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Regular research paper

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DENSITY, DISTRIBUTION AND NEST-SITES OF WOODPECKERS PICIDAE, IN A MANAGED FOREST OF WESTERN POLAND

ABSTRACT: Abundance, distribution and nest-site characteristics of woodpecker species (family Picidae), i.e., Great Spotted Woodpecker (*Dendrocopos major* L.), Middle Spotted Woodpecker (*D. medius* L.), Lesser Spotted Woodpecker (*D. minor* L.), Black Woodpecker (*Dryocopus martius* L.), Grey-faced Woodpecker (*Picus canus* Gmel.) and Wryneck (*Jynx torquilla* L.), coexisting in managed forest are described. All species preferred old deciduous forest stands (≥ 81 years old) as nest-sites, however, they differed in most aspects of nest site selection. Great- and Middle Spotted Woodpeckers excavated nest-holes most commonly in oaks (78 and 86% of nests, respectively), but Black- and Grey-faced Woodpeckers in beeches (71 and 100% of nests). However, placement of nest-holes within the same tree species differed among woodpecker species. Great Spotted- and Grey-faced Woodpeckers nested three meters lower (9 m) compared to Middle Spotted and Black Woodpeckers (12 m). Lesser Spotted- Woodpeckers excavated breeding holes relatively the highest in respect to tree height. With the exception of Lesser Spotted Woodpeckers, all species used live trees as nest sites. Weaker excavators such as Middle Spotted- and Lesser Spotted Woodpeckers, nested more frequently in limbs and branches (31 and 25% of nests, respectively) compared to strong excavators, i.e., Great Spotted-, Black- and Grey-faced Woodpeckers (<8% of nests in limbs or branches). Weaker excavators more frequently

selected dead tree fragments compared to strong excavators.

KEY WORDS: hole-nesters, breeding densities, nest-sites, managed forests

1. INTRODUCTION

Woodpeckers (Picidae) are considered to be the most demanding group of forest birds since they are associated with mature forests and depend to varying degrees on dead and decaying trees for nesting and foraging sites (e.g. Wesołowski and Tomiałojć 1986, Hågvar *et al.* 1990, Short and Horne 1990, Wesołowski 1995, Stenberg 1996). However, as a result of past human activities, e.g., deforestation, impoverishment of tree species diversity and removal of dead wood, the populations of most woodpecker species have decreased markedly in many parts of Europe (Mikusiński and Angelstam 1997, Angelstam *et al.* 2004). As major creators of holes, woodpeckers are keystone species whose presence provides a critical resource in the community and whose extinction would consequently limit the population size of secondary hole nesters and lead to a reduction of biodiversity (e.g. Newton 1994,

Weggler and Aschwanden 1999, Martin *et al.* 2004). Moreover, the usefulness of woodpeckers as part of an indicator system for assessing biodiversity in different scales has been documented (e.g. Mikusiński *et al.* 2001, Roberge and Angelstam 2006). Furthermore, some of them are considered to be a subset of a focal species, whose habitat requirements encompass those of all other species in the landscape and help to support the ecosystem of which they are a part (Angelstam *et al.* 2004).

A considerable body of detailed information concerning the abundance of the woodpeckers in the deciduous forests of Poland is derived from habitat plots smaller than 30 ha (91%, $n = 117$, Kosiński 2006), which seems to be inadequate for censusing species with very large territories, e.g. Black Woodpecker (*Dryocopus martius* L.), Grey-faced Woodpecker (*Picus canus* Gmel.) and even Lesser Spotted Woodpecker (*Dendrocopos minor* L.) (e.g. Spitznagel 1990, Wiklander *et al.* 2001). It is a fact that studies embracing small areas tend to document disproportionately high densities, whereas large-scale plots yield lower values (e.g. Gaston *et al.* 1999). In spite of the ongoing interest in nest-sites used by European woodpeckers (e.g. Wesołowski and Tomiałojć 1986, Hågvar *et al.* 1990, Glue and Boswell 1994, Stenberg 1996, Smith 1997, Fauvel *et al.* 2001, Kosenko and Kaygorodova 2003), there is a lack

of published data covering the abundance and habitat requirements of woodpecker guilds in managed forests of Central Europe (but see Noah 2000, Wübbenhorst and Südbek 2003). A simultaneous study of habitat requirements may shed light on the niche partitioning of the woodpecker species. Moreover, measuring how woodpecker species are distributed across the forest matrix and which trees are used for nesting is essential for effective species management and may enable the development of forestry operation guidelines suitable for woodpeckers. In consequence, it could help in the protection of woodpeckers and finally forest biodiversity (Mikusiński *et al.* 2001, Martin *et al.* 2004, Remm *et al.* 2006).

The aims of this paper are: (1) to investigate the abundance and distribution of woodpecker species across a large-scale study plot and (2) to describe the nest-site characteristics of co-occurring woodpecker species in managed forest in Western Poland.

2. STUDY AREA

The study was carried out on a 775 ha plot in the managed forest, called “Smoszew” Forest (17°30' E–51°40' N), Western Poland, 100 km south east of Poznań (Fig. 1). Some 97% (750 ha) of the study plot (plot A) is forested, with coniferous and deciduous stands covering approximately the same area (Table 1). The remaining 3% (25 ha) is cov-

Table 1. The area of different forest stands (in ha) in studied forest (“Smoszew” Forest; see Fig. 1). In parentheses the percentage values are given.

