Ornis Fennica 81:145–156. 2004

Nest-site selection and niche partitioning among the Great Spotted Woodpecker *Dendrocopos major* and Middle Spotted Woodpecker *Dendrocopos medius* in riverine forest of Central Europe

Ziemowit Kosiński & Aleksander Winiecki

Institute of Environmental Biology, Department of Avian Biology and Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Poland, e-mail: zkosinsk@main.amu.edu.pl

Received 4 May 2004, accepted 15 October 2004

We studied nest-site selection of the Great- and Middle Spotted Woodpecker inhabiting the riverine forest remnants of Central Poland. In addition to nest tree characteristics and location in relation to edge proximity, a comparison between nesting and random sites within the woodpeckers' territories allowed a study of the importance of stand structure on nest tree selection. Unlike the Great Spotted Woodpecker, we found that the Middle Spotted Woodpecker showed an affinity to nest near forest edges. Both species excavated nest holes within trees with a diameter at breast height larger than the diameter of available trees suitable for hole-excavation. Trees with the presence of former woodpecker holes, polyporous fungi and limb holes were highly selected, with nest chambers commonly built in dead parts of the trees (74% and 90% of nests of Great- and Middle Spotted Woodpeckers, respectively). Both the Great- and Middle Spotted Woodpeckers nested more often in trunks than in limbs, with the former species favouring live oaks and alders and the latter snags. Vegetation immediately surrounding nest trees had probably a low influence on species nest-site selection. The nest tree was, in the majority of cases, the only tree suitable for hole-excavation in the nest site. Our results suggest that gap-phase dynamics and the presence of old and dead deciduous standing trees are key components of habitat quality for breeding woodpeckers, particularly for the declining Middle Spotted Woodpecker.

1. Introduction

The habitat selection of birds is a hierarchical decision process which results from the sequence of selection responses that starts from landscape scales and proceeds to fine-scale local habitat characteristics (Hildén 1965, Cody 1985). Thus, habitat selection should be investigated in different spatial scales. An important implication of this selection paradigm is a more realistic and complete description of the specific habitat requirements of birds (e.g. Gutzwiller & Anderson 1987, Rolstad *et al.* 2000).

Nest-site selection implies the rule that some sites are preferred for nesting while others are avoided. Studies of the requirements of European woodpeckers have presented data on nest sites used: e.g. tree species, diameter of breast height, tree age, health of the tree and exact nest site (e.g. Wesołowski & Tomiałojć 1986, Hågvar *et al.* 1990, Glue & Boswell 1994, Stenberg 1996). Owing to some differences relating to geographic variation, sampling intensity and spatial scale of earlier studies, it is difficult to compare them (Hanson 1992, Schmitz 1993, Stenberg 1996, Smith 1997, Mazgajski 1998). In the case of territorial birds, such as the Great- and Middle Spotted Woodpeckers, nest-site selection takes place after the territory has been established. According to this hierarchical process nest-site selection should have been examined by analysing the habitat composition within the birds' territories. However, none of the earlier studies of both woodpeckers took this spatial and temporal pattern into consideration.

Previous investigations have rarely examined the characteristics of woodpeckers' nest sites on more than one spatial scale, although the floristic and physical characteristics of nest trees used by woodpeckers have been studied frequently. The few studies that focused on whether the surrounding vegetation influences nest tree selection suggest, however, non-conclusive results, although limited to north American birds and vegetation conditions (e.g. Gutzwiller & Anderson 1987, Li & Martin 1991, Adkins Giese & Cuthbert 2003). Moreover, selection pressures arising from the presence of different kinds of competitors and predators may affect nest site preferences, e.g. in relation to the forest edge (Short 1979, Stenberg 1996).

In Poland, Great- and Middle Spotted Woodpeckers coexist in riverine forests. Here they can reach relatively high densities when compared to other forest types, e.g. up to 2.6 pairs/10 ha compared to 1–2 pairs/10 ha in oak-hornbeam stands in the case of the Great Spotted Woodpecker, and in the case of the Middle Spotted Woodpecker up to 2.2 pairs/10 ha compared to 0.9 pairs/10 ha in continuous old oak forests (Tomiałojć & Stawarczyk 2003, Kosiński & Winiecki, in prep.). For the endangered Middle Spotted Woodpecker, riverine forests are assumed to be its original habitat (Spitznagel 1990). Being primary cavity excavators woodpeckers are seen as "key species", producing nest- and roosting sites for other birds' species and animals (e.g. Wesołowski 1989, Weggler & Aschwanden 1999). Furthermore, the Middle Spotted Woodpecker is considered to be a suite of "focal species", whose habitat requirements encompass those of all other species in the landscape (Lambeck 1997, Angelstam *et al.* 2004 in press). This multi-species approach builds on the concept of umbrella species, who need such large tracts of habitat that saving it would provide protection for a large number of other species (Martikainen *et al.* 1998, Simberloff 1998). A better insight of the habitat requirements of woodpeckers may shed light on the niche partitioning of these closely related species and are essential for effective species management. As a consequence, this could help in the protection of woodpeckers and overall forest biodiversity (Mikusiński *et al.* 2001, Nilsson *et al.* 2001).

The main goals of this study were: (1) to characterise nest trees used by the Great- and Middle Spotted Woodpeckers, (2) to compare forest structure around nest trees and random locations all over the breeding habitat, (3) to assess niche breadth and preferences of the species in relation to available tree species and their health condition, and (4) to relate nest trees distribution to edge proximity.

2. Material and methods

2.1. 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 semi-natural flood-plain forest. In Poland, riverine forests were cleared for agriculture or were lose after the rectification of rivers and building of embankments, mainly during last 200–300 years. In modern times the total area of this type of forest is estimated at 27 km^2, however, in the Wielkopolsko-Kujawska Lowland at 1.7 km^2 only (Matuszkiewicz 2001). The study was carried out on a 224 ha plot. Some 83% (185 ha) of the study plot is forested, with Quercus-Fraxinus-Ulmus (*Fraxino-Ulmetum*) woodland in the flooded parts and Quercus-Carpinus (*Stallario-carpinetum*) forest on the higher ground. The remaining study area

(17%) is formed by old river-beds and meadows. About 40% of forests of the study plot (74 ha) consists of stands older than 120 years (ca 155–165 years old), 24% (43 ha) between 81–120 years old and 28% (51 ha) between 41–80 years old. Since 1959, 40% (73.2 ha) of the forest area has been protected within two reserves: "Czeszewo" and "Lutynia". In 2004, the whole study plot (222,6 ha) was established as a nature reserve "Czeszewski Las".

