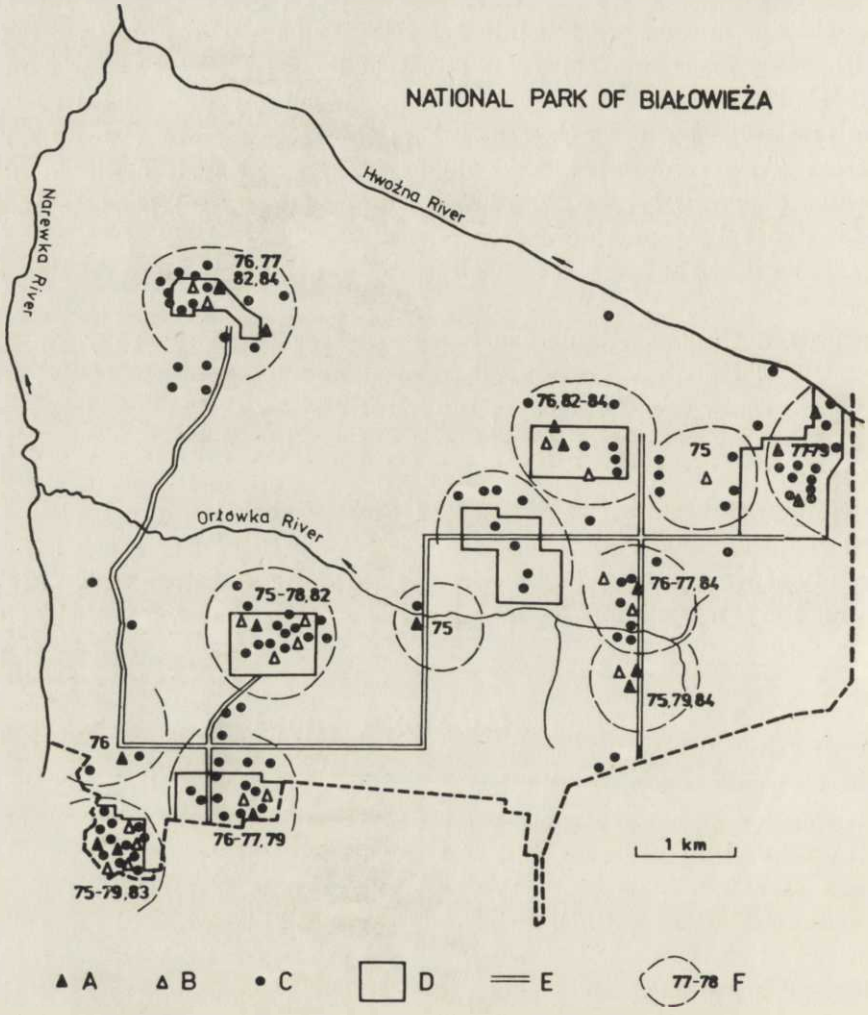

Fig. 1. Records of *Picoides tridactylus* in the Białowieża National Park, lumped observations from 1975–84

A – nest-record, B – probable nesting, C – single breeding season observation, D – census plot, E – access paths, F – cluster of breeding season observations, years of confirmed or presumed breeding are given. As the data were collected mainly within census plots and along access paths to them, the distribution of records does not show a full picture of the species distribution within the Park

Ryc. 1. Miejsca stwierdzeń dzięcioła trójpalczastego w Białowieskim Parku Narodowym w latach 1975–84

A – stwierdzenie lęgu, B – gniażdżenie prawdopodobne, C – pojedyncza obserwacja w sezonie lęgowym, D – powierzchnia próbna, E – drogi dojazdowe, F – skupienia obserwacji w sezonie lęgowym; podano lata stwierdzonego lub prawdopodobnego gniażdżenia. Ponieważ dane zbierano głównie w obrębie powierzchni próbnych i wzdłuż dróg dojazdowych, rozmieszczenie obserwacji nie daje pełnego obrazu występowania gatunku w Parku

territorial calling were on plans distinguished from non-territorial vocalizations. When possible, the sex of the observed individuals was recorded.

While visiting plots we always paid attention to distant drumming of scarcier species, first of all of *Dryocopus martius*, *Dendrocopos leucotos* and *Picoides tridactylus*, thus, covering by aural control an area much larger than the plot itself. All the records of scarce woodpeckers encountered during walking or riding by bicycle to and back through the BNP were also marked on the plans of the Park (see Figs 1 and 2).