Forest stand	Plot					
	A			B		
	< 81 years old	≥ 81 years old	Total	< 81 years old	≥ 81 years old	Total
Oak	79.6 (11)	210.1 (28)	289.7 (39)	55.5 (11)	196.0 (39)	251.5 (50)
Beech and hornbeam	18.0 (2)	18.3 (2)	36.3 (5)	15.0 (3)	18.3 (4)	33.3 (7)
Other deciduous	61.3 (8)	4.5 (1)	65.8 (9)	18.9 (4)	4.5 (1)	23.4 (5)
Coniferous	272.7 (36)	85.2 (11)	357.9 (48)	110.4 (22)	86.0 (17)	196.4 (39)
Total	431.6 (58)	318.1 (42)	749.7 (100)	199.9 (40)	304.7 (60)	504.5 (100)

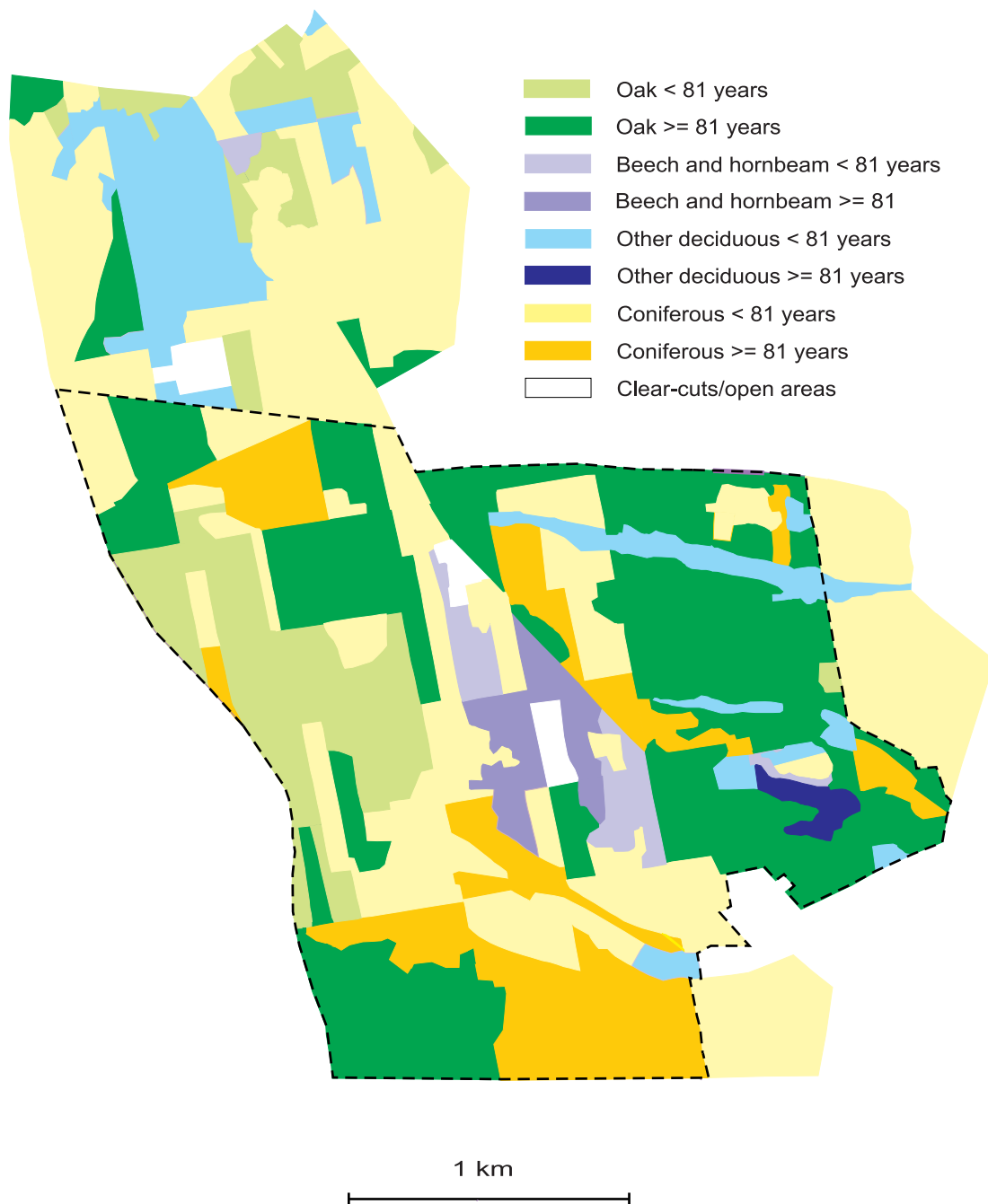


Fig. 1. Map of study area ("Smoszew" Forest). Plot A is equal to the whole study area. Smaller plot B (dashed line) was delimited inside plot A.

ered by division lines, ditches, roads and agricultural areas. Along its western and southern boundaries plot A adjoins forest stands. This area was appropriate for the estimation of the abundance of the largest and/or less numerous species, Black Woodpeckers and

Grey-faced Woodpeckers, as well as Lesser Spotted Woodpeckers. Within the study area (plot A), we delimited the smaller plot B (524 ha; Fig. 1) for the detailed censusing of the most numerous woodpecker species, i.e. Middle Spotted Woodpeckers (*Dendro-*

copos medius L.), Great Spotted Woodpeckers (*Dendrocopos major* L.) and Wrynecks (*Jynx torquilla* L.). This plot encompasses 504.5 ha of the forest. Division lines, ditches, roads and unidentified areas cover about 4% (19 ha) of plot B. In fact, the abundance of Middle Spotted Woodpeckers was initially estimated from a larger area (588 ha, see Kosiński and Winięcki 2005), however, to make the data comparable to other woodpecker species in the present analysis we used data from a smaller area.