Data was collected between 2000–2002. From mid March to the end of April the number and distribution of territorial Middle Spotted Woodpeckers were established by responses to the play-back of taped calls (for detailed description of method see Kosiński & Winiecki 2003, Kosiński *et al.* 2004). In 2001, it was not possible to estimate precisely the number of this species in the pre-breeding season because only two incomplete censuses were conducted. Three to five censuses were carried out during the pre-breeding season. This resulted in the mapping of all the territories. A search for nest holes of both species began from the end of May in 2000 and 2001 and from late April in 2002 by systematically walking each territory. Searches begun at the beginning of the breeding season in 2002 did not increase the number of nests found of the Middle Spotted Woodpecker (Kosiński & Winiecki 2003). According to the number of territories, between 46 and 53% of the Middle Spotted Woodpecker nest holes were found in 2000 and 2002. However, the number of pairs which started to breed was probably greater, up to 75% in 2002 (Kosiński & Winiecki 2003). Based on the high survival rates of the Great Spotted Woodpecker nests and the high efficiency of the nest searching methods based on begging-calls of the young, we assumed that probably all the nesting attempts were recorded in each year (Glue & Boswell 1994, Mazgajski 2002). The densities are reported as pairs per 10 ha of forest area.

The following parameters were recorded for the description of the nest site: tree species, diameter at breast height, health of the tree and exact nest site. Because a few nest sites of both species had disappeared and in some cases it was not possible to generate the random sites for nest sites, in the final analyses 41 nest trees of the Middle Spotted Woodpecker and 54 nest trees of the Great Spotted Woodpecker could be used.

In 2002 we used GPS as a method of identifying the position of trees with nest-holes. To generate the randomly selected points within the woodpeckers' territories (one per territory) this data was transferred to personal computer and transformed to the geodetic reference system. The randomisation procedure was made as a function of: (1) the distance between nest tree and random point and (2) the distance among random locations. The maximum distance between nesting trees and selected points for each woodpecker species was defined as a radius of a circle with an area equal to the male core area in the pre-breeding season. For the Middle Spotted Woodpecker this area was 7.3 ha (Pasinelli *et al.* 2001) and for the Great Spotted Woodpecker it was 3.0 ha (Osiejuk 1993, Bachmann & Pasinelli 2002). The minimum distance between nesting trees and randomly selected points for both species was defined as twice the position of error (ca 10 m). The distance between random locations was defined as no less than the maximum distance between nesting trees and corresponding random locations. Moreover, all points had to be placed within the studied area. The random locations were identified in the field using the GPS navigator.

The study was designed to determine if woodpeckers choose among habitats and trees when selecting nest sites. Following the procedures of Smith (1997), in circular plots with a radius of 10 m (0.033 ha) around each nesting tree and random location, three habitat variables were measured: number of tree stems with diameter at breast height (DBH) equal and over 10 cm (NS), number of tree species (NT), and total basal area of trees with diameter at breast height $\geq$ 10 cm (TBA). We measured all trees with DBH $\geq$ 10 cm to obtain a broader range of forest characteristics and to omit the large number of the youngest trees and shrubs. Each tree within the randomly selected points was checked by binoculars to find: old woodpecker holes, polyporous fungi and limb-holes. Their presence may indicate advanced decay inside the tree. Trees with a minimum of one of these characteristics were treated as potentially suited for nest-hole excavation (e.g. Pasinelli 2000). The tree was defined dead if during the vegetation period any signs of vital, e.g. living leaves, were observed. To separate the influence of the nest tree from the influence of the surrounding vegetation, we compared nest sites to random sites containing a tree suitable for nesting – with presence of characteristics, which indicated heartwood decay and appropriate DBH (Adkins Giese & Cuthbert 2003). Based on our data we assumed that the smallest diameter tree used for nesting in the study area was 19 cm for the Great Spotted Woodpecker and 14 cm for the Middle Spotted Woodpecker. Nesting habitats were classified as closed forest (> 25 m from an edge) and forest edge (≤ 25 from an edge) (Hansson 1992, Stenberg 1996). The forest edge was defined as the boundary between two structurally distinct habitats, e.g. forest and meadow, as well as that between forest and distinct forest gap.

We surveyed habitat variables around nesting trees and random locations in a total area of 3.6 ha for the Great Spotted Woodpecker (n = 54) and 2.7 ha (n = 41) for the Middle Spotted Woodpecker.

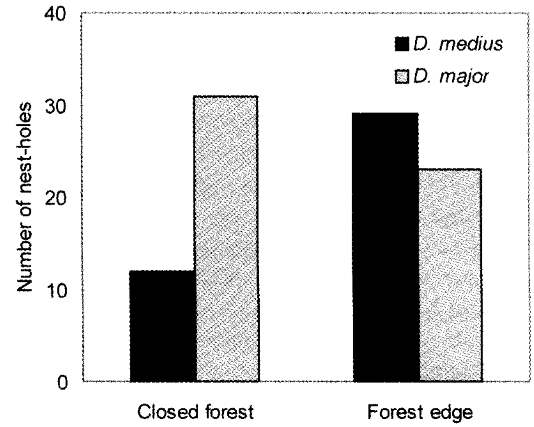

Fig. 1. Nest-site distribution of the Great and Middle Spotted Woodpecker in relation to distance from the forest edge. Closed forest > 25 m from an edge and forest edge ≤ 25 m.

2.2. Data analysis

The study was carried out over three years. Hence, it could be expected that some individuals and nest choices might be replicated, especially in the case of resident Middle Spotted Woodpeckers. However, based on observation of colour-ringed Middle Spotted Woodpeckers and shift in the nest sites in the same territories, we assumed that nest choices of both woodpecker species were independent of their previous ones.

