

## Nest site selection in middle and great spotted woodpeckers *Dendrocopos medius* & *D. major*: implications for forest management and conservation

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**Abstract** Success of species conservation depends to a large extent on comprehensive management that considers all critical aspects of a species' niche. Many studies have examined habitat factors in relation to occurrence, abundance or foraging behaviour of European woodpecker species, while relatively little is known about nest site selection. I compared habitat structures used for nesting by middle and great spotted woodpeckers *Dendrocopos medius* and *D. major* with available structures in an oak forest in the Swiss lowlands. I first tested if nest trees were randomly selected among available trees by focusing on species, condition and diameter of nest trees, and on the presence of the fruiting body (hereafter sporophore) of polypores (wood-decomposing fungi). Second, I examined if the nesting niches of the two species were differentiated. Both species showed strong preferences for oaks, large trees, dead trees and for trees with sporophores. Nest sites of the two species differed most strongly with respect to the presence of sporophores, cavity age and tree condition, pointing towards interspecific competition for nest sites. Old living or dead trees with sporophores are central components of the nesting niche of middle and great spotted woodpeckers. Conservation plans for the threatened middle spotted woodpecker have so far mostly focused on the needs in terms of distribution and foraging; future conservation strategies and forest management must take into account the preference for dead and decaying trees with sporophores as another vital resource. This will also provide benefits for other woodpecker species as well as for the community of secondary cavity nesters.

**Keywords** Dead trees · Forestry · Nesting ecology · Niche · *Piciformes* · Resource selection

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## Introduction

The removal of old and dead trees is considered to be one of the most negative aspects of intensive forestry in remaining woodlands of temperate zones. Intensively managed forests are generally younger and structurally impoverished compared to not or only extensively managed forests (e.g. Bretz Guby and Dobbertin 1996; Scherzinger 1996; Hunter 1999). This decline of tree age and structural diversity has not remained without impact on biodiversity in forest ecosystems. For example, a large proportion of saproxylic (dead-wood dependent) insects are threatened today (e.g. Speight 1989; Mawdsley and Stork 1995), and communities of these insects are generally depauperated in forests harvested since centuries (Okland 1996; Nilsson and Baranowski 1997). Besides a deficit of dead wood, managed forests often lack characteristic structures of unmanaged forests, as for example ‘legacy’ trees, i.e. old-growth trees having been spared during harvest, or having survived stand-replacing natural disturbances (Franklin 1990 cit. in Mazurek and Zielinski 2004). Such legacy trees have been shown to be important structures for a variety of wildlife species (Mazurek and Zielinski 2004 and studies therein). Overall, 40% of forest wildlife species in Europe are estimated to be threatened or in danger of extinction (INSECTA and Zaric, 1995 cit. in Bretz Guby and Dobbertin 1996).

Primary cavity-nesters (i.e. species that excavate their own breeding cavity) are particularly vulnerable to intensive forestry, despite their ability to create suitable nest sites. Many of these species require specific habitat structures for excavating their nests (e.g. Raphael and White 1984; Harestad and Keisker 1989; Martin and Eadie 1999; Conner et al. 2001; Steeger and Dulisse 2003), but these structures often coincide with those that are most efficiently removed by forestry.

As in many other species, the selection of suitable nest sites is of central importance in the life history of woodpeckers. Despite this, relatively few studies have examined nest site selection in European woodpecker species, and still fewer have addressed use in relation to available habitat structures. A general assumption seems to be that knowing both habitat selection on the landscape level and foraging requirements within habitats is sufficient to protect and promote habitats of endangered species. However, such an approach is insufficient, and many examples exist that show how structures needed for nesting differ from those required for other activities (e.g. red-cockaded woodpecker *Picoides borealis*, Jackson 2003; cavity nesting waterfowl, Eadie and Gauthier 1985; Eadie et al. 1998). Thus, the success of species conservation is contingent upon comprehensive management plans that include detailed information on all critical aspects of a species’ ecology.

A particularly striking example for the lack of information on nest site selection is the middle spotted woodpecker *Dendrocopos medius*. As a consequence of habitat destruction through intensive forestry, this species has suffered strong declines in the 20th century, resulting in highly fragmented populations throughout Europe (Pasinelli 2003). The middle spotted woodpecker belongs to the Annex I of the Birds directive of the European Union listing threatened species that require special conservation measures to be taken for their habitats. While many studies exist on habitat selection and foraging behaviour of the middle spotted woodpecker, knowledge on nest site selection in relation to available resources is very limited (reviewed by Pasinelli 2003; but see Kosinski and Winiecki 2004). A similar situation is found in the great spotted woodpecker *Dendrocopos major* (reviewed by Michalek

and Miettinen 2003). This species, however, is far more numerous and widespread than the middle spotted woodpecker and not threatened so far.