The vegetation of the study area consists of oak-dominated stands, mainly *Calamagrostio arundinaceae-Quercetum petraeae* and *Galio sylvatici-Carpinetum* association. Of 210 ha of oak stands older than 81 years, ca 53 ha (plot B) is managed as seed stands. The central part of plot B is covered by beech-stands *Luzulo pilose-Fagetum*. Moreover, single trees or groups of old beeches (*Fagus sylvatica*) are scattered throughout the whole area of plot A. The rest of the study area is dominated by Scots Pine (*Pinus sylvestris*). A small fragment of the studied forest (13.46 ha) is protected within the reserve “Dąbrowa Smoszew”. The habitat data were extracted from the official inventory and management map (scale 1:10000) of the forestry authority. The age of the forestry stands was corrected according to the date of the forestry map preparation.

3. MATERIAL AND METHODS

Data was collected between 2001–2003. The number and distribution of territorial woodpecker species, with the exception of Great Spotted Woodpeckers, was based on the playback method which has been recommended for woodpecker censuses as a way of overcoming difficulties in detection and mapping, and is widely used in field studies of different woodpecker species (e.g. Fernandez and Azkona 1996, Miranda and Pasinelli 2001, Kosiński *et al.* 2004). The playback method is based on the territory mapping technique, where all contacts with birds, either by sight or sound, are plotted on large-scale maps (Tomiałojć 1980, Bibby *et al.* 2000). In this way the number of birds holding territory on study plot can be assessed. To provoke the response

of territorial birds the taped-calls (advertising-calls, rattle-calls and drumming) were played every 150–200 metres in the case of the Middle- and Lesser Spotted Woodpecker, and 350–400 metres in the case of the Black- and Grey-faced Woodpecker. After the first bird response the taped-calls were stopped to determine the initial location of the bird. The position, behaviour (spontaneous or response to the tape-calls), type of call and number of birds recorded (single or pair) were plotted onto the forest maps according to the mapping technique rules. The field studies covered the peak of vocal and territorial activity of birds during the pre-breeding period (March–April) connected with establishing and defending territories and mates. In plot B each woodpecker species was detected during two to three (four in the case of Grey-faced Woodpecker) censuses in the pre-breeding season. In the remaining area one census was performed. The delineated territories were checked to find excavated or occupied breeding holes. Territories where no nests were found were revisited at the end of May and at the beginning of June for the detection of holes with nestlings. The estimation of the number of Great Spotted Woodpeckers was based on the nest searching method. Due to the high efficiency of nest searching method and the high survival rates of nests, this method makes it possible to assess the population size with high efficiency (e.g. Glue and Boswell 1994, Kosiński and Ksyt 2006). In consecutive years, observations were conducted for 27 days (118 h) in 2001, 43 days (290 h) in 2002 and 24 days (154 h) in 2003.

For some species with well known preferences for breeding in deciduous forests two measures of density were calculated: (1) crude density, based on the total forest area of the study plot, and (2) ecological density, based on potential habitat that the species use (Gaston *et al.* 1999). Since smooth-barked deciduous forests (< 200 years old), such as beech woods, are considered to be unsuitable for Great Spotted Woodpeckers, Middle Spotted Woodpeckers (e.g. Hertel 2003, Winter *et al.* 2005, Kosiński 2006) and probably for Lesser Spotted Woodpeckers, those forest stands were excluded from the area of potential habitats.

Nine parameters of nest-sites were recorded: tree viability according to the scale as described by Hågvar *et al.* 1990, part of tree (trunk *vs.* limb/branch) and their viability (live *vs.* dead), diameter at breast height (dbh), tree and nest height, orientation of entrance hole (to nearest 10°) and state of exact nest site. Due to the small sample sizes of some classes, tree viability was finally attributed to one of three categories: living tree (Hågvar's class 1 and 2), tree still alive (only one or a few branches with living leaves) and dead tree (Hågvar's class 4 to 6). In some cases not all measurements were available for each nest, and thus sample size may differ in subsequent analyses. The Global Positioning System (GPS) was used to identify the position and distance between neighbouring occupied nest-holes.

We used every nesting attempt as an independent data point, including nest-holes inhabited in more than one year (three nest-holes in Great Spotted Woodpeckers and two nest-holes of Black Woodpeckers). To characterise Great Spotted Woodpecker nest-sites we also used incomplete data obtained in 2001 ($n = 27$ nests). Since most variables were either nonnormally distributed or had unequal variances, we used Kruskal-Wallis tests to compare nest tree characteristics among three woodpecker species with more than 10 nests (Great Spotted Woodpecker, Middle Spotted Woodpecker and Black Woodpecker). Variables with significant Kruskal-Wallis tests were tested post hoc with pairwise Mann-Whitney U tests to identify the difference between woodpecker species. As the repeated use of statistical tests increases the probability of committing a type I error, we used the Bonferroni correction for multiple comparisons. Data on nest-hole orientation were analysed using angular statistics. The distribution of entrance exposures was tested using the Rayleigh test (Zar 1984).