The niche breadth of the both species was calculated by the Freeman-Tukey (*FT*) index (Waite 2000). This measure takes into account the availability of resource classes (*R*). We used all tree species with appropriate DBH and dead trees as a separate category to define the number of resource classes. The *FT* index of niche breadth varies from 0 to 1.0. The maximum value of 1.0 implies that the species distribution does not differ from a random pattern of resource class occupation. The *FT* measure is much less sensitive to rare resources. The chi-squared goodness-of-fit statistic, with $R - 1$ degrees of freedom, was used to test the hypothesis that $FT = 1$ (Waite 2000). We calculated individual selection indices as the proportion of nest trees to the proportion of available trees. Based on Bonferroni inequality for individual selection indices 95% confidence limits (CL) were constructed (Manly *et al.* 1993). A value > 1 implies positive selection and a value < 1 negative selection of tree species. Negative lower limits were changed to 0.00 since negative values of confidence limits are not possible.

Because none of the habitat measures were normally distributed, we used nonparametric tests for comparing the difference between nesting sites and random sites. All statistics were performed with the statistical package STATISTICA (StatSoft, Inc. 2003).

3. Results

3.1. Numbers

The number of the Great Spotted Woodpecker was estimated at 48 pairs in 2000 (2.6 pairs/10 ha), 32 pairs in 2001 (1.7 pairs/10 ha) and 24 pairs in 2002 (1.3 pairs/10 ha). The number of Middle Spotted Woodpecker territories varied from 38 in 2000 (2.1 territories/10 ha) to 33 in 2002 (1.8 territories/10 ha).

3.2. Habitat selection

The two woodpecker species differed according to nest location in relation to the forest edge ($\chi^2 = 6.36$, df = 1, P = 0.012, statistic with Yates' correction is given). Most of the Middle Spotted Wood-

Table 1. Comparison of nesting habitats and random locations in woodpecker territories containing all trees with DBH ≥ 10 cm (A) and trees suitable for hole excavation (B). NS = number of stems, TS = tree species, TBA = total basal area (m^2). Mean (median), standard deviation (SD), Z-values and probability of Wilcoxon test are given.

Variable		Nesting habitat Mean (Me) ± SD	Random location Mean (Me) ± SD	Z	P
Great Spotted Woodpecker (n = 54)					
NS	A	15.3 (14.5) ± 7.0	15.2 (15.0) ± 6.8	0.24	0.808
	B	0.13 (0.0) ± 0.44	0.48 (0.0) ± 0.82	2.41	0.016
TS	A	3.6 (3.0) ± 1.3	3.6 (3.0) ± 1.2	0.11	0.909
	B	0.13 (0.0) ± 0.44	0.35 (0.0) ± 0.55	2.03	0.042
TBA	A	2.5 (2.4) ± 0.8	2.1 (2.0) ± 0.7	2.35	0.019
	B	0.03 (0.00) ± 0.12	0.23 (0.00) ± 0.41	3.28	0.001
Middle Spotted Woodpecker (n = 41)					
NS	A	14.4 (12.0) ± 6.1	12.3 (6.0) ± 5.6	1.78	0.076
	B	0.17 (0.00) ± 0.44	0.63 (1.00) ± 0.66	2.98	0.003
TS	A	3.8 (4.0) ± 1.2	3.2 (3.0) ± 1.2	2.45	0.014
	B	0.15 (0.0) ± 0.36	0.59 (1.0) ± 0.59	3.08	0.002
TBA	A	2.7 (2.4) ± 1.1	2.0 (1.9) ± 0.9	2.96	0.003
	B	0.1 (0.0) ± 0.36	0.19 (0.05) ± 0.30	2.19	0.028

pecker's nests (71%, n = 41) were located close to or on the forest edge (≤ 25 m from an edge). Nest-holes of the Great Spotted Woodpecker were excavated more frequently (57%, n = 54) within closed forest (> 25 m from an edge) (Fig. 1). In the case of the Middle Spotted Woodpecker the habitat structure did not differ between edge and closed forest (Mann-Whitney U test, P > 0.05), however, a decrease in the number of stems in the proximity of forest edge compared to closed forest (Median = 12 and 17 respectively) was connected with an increase of the total basal area (Median = 2.5 m^2 and 2.3 m^2 respectively). The number of stems in nest sites of the Great Spotted Woodpecker was significantly higher in closed forest than in edge proximity (Mann-Whitney U test, Z = –2.78, P = 0.005, Median = 18 and 11 respectively). Comparing the habitat structure around the Great Spotted Woodpecker nesting trees versus random locations, we found that the total basal area of tree boles was significantly higher in nest sites (Table 1). In the case of the Middle Spotted Woodpecker both the number of tree species and the total basal area of tree boles in nesting locations were significantly higher than in the random points. When we compared the habitat structure around nesting trees between both species we found that there were no statistically significant differences between any of the habitat measurements (Mann-Whitney U test, P > 0.05).

It was detected that the number of stems, number of tree species as well as the basal area of trees suitable for nesting were significantly higher in random sites compared to nesting sites (Table 1).

Table 2. Trees used by Great and Middle Spotted Woodpeckers. Pooled data from all years are given.

Species	Great Spotted Woodpecker		Middle Spotted Woodpecker	
	Trees			
	Alive	Dead	Alive	Dead
Oak *Quercus robur*	37	1	20	2
Ash *Fraxinus excelsior*	11	0	8	2
Alder *Alnus glutinosa*	2	0	0	2
Linden *Tilia cordata*	1	0	0	0
Poplar *Populus sp.*	1	0	2	0
Hornbeam *Carpinus betulus*	1	0	0	0
Field maple *Acer campestre*	0	0	2	0
Birch *Betula verrucosa*	0	0	0	2
Willow *Salix sp.*	0	0	1	0
Total	53	1	33	8

Table 3. Freeman-Tukey (*FT*) index of niche breadth of the Great Spotted Woodpecker (GSW) and Middle Spotted Woodpecker (MSW). 95% confidence limits (CL) and chi-squared goodness-of-fit statistic are given.

