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Nest sites of Great Spotted Woodpeckers *Dendrocopos major* and Middle Spotted Woodpeckers *Dendrocopos medius* in near-natural and managed riverine forests

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Abstract. The main goals of this study were to determine whether woodpeckers differ in nest-site selection between near-natural old-growth forests protected for ca. 50 years and managed forests. Great Spotted Woodpeckers preferred oaks as nest sites, but Middle Spotted Woodpeckers selected dead trees as well as live ashes and oaks. It was found that the degree of silviculture did not affect the preference for tree species between long-term protected and managed areas in either *Dendrocopos* species. However, the share of ashes as nesting trees for Middle Spotted Woodpeckers was distinctly smaller in managed stands. In primeval *Quercus-Fraxinus-Ulmus* riverine forests ashes are thought to have played an important role as a nest-site for this species. In unmanaged forests both woodpeckers nested in trees of a larger diameter, at a nearly twofold higher rate than in managed stands. Nest-height was influenced by tree diameter. However, these relationships varied between the two woodpecker species, in relation both to the type of management and to the tree species, and were the most pronounced in Middle Spotted Woodpeckers nesting in ashes in near-natural stands. The type of management did not affect the placements of nest-holes in relation to tree condition, state of tree stump and condition of the wood in either species. However, in comparison to the near-natural forests, both species excavated holes more frequently than expected in tree-trunks in the managed stands. The results of the present work suggest a convergence of some nest-site characteristics in managed forests.

Key words: nest-site selection, riverine forests, stand structure, forest management, nest-site convergence

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INTRODUCTION

Nest-site selection may be affected by many factors operating in different spatial scales (Hilden 1965, Johnson 1980, Gutzwiller & Anderson 1987, Rolstad et al. 2000). Studies of the nest-site requirements of woodpeckers within the home range (third-order selection sensu Johnson 1980), suggest that distance to the forest edge (Short 1979, Stenberg 1996, Kosiński & Winiecki 2004), density of the surrounding vegetation and availability of trees suitable for hole excavation (Gutzwiller & Anderson 1987, Li & Martin 1991, but see Adkins Giese & Cuthbert 2003, Kosiński & Winiecki 2004) seem to be important in selection processes. However, since forest management influences stand structure by simplifying age, tree species composition and spatial structure of habitat, it may reduce the resources preferred for habitat use and nest-site selection of woodpeckers (e.g. Wesołowski 1995, Dobkin et al. 1995, Winter et al. 2005). Moreover, the excavating morphology of woodpecker species may create additional constraints on the nest-site selection of individual species (Jenni 1981).

The nest-sites of Great- and Middle Spotted Woodpeckers have been described frequently across the geographic range of both the species (e.g. Pettersson 1985, Stenberg 1996, Smith 1997, Yamauchi et al. 1997, Mazgajski 1998, Kossenko & Kaigorodova 2003, Bai et al. 2005). However, comparative studies of the species living in sympatry are scarce (Wesołowski & Tomiałojć 1986, Günther 1993, Mazgajski 1997, Fauvel et al. 2001, Kosiński & Winiecki 2004).

Great- and Middle Spotted Woodpeckers are taxonomically related species, coexisting in old, deciduous forests (del Hoyo et al. 2002, Kosiński 2006). Both the species are primary excavators. Nest-holes are excavated more often in trunks with the presence of decaying or dead wood (e.g. Wesołowski & Tomiałojć 1986, Smith 1997, Mazgajski 1997). However, it has been reported that both woodpecker species differ with respect to the nest-tree selection, nest height and orientation of the nest entrance (e.g. Tomiałojć & Wesołowski 1986, Fauvell et al. 2001, Kosiński & Winiecki 2004). It was suggested that some of these differences might have evolved to reduce interspecific competition between Great- and Middle Spotted Woodpeckers (Günther 1993) or could be affected by their different excavating morphology (Jenni 1981). Contemporaneous studies covering both congeneric and ecologically similar species should be useful in characterizing niche partitioning among species. Moreover, determining which trees are used and preferred for nesting is essential for effective species management.

Riverine forests are among the richest and most complex ecosystems in Europe (Tucker & Evans 1997), where both species probably occur in optimal conditions (e.g. Spitznagel 1990). Consequently, such habitats offer opportunities to advance our knowledge of species habitat requirements in conditions close to natural. It should be pointed out that none of the earlier studies considering nest-site characteristics of both woodpeckers were conducted in hardwood *Quercus-Fraxinus-Ulmus* riverine forest (see Wesołowski & Tomiałojć 1986).

In this paper we examine 1) if woodpeckers differ in nest-tree selection in near-natural old-growth stands protected for ca. 50 years and, by contrast, in managed (logged) riverine forests and 2) whether the type of silviculture affects the parameters of nesting trees and distribution of nest-holes within trees. Finally, we discuss whether the type of management might affect niche partitioning between both woodpecker species.

STUDY AREA

The study was carried out in the riverine forest of the Warta river valley, Central Poland, near Czeszewo (17°31'E, 52°09'N), 50 km south east of Poznań. This woodland is a remnant of an ancient flood-plain forest, which in the past covered narrow, alluvial strips along major European rivers (review in Tucker & Evans 1997). Floodplain deciduous forests were cleared and converted into meadows or were lost after rectification of rivers and the building of embankments. In modern times, the total area of riverine forest in Poland is estimated at 27 km^2, however, in the Wielkopolsko-Kujawska Lowland (19 032 km^2), where this study took place, only 1.7 km^2 (0.009%) exists (Matuszkiewicz 2001).