All signs of breeding activities, *i.e.* hole-excavation, copulation, collecting

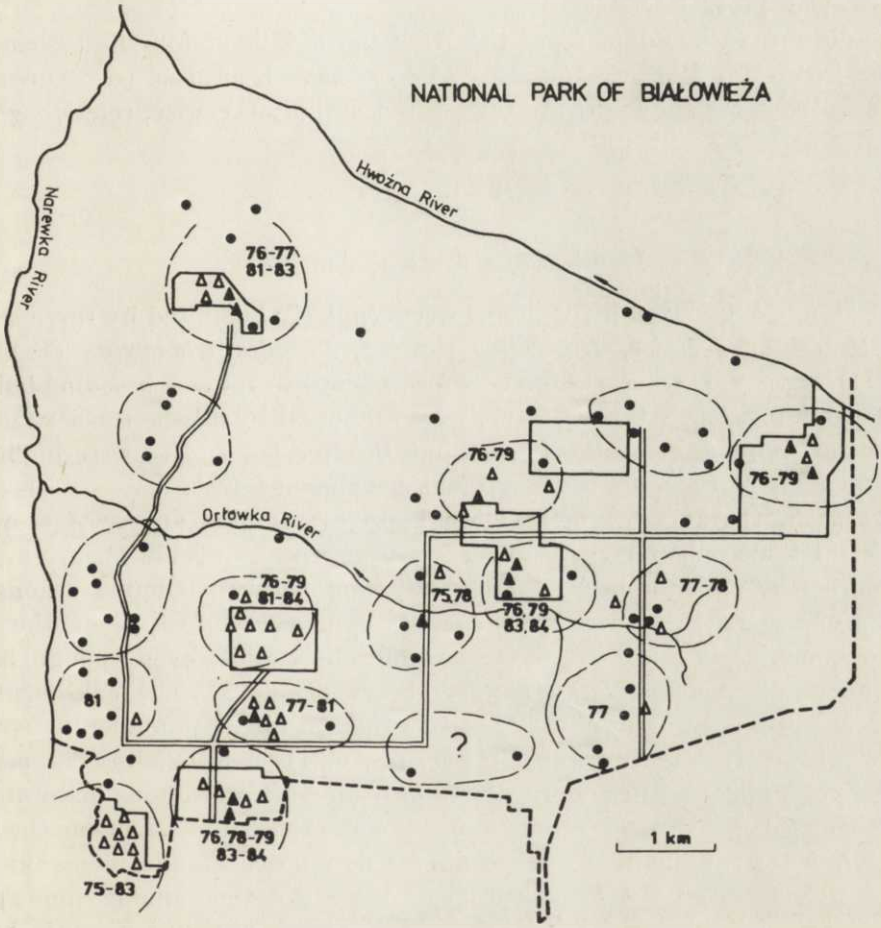

Fig. 2. Records of *Dendrocopos leucotos* in the Białowieża National Park, lumped observations from 1975–84

For explanations see Fig. 1

Ryc. 2. Miejsca stwierdzeń dzięcioła białogrzbietego w Białowieskim Parku Narodowym w latach 1975–84

Objaśnienia – patrz ryc. 1

food for young, feeding nestlings, presence of newly fledged families were recorded on the plans. Nest finding is an important element in the "combined mapping". As the nestlings of woodpeckers (at least some) were quite noisy the nests could be found most easily during the nestling period. About 80 % of *Dendrocopos major* and *D. medius* nests, and about 70 % of nests of *D. leucotos* and *D. minor* were found during this period. The holes were observed only from the ground. Some parameters, such as species of tree, the height above the ground and entrance orientation were noted almost in every case. Recording of other parameters, such as the position of a hole in a living versus a dead tree was less consistent. The holes, if occupied, were checked on every consecutive visit to the plot.

In addition to our data from the BNP the details of four nest-records of *Picoides tridactylus* from the Augustów Forest have been used (see Appendix).

All probabilities shown in the text, if not stated otherwise, refer to χ^2 test.

RESULTS

Habitat distribution, densities

The stands dominated by coniferes were regularly inhabited by three species only: *Dendrocopos major*, *Dryocopus martius*, *Picoides tridactylus* (Tables 1 and 2). Even they, however, did not prefer this forest type as a breeding habitat. The swampy forests on the contrary, were inhabited by all the species and the densities or frequencies of all of them but *Dendrocopos medius* were higher, or at least equal, to those found in the oak-hornbeam forest.

As regards the densities of individual species our data are satisfactory for such calculations only for three most numerous species (Table 1).

Dendrocopos major appears to be fairly uniformly distributed among the habitats of the BNP. It occupied all types of mature forest, being the most numerous species in the swampy and coniferous stands, even though in the latter its absolute densities were much lower (Table 1). The oak-hornbeam stands were the only habitat where it was the second most numerous species, being significantly less numerous (t test, $p < 0.01$) than *Dendrocopos medius*.

Dendrocopos medius nested regularly only in both deciduous habitats, although sometimes it was also observed in the coniferous stands. Outside the BNP it even bred exceptionally in the coniferes dominated stands, being in such cases attached to groups of mature oak trees standing among pine-spruce stand. Its densities in the BNP oak-hornbeam stands were significantly higher (Table 1) than in the swampy ones.

Dendrocopos minor bred only in deciduous habitats (Table 1), yet its densities were far lower — three to five times — than of the previous two species.

The remaining three species (*Dendrocopos leucotos*, *Picoides tridactylus*, *Dryocopus martius*) were so scarce that even in the most extensive of our double-

Table 1. Mean densities of woodpeckers in the Białowieża National Park

The densities shown in the first two columns have been calculated by dividing the total number of territories by the total area censused in that year and habitat. Probabilities shown refer to Student's t test

Tabela 1. Przeciętne zagęszczenie dzięciołów w Białowieskim Parku Narodowym

Zagęszczenia podane w pierwszych dwóch kolumnach wyliczono dzieląc ogólną liczbę stwierdzonych terytoriów przez łączną powierzchnię kontrolowaną w danym roku i siedlisku. Podane prawdopodobieństwa obliczono testem t Studenta