Species	*FT*	95% CL	χ^2	df	P
GSW	0.766	0.673–0.844	101.2	10	< 0.001
MSW	0.741	0.630–0.835	85.0	10	< 0.001

3.3. Selection of trees

Oaks and ashes were the most common nest trees used for nest-hole excavation (Table 2). The Middle Spotted Woodpecker excavated 68% (n = 41) of its holes in oaks and ashes but the Great Spotted Woodpecker – 91% (n = 54). The niche breadth of the Great Spotted Woodpecker was similar to that of the Middle Spotted Woodpecker (Table 3). In both cases the distribution of tree species used differed from a random pattern of resource class occupation. In the case of the Great Spotted Woodpecker a positive selection for oaks and alders was found but in the case of the Middle Spotted Woodpecker a highly positive selection for dead trees was recorded (Table 4). Trees with the presence of old woodpecker holes, polyporous fungi and limb holes were highly selected by both woodpecker species (Table 5). Both species excavated nest holes within trees with a diameter at breast height higher than the diameter of potentially available trees (Table 6). The median diameter of nest trees

Table 4. Selection indices for nesting tree species. Pooled data from all years are given.

Tree species	Alive/ dead	Nests	Proportion of nests	Available trees	Proportion of trees	Selection index	95% CL
Great Spotted Woodpecker							
Oak	A	37	0.685	109	0.224	3.06	2.76–3.36
Ash	A	11	0.204	136	0.279	0.73	0.00–1.81
Alder$_1$	A	2	0.037	5	0.010	3.61	2.27–4.94
Linden$_2$	A	1	0.190	50	0.103	0.18	0.00–8.23
Poplar$_3$	A	1	0.190	0	0.000		
Hornbeam$_4$	A	1	0.190	101	0.207	0.09	0.00–10.84
Other$_5$	A	0	0.000	83*a*	0.170	0.00	
Other	D	1	0.190	3*b*	0.006	3.01	0.93–5.08
Total		54		486			
Other$_{(1–5)}$		5	0.093	239	0.491	0.19	0.00–2.65
Middle Spotted Woodpecker							
Oak	A	20	0.488	141	0.330	1.48	1.01–1.94
Ash	A	8	0.195	70	0.164	1.19	0.28–2.10
Field maple$_1$	A	2	0.049	21	0.049	0.99	0.00–3.13
Poplar$_2$	A	2	0.049	15	0.035	1.39	0.00–3.21
Willow$_3$	A	1	0.024	0	0.000		
Other$_4$	A	0	0.000	170*c*	0.398	0.00	
Other	D	8	0.195	10*d*	0.023	8.33	7.96–8.71
Total		41		427			
Other$_{(1–4)}$	A	5	0.122	206	0.482	0.25	0.00–3.51

a – Elm (16), field maple (34), maple (2), scots pine (31).
b – Ash (2), alder (1).
c – Hornbeam (105), linden (30), elm (30), birch (1), maple (4).
d – Oak (2), hornbeam (1), ash (3), elm (2), poplar (2).

Table 5. Selection indices for trees with characteristics suited (Yes/Not) for cavity excavation (see Material and methods). Only live trees are considered. Pooled data from all years are given.

Tree species	Yes/Not	Nests	Proportion of nests	Available trees	Proportion of trees	Selection index	95% CL
Great Spotted Woodpecker							
Oak	N	5	0.094	91	0.188	0.50	0.00–2.00
	Y	32	0.604	18	0.037	16.23	16.12–16.35
Ash	N	1	0.019	130	0.269	0.07	0.00–8.58
	Y	10	0.189	6	0.012	15.22	15.01–15.43
Other	N	1	0.019	234*a*	0.483	0.04	0.00–9.64
	Y	4	0.075	5*b*	0.010	7.31	6.82–7.79
Total		53		484			
Middle Spotted Woodpecker							
Oak	N	0	0.000	129	0.309	0.00	–
	Y	20	0.606	12	0.029	21.06	20.96–21.16
Ash	N	2	0.061	63	0.151	0.40	0.00–2.54
	Y	6	0.182	7	0.017	10.83	10.58–11.09
Other	N	2	0.061	201*c*	0.482	0.13	0.00–3.11
	Y	3	0.091	5*d*	0.012	7.58	7.15–8.02
Total		33		417			

a – Hornbeam (101), linden (50), elm (16), field maple (30), maple (2), alder (4), scots pine (31).
b – Field maple (4), alder (1).
c – Hornbeam (101), linden (29), elm (30), field maple (21), maple (4), birch (1), poplar (15).
d – Hornbeam (4), linden (1).

at breast height did not differ between species (Mann-Whitney U test, Z = –0.26, P = 0.822). However, when the stem diameter of single tree species between both woodpecker species was compared, a significant difference in DBH for ash was found (Mann-Whitney U test, Z = –2.23, P = 0.026). Great- and Middle Spotted Woodpeckers nested more often in trunks than in limbs. The proportion of holes excavated in trunks was 63% (n = 41) in the Middle Spotted Woodpecker and 80% (n = 54) in the Great Spotted Woodpecker. Nest chambers were commonly sited in dead parts of trees (90% and 74% respectively). There were no differences in frequency of nest location and condition of substrates between woodpeckers (χ^2 = 7.83, df = 4, P = 0.098).

Table 6. The selection of nest tree diameter (DBH in cm) for the Great and Middle Spotted Woodpecker. Mean (median), standard deviation (SD), numbers of trees inspected (n), Z-values and probability of Mann-Whitney U test are given. In the case of the Great Spotted Woodpecker only live trees are considered.