Field work was carried out on a 224 ha plot, which encompasses 185 ha of forest (Fig. 1). The vegetation consists of *Quercus-Fraxinus-Ulmus* (*Fraxino-Ulmetum*) woodland in the flooded parts and *Quercus-Carpinus* (*Stellario-carpinetum*) forest on the higher ground. The rest of study area (39 ha, 17%) is formed by old river-beds and meadows. The study forest differs in terms of age, species composition and spatial structures as a consequence of previous human impact. About 40% of tree stands on the study plot (74 ha) were ca. 155–165 years old, 24% (43 ha) — 81–120 years old, 28% (51 ha) — 41–80 years old and 4% (10 ha) — ≤ 40 years old; ca. 4% (8 ha) was covered by coniferous stands. Since 1959, the oldest near-natural stands have been protected within two

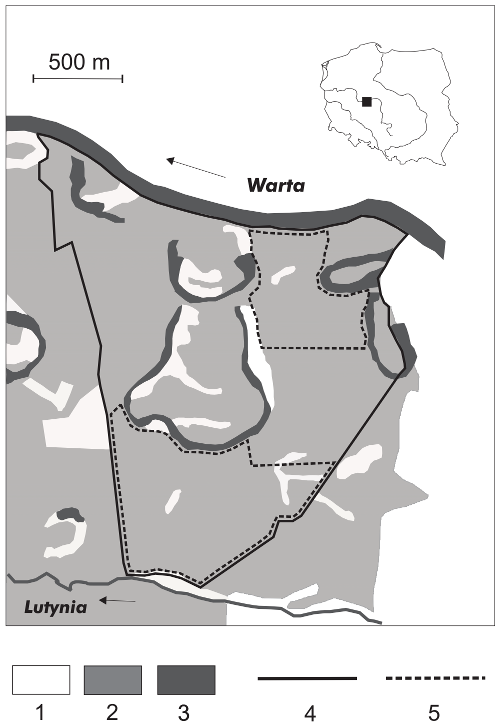

Fig. 1. Location of the study area; 1 — open areas, 2 — forests, 3 — rivers and old river-beds, 4 — nature reserve "Czeszewski Las", 5 — near-natural forests protected for ca. 50 years.

reserves ("Czeszewo" and "Lutynia") and nearly unmanaged. However, due to an increasing number of dead trees, over a total area of 7.3 ha, logging took place in 1993–1994. In consequence, man-made gaps covered by young stands came into being. Moreover, until 2002, naturally downed logs suitable for treatment as a raw material were removed from both natural reserves. The rest of study area has been severely altered by silviculture and is covered by younger and simplified tree stands. In 2004, the whole study plot (222.6 ha) was declared a nature reserve "Czeszewski Las".

MATERIALS AND METHODS

Data were collected in 2000–2005 for Middle- and 2001–2005 for Great Spotted Woodpeckers. To estimate the number and distribution of Middle Spotted Woodpecker territories in each of the pre-breeding seasons (the latter half of March to the end of April), four to five complete censuses based on the playback method were performed (Pasinelli et al. 2001, Kosiński & Winiecki 2003, Kosiński et al. 2004). This resulted in the mapping of all the territories. The number of Middle Spotted Woodpecker territories varied from 38 in 2000 (2.1 territories/10 ha of forest area) to 29 in 2003 (1.6 territories/10 ha). A search for nest-holes of Middle Spotted Woodpeckers began in late April. We systematically checked each territory. Territories where no nests were found or nests were abandoned (ca. 60–70% in each year) were revisited in the second part of May and at the beginning of June for the detection of calling nestlings. In this way 12–25 (46–86%) nest-sites were found each year. No playback censuses were conducted for Great Spotted Woodpeckers. The nest-holes of Great Spotted Woodpeckers were found at the beginning of the breeding season either by the sound of excavation or signs of wood-boring, e.g. wood chips on the ground, as well as by observations of adults and begging-calls of the young during the latter period. Based on the high survival rates of Great Spotted Woodpecker nests (e.g. Mazgajski 2002, Kosiński & Ksit in press) and the high efficiency of these nest searching methods, it was assumed that all the nesting attempts were recorded in each year. The number of Great Spotted Woodpecker terri-tories varied from 24 in 2002 (1.3 pairs/10 ha of forest area) to 45 pairs in 2004 (2.5 pairs/10 ha).

In order to determine the presumed effects of silviculture on nest-site selection of woodpeckers the territories were divided into two categories: territories within nearly unmanaged and protected forests (PF) and managed forest (MF). In each of the 54 territories of Great Spotted Woodpeckers in 2001–2002 and 92 territories of Middle Spotted Woodpeckers in 2000–2004, one randomly selected circular plot with a radius of 10 m (0.033 ha) was established (for detailed procedure see Kosiński & Winiecki 2004). In each plot all trees with diameter at breast height (DBH) sufficiently large for hole excavation (≥ 14 cm for Middle Spotted Woodpeckers and ≥ 19 cm for Great Spotted Woodpeckers; own data) were recorded. To test the effect of silvicultural practice on nesting tree characteristics we analysed only those territories in which nest-site and random site encompassed the same type of habitat (e.g. managed forest). In this way 51 territories of Great- and 78 of Middle Spotted Woodpeckers were included in the analyses. Further, individual selection indices were calculated to determine nest-site selection in relation to the availability of different tree species. Based on the Bonferroni inequality for individual selection indices 95% simultaneous confidence intervals (CI) were constructed (Manly et al. 1993). An index value > 1 implies positive selection and a value < 1 indicate avoidance of tree species. The selection coefficient is then declared significantly different from 1 if the confidence interval does not contain the value 1. Negative lower limits were changed to 0.00 since negative values of confidence limits are not possible.

Eight parameters of nest-sites were recorded: tree species, tree viability, part of tree (trunk vs. limb/branch) and its viability (live vs. dead), diameter at breast height, nest height, orientation of entrance hole (to nearest 10°; not reported in this paper) and condition of wood at nest site. Tree viability was attributed to one of three categories: living tree, tree still alive (only one or a few branches with living leaves) and dead tree. A SUUNTO Height Meter PM-5/1520 was used to measure nest height. In some cases not all measurements were available for each nest, and thus sample size may differ in subsequent analyses.