Species Gatunek	Habitat Siedlisko	Number of years Liczba lat	Density (territories/10 ha) — Zagęszczenie (terytoriów/10 ha)		
			$\bar{x}$ (S.D.)	Range Zakres	Maximum within single plot Maksymalne na pojedynczej powierzchni
All species Wszystkie gatunki	Ash-alder Łęg	9	2.3 (0.47)	1.6–3.2	3.4
	Oak-hornbeam Grąd	9	2.1 (0.50) — NS; $p < 0.001$; $p < 0.001$	1.2–2.7	3.3
	Coniferous Bór	9	0.4 (0.29)	0.1–0.8	1.0
Dendrocopos major	Ash-alder Łęg	9	0.9 (0.46)	0.4–1.9	2.0
	Oak-hornbeam Grąd	9	0.7 (0.28) — NS; $p < 0.05$; $p < 0.01$	0.3–1.1	1.5
	Coniferous Bór	9	0.4 (0.24)	0.1–0.7	0.8
Dendrocopos medius	Ash-alder Łęg	9	0.7 (0.17)	0.5–1.0	1.1
	Oak-hornbeam Grąd	9	1.0 (0.15) — $p < 0.01$	0.8–1.2	1.6
	Coniferous Bór	9	–	–	–
Dendrocopos minor	Ash-alder Łęg	9	0.3 (0.15)	0.1–0.6	0.8
	Oak-hornbeam Grąd	9	0.2 (0.10) — NS	0.1–0.4	0.6
	Coniferous Bór	9	–	–	–

plots the number of pairs of any of them hardly ever exceeded one in a season per plot. An attempt to calculate densities from such small samples would not give realistic figures, hence, their distribution has been presented only in a semi-quantitative form, *i.e.* as frequencies with which they were recorded as breeding species in different habitats (Table 2). However, taking into account the almost total absence of density evaluations from the lowland of Central Europe for *Dendrocopes leucotos* and *Picoides tridactylus* we decided to present pictures of

Table 2. Number and percentage of plot-years of censuses with the breeding of *D. leucotos*, *D. martius* and *P. tridactylus* in relation to habitat type

Habitat distribution of *D. leucotos* and *P. tridactylus* differs significantly from the distribution of the number of plot-years among the habitats ($p < 0.001$ and $p < 0.01$ respectively), but that of *D. martius* is very similar to it ($p > 0.7$)

Tabela 2. Liczba i udział procentowy jednorocznych liczeń na pojedynczych powierzchniach próbnych, na których stwierdzono gnieżdżenie dzięciołów białogrzbietego, czarnego i trójpalczastego, w zależności od typu siedliska

Rozmieszczenie siedliskowe dzięciołów białogrzbietego i trójpalczastego różni się istotnie od rozkładu liczb liczeń w różnych siedliskach ($p < 0{,}001$ i $p < 0{,}01$), natomiast rozmieszczenie dzięcioła czarnego jest do niego podobne ($p > 0.7$)

Habitat Siedlisko	Total number of plot-years censused Suma jednorocznych liczeń na pojedynczych powierzchniach		*D. leucotos*		*D. martius*		*P. tridactylus*	
	N	%	*N*	%	*N*	%	*N*	%
Ash-alder Łęg	20	100	20	100	10	50	15	75
Oak-hornbeam Grąd	40	100	28	70	15	37	7	17
Coniferous Bór	21	100	2	9	10	48	8	38
All habitats Wszystkie siedliska	81	100	50	62	35	43	30	37

their distribution in fragments of the BNP more frequently penetrated during our work (Figs 1 and 2). In spite of the obvious incompletness of these data they suggest that breeding densities of both species in the BNP are as a rule somewhere around 1 pair/km² in their best habitats, and much lower if calculated per the whole BNP area.

Dendrocopos leucotos occupied mainly the deciduous habitats, with clear preference of swampy stands, in which it was recorded with a 100 % frequency (Table 2), and where most of its nests were found. *Picoides tridactylus* was recorded in all the habitats studied but, as in the previous species, the ash-alder

stands were its preferred breeding habitat. Only *Dryocopus martius* was fairly uniformly distributed throughout the BNP forests without showing any clear-cut habitat preferences (Table 2).

Population fluctuations

An analysis of year-to-year changes in numbers was possible only in the two most numerous species (Fig. 3). The numbers of *Dendrocopos medius* appeared to be relatively stable; the minima and maxima differing only by a factor of two. The numbers of *Dendrocopos major* varied much more; the maximum values were 4.5-fold higher than the minimum. Changes in numbers of *Dendrocopos major* were correlated neither with mean temperatures of the preceding winter, nor with changes in numbers of *Dendrocopos medius* as potential competitor. We suspect that they may rather reflect the events connected with the

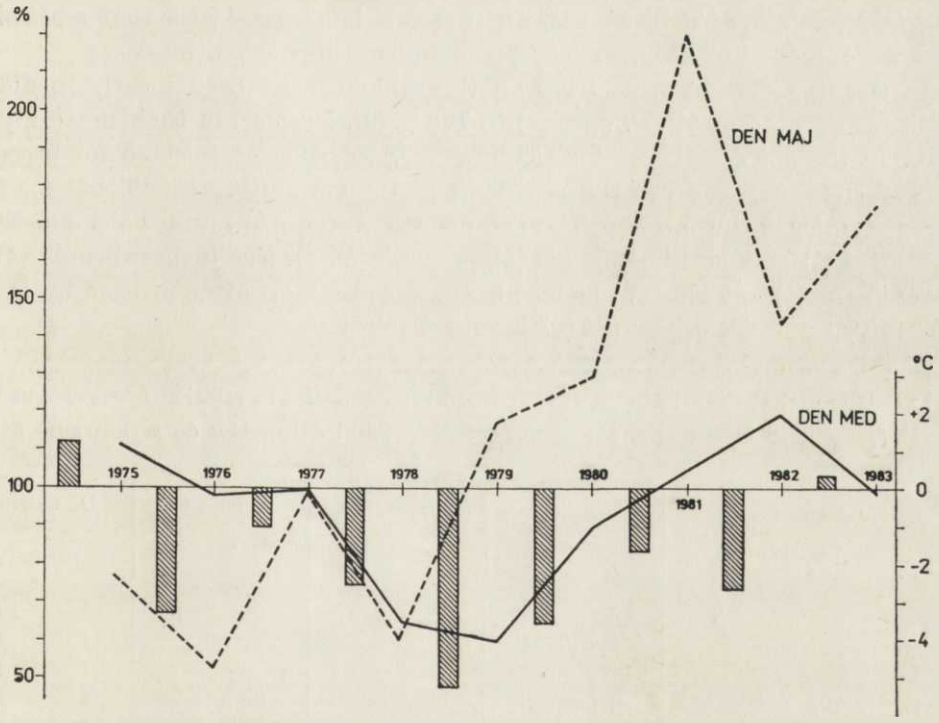

Fig. 3. Population indices of *Dendrocopos medius*, *D. major* and mean temperatures December-March (bars)