Tree species	Available trees Mean (Me) ± SD	n	Nest trees Mean (Me) ± SD	n	Z	P
Great Spotted Woodpecker						
Oak	50.4 (46.5) ± 17.4	109	58.9 (55.1) ± 17.5	37	2.77	0.005
Ash	36.8 (32.5) ± 16.9	136	48.3 (43.6) ± 22.0	11	1.79	0.072
Other	30.5 (28.3) ± 9.8	239	49.2 (44.6) ± 12.2	5	3.21	<0.001
Middle Spotted Woodpecker						
Oak	45.6 (43.9) ± 19.1	141	71.3 (52.1) ± 47.0	20	2.64	0.008
Ash	31.8 (27.5) ± 15.6	70	78.5 (77.4) ± 29.3	8	3.96	<0.0001
Other	24.6 (21.0) ± 10.7	206	39.1 (34.7) ± 20.8	5	1.58	0.113
Dead trees	29.1 (27.2) ± 10.0	10	51.5 (44.1) ± 22.0	8	2.62	0.009

4. Discussion

4.1. Habitat selection

The nest-site selection strategies of woodpeckers may reflect predation and the risk of klepto-parasitism, food availability and microclimate (Short 1979, Li & Martin 1991, Wiebe 2001). It has been suggested that nesting in closed forest gives better shelter from aerial predators, as well as some arboreal predators (Short 1979, Stenberg 1996). The hole diameter of the Great Spotted Woodpecker, as well as that of the Middle Spotted Woodpecker, is narrow enough to prevent predation by Pine Marten *Martes martes*, which are responsible for some nest failures of forest cavity nesting birds (e.g. Sonerud 1985, Walankiewicz 2002).

None of the four direct observations of Pine Marten, which tried to plunder the nests in the study area, were successful. The preference of the Middle Spotted Woodpecker for nesting on the forest edge is probably related to their foraging behaviour. It was found that this species prefer deciduous forest with rather open canopies and free-standing, medium-size oak crowns as foraging sites (Pasinelli & Hegelbach 1997). In riverine forests these types of crowns are restricted to the forest edge, mainly old river-beds, and to forest gaps. Less dense forest structures might be preferred as foraging sites due to the greater exposure to sunlight and, in consequence, greater abundance of arthropods, as well as greater accessibility for foraging birds (Nicolai 1986, Pasinelli & Hegelbach 1997, Jokimäki *et al.* 1998, Pasinelli 2000). Nest location close to the preferred foraging habitat may reduce the energy cost of rearing young. In spite of the lack of any significant differnces between nest sites of the Middle Spotted Woodpecker situated in closed forest and forest edge, the adverse trend between number of stems and total basal area between both sites should be emphasized.

This suggests that in the proximity of forest edge birds might select habitats with older trees compared to the forest interior. The Great Spotted Woodpecker is a generalist species according to habitat selection, food composition, prey size utilization and foraging behaviour (e.g. Jenni 1983, Török 1990, Osiejuk 1996). In general, it is likely that the distribution of the Great Spotted Woodpecker is mainly affected by the presence of suitable nest sites than by food.

The differences between species' nest sites and random locations in terms of structural characteristics suggests that nest-site selection was non-random with respect to the total basal area (for both species) and the number of tree species (for the Middle Spotted Woodpecker). However, it was found that vegetation immediately surrounding nest trees may have a minimal influence on the woodpecker nest-site (Gutzwiller & Anderson 1987, Adkins-Giese & Cuthbert 2003). We found that the number of stems and total basal area were higher in random sites than in nest sites. The low values of both structural characteristics in nest sites suggests that, in most cases, nest trees were the only trees suitable for hole-excavation in each of the nest sites. It is questionable why the Middle Spotted Woodpeckers prefer sites characterised by a higher diversity of vegetation. The benefits of nesting in a more diverse and dense habitat could be explained in terms of reduced predator efficiency (Li & Martin 1991). However, loud nestling voices are probably easy to detect for predators. On the other hand, it could be explained by the fact that a more diverse habitat supported a higher biomass of arthropods and trees surrounding the nest tree may be used as foraging sites (Adkins Giese & Cuthbert 2003). However, we did not observe woodpeckers foraging near nest sites. Furthermore, it was revealed that the availability of large oaks preferred as foraging habitat is a crucial factor, which determines the presence of this species all through the year, as well as the home range size (Pasinelli & Hegelbach 1997, Pasinelli 2000). It also could be argued that nesting in such habitats is simply a result of forming different succesional stages beneath the canopy of the largest trees, which are used as nest sites by woodpeckers. The lack of interspecific differences between the habitat structures around nesting trees is to be expected from their similar habitat associations, the high overlap of the home ranges and core areas of both species and the low level of interspecific competition between these two woodpecker species (Bachmann & Pasinelli 2002, but see Günther 1993). For example, in 2003, nests of both species were recorded in neighbouring willow trees at a distance of five metres.

4.2. Nest-site selection

Earlier findings suggest that the nest-site selection of the Great- and Middle Spotted Woodpeckers depends on accessibility of trees and places suited for nest-hole excavation. The niche breadth values suggested that both species use similar states of resources in our study area. However, detailed analysis showed that both woodpeckers differed according to preference of nesting trees and their health. The Great Spotted Woodpecker preferred oaks and alders but the Middle Spotted Woodpecker selected dead trees. Comparable data from primeval forest of the Białowieża National Park showed different preferences according to nest-tree selection. Overall, in ash-alder stands both woodpeckers selected alder, however, in oak-hornbeam stands the Middle Spotted Woodpecker preferred hornbeam and oak while the Great Spotted Woodpecker – aspen *Populus tremula* (Wesołowski & Tomiałojć 1986). Moreover, despite the differences in sample surveys and spatial scale, studies concerning the proportion of nests according to the availability of substrates showed that aspen was the most favoured tree species in Norway and Sweden (Hågvar *et al.* 1990, Hansson 1992, Stenberg 1996). In Central Poland the alder was preferred in oak-hornbeam forest with an admixture of ash-alder stands but oaks and aspen in clear oak-hornbeam forest (Mazgajski 1998). In Southern England, the Great Spotted Woodpecker selected dead trees, mainly birch *Betula* spp. (Smith 1997). It should be emphasized that aspen and birch are very scarce substrates in our study area. It is worth noting that despite the low availability of alder (1% of all trees), there was highly positive selection for this species. In the case of the Middle Spotted Woodpecker the comparable data are very scarce, however, the studies of Mazgajski (1997) indicate preference for oaks in comparison with tree species availability. These data suggest that habitat-selection responses of the species may vary geographically, e.g. as an effect of tree-species composition.