To test the differences between nest-tree characteristics the variables were log-transformed to normalise values. Levene's test was used to test the equality of variance among the compared samples. When the variances were the same, t-test was used to compare the means. In other cases the nonparametric Mann-Whitney U test was used.

The frequency distributions within the categorical variables were tested using the χ^2 test. When there were only two categories in a distribution (df = 1), statistic with Yates' correction is given. We used the Pearson correlation coefficient to determine correlation between nest-height and tree diameter.

Statistical tests were carried out using STATISTICA 6.0 (StatSoft, Inc. 2003). Values reported are means ± standard deviations and 95% confidence limits for the means (CL). All tests are 2-tailed.

RESULTS

Nest-tree preferences

Both species most commonly used oaks (Table 1). However, in near-natural, formerly protected forests, Middle Spotted Woodpeckers excavated their holes mainly in ashes. Despite the lack of any significant differences in frequency of nest location in oaks, ashes and other species between the years, the proportion of Middle Spotted Woodpecker nests found in ashes in 2003–2004 (41% of all nesting trees, n = 51) was approximately twice higher than in other years (23% of all trees, n = 69). Moreover, in unmanaged stands the proportion of holes in ashes in 2003–2004 was approximately two-fold higher than in oaks (56% vs 31% in 2003, n = 16, and 60% vs 27% in 2004, n = 15).

Great Spotted Woodpeckers strongly preferred oaks, especially in near-natural, protected forests (Table 2). Furthermore, there was also a highly positive selection for dead trees in managed forests, however, the amount of substrate which was used and available was very small. Middle Spotted Woodpeckers clearly preferred dead trees, especially in protected stands. Ashes and oaks were also more frequently used than expected relative to their abundance, both in managed and protected stands. Moreover, willows were highly preferred in managed forests but there only few trees were used or available.

Characteristics of nest-sites

The average breast height diameter (DBH) of the nesting trees was 57.9 ± 20.4 cm (CL: 54.8–60.9, range 20.7–134.1, n = 173) in Great Spotted Woodpeckers and 62.1 ± 28.6 cm (CL: 56.9–67.3, range 14.0–197.5, n = 119) in Middle Spotted Woodpeckers, and did not differ significantly between species (t_{290} = -0.81, p = 0.42).

In protected stands, both species excavated nest-holes in trees with larger DBH than in the managed forests (Great Spotted Woodpecker: t_{171} = 7.61, p < 0.0001, Middle Spotted Woodpecker: t_{117} = 2.79, p = 0.006; Fig. 2). However, the diameter of nest trees of Great- and Middle Spotted Woodpeckers did not differ either in protected (Mann-Whitney U test, Z = 0.59, p = 0.56) or managed stands (Mann-Whitney U test, Z = -1.21, p = 0.23).

When the stem diameter of the two most commonly used tree species was compared, it was found that the DBH of oaks and ashes used by Great- and Middle Spotted Woodpeckers was significantly larger in protected than in managed forests, but the diameter of other species (pooled in one category) did not differ significantly (Table 3).

The average height of the nest entrance from the ground level was 10.0 ± 6.2 m (CL: 9.1–11.0, range 0.91–26, n = 170) in Great Spotted Woodpeckers and 11.3 ± 7.0 m (CL: 10.0–12.6, range 0.95–28, n = 114) in Middle Spotted Woodpeckers,

Table 1. Trees used by Great and Middle Spotted Woodpeckers. Pooled data from all years are given. PF — protected forests, MF — managed forests, N — sample size.

Species	Great Spotted Woodpecker				Middle Spotted Woodpecker			
	PF	MF	Total		PF	MF	Total	
	N	N	N	%	N	N	N	%
Quercus robur	57	61	118	68.2	25	36	61	50.8
Fraxinus excelsior	21	15	36	20.8	30	7	37	30.8
Carpinus betulus	4	0	4	2.3	2	1	3	2.5
Alnus glutinosa	1	3	4	2.3	1	3	4	3.3
Salix sp.	0	4	4	2.3	1	2	3	2.5
Tilia cordata	0	3	3	1.3	0	0	0	0.0
Populus sp.	0	2	2	1.2	0	4	4	3.3
Acer campestre	0	1	1	0.6	3	0	3	2.5
Betula verrucosa	0	1	1	0.6	1	3	4	3.3
Ulmus sp.	0	0	0	0.0	1	0	1	0.8
Total	83	90	173	100.0	64	56	120	100.0

Table 2. Selection indices for nesting tree species in protected forests (PF) and managed forests (MF). Pooled data from all years are given. *a* — *Tilia cordata* (24), *Acer campestre* (16), *Ulmus* sp. (9), *Acer platanoides* (2), *b* — *Fraxinus excelsior* (1), *c* — *Carpinus betulus* (38), *Pinus sylvestris* (31), *Acer campestre* (18), *Ulmus* sp. (7), *d* — *Quercus robur* (1), *e* — *Fraxinus excelsior* (1), *Alnus glutinosa* (1), *f* — *Tilia cordata* (46), *Ulmus* sp. (25), *Picea excelsa* (6), *Acer platanoides* (5), *Alnus glutinosa* (5), *Betula verrucosa* (1), *g* — *Fraxinus excelsior* (4), *Quercus robur* (2), *Carpinus betulus* (1), *h* — *Fraxinus excelsior* (4), *Ulmus* sp. (1), *i* — *Carpinus betulus* (147), *Acer campestre* (58), *Tilia cordata* (51), *Ulmus* sp. (35), *Picea excelsa* (1), *Betula verrucosa* (1), *j* — *Quercus robur* (1), *Betula verrucosa* (1), *Alnus glutinosa* (1), *k* — *Fraxinus excelsior* (3), *Quercus robur* (2), *Ulmus* sp. (2), *Populus* sp. (2), *Carpinus betulus* (1).