The high survival rates of Great Spotted Woodpecker nests and the high efficiency of the nest searching method suggest that probably all the nesting attempts of this species were recorded. Therefore, the spatial distribution of Great Spotted Woodpecker nests could be assessed over the whole area of the study plot. The distribution of Middle Spotted Woodpecker nest-sites was re-

corded on a smaller plot (78.2 ha) in 2003, where all breeding attempts were found (see Kosiński *et al.* 2004). The horizontal distribution of nest-holes on the study plot was tested with the aggregation index of Clark and Evans (R), and corrected for the edge effects (Waite 2000). R -values which equal 1 indicate a random distribution, values larger than 1.0 indicate a tendency to regular distribution, and values below 1.0 a tendency to clustered distribution. Significant departures of R from 1.0 were tested by a z -test. The null hypothesis was rejected at the $P = 0.05$ if $z > |1.96|$.

All statistics were performed with the statistical package STATISTICA (StatSoft, Inc. 2005). Values reported are means \pm standard deviations. All tests are 2-tailed.

4. RESULTS

4.1. Distribution and density

All woodpecker species preferred old deciduous forests as nest sites. Of 151 breeding holes of Great Spotted Woodpeckers found in 2002–2003, 114 (75%) were located in stands older than 80 years, which covered 44% of plot B, and 11 (7%) in stands 41–80 years old (13% of plot B, Table 1). The remaining portion of nests ($n = 26$) were excavated mostly, with one exception, in coniferous stands older than 81 years. Other woodpecker species inhabited old deciduous forests (≥ 81 years old) exclusively.

The population of Great Spotted Woodpeckers was the most abundant, and their crude density was three times higher than the population of Middle Spotted Woodpeckers (Table 2). The ecological density (including area of habitats that the species potentially uses) of Great Spotted Woodpeckers based on an area of rough-barked deciduous stands (274.9 ha, Table 1) varied from 2.1 pairs 10 ha^{-1} in 2002 ($n = 57$ pairs) to 2.5 pairs 10 ha^{-1} in 2003 ($n = 68$ pairs). The density of Middle Spotted Woodpecker territories varied from 0.9 territories 10 ha^{-1} in 2001 to 1.0 territories 10 ha^{-1} in 2003, respectively. The less numerous species inhabiting exclusively rough-barked stands was the Lesser Spotted Woodpecker – 0.1–0.2 pairs 10 ha^{-1} (1.5–2.2 pairs 100 ha^{-1}). Territories of Black

Table 2. Number of territories, number of nest-holes found (in parentheses) and density of woodpecker species in studied forest. Plot A (750 ha of forest area), plot B (504 ha of forest area; see Fig. 1), m – number of unpaired males.

Species	Plot	Number of territories			Density	
		2001	2002	2003	pairs 10 ha ⁻¹	pairs 100 ha ⁻¹
Great Spotted Woodpecker (<i>Dendrocopos major</i>)	B	-	(72)	(79)	1.4-1.5	14.3-15.7
Middle Spotted Woodpecker (<i>Dendrocopos medius</i>)	B	25+2m (15)	23+3m (12)	26+2m (21)	0.5-0.6	5.2-5.6
Black Woodpecker (<i>Dryocopus martius</i>)	A	6-7 (2)	7 (6)	9+1m (7)	≤0.1	0.8-1.3
	B	5-6 (1)	6 (5)	8+1m (6)	0.1-0.2	1.0-1.8
Lesser Spotted Woodpecker (<i>Dendrocopos minor</i>)	A	6 (1)	4 (1)	-	≤0.1	0.5-0.8
	B	5 (1)	4 (1)	6 (2)	≤0.1	0.8-1.1
Grey-faced Woodpecker (<i>Picus canus</i>)	A	3 (1)	3 (2)	2-3 (2)	<0.1	0.3-0.4
	B	3 (1)	3 (2)	2-3 (2)	<0.1	0.4-0.6
Wryneck (<i>Jynx torquilla</i>)	B	3 (2)	3 (0)	2 (0)	<0.1	0.4-0.6

Woodpeckers and Grey-faced Woodpeckers encompassed all types and age classes of woodland. In each breeding season two pairs of Black Woodpeckers and additionally one male in 2003, as well as one pair of Grey-faced Woodpeckers used space which extended beyond the western boundary of the study area. However, in all cases most of the territory areas encompassed the study plot B. Moreover, Grey-faced Woodpecker territories were found on plot B, only.

The mean distance between the two closest nests of neighboring Great Spotted Woodpecker pairs was 0.16 ± 0.06 km (range: 0.03–0.35 km, $n = 72$) in 2002 and 0.16 ± 0.07 km (0.06–0.44 km, $n = 78$) in 2003. The horizontal distribution of nest-holes tends to have a regular distribution ($R = 1.14$, $z = 2.11$ in 2002 and $R = 1.18$, $z = 2.85$ in 2003). The mean distance between two neighboring nests of Middle Spotted Woodpeckers in 2003 was 0.19 ± 0.07 km ($n = 19$). The index value of spatial distribution in Middle Spotted Woodpeckers in an area of 78.2 ha ($R = 1.46$, $n = 10$ nests), suggests a tendency for regular distribution, however, the null hypothesis of random distribution could not be rejected ($z = 0.89$). The mean distance between two neighbouring nests of Black Woodpeckers

was 0.91 ± 0.43 km (0.40–1.65 km, $n = 11$, data from all years were pooled).

4.2. Tree characteristics

Oaks were the most commonly used tree species among Great Spotted- and Middle Spotted Woodpeckers, and beeches were the most frequently inhabited by Black- and Grey-faced Woodpeckers (Table 3).