The Middle Spotted Woodpecker was predicted to have a weaker excavating morphology and to choose softer or decayed wood than would the Great Spotted Woodpecker (Jenni 1981). Our study confirms this pattern. Similarly, in primeval forest Middle Spotted Woodpeckers excavated nest holes more frequently in dead or decaying wood than Great Spotted Woodpeckers (Wesołowski & Tomiałojć 1986). The Middle Spotted Woodpeckers' preference for habitats with a lot of dead wood has been noted by several other authors (Günther 1992, Günther & Hellmann 1997, Walankiewicz *et al.* 2002). However, the detailed analysis of foraging trees suggests that dead trees are used randomly for foraging according to their availability (Pasinelli & Hegelbach 1997, see also Pasinelli 2000). Our findings and literature data suggest that the importance of dead wood for this woodpecker in breeding season is mainly connected with its choice of the location of breeding holes (Günther 1992, Wesołowski 1989) and to a lesser extent as foraging trees.

When the abundance of snags is limited, it could be expected that woodpeckers would prefer live trees with signs of suitability for nest excavation, such as old woodpecker holes, polyporous fungi and limb holes (e.g. Wesołowski & Tomiałojć 1986, Smith 1997, Pasinelli 2000, but see Mazgajski 1998). The results of our study confirm this assumption. However, Schepps *et al.* (1999) have found that the external characteristics of suitability to nest excavation do not effectively reflect the subtle changes in tree hardness that appear to be recognised by birds during nest-site selection. In fact, we have found that both species excavated nest holes in trees without these characteristics. This does not mean that these trees were fully vital. Organoleptic analyses of wood shavings thrown out during nest-hole excavation suggest that all birds excavate holes in soft or decaying wood (Kosiński *et al.* unpubl. data). Therefore, it is possible that in earlier studies signs of weakness were frequently unrecognised by observers, especially when wood shavings were not examined (see also Wesołowski & Tomiałojć 1986).

It was found that both woodpecker species selected nest sites in larger diameter trees. It is possible that the number of sites potentially suitable for nest-hole excavation in such trees is larger than in younger trees with smaller diameter. Nesting in larger diameter trees may positively affect the microclimate of nest-holes and their sizes and, in consequence, clutch-size and other reproductive parameters. Nests in small and dead trees are the coldest during incubation and seem to be energetically more expensive for adults and nestlings than warmer nests (Wiebe 2001), moreover, in small nests crowding may reduce nestling survival (Wiebe & Swift 2001).

Earlier studies have reported that among other things the stem diameter at breast height increased with the increasing size of the bird (e.g. Hågvar *et al.* 1990, Stenberg 1996). Our data does not confirm this pattern (see also Wesołowski 1989, Mazgajski 1997). However, Günther (1993) reported an adverse trend at the diameter of the trunk at the hole. Furthermore, like other studies (Wesołowski & Tomiałojć 1986, Günther 1993, but see Mazgajski 1997), we have found that the Middle Spotted Woodpecker excavates his holes at an average of 2–3 metres higher than the Great Spotted Woodpecker, as well as more frequently in limbs and dead parts of trees compared to the Great Spotted Woodpecker (Kosiński *et al.* in prep.). These patterns are in agreement with findings that tree hardness decreases with height and trees are softest at the height of the nest (Schepps *et al.* 1999).

4.3. Management implications and conclusion

We found that nesting sites and random sites of both woodpecker species differed from each other. However, the adaptative role for nesting in more diverse habitats by the Middle Spotted Woodpecker is unclear. Our data confirms an earlier assumption suggesting that woodpeckers may select suitable trees independent of the surrounding vegetation (Adkins Giese & Cuthbert 2003). We provide the first evidence that the Middle Spotted Woodpecker favourably selects snags for nest sites. Moreover, we have documented that soft or decaying substrates are important in terms of their excavation potential for both woodpeckers and in nest-site selection. This implies, among others, that forest management should focus on the maintenance of standing dead or decaying trees with appropriate diameter and economically less important trees with polyporous fungi and old cavities (e.g. Smith 1997, Pasinelli 2000, Walankiewicz *et al.* 2002). Such trees may be used for nesting in the future and would also be valuable for other hole-nesting species (e.g. Newton 1994, Weggler & Aschwanden 1999). It was suggested that to support the Middle Spotted Woodpecker long-term, a continuous supply of trees of all age categories is needed, moreover, a high density of old oaks and ashes (in riverine forests), most suitable for feeding throughout the year, is of crucial importance (Pasinelli & Hegelbach 1997, Pasinelli 2000). The strong affinity of the Middle Spotted Woodpecker to forest edges confirms the suggestions that the preferred habitat of this species is characterised by small-gap dynamics (Angelstam *et al.* 2004 in press). Therefore, the promotion of natural processes in modern forestry could provide for the creation of habitats suitable for the Middle Spotted Woodpecker.

To maintain valuable populations of woodpeckers, we should have a knowledge of the critical level of resources such as potential nest trees. The number of trees suited for nest-hole excavation is one of the main factors, which determine the carrying capacity of the habitat (Smith 1997, Walankiewicz *et al.* 2002). For example, the densities of large oaks and of potential nest trees simultaneously interact with the home range size of the Middle Spotted Woodpecker (Pasinelli 2000). The number of snags in the remnant of the European primeval forests of the Białowieża National Park is 27/ha (Walankiewicz *et al.* 2002). Pasinelli (2000) has shown that an average home range of the Middle Spotted Woodpecker contained 26 potential cavity trees per ha. Based on our sample surveys we determined the density of potential nest trees in our study area at 13 trees/ha in the case of the Middle Spotted Woodpecker and 11 trees/ha in the case of the Great Spotted Woodpecker. However, when the number of nest trees was included, the density increases to 26 trees/ha and 24 trees/ha, respectively. Hence, a detailed inventory of trees suitable for hole-excavation in areas of different woodpecker densities would be valuable for assessing the critical level of this resource (Pasinelli 2000).