Here, my first goal is to examine habitat structures used for nesting by middle and great spotted woodpeckers in a central European oak forest. Specifically, I test whether nest trees are a random sub-sample of available trees by focusing on species, condition and diameter of nest trees, and on the presence of fruiting bodies (or sporophores) of polypores (wood-decomposing fungi). This information will then be used to suggest guidelines for forest management.

A second goal is to compare the nest sites of middle spotted and great spotted woodpeckers, which allows insight into niche differentiation in terms of the nesting ecology of these species. The competitive exclusion principle (Gause's principle) states that two species that compete for the same resources cannot stably coexist (Gause 1934). Given that middle and great spotted woodpeckers are morphologically very similar and are often syntopic, many studies have focused on niche differentiation in terms of foraging behaviour and habitat use of these species to explain their coexistence (e.g. Jenni 1983; Lovaty 1985; Török 1990; Michalek 1994; Hertel 2003). Much less is known about niche differentiation with respect to nesting, although this may be at least as important as interspecific differences in foraging and habitat use for explaining coexistence.

## Methods

### Study site

From 1993–1999, nest site selection of the two woodpecker species was examined in the northeastern part of the Swiss lowlands. The study area (47°37'N, 8°37'E; 120 ha, 380 m a.s.l.) was situated in the Niderholz, an 800-ha forest, 35 km north of Zurich near the Rhine River. The Niderholz is one of the most important breeding areas of the middle spotted woodpecker in Switzerland, hosting 40–60 breeding pairs, although substantial declines have recently been noticed (Bühlmann et al. 2003). The Niderholz consists of an old oak–hornbeam forest managed for centuries as coppice-with-standards (Mittelwald), a forestry practice that results in a two-layered forest with large trees forming the canopy and small trees below the canopy. In the study area, the canopy is dominated by oak *Quercus* sp., with occasional Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, and Norway maple *Acer platanoides*, whereas the dominant tree species below the canopy are hornbeam *Carpinus betulus* and lime *Tilia* sp. The study area is surrounded by deciduous and coniferous forest of varying tree species composition and age classes, with some further oak–hornbeam forest stands (Pasinelli 2000a).

Over the course of the study, breeding densities of middle and great spotted woodpeckers averaged 0.83 and 2.03 pairs 10 ha<sup>-1</sup>, respectively, in the study area. Besides the two target species of this study, four other woodpecker species regularly breed in the Niderholz, these being black woodpecker *Dryocopus martius*, grey-faced woodpecker *Picus canus*, green woodpecker *P. viridis* and lesser spotted woodpecker *Dendrocopos minor*.

## Nest trees and available habitat

Nests were searched each year from mid-April to mid-June. This time span covers the usual nesting period of both woodpecker species in Central Europe (Michalek and Miettinen 2003; Pasinelli 2003). From 1993–1996, nests of the middle spotted woodpecker were found by following individuals carrying radio transmitters that had been attached to them during a project on the ecology of this species (for details see Pasinelli 2000a, b, 2001; Pasinelli et al. 2001). From 1997–1999, nests were searched by acoustically locating the chirping begging calls of young and/or by following parents carrying food in their beaks. Annually, 7–13 territories were searched for nests. In the great spotted woodpecker, some nests were detected during cavity construction, but most were found in the nestling stage by acoustically locating the loud chirping begging calls of young and/or by following parents carrying food in their beaks. Annually, 18–29 territories were searched for nests in this way.

Some nests may have gone undetected if the brood died before it could be found, particularly during the very wet breeding season of 1995 (cf. Pasinelli 2001). However, daily survival rates of nests and nesting success of both woodpecker species are very high (Glue and Boswell 1994; Smith 1997; Michalek and Miettinen 2003), so that the majority of nests probably survived long enough to be found.