The mean diameter of the nesting tree at breast height (dbh) varied between ca 48 cm in Great- and Lesser Spotted Woodpeckers to 56 cm in Middle- and Grey-faced Woodpeckers (Table 4). Median nest-tree dbh differed significantly among the three most numerous woodpecker species (Kruskal-Wallis ANOVA $H_3 = 12.85$, $P = 0.0016$). Middle Spotted Woodpeckers excavated nest-holes within trees with a dbh higher than Great Spotted Woodpeckers (Mann-Whitney U test, $Z = -0.77$, $P < 0.001$).

Great Spotted- and Grey-faced Woodpeckers excavated their breeding holes at approximately three meters lower compared to other species (Table 4). Median nest height varied significantly across the three most numerous species (Kruskal-Wallis ANOVA $H_3 = 24.31$, $P < 0.0001$). Middle Spotted- and

Table 3. Nest-trees used by woodpecker species in studied forest in 2001–2003. Number of nest-holes found (N) and percentage values (%) in particular tree species are given. * – data from plot A, ** – data from plot B.

Species	Great Spotted Woodpecker (<i>D. major</i>)**		Middle Spotted Woodpecker (<i>D. medius</i>)**		Black Woodpecker (<i>D. martius</i>)*		Lesser Spotted Woodpecker (<i>D. minor</i>)*		Grey-faced Woodpecker (<i>P. canus</i>)**		Total N
	N	%	N	%	N	%	N	%	N	%	
<i>Quercus robur</i>	141	77	42	86	0	0	1	25	0	0	184
<i>Fagus sylvatica</i>	8	4	1	2	10	71	0	0	5	100	24
<i>Alnus glutinosa</i>	7	4	5	10	2	14	1	25	0	0	15
<i>Pinus sylvestris</i>	13	7	0	0	1	7	0	0	0	0	14
<i>Carpinus betulus</i>	4	2	1	2	1	7	2	50	0	0	8
<i>Picea abies</i>	4	2	0	0	0	0	0	0	0	0	4
<i>Betula verrucosa</i>	3	2	0	0	0	0	0	0	0	0	3
<i>Populus</i> sp.	1	<1	0	0	0	0	0	0	0	0	1
<i>Tilia cordata</i>	1	<1	0	0	0	0	0	0	0	0	1

Table 4. Descriptive statistics for nest-trees used by woodpeckers in studied forest in 2001–2003. Mean, standard deviation (SD), minimum-maximum (in parentheses) and numbers of nest-holes (N) are given. * – data from plot A, ** – data from plot B.

Characteristics	Great Spotted Woodpecker (<i>D. major</i>)**		Middle Spotted Woodpecker (<i>D. medius</i>)**		Black Woodpecker (<i>D. martius</i>)*		Lesser Spotted Woodpecker (<i>D. minor</i>)*		Grey-faced Woodpecker (<i>P. canus</i>)**	
	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N
Diameter at breast height (cm)	47.5 ± 16.9	176	56.2 ± 17.1	49	51.2 ± 8.1	14	47.8 ± 42.5	4	56.1 ± 13.6	5
	(19.1-111.5)		(25.5-95.5)		(38.2-66.9)		(25.5-111.5)		(41.4-70.1)	
Nest height (m)	8.7 ± 4.8	177	12.4 ± 5.8	49	12.4 ± 2.8	14	12.0 ± 7.0	4	9.3 ± 4.0	5
	(0.9-20.0)		(5.0-25.0)		(8.0-17.0)		(6.0-21.0)		(4.0-13.0)	
Tree height (m)	25.8 ± 6.5	174	29.0 ± 4.0	49	28.8 ± 4.8	13	19.8 ± 9.3	4	29.0 ± 4.8	4
	(6-38)		(19-36)		(16-34)		(12-33)		(22-32)	
Relative nest height (m)*	0.34 ± 0.18	173	0.43 ± 0.20	49	0.44 ± 0.16	13	0.59 ± 0.14	4	0.36 ± 0.01	4
	(0.05-0.90)		(0.16-0.92)		(0.24-0.88)		(0.40-0.74)		(0.30-0.41)	

* Nest height divided by tree height

Table 5. Placements of woodpecker nest-holes in relation to tree condition, tree fragment and state of nest-site. Number of nest-holes found (N) and percentage values (%) in each placement category are given. * – data from plot A, ** – data from plot B.

Placement	Great Spotted Woodpecker (<i>D. major</i>)**		Middle Spotted Woodpecker (<i>D. medius</i> **)		Black Woodpecker (<i>D. martius</i>)*		Lesser Spotted Woodpecker (<i>D. minor</i>)*		Grey-faced Woodpecker (<i>P. canus</i>)**	
	N	%	N	%	N	%	N	%	N	%
Tree condition										
Live	143	79	37	76	10	71	1	25	5	100
Still alive	25	14	12	24	3	21	3	75	0	0
Dead	7	4	0	0	1	7	0	0	0	0
Part of tree										
Trunk	164	92	34	69	13	93	3	75	5	100
Limb/branch	15	8	15	31	1	7	1	25	0	0
State of tree fragment										
Live	150	84	33	67	11	79	0	0	5	100
Dead	29	16	16	33	3	21	4	100	0	0
State of nest-site										
Live	25	14	3	6	7	50	0	0	0	0
Dead	154	86	46	94	7	50	4	100	5	100

Black Woodpeckers nested significantly higher than Great Spotted Woodpeckers (Mann-Whitney U test, $Z = 4.19$, $P < 0.0001$ and $Z = 3.12$, $P < 0.002$, respectively). Nest height was positively correlated with tree height in Great Spotted Woodpeckers ($r_s = 0.56$, $P < 0.0001$, $n = 173$) and was close to significance in Middle Spotted Woodpeckers ($r_s = 0.27$, $P = 0.058$, $n = 49$). Finally, the relative nest height varied significantly across species (Kruskal-Wallis ANOVA $H_3 = 13.69$, $P = 0.001$), being higher in Middle Spotted- and Black Woodpeckers than in Great Spotted Woodpeckers (Mann-Whitney U test, $Z = 3.13$, $P < 0.002$ and $Z = 2.35$, $P < 0.019$, respectively). It is worth noting that Lesser Spotted Woodpeckers excavated breeding holes relatively higher in respect to tree height (Table 4).