	Tree species	Alive/dead	Nests	Proportion of nests	Available trees	Proportion of trees	Selection index	95% CL
				Great Spotted Woodpecker				
PF	*Quercus robur*	A	18	0.857	27	0.153	5.62	5.42–5.82
	Fraxinus excelsior	A	2	0.095	40	0.226	0.42	0.00–2.49
	Carpinus betulus	A	1	0.048	58	0.328	0.15	0.00–4.78
	Other	A	0	0.000	51*a*	0.288	0.00	
	Other	D	0	0.000	1*b*	0.006	0.00	
	Total		21		177			
MF	*Quercus robur*	A	18	0.600	70	0.263	2.28	1.93–2.63
	Fraxinus excelsior	A	8	0.267	70	0.263	1.01	0.22–1.81
	Alnus glutinosa	A	1	0.033	5	0.019	1.77	0.00–3.74
	Tilia cordata	A	1	0.033	25	0.094	0.35	0.00–4.57
	Populus sp.	A	1	0.033	0	0.000		
	Other	A	0	0.000	94*c*	0.353	0.00	
	Other	D	1*d*	0.033	2*e*	0.008	4.43	3.19–5.68
	Total		30		266			
				Middle Spotted Woodpecker				
PF	*Quercus robur*	A	13	0.342	74	0.174	1.97	1.51–2.43
	*Fraxinus excel*sior	A	14	0.368	73	0.171	2.15	1.72–2.58
	Acer campestre	A	3	0.079	23	0.054	1.46	0.27–2.66
	Carpinus betulus	A	1	0.026	163	0.383	0.07	0.00–7.77
	Other	A	0	0.000	88*f*	0.207	0.00	
	Other	D	7*g*	0.184	5*h*	0.012	15.69	15.45–15.94
	Total		38		426			
MF	*Quercus robur*	A	26	0.650	272	0.417	1.56	1.24–1.88
	*Fraxinus excel*sior	A	7	0.175	48	0.074	2.38	1.76–3.00
	Populus sp.	A	2	0.050	27	0.041	1.21	0.00–2.83
	Salix sp.	A	2	0.050	3	0.005	10.88	10.32–11.45
	Other	A	0	0.000	293*i*	0.449	0.00	
	Other	D	3*j*	0.075	10*k*	0.015	4.90	4.21–5.58
	Total		40		653			

and did not differ significantly between species (t_{282} = -0.85, p = 0.40). However, comparisons between protected and managed forests indicate that both species nested almost twofold higher (1.7 and 1.9 respectively) in protected forests than in managed stands (Great Spotted Woodpeckers: t_{168} = 4.96, p < 0.0001, Middle Spotted Woodpeckers: t_{112} = 5.10, p < 0.0001; Fig. 3).

The average height of nest-holes excavated in ashes and oaks was larger in protected than in managed forests (Table 3). More than 70% of nest-holes of both species in managed stands were located below 10 m, but in protected forests holes were the most frequently excavated between 5 and 25 m.

Nest-heights were significantly positively affected by the DBH of nest trees both in Great Spotted Woodpeckers (Pearson correlation, r = 0.31, p < 0.001, n = 170; nest-height and DBH log-transformed) and Middle Spotted Woodpeckers (r = 0.55, p < 0.001, n = 114). This relationship varied at an intraspecific level, being more pronounced in ashes (Great Spotted Woodpeckers: r = 0.58, p < 0.001, n = 35; Middle Spotted Woodpeckers: r = 0.67, p < 0.001, n = 34) than in oaks (r = 0.25, p = 0.008, n = 116 and r = 0.35, p = 0.008, n = 56, respectively). The strength of correlations varied between protected and managed forests both in Great- and Middle Spotted Woodpeckers (Fig. 4; two Middle Spotted Woodpecker holes in MF excavated in oaks with DBH > 180 cm, and two Great Spotted Woodpecker holes in MF excavated in oaks with DBH > 120 cm were removed from analysis). In managed stands there was a weak and not statistically significant correlation between DBH and nest height in Great

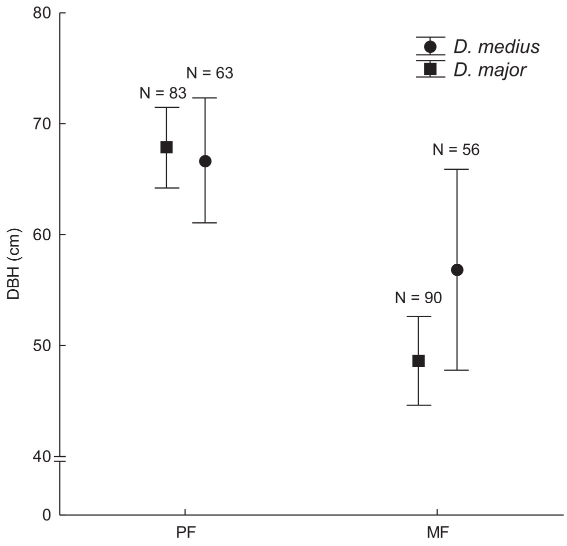

Fig. 2. Diameter of the nesting trees (DBH) of Great Spotted Woodpeckers and Middle Spotted Woodpeckers in protected forests (PF) and managed forests (MF). Means and 95% confidence limits are given.