For each active nest cavity, the following parameters were recorded: tree species, condition of the cavity tree (hereafter referred to as tree condition) and of the substrate containing the cavity (substrate condition) as either alive or dead, diameter at breast height (dbh; recorded after the young had left the cavity), substrate diameter at cavity entrance (estimated by comparing with the breadth of the woodpecker's dorsum), type of substrate containing the cavity (substrate type: trunk or limb), position of substrate containing the cavity (substrate position: vertical or inclined), height of cavity entrance above ground (cavity height, estimated visually), cavity age (freshly excavated before breeding season yes or no), presence or absence of one or more fruiting bodies (hereafter referred to as sporophores) of polypores (wood-decomposing fungi, with sporophores on the tree surface  $\geq 3$  cm in length or breadth) within 1 m of the cavity entrance (sporophore).

Data on available habitat were sampled in the winter months following breeding attempts on 286 circular plots of 0.03 ha, located at the intersections of an 150 m by 80 m grid placed randomly over the study area. The area sampled corresponded to 7.2% of the total study area. For every tree on each plot, species identity, dbh ( $\geq 8$  cm), tree condition, and occurrence of one or more sporophores were recorded. These data were used to determine resource availability, which then was compared with nest tree characteristics.

## Statistical analysis

In both woodpecker species, cavities are mainly constructed by males, which may live for several years in the breeding territories once selected (Michalek and Miettinen 2003; Pasinelli 2003). Some individuals may thus have contributed more than one observation to the data, but to retain as much information as possible, each nest was considered as one independent observation for two reasons. First, based on data of marked middle spotted woodpeckers, only a small fraction of individuals was present for more than one breeding season (three males and two females out of 26 marked individuals, with two males being present in three, the other individuals in

2 years). Second, intra-individual variation in nest site selection is presumably high (own observation), although detailed studies are lacking. Besides these potential intra-individual dependencies, cavity-related dependencies due to the use of the same cavity or nest tree by the birds in more than 1 year may arise. Of the 196 breeding cavities examined here (see Results), six cavities and 10 nest trees were used more than once by the great spotted woodpecker, the corresponding numbers in the middle spotted woodpecker being 0 cavities and four nest trees. However, because structural attributes related to a cavity do not necessarily remain constant over time, I considered the use of a cavity in a given year as independent from the use of the same cavity in another year. Structural attributes such as tree dbh or substrate diameter increase with time, while other attributes such as the presence of sporophores or cavity age can change between years. Note that results did not change if each tree and cavity was used only once (data not shown).

Following Manly et al. (1993), selection indices were used to see if one resource was preferred, avoided or used as expected based on its availability (see below). Selection indices were calculated by dividing the proportion of a used resource by its proportional availability. A selection index significantly greater than one indicated preference, while a value significantly smaller than one implied avoidance. A selection index was considered to be significantly different from one if the simultaneous 95% Bonferroni confidence interval calculated over all categories did not contain the value one (Manly et al. 1993), i.e. the null hypothesis of use being proportional to availability was rejected. To calculate the proportion of available trees, I only considered those trees with a dbh of at least 20 cm and 15 cm in middle spotted and great spotted woodpecker, respectively, since these are the minimum dbh of nest trees recorded for these two species so far (Michalek and Miettinen 2003; Pasinelli 2003). Consideration of all trees ( $\geq 8$  cm) would have led to trivial results, since most trees had very small dbh and for that reason were unsuitable for cavity construction. It should be noted that the selection analyses were redone for the great spotted woodpecker by considering only those trees with a dbh of at least 20 cm as available (as in the middle spotted woodpecker), but since all results were identical to using 15 cm as the limit for available trees, I will not consider them further in the result section.

Nest sites of the two woodpecker species were compared with logistic regression (PROC LOGISTIC, SAS Institute Inc 1999–2001), using species as the categorical dependent variable. Categorical explanatory variables were tree condition, substrate condition, substrate type, substrate position, cavity age, and sporophore. Continuous explanatory variables were dbh of cavity tree, substrate diameter and cavity height. Results did not change if cavity height was treated as categorical variable, with height above ground assigned to one of six categories (<5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m,  $\geq 25$  m) (data not shown). Tree species was excluded from this analysis, since the majority of the cavities of both woodpecker species was built in oaks (see Results).