Great Spotted Woodpeckers, Middle Spotted Woodpeckers, Black Woodpeckers and Grey-faced Woodpeckers primarily used live trees, while Lesser Spotted Woodpeckers selected decaying trees (Table 5). There were no inter-species differences in the viability of trees used by Great Spotted-, Middle Spotted-, and Black Woodpeckers ($\chi^2 = 5.33$, $df = 4$, $P = 0.255$). All woodpecker species excavated nest-holes mainly in trunks and generally in live parts of the tree, except for Lesser Spotted Woodpeckers. However, there were some differences between the three most numerous species. Middle Spotted Woodpeckers nested more frequently than expected in limbs and branches ($\chi^2 = 17.45$, $df = 2$, $P < 0.001$) and in dead tree fragments ($\chi^2 = 6.57$, $df = 2$, $P = 0.037$) than Great Spotted Woodpeckers (Table 5). Black Woodpeckers did not show any preferences. Nest-holes were most frequently excavated in the dead or decaying part of tree fragments, e.g. in limb-holes, open wounds/scars and close to the fruiting body of tree fungus (Great Spotted Woodpecker – 81%, $n = 179$, Middle Spotted Woodpecker – 78%, $n = 49$), as well as in the base of dead or broken limbs (5% and 10%, respectively). Middle Spotted Woodpeckers excavated nest holes more frequently than expected in dead substrate while Black Woodpeckers in live substrate ($\chi^2 = 17.08$, $df = 2$, $P < 0.001$). It should be pointed out that all Lesser Spotted Woodpeckers' nest-holes were excavated in dead tree fragments.

The frequency distribution of nest-hole orientation did not differ from uniform distribution for Great Spotted Woodpeckers and Black Woodpeckers (Rayleigh test of uniformity, $P = 0.55$, $n = 166$ and $P = 0.46$, $n = 13$, respectively), and was significantly nonuniform for Middle Spotted Woodpeckers (Rayleigh test, $P = 0.05$). The distribution of nest-hole orientation for Middle Spotted Woodpeckers was biased toward the SEE and the mean angle of nest-hole exposure was 116.6° (95% confidence limit: 71.9 – 161.2 , $n = 45$).

5. DISCUSSION

In our study area we have found all six species of woodpeckers inhabiting lowland forests of Western Poland, among others the Grey-faced Woodpecker, a new breeding species in this region, its distribution range now shifting northward in Poland (Kempa and Kosiński 2003, Tomiałojć and Starwarczyk 2003).

It was suggested that the occurrence of several woodpecker species indicates some properties of naturally dynamic forest and forested landscape (Mikusiński and Angelstam 1997). Among the six species of woodpeckers occurring in the study forest ("Smoszew" Forest), four species (Lesser Spotted Woodpecker, Middle Spotted Woodpecker, Grey-faced Woodpecker, Black Woodpecker) are considered to be specialized forest birds sensitive to different attributes of the forest landscape (Angelstam *et al.* 2004). In the case of Lesser Spotted Woodpeckers and Middle Spotted Woodpeckers those attributes are related to the presence of older deciduous-dominated forests with dead or decaying trees as nesting and foraging-sites, but Grey-faced Woodpeckers and Black Woodpeckers are adapted for nesting in large trees and foraging in young forest stands abundant in ants. Our results suggest that the "Smoszew" Forest should be treated as a local or even regional hotspot of woodpecker diversity. Since the woodpecker species richness is an effective predictor of the number of forest bird species, the "Smoszew" Forest is probably an area of potentially high diversity for the entire bird community (Mikusiński *et al.* 2001).

The breeding densities found in the study area varies greatly between species, mainly as an effect of the differential area requirements of species. The territory size of woodpecker species in the breeding season are generally related to the degree of specialization, e.g. being lower in Great Spotted Woodpeckers (ca 3 ha), which is a generalist species, than in Middle Spotted Woodpeckers (ca 7 ha) and Lesser Spotted Woodpeckers (ca 40 ha) which are the most specialized forest birds (Pasinelli *et al.* 2001, Bachmann and Pasinelli 2002, Wiklander *et al.* 2001, see also Spitznagel 1990). Moreover, the densities in a given locality might depend on the plot size and area of habitats included in the area measurement. Therefore, the resultant density can vary between different plots (Gaston *et al.* 1999, Kosiński and Winiecki 2005). Furthermore, year-to-year variation in the abundance of some species, e.g. Great Spotted Woodpeckers, may additionally affect breeding density (Wesołowski and Tomiałoć 1997). In consequence, all comparisons should be made carefully and meet the above-mentioned objections. The ecological density of Great Spotted Woodpeckers was similar to that obtained from large-scale studies in an old deciduous riverine forest (nature reserve “Czeszewski Las” – “Czeszewski” Forest), ca 50 km north of the “Smoszew” Forest, at the same time (1.3 and 2.4 pairs 10^{-1} ha of forest area in 2002 and 2003 respectively, own data). It should be stated that the number of Great Spotted Woodpecker pairs in the reserve “Czeszewski Las” (“Czeszewski” Forest) in 2002 was the lowest during 2000–2006, own unpubl. data). Long-term studies in the primaeval temperate forests of the Białowieża National Park indicate an approximately two-fold lower density of Great Spotted Woodpeckers (e.g. Tomiałoć and Wesołowski 1994). The ecological density based on habitats that Middle Spotted Woodpeckers potentially use was similar to those in other large-scale oak-dominated plots in Western Poland (Kosiński and Winiecki 2005) and close to those in typical lowland forest habitats in Europe (Pasinelli 2003). The ecological density of Lesser Spotted Woodpeckers (see above) was similar to that obtained during large-scale studies in floodplain and alder-dominated alluvial for-