The values presented show how much and in which direction the number of birds breeding in a compared year differed from their number in the same plots in 1977

Ryc. 3. Wskaźniki liczebności dzięciołów średniego (DEN MED) i dużego (DEN MAJ) oraz przeciętne temperatury w okresie XII–III (słupki)

Przedstawione wartości pokazują o ile i w jakim kierunku liczebność ptaków gnieżdżących się w porównywanym roku różniła się od ich liczebności na tych samych powierzchniach w 1977

irruptive movements over larger parts of the continent known to occur in this species (GLUTZ and BAUER 1980). In *Dendrocopos medius* the correlation between winter temperatures and the population index was stronger ($r = 0.56$, $p < 0.10$), though not significant either. Even in this species, however, the most severe winter 1978/79 had no clear detrimental impact, its 1979 density remaining on the same low level as in 1978.

Nest-sites

As a rule woodpeckers excavate new holes each spring. Only five cases (3.8 %) were observed when holes from previous years were occupied by *Dendrocopos major*; it once occupied an old hole of *Picoides tridactylus* and four old holes of its own species.

In all habitats *Picoides tridactylus* excavated most of their holes in spruces (Table 3), whereas other woodpeckers utilized this tree only exceptionally (p at least < 0.05, *cf* Tables 3 and 4). It should be stressed here that most of its holes were in dead or dying spruces, frequent in this ancient forest.

In swampy stands birds from all the other species bred mostly in alders, which constituted 68 % (*D. medius*) to 100 % (*D. leucotos*) of their nesting trees there. In the oak-hornbeam forest, however, tree-species selected for breeding differed significantly from those utilized in the swampy forest (Table 4). *Dendrocopos major* in the oak-hornbeam stands excavated its nesting holes mostly in aspens (40 %) and hornbeams (24 %), whereas *D. medius* in hornbeams (41 %) and oaks (31 %) — Table 4. The hornbeam was also most often utilized by *D. leucotos* (50 %) and *D. minor* (86 %) in this habitat.

Table 3. The distribution of holes of four woodpecker species in relation to species of trees
Tabela 3. Gatunki drzew używane przez cztery gatunki dzięciołów do wykuwania dziupli

Tree species Gatunek drzewa	*D. minor*		*P. tridactylus*		*D. leucotos*		*D. martius*	
	N	%	*N*	%	*N*	%	*N*	%
Alnus glutinosa	9	47	3	16	4	29	1	14
Fraxinus execlsior	4	21	—		—		1	14
Picea excelsa	—		13	68	—		1	14
Carpinus betulus	6	32	—		5	36	1	14
Quercus robur	—		—		2	14	—	
Acer platanoides	—		—		—		1	14
Betula spp.	—		—		1	7	—	
Populus tremula	—		2	11	1	7	—	
Pinus silvestris	—		1	5	—		2	28
"dead tree" „martwe drzewo"	—		—		1	7	—	
Total — Razem	19	100	19	100	14	100	7	100

Table 4. The distribution of nest-holes of *D. medius* and *D. major* in relation to tree-species and habitat

The inter-habitat differences in distribution of tree-species chosen for breeding are in both species significant ($p < 0.001$). *D. medius* differs from *D. major* ($p < 0.001$) in its selection of nest-trees in the oak-hornbeam stands

Tabela 4. Umieszczenie dziupli dzięciołów średniego i dużego w zależności od gatunku drzewa i siedliska

Międzysiedliskowe różnice w częstości wybierania poszczególnych gatunków drzew do gnieżdżenia są u obu gatunków istotne ($p < 0,001$). Dzięcioł średni różni się istotnie od dzięcioła dużego częstością wyboru różnych gatunków drzew w grądach ($p < 0,001$)

Tree species Gatunek drzewa	*D. medius*				*D. major*				
	Ash-alder Łęg	Oak-hornbeam Grąd	Total Razem *N*	%	Ash-alder Łęg	Oak-hornbeam Grąd	Coniferous Bór	Total Razem *N*	%
Alnus glutinosa	15	–	15	21	37	–	–	37	28
Fraxinus excelsior	2	1	3	4	3	4	–	7	5
Carpinus betulus	–	21	21	29	–	17	1	18	14
Quercus robur	2	16	18	25	–	10	2	12	9
Acer platanoides	1	4	5	7	–	4	–	4	3
Tilia cordata	–	2	2	3	–	1	–	1	1
Populus tremula	–	–	–		3	28	7	38	29
Betula spp.	–	–	–		–	4	4	8	6
Pinus silvestris	–	–	–		–	–	4	4	3
Picea excelsa	2	1	3	4	–	2	1	3	2
Ulmus spp.	–	1	1	1	–	–	–	–	
"dead tree" „martwe drzewo"	–	5	5	7	–	–	–	–	
Total – Razem	22	51	73	100	43	70	19	132	100

Because of the lack of quantitative data a direct comparison of tree-species utilization by woodpeckers, and their availability in the forest, is impossible at the moment. Yet, in some cases the differences were so striking that they can be indicated here. Namely, though spruce is the most numerous tree species in the coniferous stands and constitutes a quarter or more of all tress in the deciduous stands, it is clearly avoided by all species but *Picoides tridactylus* (*cf* Tables 3 and 4). On the contrary, the aspen is rather a scarce species in our study plots, constituting on the average one percent or so of the tree community. Yet it is clearly preferred by *Dendrocopos major* which made almost 30% of their holes in this tree. Another preferred tree is the alder. It accounts for only a quarter up to a half of the tree stands in swampy places yet the majority of holes of almost all species found in such areas were made in it (*cf* Tables 3 and 4).