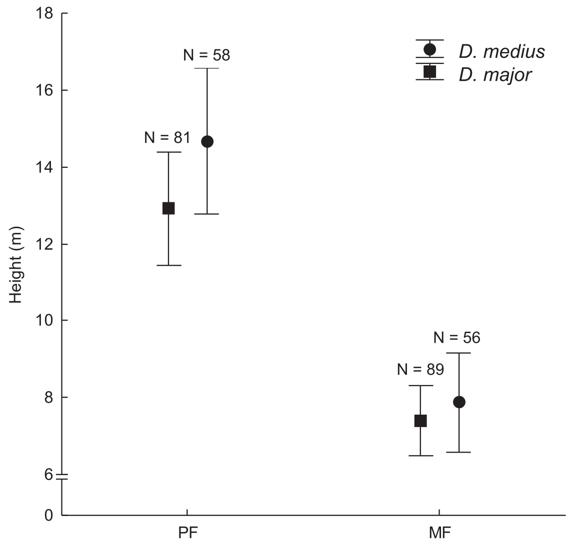

Fig. 3. Nest height of Great- and Middle Spotted Woodpeckers in protected forests (PF) and managed forests (MF). Means and 95% confidence limits are given.

Spotted Woodpeckers. However, at an intraspecific level, this relationship was significant only in the case of ashes in near-natural forests (Middle Spotted Woodpecker: r = 0.77, p < 0.001, n = 27, Great Spotted Woodpecker: r = 0.60, p = 0.005, n = 20).

Great Spotted Woodpeckers excavated nest-holes significantly more frequently in vital trees ($\chi^2 = 14.53$, df = 2, p < 0.001), in trunks ($\chi^2 = 13.69$, df = 1, p < 0.001) and live tree fragments ($\chi^2 = 27.24$, df = 1, p < 0.001) compared to Middle Spotted Woodpeckers (Table 4). However, both woodpecker species used dead or decaying parts of tree fragments with similar frequency ($\chi^2 = 2.82$, df = 1, p = 0.09). The majority of nest-holes were excavated in limb-holes, open wounds/scars and close to the fruiting body of tree fungus (Great Spotted Woodpecker: 65%, n = 168, Middle Spotted Woodpecker: 70%, n = 116), as well as in the base of dead or broken limbs (18% and 21%, respectively).

The type of management did not affect the placements of nest-holes in relation to tree

Table 3. Diameters at breast height (DBH) and height of nest-holes of woodpeckers in protected (PF) and managed forests (MF). Mean ± standard deviation, number of nest trees in brackets, Z — values and probability of Mann-Whitney U test are given.

Tree species	Type of management		Z	p
	PF	MF		
Great Spotted Woodpecker				
DBH				
Quercus robur	71.5 ± 15.5 (57)	51.1 ± 21.3 (61)	-6.01	< 0.0001
Fraxinus excelsior	51.1 ± 17.0 (21)	41.3 ± 12.8 (15)	-3.48	< 0.001
Other	46.2 ± 4.0 (5)	45.9 ± 11.8 (14)	-0.79	0.431
Height				
Quercus robur	12.2 ± 6.1 (56)	7.1 ± 4.3 (60)	-4.34	< 0.0001
Fraxinus excelsior	16.6 ± 6.9 (20)	8.5 ± 4.3 (15)	-3.20	0.001
Other	6.6 ± 4.1 (5)	7.6 ± 4.4 (14)	0.19	0.853
Middle Spotted Woodpecker				
DBH				
Quercus robur	70.6 ± 19.5 (24)	61.6 ± 36.7 (36)	-2.91	0.004
Fraxinus excelsior	72.3 ± 19.7 (30)	61.5 ± 29.3 (7)	-1.40	0.163
Other	37.3 ± 15.2 (9)	41.4 ± 23.1 (13)	0.43	0.664
Height				
Quercus robur	12.0 ± 4.7 (22)	7.2 ± 4.3 (36)	-3.68	0.0002
Fraxinus excelsior	19.9 ± 5.6 (27)	15.1 ± 2.8 (7)	-2.33	0.020
Other	5.6 ± 2.9 (9)	5.7 ± 3.1 (13)	0.10	0.920