ests in Germany (Spitznagel 1990, Noah 2000), and close to that obtained in primaeval oak-linden-hornbeam forest plots (each of ca 30 ha in size) in the Białowieża National Park (0.1–0.3 pairs 10 ha^{-1} , Tomiałoć and Wesołowski 1994). Black Woodpecker density was among the highest reported in Europe (e.g. Nilsson 1997, Wübbenhorst and Südbeck 2003). However, this value may be slightly inflated by the fact that some pairs used space outside the study area. It is worth noting that similar densities have been found in mixed beech and coniferous forests (Nilsson 1997). There is lack of accurate estimation regarding Grey-faced Woodpecker breeding densities in Poland (Tomiałoć and Stawarczyk 2003). However, the density obtained in the “Smoszew” Forest was similar to that reported from the floodplain forest in Germany (Spitznagel 1990) and seems to be typical of Central European densities (Saari and Südbeck 1997). The population of Wrynecks was the least numerous and its density was also very low compared to other large-scale studies (Tomiałoć and Stawarczyk 2003). The cause of the very low density of this secondary-hole nester is not known. There were many sites with a combination of deciduous woodland, young forest stands and clear cuts potentially suitable for breeding and foraging.

Although the study plot had been strongly altered by forestry practices and was covered by a matrix of different forest stands, nest-sites of Great Spotted Woodpeckers were regularly distributed. This distribution pattern may be affected by the lower demands of this species related to the type and age of forest stands; e.g. it was found that Great Spotted Woodpeckers inhabiting deciduous forests avoid young stands (< 40 years old), and tends to avoid alder-dominated and beech forests (Kosiński 2006). Therefore, spatial distribution may be more strongly affected by territorial behaviour than by habitat quality. In the case of Middle Spotted Woodpeckers the presence of trees suitable for excavation or the proximity of preferred foraging sites may be more important for nest-hole distribution than other factors, especially in managed forests (Kosiński and Winiecki 2004). The distribution of Black Woodpecker nest-sites was probably affected by the distribution of

suitable nest sites, i.e. patches of beech stand. However, other factors such as the presence of foraging sites, habitat fragmentation and territorial behaviour might affect their distribution (Tjernberg *et al.* 1993). It should be pointed out that the mean distance between the nearest occupied nests was close to that obtained in the Italian Western Alps (Bocca and Rolando 2003) and six times lower than in Central Finland (Tjernberg *et al.* 1993).

We did not examine tree species availability in the "Smoszew" Forest, however, it could be stated that Great- and Middle Spotted Woodpeckers preferred oaks as nest sites. Similar results were obtained in riverine forests (Kosiński and Winiecki 2004, Kosiński *et al.* 2006) and oak-hornbeam forests (Mazgajski 1997), where oaks were selected relative to what was available. The most likely reason that both woodpecker species prefer oaks in managed oak-dominated forests is the lack of any other tree species suitable for hole excavation. Another deciduous tree species, which forms tree stands, is the hornbeam. However, live, hardwood hornbeams seem to be unsuitable for excavation (see also Wesołowski and Tomiałojć 1986). It was found that in more diverse riverine forests, Middle Spotted Woodpeckers also preferred ashes *Fraxinus excelsior* (Kosiński *et al.* 2006). In the primeval ash-alder stands of the Białowieża National Park both species preferred alders *Alnus glutinosa* (Wesołowski and Tomiałojć 1986). In Northern and Eastern Europe woodpecker species select aspen *Populus tremula* because they are susceptible to heartwood that makes excavation easier (Hågvar *et al.* 1990, Stenberg 1996, Kosenko and Kaygorodova 2003, Remm *et al.* 2006).

Contrary to previous studies we did not find Middle Spotted Woodpecker nests in dead trees, although such trees were highly preferred in other sites (Wesołowski and Tomiałojć 1986, Kosiński and Winiecki 2004, Kosiński *et al.* 2006). This may be a result of the scarcity of dead trees with sufficient diameter for hole-excavation in intensively managed forests or, less-likely, interspecific competition for nest-sites with Great Spotted Woodpeckers.

Since Black Woodpeckers and Grey-faced Woodpeckers excavated nest-holes almost exclusively in beeches, which were scattered in small patches throughout the whole study area, it seems to be obvious that this tree species was preferred. Although old deciduous stands constitute an important element of the Black Woodpeckers' habitat in European temperate forests, beech stands seem to be preferred (Lang and Rost 1990, Lange 1996, Wübbenhorst and Südbeck 2003). Since both woodpecker species excavate holes accessible to Pine Martens *Martes martes* (Nilsson *et al.* 1991), nesting in smooth-barked trees provides probably the best protection from this and other arboreal predators.