Acknowledgments. We are grateful to Jarocin Forest District for kindly providing help with accommodation. We are indebted to L. Kuczyński for methodological discussion and creating the randomisation procedure. P. Fayt, J. Jokimäki and P. Tryjanowski provided constructive comments and suggestions that improved the paper. We thank R. Kippen for improving the English. This study was supported by grant 3 P04F 001 22 from the Polish Science Research Committee.

Käpytikan ja tammitikan pesäpaikan-valinnasta Keski-Euroopan jokivarsimetsissä

Artikkelin kirjoittajat tutkivat käpytikan ja tammitikan pesäpaikanvalintaa Puolan keskiosien jokivarsimetsissä vuosina 2000–2002. Tutkimuksessa tarkasteltiin pesäpuun laatua ja pesäpuun etäisyyttä metsäreunasta. Myös metsikkörakenteen vaikutusta pesäpuun valintaan tutkittiin. Toisin kuin käpytikka, tammitikalla oli taipumus pesiä lähellä metsänreunaa. Molemmat tutkimuslajit koversivat pesäkolon keskimääräistä paksumpiin puihin. Tikat suosivat pesäpuinaan erityisesti puita, joissa oli entuudestaan tikankoloja, kääpiä tai oksanhaarassa olevia koloja. Pesäkolo koverrettiin yleensä puun kuolleeseen osaan. Molemmat lajit pesivät useammin puun runko-osissa kuin oksastossa. Käpytikka suosi pesäpuinaan eläviä tammia ja leppiä, kun taas tammitikka suosi pökkelöitä. Pesäpuun ympäristön kasvillisuuden havaittiin vaikuttavan varsin vähän lajien pesäpuun valintaan. Useimmiten pesäpuu oli ainoa tarjolla oleva sopiva puu pesäntekoon. Tutkimustulosten mukaan pienaukkodynamiikka ja vanhat ja kuolleet lehtipuut vaikuttavat merkittävästi tikkojen, erityisesti tammitikan habitaatin laatuun.

References

Adkins Giese, C.L. & Cuthbert, F.J. 2003: Influence of surrounding vegetation on woodpecker nest tree selection in oak forests of the Upper Midwest, USA. — For. Ecol. Manage. 179: 523–534.

Angelstam, P., Roberge, J.-M., Lõhmus, A., Bergmanis, M., Brazaitis, G., Breuss, M., Edenius, L., Kosinski, Z., Kurlavičius, P., Lārmanis, V., Lūkins, M., Mikusinski, G., Račinskis, E., Strazds, M. & Tryjanowski, P. 2004: Habitat modelling as a tool for landscape-scale conservation – a review of parameters for focal forest birds. In: Angelstam, P., Breuss, M. & Roberge, J.-M. (eds.), Targets and tools for the maintenance of forest biodiversity. — Ecol. Bull. 51 (still in press).

Bachmann, S. & Pasinelli, G. 2002: Raumnutzung syntop vorkommender Buntspechte Dendrocopos major und Mittelspechte D. medius und Bemerkungen zur Konkurrenzsituation. — Ornithol. Beob. 99: 33–48.

Cody, M.L. 1985: Habitat selection in birds. — Academic Press, Orlando. 558 pp.

Glue, D.E. & Boswell, T. 1994: Comparative nesting ecology of the three British breeding woodpeckers. — Brit. Birds 87: 253–269.

Gutzwiller, K.J. & Anderson, S.H. 1987: Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. — Condor 89: 534–548.

Günther, E. 1992: Untersuchung zum Brutbestand, zur Bestandsentwicklung und zum Habitat des Mittelspechtes (Dendrocopos medius) im nordöstlichen Harz (Sachsen-Anhalt). — Orn. Jber. Mus. Heineanum 10: 31–53.

Günther, E. 1993: Zur Wahl des Höhlenstandortes von Bunt- und Mittelspecht (Dendrocopos major und D. medius) im nordöstlichen Harz (Sachsen-Anhalt). — Orn. Jber. Mus. Heineanum 11: 67–73.

Günther, E. & Hellman, M, 1997: Der Mittelspecht und die Buche: Versuch einer Interpretation seines Vorkommens in Buchenwaldern. — Orn. Jber. Mus. Heineaunum 15: 97–108.

Hågvar, S., Hågvar, G. & Mønness, E. 1990: Nest site selection in Norvegian woodpeckers. — Holarct. Ecol. 13: 156–165.

Hansson, L. 1992: Requirements by the Great Spotted Woodpecker Dendrocopos major for a suburban life. — Ornis Svecica 2: 1–6.

Hildén, O. 1965: Habitat selection in birds: a review. — Ann. Zool. Fenn. 2: 53–75.

Jenni, L. 1981: Das Skelettmuskelsystem des Halses von Buntspecht und Mittelspecht Dendrocopos major und medius. — J. Orn. 122: 57–61.

Jenni, L. 1983: Habitatnutzung, Nahrungserwerb und Nahrung von Mittel- und Buntspecht (Dendrocopos medius und D. major) sowie Bemerkungen zur Verbreitungsgeschichte des Mittelspechts. — Ornithol. Beob. 80: 29–57.

Jokimäki, J., Huhta, E., Itämies, J. & Rahko, P. 1998: Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. — Can. J. For. Res. 28: 1068–1072.

Kosiński, Z. & Winiecki, A. 2003: Estimation of the Middle Spotted Woodpecker Dendrocopos medius numbers – a comparison between the mapping technique combined with audio stimulation and the nest searching method. — Not. Orn. 44: 43–55. (In Polish with English summary).

Kosiński, Z., Kempa, M., Hybsz, R. 2004: Accuracy and efficiency of different techniques for censusing territorial Middle Spotted Woodpeckers Dendrocopos medius. — Acta Ornithol. 39: 29–34.

Lambeck, R.J. 1997: Focal species define landscape requirements for nature conservation. — Conserv. Biol. 11: 849–856.

Li, P. & Martin, T.E. 1991: Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. — Auk 108: 405–418.

Manly, B., McDonald, L. & Thomas, D. 1993: Resource selection by animals. Statistical design and analysis for field studies. — Chapman and Hall, London. 177 pp.