The proportion of holes excavated in dead or decaying wood, *i.e.* in places described as "rotten, dead, broken, stump, under bracket fungus" and the like,

varied among the species. *Dendrocopos major* excavated only 26.3 % of its holes in such places, significantly less ($p < 0.001$ for each comparison) than *D. medius* — 52.6 % or the other species (71–79 %). It should be emphasised, however, that the percentages shown here have only an approximate value, and do not reflect precisely the real proportion of holes made in dead and decaying wood. The proportion could be somewhat higher as it was often impossible to decide from the ground if the wood was dead or not.

The woodpeckers in the BNP excavated their holes 2–35 m above the ground (Fig. 4). Holes (not shown in the Figure) of *Dryocopus martius* were on the average situated about 16 (8–25) m above the ground. *Dendrocopos leucotos* was nesting the highest, its mean hole-height was almost eight metres higher than that of the lowest nesting species — *Picoides tridactylus* (Fig. 4).

Orientation of hole-entrances of two most numerous species has been presented in Figure 5.

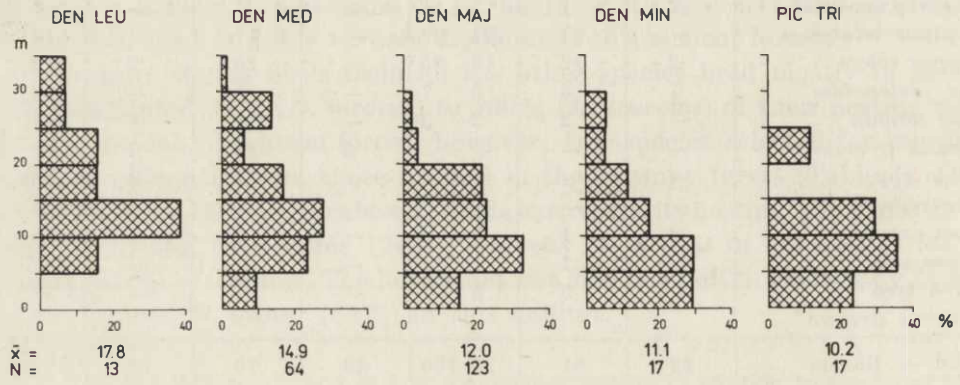

Fig. 4. Percentage distribution of hole-heights in *Dendrocopos leucotos*, *D. medius*, *D. major* *D. minor* and *Picoides tridactylus*

The hole-height distribution in *D. medius* differs significantly from that in *D. major* ($p < 0.02$) and *P. tridactylus* ($p < 0.05$). Differences between the distributions in other species are not significant

Ryc. 4. Rozkład procentowy wysokości położenia dziupli dzięciołów białogrzbietego (DEN LEU), średniego (DEN MED), dużego (DEN MAJ), małego (DEN MIN) i trójpalczastego (PIC TRI)

Rozkład wysokości położenia dziupli u dzięcioła średniego różni się istotnie od rozkładów u dzięciołów dużego ($p < 0,02$) i trójpalczastego ($p < 0,05$). Różnice między rozkładami u pozostałych gatunków są nieistotne

Timing of breeding

Because all holes were checked only from a distance no direct observation on the timing of egg-laying is available. However, with the data at hand, it is possible to approximately estimate the time of fledging (Table 5). Exact dates of nest leaving by young woodpeckers were recorded only exceptionally. Usually during one visit parents feeding young or nestlings calling loudly were

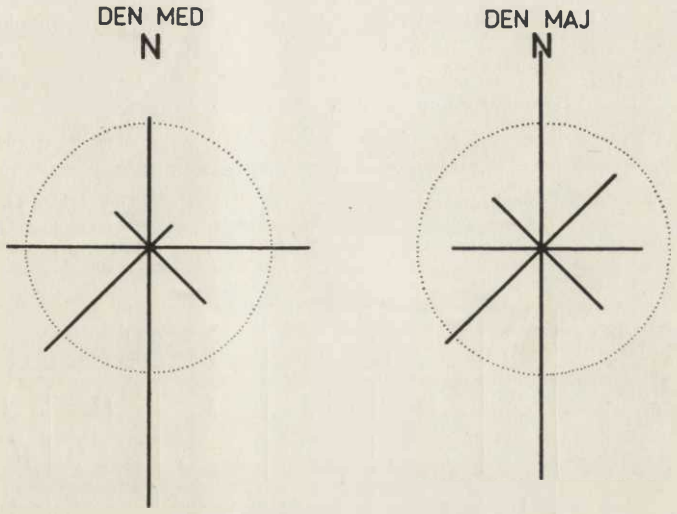

Fig. 5. Percentage distribution of hole-entrance exposures in *Dendrocopos medius* (N = 62) and *D. major* (N = 119)

If hole-entrances were oriented randomly in respect to compass directions one would expect all lines to be equal in length to the radii of circles marked with dotted line. *D. medius* excavates more holes than expected in the southern ($p < 0.02$) and *D. major* more holes than expected in the southern ($p < 0.01$) and the northern ($p < 0.05$) sides of trees