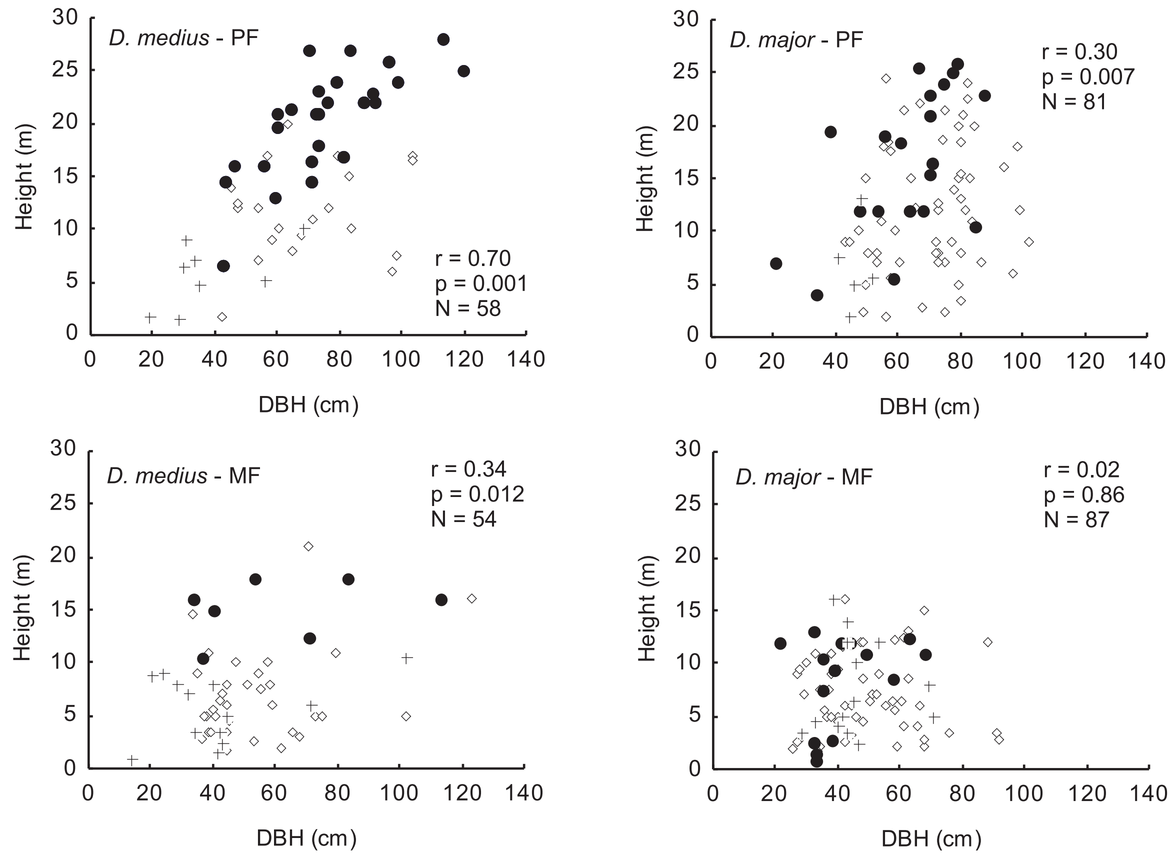

Fig. 4. Relation between tree diameter (DBH) and nest height in Middle — and Great Spotted Woodpeckers in protected (PF) and managed forests (MF). Dots — ashes, diamonds — oaks, crosses — other tree species. Correlation coefficients are based on log-transformed variables.

condition, state of tree fragment and condition of wood in either Great- or Middle Spotted Woodpeckers (χ^2-test, $p > 0.05$ in all cases). However, in managed stands, both species excavated nest-holes significantly more frequently than expected in trunks compared to the protected forests where limbs and branches were used commonly (Great Spotted Woodpecker: $\chi^2 = 10.51$, df = 1, p = 0.001, Middle Spotted Woodpecker: $\chi^2 = 8.11$, df = 1, p = 0.004, Table 4).

Table 4. Placements of woodpecker holes in relation to tree condition, fragment, and state of nest-site in protected (PF) and managed forests (MF). Nest-holes from all years are pooled. N — sample size.

Placement	Great Spotted Woodpecker				Middle Spotted Woodpecker			
	PF	MF	Total		PF	MF	Total	
	N	N	N	%	N	N	N	%
Tree condition								
Live	71	78	149	86.1	48	38	86	72.3
Still alive	8	7	15	8.7	4	6	10	8.4
Dead	4	5	9	5.2	11	12	23	19.3
Part of tree								
Trunk	57	81	138	81.2	29	42	71	60.7
Limb/branch	24	8	32	18.8	32	14	46	39.3
State of tree fragment								
Live	60	77	137	80.6	26	33	59	49.2
Dead	21	12	33	19.4	35	23	58	48.3
Condition of wood at nest-site								
Live	14	15	29	17.3	3	8	11	9.5
Dead	65	74	139	82.7	57	48	105	90.5

DISCUSSION

Nest-site selection

Great Spotted Woodpeckers preferred oaks as nest sites but Middle Spotted Woodpeckers selected dead trees as well as live ashes and oaks. These results differed slightly from our previous data (Kosiński & Winiecki 2004) in which it was found that Great Spotted Woodpeckers preferred mostly oaks but Middle Spotted Woodpeckers selected dead trees and oaks. In our opinion, these discrepancies (mainly the positive selection for ashes among Middle Spotted Woodpeckers) might be affected by two factors. First, in earlier studies we combined data from managed and protected stands in one sample. In this way, some territories encompassed both managed and protected forests that differed in tree species composition. Second, the positive selection for ashes could be connected either with the increase of our experience which has improved in the detection of highly situated nests in ashes or with inter-seasonal variation in nest-site availability in different tree species. The latter factor might be confirmed by the fact that in 2005 only 22% of nests (n = 23) were found in ashes, despite the fact that the study area was checked with the same intensity as in previous years (e.g. 2003–2004). It is worth noting that silviculture did not affect the preference for tree species between long-term protected and managed areas in Great- and Middle Spotted Woodpeckers. However, the simplification of tree species composition in managed stands and its lower age compared to protected forests has caused a strong reduction in the share of ashes suitable as nesting trees for Middle Spotted Woodpeckers. This suggests that in primeval hardwood *Quercus-Fraxinus-Ulmus* riverine forests this tree species probably played an important role as a nest-site for Middle Spotted Woodpeckers. It should be pointed out that Middle Spotted Woodpeckers were practi-cally absent from mainly ash-dominated stands younger than ca. 80 years old, which were frequently inhabited by Great Spotted Woodpeckers (see also Kosiński 2006).

The few studies that have focused on nest-site selection in relation to the availability of tree species suggest that utilisation of nesting trees may vary geographically as an effect of tree species composition (Wesołowski & Tomiałojć 1986, Hågvar et al. 1990, Stenberg 1996, Mazgajski 1998, Kosiński & Winiecki 2004) and its susceptibility to heartwood rot (e.g. Martin et al. 2004). Data from primeval forests of the Białowieża National Park showed that in swampy ash-alder stands both species selected alder, but in oak-hornbeam forests Great Spotted Woodpeckers preferred aspen *Populus tremula* while Middle Spotted Woodpeckers preferred hornbeam and oak (Wesołowski & Tomiałojć 1986). It should be pointed out that alders and aspens are scarce in our study area. Our data suggest that other factors such as silvicultural practice and temporal variation of substrate availability may affect nest-site selection and modify selection indices.