Martikainen, P., Kaila, L. & Haila, Y. 1998: Threatened beetles in White-backed Woodpecker habitats. — Conserv. Biol. 12: 293–301.

Matuszkiewicz, J.M. 2001: Zespoły leśne Polski. — Wydawnictwo Naukowe PWN, Warszawa. 358 pp. (In Polish).
Mazgajski, T.D. 1997: Changes in the numbers and nest sites of the Great Spotted Woodpecker Dendrocopos major and the Middle Spotted Woodpecker D. medius in the Las Bielański Reserve in Warsaw. — Ochr. Przyr. 54: 155–160. (In Polish with English summary).
Mazgajski, T.D. 1998: Nest-site characteristics of Great Spotted Woodpecker Dendrocopos major in Central Poland. — Pol. J. Ecol. 46: 33–41.
Mazgajski, T.D. 2002: Nesting phenology and breeding success in Great Spotted Woodpecker Picoides major near Warsaw (Central Poland). — Acta Ornithol. 37: 1–5.
Mikusiński, G. & Angelstam, P. 1997: European woodpeckers and anthropogenic habitat change: a review. — Vogelwelt 118: 277–283.
Mikusiński, G., Gromadzki, M. & Chylarecki, P. 2001: Woodpeckers as indicators of forest bird diversity. — Conserv. Biol. 15: 208–217.
Newton, I. 1994: The role of nest sites in limiting the numbers of hole-nesting birds: a review. — Biol. Conserv. 70: 265–276.
Nicolai, V. 1986: The barks of trees: thermal properties, microclimate and fauna. — Oecologia 69: 148–160.
Nilsson, S.G., Hedin, J. & Niklasson, M. 2001: Biodiversity and its assessment in boreal and nemoral forests. — Scand. J. For. Res. 3: 10–26.
Osiejuk, T.S. 1993: Wybiórczość środowiskowa a wielkość terytorium u ptaków żerujących na korze drzew. — MSc thesis, University of Adam Mickiewicz, Poznań. 46 pp. (In Polish).
Osiejuk, T.S. 1996: Locomotion patterns in wintering bark-foraging birds. — Ornis Fenn. 73: 157–167.
Pasinelli, G. 2000: Oaks (Quercus sp.) and only oaks? Relations between habitat structure and home range size of the middle spotted woodpecker (Dendrocopos medius). — Biol. Conserv. 93: 227–235.
Pasinelli, G. & Hegelbach, J. 1997: Characteristics of trees preferred by foraging middle spotted woodpecker Dendrocopos medius in Northern Switzerland. — Ardea 85: 203–209.
Pasinelli, G., Hegelbach, J. & Reyer, H.-U. 2001: Spacing behavior of the Middle Spotted Woodpecker in Central Europe. - J. Wildl. Manage. 65: 432–441.
Rolstad, J., Løken, B. & Rolstad, E. 2000: Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. — Oecologia 124: 116–129.
Schepps, J., Lohr, S. & Martin, T.E. 1999: Does tree hardness influence nest-tree selection by primary cavity nesters? — Auk 116: 658–665.
Schmitz, L. 1993: Distribution et habitat du Pic mar (Dendrocopos medius) en Belgique. — Aves 30: 145–166.
Simberloff, D. 1998: Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? — Biol. Conserv. 83: 247–257.
Short, L.L. 1979: Burdens of the Picid hole-excavating habit. — Wilson Bull. 91: 16–28.
Smith, K.W. 1997: Nest site selection of the Great Spotted Woodpecker Dendrocopos major in two oak woods in Southern Englands and its implications for woodland management. — Biol. Conserv. 80: 283–288.
Sonerud, G.A. 1985: Nest hole shift in Tengmalm's owl Aegolius funereus as defence against nest predation involving long-term memory in the predator. — J. Anim. Ecol. 54: 179–192.
Spitznagel, A. 1990: The influence of forest management on woodpecker density and habitat use in floodplain forests of the Upper Rhine Valley. — In: Carlson, A. & Aulén, G. (eds.), Conservation and management of woodpecker populations: 117–145. Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Report 17. Uppsala, Sweden. 164 pp.
StatSoft, Inc. 2003: STATISTICA (data analysis software system), version 6. www.statsoft.com.
Stenberg, I. 1996: Nest site selection in six woodpecker species. — Fauna norv. Ser. C, Cinclus 19: 21–38.
Tomiałojć, L. & Stawarczyk, T. 2003: The avifauna of Poland. Distribution, numbers and trends. — PTPP "pro Natura", Wrocław. 870 pp. (In Polish with English summary).
Török, J. 1990: Resource partitioning among three woodpecker species Dendrocopos spp. during the breeding season. — Holarct. Ecol. 13: 257–264.
Waite, S. 2000: Statistical ecology in practice. — Pearson Education Limited, Harlow. 414 pp.
Walankiewicz, W. 2002: Nest predation as a limiting factor to the breeding population size of the Collared Flycatcher *Ficedula albicollis* in the Białowieża National Park (NE Poland). — Acta Ornithol. 37: 91–106.
Walankiewicz, W., Czeszczewik, D., Mitrus, C. & Bida, E. 2002: Snag importance for woodpeckers in deciduous stands of the Białowieża Forest. — Not. Orn. 43: 61–71. (In Polish with English summary).
Weggler, M. & Aschwanden, B. 1999: Angebot und Besetzung natürlicher Nisthöhlen in einem Buchenmischwald. — Orn. Beob. 96: 83–94.
Wesołowski, T. 1989: Nest-sites of hole-nesters in a primaeval temperate forest (Białowieża National Park, Poland). — Acta Ornithol. 25: 321–351.
Wesołowski, T. & Tomiałojć, L. 1986: The breeding ecology of woodpeckers in a temperate primaeval forest – preliminary data. — Acta Ornithol. 22: 1–21.
Wiebe, K.L. 2001: Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? — Auk 118: 412–421.
Wiebe, K.L. & Swift, T.L. 2001: Clutch size relative to tree cavity size in Northern Flickers. — J. Avian Biol. 32: 167–173.