Ryc. 5. Rozkład procentowy ekspozycji otworów dziupli u dzięciołów średniego (N = 62) i dużego (N = 119)

Jeśli otwory dziupli byłyby, w stosunku do stron świata, skierowane losowo, to należałoby oczekiwać, że wszystkie linie będą miały jednakową długość, równą promieniowi okręgów zaznaczonych linią kropkowaną. W stosunku do wartości oczekiwanych dzięcioł średni wykuwa więcej dziupli o ekspozycji południowej ($p < 0{,}02$), a dzięcioł duży więcej dziupli o ekspozycji południowej ($p < 0{,}01$) i północnej ($p < 0{,}05$)

recorded and next time when the hole was visited no sings of birds presence were observed. Thus it has been assumed that in such cases young fledged half way (4–5 days) between the two check-visits.

As follows from the Table 5 fledglings of *Dendrocopos leucotos* were appearing mostly in the last ten-day period of May, about twenty days earlier than the fledglings of *D. minor*, *D. major* and *D. medius*. The main fledging period of the latter species fell on mid-June. *Picoides tridactylus* was the latest species then, its fledglings appearing mainly in the second and third ten days periods of June.

According to the data collated by Glutz and Bauer (1980) the period of time passing between the laying of the first egg and fledging is about 45 days in *Dendrocopos leucotos* and 35–40 days in the other species. By subtracting this amount of time from the fledging dates presented in Table 5 one can calculate that in the BNP *Dendrocopos leucotos* starts to lay eggs in the first ten-day period of April; *D. major*, *D. medius* and *D. minor* commence egg-laying in the last days of April but their main laying periods are in the first ten-day period of May. Finally, *Picoides tridactylus* starts egg-laying in the first ten-day period of May and continues throughout this month.

Table 5. The distribution of estimated fledging times of different woodpecker species in the consecutive ten-day periods

The distribution of fledging dates of *D. leucotos* differs significantly ($p < 0.01$) from those of all the other species, whereas that of *P. tridactylus* differs significantly ($p < 0.05$) from those of all the species but *D. medius*

Tabela 5. Rozkład przybliżonych terminów wylotu młodych z dziupli u różnych gatunków dzięciołów w kolejnych dekadach

Rozkład terminów wylotu młodych dzięciołów białogrzbietych różni się istotnie od rozkładu terminów wszystkich pozostałych gatunków ($p < 0.01$), a rozkład terminów wylotu młodych dzięciołów trójpalczastych różni się istotnie od takiego rozkładu u wszystkich porównywanych gatunów poza dzięciołem średnim ($p < 0.05$)

Species Gatunek	*N*	May Maj				June Czerwiec						July Lipiec	
		II		III		I		II		III		I	
		N	%	*N*	%	*N*	%	N	%	N	%	N	%
D. leucotos	10	2	20	5	50	2	20	—		1	10	—	
D. minor	9	—		—		1	11	8	89	—		—	
D. medius	65	—		—		12	18	48	74	5	8	—	
D. major	128	—		—		23	18	83	65	20	16	2	2
P. tridactylus	11	—		—		—		5	45	4	36	2	18

DISCUSSION

Habitat distribution of woodpeckers in the BNP quite well fits the descriptions of their habitat preferences elsewhere, *e.g.* in Central Europe (papers cited in Glutz and Bauer 1980), the Soviet Union (Dementev *et al.* 1951), Finland (Pynnönen 1939, Haapanen 1965), Norway (Håland and Toft 1983) or Japan (Matsuoka 1979). Two species, however, show some peculiarities which are worth discussing.

Firstly, it has been repeatedly reported that the distribution of *Dendrocopos medius* is strongly dependent on the presence of old oak woodland (*e.g.* Voous 1947, Blume 1968, Schubert 1978, Ahlén *et al.* 1978, Bauer and Glutz 1980, Müller 1982). The data from the BNP, where *D. medius* breeds regularly in swampy stands, containing hardly any oak tree, suggest that the restriction to oak woodland visible elsewhere in Europe has probably been brought about by man's destruction of some of its primaeval habitats — *i.e.* riverine forests.

Secondly, throughout its range *Picoides tridactylus* is a species of coniferous forest. The nominate subspecies *P. t. tridactylus*, with which the Białowieża birds belong (Tomiałojć 1972), breeds almost exclusively in the zone of pine and spruce boreal forests, and only in some places in northern Fennoscandia does it enter birch woods (Glutz and Bauer 1980, Maltchevskiy and Pukinskiy 1983). Observations from the BNP show, however, that this species breeds with the highest frequency in swampy ash-alder stands in which spruces constitute only an admixture. Even when it breeds in other types of stands

there it chooses the wettest parts of them (all the nests found in the oak-hornbeam and coniferous stands were situated in such places). The same situation was recorded in the Augustów Forest as well — four nests found there were situated in wet fragments in the vicinity of forest lakes (see Appendix).

There can be two explanations of this pattern. Firstly, the Białowieża Forest constitutes the southernmost fringe of the breeding range of this boreal form. Thus one can suppose that, in such conditions, such wet and cool habitats fit best its microclimatic requirements.

An alternative interpretation can be, however, that the pattern is some kind of an artifact. This species needs an amount of dead or dying spruces for foraging, and these are mostly found in swampy places, either left aside as nature reserves, or, when in a managed forest, are exploited by man less intensively because of difficulty in access to such sites.

A comparison of *Dendrocopos minor* densities recorded in the BNP with those found elsewhere shows that the values from the BNP (0.2–0.3 p/10 ha) belong to the highest known from literature (see data from bigger plots presented by Schiermann 1930, Schumann 1973, Głowaciński 1975, Lovaty 1980). This possibly reflects the very old age of the BNP stands containing large amount of soft-timber decaying branches of large trees.