In near-natural unmanaged forests both woodpeckers nested in larger diameter trees and nearly twofold higher than in managed stands. This phenomenon probably reflects the differences in tree-size between the managed and unmanaged parts of the study area affected by the age of forest stands. We have found that nest-height was affected by tree diameter. However, these relationships varied between woodpecker species both in relation to the type of management and tree species, being the strongest in Middle Spotted Woodpeckers nesting in ashes in near-natural stands. Moreover, it was found that Middle Spotted Woodpecker holes were placed higher in ashes than in oaks. It is interesting to speculate as to why Middle Spotted Woodpeckers should prefer to nest high in ashes. This may result from this distribution of preferred nest sites. Ash is a tall tree species and reaches terminal age more rapidly than e.g. oaks. In old ashes the upper branches and the top of tree die back creating places for nest-hole excavation (Authors' own obs.). Moreover, since the hardness of trees decreased with their increasing height (Schepps et al. 1999), their upper and external parts seem to be more suitable for weaker excavators such as Middle Spotted Woodpeckers (Jenni 1981). A much higher proportion of Middle Spotted Woodpecker holes in ashes were situated in limbs and branches (76%, n = 37) compared to that excavated in such structures by Great Spotted Woodpeckers (29%, n = 35). However, data from swampy ash-alder stands in primeval forests suggests that ashes might be preferred trees only in certain habitats, e.g. in hardwood *Quercus-Fraxinus-Ulmus* riverine forests, and that they constitute an unfavourable substrate for excavation compared to alders (Wesołowski & Tomiałojć 1986). Sites suitable for hole excavation in oaks, such as limb-holes and open wounds/scars, occur more frequently in trunks, and their presence seems to be less dependent on tree-size. Therefore, the nest-height was less affected by the tree diameter in both woodpecker species. Since oaks and ashes offer different structures suitable for hole excavation, it could be stated that nest-sites of Middle Spotted Woodpeckers in near-natural riverine forests, where ashes were used more frequently, are more diverse than in more simplified managed stands.

We have found that irrespective of the type of management Middle Spotted Woodpeckers excavated nest-holes more frequently in dead and soft wood than Great Spotted Woodpeckers (Wesołowski & Tomiałojć 1986, Günther 1993, Kossenko & Kaygorodova 2003). These differences seem to be a result of the less specialised and simpler neck muscles of Middle Spotted Woodpeckers compared to the latter species which are less suitable for drumming and excavation (Jenni 1981). It was suggested that Middle Spotted Woodpeckers' preference for nesting in higher and weaker parts of trees might have evolved to reduce interspecific competition with Great Spotted Woodpeckers (Günther 1993, see also Pasinelli 2003). It has also been speculated that the smaller nest-holes of Middle Spotted Woodpeckers excavated into thin fragments could not be taken over and enlarged by Great Spotted Woodpeckers. However, we did not find any differences in most nest-hole dimensions (Z. Kosiński, P. Ksit, unpubl. data).

The diameter of nesting trees of Great- and Middle Spotted Woodpeckers was generally higher to those reported from other sites in the temperate forests of Central and Western Europe (recent reviews in Michalek & Miettinen 2003, Pasinelli 2003). The lowest values were reported mainly from Eastern and Northern Europe where species nest more frequently in relatively small-sized tree species such as aspen (e.g. Hågvar et al. 1990, Stenberg 1996, Kosenko & Kaygorodova 2003). Some studies have reported that Middle Spotted Woodpeckers use larger diameter trees compared to Great Spotted Woodpeckers (Wesołowski & Tomiałojć 1986, Fauvel et al. 2001), but we did not find such differences. However, we have found that in the study area both woodpecker species selected trees with significantly larger diameters than potentially available trees (Kosiński & Winiecki 2004).

The average height of nest-holes above the ground of Great- and Middle Spotted Woodpeckers was generally higher than in other intensively studied populations (e.g. Fauvel et al. 2001, Kosenko & Kaygorodova 2003, recent reviews in Michalek & Mietttinen 2003, Pasinelli 2003). The nest-height of Great- and Middle Spotted Woodpeckers in near-natural stands (12.9 m and 14.7 m respectively) was similar to that found in the primeval temperate forests of the Białowieża National Park (Wesołowski & Tomiałojć 1986). As stated earlier, the differences in nest-height might be a product of forest age as well as the size of preferred tree species. For example, Kossenko & Kaygorodova (2003) found that in Eastern Europe Middle Spotted Woodpeckers nested more frequently in aspen. This short-living tree species rarely grows to a large size and, in consequence, nest-holes are excavated at relatively low height (see also Hågvar et al. 1990, Stenberg 1996).

Does the type of management affect niche partitioning of woodpecker species?

Our data suggests that silviculture affects nest tree selection, as well as modifying parameters of nesting trees and distribution of nest-holes within trees in Great- and Middle Spotted Woodpeckers. Generally, we have found a convergence of some nest-site characteristics in managed stands where both species commonly used oaks and excavated holes more frequently in trunks compared to near-natural stands. In consequence, niche partitioning between Great- and Middle Spotted Woodpeckers in managed forests seems to be weaker than in near-natural stands. It is questionable as to whether convergence of nest-sites affects interspecific competition between both woodpecker species and, as a consequence, population parameters, e.g. population density. We have no data concerning the intensity of conflicts between both woodpecker species in near-natural and managed stands and competition for nest-sites. However, other studies suggest a very low level of interspecific competition between these two *Dendrocopos* species living in sympatry (Bachmann & Pasinelli 2002). On the other hand, lower densities of Middle Spotted Woodpeckers in other managed and even very old oak stands (e.g. Kosiński & Winiecki 2005) suggest that simplifying tree species composition and spatial structure of tree stands may reduce the abundance of this species (Spitznagel 1990, Pavlik 1994). This could be a result of both the lower availability of large rough-barked trees, being related to potential food abundance, and of potential nest trees, being related to reproduction. It was found that both factors determine home range size in Middle Spotted Woodpeckers (Pasinelli 2000). Wesołowski & Tomiałojć (1986) suggest that in primeval forests woodpecker species also "tended rather to converge (…) in many niche parameters" especially in swampy ash-alder stands, e.g. where it has been found that all species excavated their breeding holes mostly in alder. However, in primeval forests both woodpecker species reach lower densities compared to the studied forests. Moreover, Hågvar et al. (1990) revealed that four woodpecker species in Norway, commonly using aspen as nest-sites, differed in respect to nest-height above the ground. Therefore, it could be suggested that in some habitats characterised by the presence of a large number of short-living tree species, such as alder and aspen (e.g. Tomiałojć et al. 1984, Stenberg 1996), which seem to be most suitable for hole-excavation, the competition for nest-sites should be limited. In the case of our study area, the different distribution of both species in relation to the forest edge (Kosiński & Winiecki 2004), preference for different tree species and tree decay stage is probably crucial for reducing any potential inter-spe-cific conflicts (see also Bachmann & Pasinelli 2002).