In opposition to other studies (e.g. Hågvar *et al.* 1990, Stenberg 1996), the average diameter of the nesting tree at breast height, tree height and nest height did not increase with the body size of woodpecker species. The choice of thin stems or fragments by the smallest species was explained by a lower risk of the nest-hole being taken over and enlarged by larger woodpeckers (e.g. Short 1979, Günther 1993). However, in other studies (Kosiński and Ksit 2007), we have found that structurally smaller Middle Spotted Woodpeckers excavated nest-holes similar in size compared to Great Spotted Woodpeckers. Moreover, it was found that Middle Spotted Woodpeckers excavated holes in thicker trees than Great Spotted Woodpeckers (Wesołowski and Tomiałojć 1986, Mazgajski 1997, Fauvel *et al.* 2001, but see Kosiński and Winiecki 2004, Kosiński *et al.* 2006). It is likely that in oak-dominated forests, the larger and older trees have a higher susceptibility to injury and infected by tree fungus and, in consequence, are more suitable for weak excavators, e.g. Middle Spotted Woodpeckers (Jenni 1981). Secondly, since the hardness of trees decreased with their increasing height (Shepps *et al.* 1999), nesting in higher and softer parts may be beneficial for species with weaker excavating abilities. This statement is supported by the fact that smaller woodpecker species excavated nest-holes relatively higher, more frequently in limb/branch and generally in weakened and dead tree fragments compared to larger species (see also Hågvar *et al.* 1990). In the case

of Black Woodpecker holes, nesting at greater height may be a form of protection against Pine Martens. Moreover, preference for nest-sites in live substrate may positively affect the nest microclimate and, in consequence, reproductive success and offspring fitness (Rolstad *et al.* 2000, Wiebe 2001). Furthermore, such nest-holes may be used successfully over a longer period (but see Nilsson *et al.* 1991).

Since nest-site preferences appear to be influenced by microclimatic conditions it could be expected that woodpeckers would prefer to orient nest-holes to direct insolation, i.e., towards the southeast (e.g. Hooge *et al.* 1999, Wiebe 2001). However, we have found that only Middle Spotted Woodpeckers preferred southeasterly directions (see also Wesołowski and Tomiałojć 1986, Fauvel *et al.* 2001). Moreover, in the other studies it was found that nest-holes of Great- and Middle Spotted Woodpeckers were oriented without any preferences (Kosiński *et al.* unpubl. data). These inconsistent data suggest that there are some constraints to nesting in optimal conditions, e.g., insufficient number of nest-sites (Hooge *et al.* 1999), interspecific competition for nest-sites (Smith 2005), and habitat context (Stenberg 1996). Secondly, recent study suggests that during the breeding season, when more inhabitants (nestlings) are consuming oxygen, woodpeckers might suffer from hypoxic conditions in the nest-hole (Ar *et al.* 2004). This effect may be pronounced when no wind is present, e.g., when nest-hole orientation differs from the prevailing wind directions.

Since woodpecker species differ in their habitat requirements it seems to be obvious that there can be no single method for the management of all woodpecker species. Our results imply that in the case of Great- and Middle Spotted Woodpecker nest-sites, forest management should focus on large (dbh > 30 cm in Great Spotted Woodpeckers and > 40 cm in Middle Spotted Woodpeckers) deciduous trees, mainly oaks. Since the presence of Great- and Middle Spotted Woodpeckers is related to older and rough-barked tree stands (Kosiński 2006), the maintenance of valuable populations of both species requires a continuous supply of

oak-dominated forest older than 80 or even 120 years appropriate for nesting and foraging (Pasinelli 2000, Kosenko and Kaygorodova 2001, Kosiński and Winiecki 2005). This target seems to be especially important for the Middle Spotted Woodpecker. In the case of Black- and Grey-faced Woodpeckers, thick (dbh > 40 cm) and even scatter-distributed groups of beech trees seem to be crucial for supporting both species long-term. Moreover, Black Woodpeckers and Grey-faced Woodpeckers may benefit from man-made altered composition and configuration of forest stands since they are adapted to nesting in old-deciduous stands and foraging in clear cuts or young forest stands.

6. CONCLUSIONS

In the study area called “Smoszew” Forest, 775 ha in size, we found all six woodpecker species, i.e. Great Spotted Woodpecker, Middle Spotted Woodpecker, Lesser Spotted Woodpecker, Black Woodpecker, Grey-faced Woodpecker and Wryneck, inhabiting lowland forests of Central and Western Poland. Therefore, this place should be treated as a local or regional hotspot of woodpecker diversity. The density of woodpecker species varied greatly between species, mainly as an effect of their ecological specialization. Black Woodpeckers had the highest breeding density reported to date in Central Europe. We found that all species preferred old deciduous forests (> 80 years old) for nest sites. Great- and Middle Spotted Woodpeckers nested more frequently in live oaks, while Black- and Grey-faced Woodpeckers preferred live beeches. In contrast with other studies, the average diameter of the nesting tree at breast height, tree height and nest height did not increase with the body size of the woodpecker species. Middle- and Lesser Spotted Woodpeckers nested more frequently in limbs/branches and/or in dead substrate than Great Spotted Woodpeckers or Black Woodpeckers due to their weaker excavation abilities. Our results imply that in order to preserve the nest-sites for Great- and Middle Spotted Woodpeckers, forest management should focus on large oaks. Black Woodpeckers and Grey-faced Woodpeckers benefit from old

and scattered groups of beech trees, as well as from the presence of man-made young coniferous stands that are used for foraging.

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