The densities of *Dendrocopos medius* recorded in the oak-hornbeam stands in the BNP fall well into the range of values recorded in similar forest elsewhere (Pfeifer and Keil 1961, Ferry and Frochot 1965, Ruge 1971, Jenni 1977). Densities higher than those in Białowieża, reaching 1.6 p/10 ha were reported only from southern France (Lovaty 1980), the Odra river valley in Poland (Tomiałojć and Profus 1977) and from some parts of Switzerland (Bühler 1976 following Jenni 1977).

Surprisingly enough, in spite of the large quantity of dead timber in the primaeval forest the densities of *Dendrocopos major* in the BNP are rather low. With average values 0.6–0.8 p/10 ha in deciduous habitats and maximum value 2 p/10 ha the Białowieża stands fall well below the maximum densities recorded in the GDR, the FRG, Switzerland (papers cited in Glutz and Bauer 1980). The reason for these differences in numbers are not clear, the one possible contributing factor might be much greater fragmentation of forests in other parts of Europe and the so called "island effect".

In comparison to other areas of Europe the nesting habitats of woodpeckers in the BNP show many peculiarities. All the species breed much higher there than anywhere else (Blagosklonov 1968, Haftorn 1971, Ezhova 1977, Schubert 1978, Matsuoka 1979, papers cited in Glutz and Bauer 1980, Håland and Toft 1983, Palm in Rutschke 1983). This regional difference certainly reflects the exceptional height of Białowieża trees, which could reach 42–43 m (oak, lime), 45 m (pine) or even 55 m (spruce) — Faliński (1977), Tomiałojć *et al.* (1984).

The utilization of trees for nesting by Białowieża *Dendrocopos major*, and

especially its high preference of aspens, is similar to that recorded in other parts of Poland (Steinfatt 1937, Grądziel 1977), in the region of Moscow, Voronezh and Leningrad of the Soviet Union (Blagosklonov 1968, Ezhova 1977, Maltchevskiy and Pukinskiy 1983) or in Finland (Pynnönen 1939, Haapanen 1965). On the other hand, the nesting-tree selection of *Dendrocopos medius*, *D. leucotos* and *Picoides tridactylus* shows several differences when compared with data from other regions. In the case of *Dendrocopos medius*, according to Glutz and Bauer (1980), various species of oaks are preferred, whereas in Białowieża, besides the oaks, hornbeams and alders are also frequently used. Similarly, the majority of *Dendrocopos leucotos* holes in the BNP are placed in hornbeams and alders, whereas birches and aspens prevail in Norway (Haftorn 1971, Håland and Toft 1983) and sycamore *Acer pseudoplatanus* and beeches in the Alps (Ruge and Weber 1974).

A very sharp preponderance of spruce as a nesting tree by *Picoides tridactylus* in the BNP does not fit the pattern found elsewhere. In Norway this species nests mostly in aspens and birches or pines, while spruces constituted only 24% of 37 nesting trees studied (Haftorn 1971). In the Leningrad province nests were found only in birches and aspens (Maltchevskiy and Pukinskiy 1983). This difference, again, might be the result of the primaeval character of the BNP stands where many dead spruces are left standing, while in other managed forests they are usually removed and birds are forced either to excavate their holes in living spruces or in deciduous soft-timber trees.

Several pieces of evidence, both presented above or found in historical data referring to former distribution of woodpeckers in Poland, suggest that the numbers of two scarce species (*Dendrocopos leucotos* and *Picoides tridactylus*) must have decreased very much because of forest management. Human activity leads to the disappearance of soft-timber tree species and of dead or dying trees from our forests. Therefore, one can hypothesize that some centuries ago *Picoides tridactylus* must have been distributed throughout the whole range of the native spruce. Under the pressure of forest management it has recently been restricted only to some protected or hardly accessible forest sections. Similar explanation could most probably be suggested for *Dendrocopos leucotos*, which still during the 19th century was a widespread though scarce breeder in the whole area east of the Vistula river (Taczanowski 1882) except Masuria (Tischler 1941). Some old data from 19th century permit the claim that it once used to breed even in Silesia, but got extinct under the pressure of conifere monoculture planting. The future of both species in Poland is clearly dependent on the amount of ancient remnants in our forests put under legal protection as nature reserves, as well as, on a turn to more biological forest management of the remaining forests.

The breeding period of Białowieża woodpeckers does not basically deviate from that recorded elsewhere in Central Europe (Glutz and Bauer 1980). That *Dendrocopos leucotos* starts breeding much earlier than other species do,

as observed in the BNP, was also found during 19th century for the Lublin and Warsaw provinces (TACZANOWSKI 1882), and more recently the Alps (RUGE 1974), near Leningrad (MALTCHEVSKIY and PUKINSKIY 1983) and in Japan (MATSUOKA 1979). MATSUOKA suggests that its earlier breeding serves as an adaptation to the early-spring peak in the availability of coleopterean larvae — the main food item brought to the nestlings. *Dendrocopos major* and *Dendrocopos kizuki*, breeding later, feed their nestlings mainly with caterpillars which appear later in the season.