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STRESZCZENIE

[Charakterystyka miejsc gniazdowania dzięcioła dużego i dzięcioła średniego w lesie łęgowym seminaturalnym i użytkowanym gospodarczo]

Celem badań było określenie czy sposób użytkowania lasu wpływa na wybór drzewa gniazdowego i cechy charakteryzujące sposób umieszczenia dziupli przez dzięcioła dużego i dzięcioła średniego. Badania prowadzono w latach 2000–2005 w lasach łęgowych w dolinie Warty koło Czeszewa w Wielkopolsce (rezerwat "Czeszewski Las", Fig. 1). Ogółem znaleziono i opisano 173 lęgowe dziuple dzięcioła dużego i 120 dziupli dzięcioła średniego.

Najczęściej wykorzystywanym przez oba gatunki dzięciołów drzewem gniazdowym był dąb, a w części seminaturalnej także jesion (Tab. 1). Sposób użytkowania lasu nie wpływał na wybór gatunku drzewa gniazdowego. Częściej niż wynikałoby to z dostępności poszczególnych gatunków drzew dzięcioł duży preferował dęby, podczas gdy dzięcioł średni wykuwał dziuple w martwych drzewach różnych gatunków oraz żywych dębach i jesionach (Tab. 2). Uzyskane dane wskazują, że w naturalnych nadrzecznych lasach łęgowych jesion stanowił prawdopodobnie istotne miejsce gniazdowania dla dzięcioła średniego.

W starych, seminaturalnych łęgach oba gatunki dzięciołów wykuwały dziuple w drzewach o większej średnicy i wyżej niż w lasach użytkowanych gospodarczo (Fig. 2 i 3). Zjawisko to odzwierciedla zapewne zróżnicowanie rozmiarów drzew wynikające z ich wieku. Analizując poszczególne gatunki drzew stwierdzono, że różnice te były istotne w przypadku dębu i jesionu, natomiast w obrębie innych gatunków drzew (połączonych w jedną kategorię), różnic takich nie odnotowano (Tab. 3).

Wysokość umieszczenia dziupli była dodatnio skorelowana ze średnicą drzewa (dzięcioł duży: $r = 0.31$, $p < 0.001$, $n = 170$; dzięcioł średni: $r = 0.55$, $p < 0.001$, $n = 114$). Związek ten był najsilniejszy w przypadku dziupli dzięcioła średniego wykuwanych w jesionach. Co więcej, zależność ta była silniejsza w lasach seminaturalnych niż użytkowanych gospodarczo (Fig. 4). Uzyskane wyniki wskazują, że formowanie się odpowiedniego do wykuwania dziupli substratu zachodzi odmiennie u różnych gatunków drzew. Jesiony dojrzewają szybciej i żyją krócej w porównaniu z dębami. Obumierające lub martwe górne konary jesionów oraz malejąca wraz z wysokością twardość drewna sprawia, że w szczytowych ich par-tiach tworzą się odpowiednie dla dzięcioła średniego miejsca gniazdowania. Preferowanie martwego substratu przez dzięcioła średniego ma związek ze słabiej niż u dzięcioła dużego rozwiniętymi mięśniami szyi, co utrudnia wykuwania dziupli. W przypadku dębów oba gatunki

dzięciołów wykorzystywały przede wszystkim blizny lub fragmenty pni w miejscu odłamanych konarów. Obecność wymienionych struktur wydaje się być niezależna od rozmiaru dębów, stąd związek między wysokością umieszczenia dziupli a średnicą drzew był słabszy.

W porównaniu z dzięciołem średnim, dzięcioł duży istotnie częściej wykuwał dziuple w żywych drzewach, w pniach i żywych fragmentach drzew (Tab. 4). Mimo tych różnic większość dziupli obu gatunków znajdowała się w miejscach martwych lub obumierających, na przykład w bliznach i w sąsiedztwie owocników grzybów (hub). Charakter użytkowania lasu nie wpływał na częstość wykuwania dziupli w drzewach charakteryzujących się odmienną kondycją bądź stanem fragmentu będącego miejscem gniazdowania. Charakterystyczne, iż w porównaniu z lasami seminaturalnymi w lasach użytkowanych gospodarczo oba gatunki dzięciołów gnieździły się istotnie częściej w pniach.

Prezentowane wyniki wskazują na większe zróżnicowanie nisz gniazdowych obu gatunków dzięciołów, szczególnie dzięcioła średniego, w lasach seminaturalnych w porównaniu z lasami użytkowanymi gospodarczo. Konwergencja nisz gniazdowych w lasach gospodarczych obejmuje przede wszystkim wykorzystywanie dębów jako miejsc gniazdowania, wykuwanie dziupli w pniach i na tej samej wysokości. Czynnikami kształtującymi podział nisz gniazdowych między badanymi gatunkami dzięciołów wydają się być zróżnicowane ze względów morfologiczno-anatomicznych możliwości drążenia dziupli. Zasugerowano, że upodobnienie nisz gniazdowych obu badanych gatunków może obniżać liczebność dzięcioła średniego w lasach gospodarczych. Powyższy spadek liczebności jest prawdopodobnie pochodną ograniczenia dostępności preferowanych drzew gniazdowych a nie interakcji międzygatunkowych.

T. Cofta