The last problem worth discussing here is the question of co-occurrence of different woodpecker species. Classical theories of community ecology (*e.g.* MACARTHUR and LEVINS 1967, MACARTHUR 1968, LACK 1971) would predict that in such species-rich guilds there are numerous mechanisms which could decrease niche overlaps, thus enabling birds to avoid interspecific competition. The data collected in the BNP suggest, however, that the species studied tended rather to converge (instead of diverging as predicted by the theories) in many niche parameters. It was not unusual to find all six species breeding simultaneously within the same plot. The swampy ash-alder stands were preferred by virtually all species but *Dendrocopos medius*, though even the latter one still bred in a relatively high density there. Furthermore, the species which in other habitats differed in their choice of nest-trees, in the ash-alder stands all excavated their holes mostly in one species — the alder. Moreover, the breeding seasons of *Dendrocopos minor*, *D. medius* and *D. major* overlapped completely, thus their nestlings appeard simultaneously and peak demand for food coincided.

An analysis of all these observations arouses doubts whether the breeding woodpeckers were really attempting to avoid niche overlap with the congenerics. It seems rather that some other selective pressures such as for example seasonal and spatial distribution of food resources and safety from predators (TOMIAŁOJĆ *et al.* 1984) were more influential in shaping their ecology.

It is impossible to solve this problem with the data at hand. To answer this question detailed comparative study of foraging behaviour and interspecific interactions of woodpeckers in the BNP would be needed.

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APPENDIX

Nest-records of *Picoides tripactylus* in the Augustów Forest

The Augustów Forest lies in the NE corner of Poland and has much more northern character than the Białowieża Forest, being mostly composed of pine-spruce coniferous stands.

2 June 1860 — hole with 7 newly hatched young in a strongly decayed stump of aspen, 5.5 m above the ground, in a swampy forest stand (Taczanowski 1882);

5 June 1968 — hole with young in spruce, 10 m height.
Habitat: cool spruce stand with aspen, birch and alder on a peninsula on Lake Tobołowo (K. Janowski and L. Tomiałojć unpubl.);

11 June 1968 — hole with young, in spruce, 8 m height.
Habitat: spruce stand with some alder and pine, on a *Sphagnum bog*, on Lake Wiłkokuk (KJ and LT);

13 June 1968 — hole with young, in aspen, 8 m height.
Habitat: spruce-pine stand with some aspen, 20 m from a small forest lake (KJ and LT).

STRESZCZENIE

[Ekologia rozrodu dzięciołów w pierwotnym lesie strefy umiarkowanej — dane wstępne.]

Obserwacje prowadzono w latach 1975–84 w klimaksowych zespołach łęgów, grądów i borów Białowieskiego Parku Narodowego. Analizowane są dane dotyczące dzięcioła dużego *Dendrocopos major*, dzięcioła średniego *D. medius*, dzięciołka *D. minor*, dzięcioła białogrzbietego *D. leucotos*, dzięcioła czarnego *Dryocopus martius* i dzięcioła trójpalczastego *Picoides tridactylus*.

Ogólne zagęszczenie dzięciołów w borach (0.4 p/10 ha) było znacznie niższe niż w grądach i łęgach (2.1–2.3 p/10 ha) — tab. 1. W borach występowały regularnie tylko trzy gatunki (dzięcioły duży, czarny, trójpalczasty). Występowanie dzięcioła średniego, dzięciołka i dzięcioła białogrzbietego było ograniczone do lasów liściastych, przy czym dzięcioł średni preferował grądy, a białogrzbiety łęgi (tab. 1 i 2). Dzięcioł trójpalczasty, chociaż gnieździł się we wszystkich siedliskach, najliczniej występował w łęgach (tab. 2). Zagęszczenia dzięciołów białogrzbietego i trójpalczastego były bardzo niskie, rzędu 1 p/km^2 lub mniej (ryc. 1 i 2).

Dzięcioł duży wykazywał znacznie silniejsze wahania liczebności niż dzięcioł średni. Zmiany liczebności obu gatunków nie były ze sobą skorelowane (ryc. 3).

Dzięcioł trójpalczasty wykuwał dziuple głównie w martwych świerkach, podczas gdy inne dzięcioły unikały tego drzewa (tab. 3 i 4). W łęgach dzięcioły gnieździły się najczęściej w olchach, natomiast w grądach dzięcioł duży gnieździł się głównie w osikach, a dzięcioł średni, dzięciołek i dzięcioł białogrzbiety w grabach. Wszystkie gatunki, z wyjątkiem dzięcioła dużego, wykuwały większość swoich dziupli w martwym drewnie.

Dziuple zakładane były na wysokości 2–35 m, przeciętnie najwyżej gnieździł się dzięcioł białogrzbiety, a najniżej dzięcioł trójpalczasty (ryc. 4).

Najwcześniej przystępował do lęgów dzięcioł białogrzbiety. Pisklęta z najwcześniejszych lęgów tego gatunku opuszczały dziuple w końcu drugiej dekady maja. Najpóźniej przystępował do lęgów dzięcioł trójpalczasty; pisklęta tego gatunku nie opuszczały dziupli przed drugą dekadą czerwca (tab. 5).

Preferencje siedliskowe dzięciołów w BPN były zasadniczo zgodne z podawanymi w literaturze, cechę specyficzną stanowiło częste gniażdżenie dzięcioła trójpalczastego w łęgach i wysoka liczebność dzięcioła średniego w tym typie siedliska.

W BPN dziuple były wykuwane znacznie wyżej niż na innych obszarach; również gatunki drzew, w których znajdowały się dziuple, różniły się od wykorzystywanych w tym celu gdzie indziej. Różnice te wynikają prawdopodob-

nie z nadzwyczajnej wysokości drzewostanów w BNP i ich zachowania w pierwotnym stanie.

Podkreślona została konieczność wzięcia pod ochronę także w innych częściach Polski fragmentów naturalnych lasów stanowiących środowisko dzięciołów białogrzbietego i trójpalczastego, gatunków zagrożonych wyginięciem w naszym kraju.