Results of multiple regression analysis may be compromised by strong correlations among the explanatory variables (Chatterjee and Price 1991; Menard 1995). Spearman rank correlations indicated two pairs of highly correlated explanatory variables ( $r > 0.7$ ), these being tree condition with substrate condition ( $r_s = 0.80$ ,  $n = 107$ ) and substrate type with substrate position ( $r_s = 0.78$ ,  $n = 107$ ), respectively. I therefore analysed five models, starting with a global model containing all explanatory variables. Then, reduced models were analysed by including only one

member of each of the two strongly related variable pairs along with all the other explanatory variables; by altering which of the highly related variables were included, four such reduced models could be analysed. For each model, I then calculated Akaike's Information Criterion (=AIC, Akaike 1973; Burnham and Anderson 1998) corrected for small sample sizes (AICc, Burnham and Anderson 1998). The model with the lowest AICc value is considered the most parsimonious one, i.e. explaining most of the variance with the fewest parameters (Burnham and Anderson 1998; Anderson et al. 2000; Burnham and Anderson 2001). Akaike model weights were calculated to determine the level of support for each of the five models by the data (Burnham and Anderson 1998). Model weights add up to 1 (by definition), with higher weights indicating better explanatory power. Effect sizes of parameters were calculated with model averaging (Burnham and Anderson 1998; Johnson and Omland 2004). Similarly, model-averaged standard errors (SE) were calculated for parameter estimates following Johnson and Omland (2004). All effect sizes in the results section refer to these weighted averages and SE. Finally, I checked the fit of each model with residual analysis (McCullagh and Nelder 1989).

## Results

In total, 57 nest cavities of middle spotted woodpeckers were found, 52 of which had been built in oaks. In the great spotted woodpecker, 139 nest cavities were located, and 137 of them had been constructed in oaks. Given the prevalence of oaks as nest trees, I focused on availability and use of oaks versus all other tree species in the analyses of nest tree species selection.

### Characteristics of nest trees

Both woodpecker species significantly preferred oaks as nest trees, while other tree species were avoided, as indicated by the selection indices and their associated confidence intervals (Table 1). Both woodpecker species most often built their nest cavity in living trees, which were much more abundant than dead trees. However, when comparing available and used trees, the selection indices indicated a strong preference for dead trees and an avoidance of living trees in the middle spotted woodpecker. Similarly, the great spotted woodpecker clearly preferred dead trees, but used living ones almost as expected from their availability (Table 1). Trees with large fruit bodies (sporophores) of polypores were very rare in the study area, but such trees were nevertheless strongly selected as nest trees in both woodpecker species.

Close inspection of Table 1 shows that most nest trees used by the middle spotted woodpecker were oaks and that most nest trees had sporophores. Thus, the positive selection of oaks and of trees with sporophores may not be independent of each other, since oaks (not least due to their age) may be more likely than other tree species to have sporophores. However, there was no such association between nest tree species and the presence of sporophores (Fisher's exact test  $P > 0.99$ ,  $n = 57$ , Table 2). Similarly, in the great spotted woodpecker no significant association between nest tree species and the presence of sporophores was found ( $P > 0.52$ ,  $n = 139$ , Table 2).

**Table 1** Selection of nest trees in middle (msw) and great spotted woodpeckers (gsw)

	Tree species		Tree condition		Sporophore present	
	Oak	Other	Alive	Dead	Yes	No
<b>MSW</b>						
Availability <sup>a</sup>	263	445	704	4	27	681
%	37.15	62.85	99.44	0.56	3.81	96.19
Use	52	5	44	13	52	5
%	91.23	8.77	77.19	22.81	91.23	8.77
Selection index	2.46	0.14	0.78	40.37	23.92	0.09
95% CI	2.23–2.68	0.01–0.27	0.65–0.90	18.32–62.41	21.72–26.12	0.00–0.18
<b>GSW</b>						
Availability <sup>b</sup>	274	753	1020	7	27	1000
%	26.68	73.32	99.32	0.68	2.63	97.37
Use	137	2	130	9	43	96
%	98.56	1.44	93.53	6.47	30.94	69.06
Selection index	3.69	0.02	0.94	9.50	11.77	0.71
95% CI	3.61–3.78	–0.01–0.05	0.90–0.99	2.64–16.36	8.43–15.11	0.62–0.80

See text for calculation of selection indices. The variable ‘sporophore present’ refers to the occurrence of a sporophore of  $\geq 3$  cm length or breadth of one or more polyporous fungi

<sup>a</sup> based on trees  $\geq 20$  cm dbh

<sup>b</sup> based on trees  $\geq 15$  cm dbh

**Table 2** Occurrence of sporophores in relation to species and condition of nest trees in middle (msw) and great spotted woodpeckers (gsw)

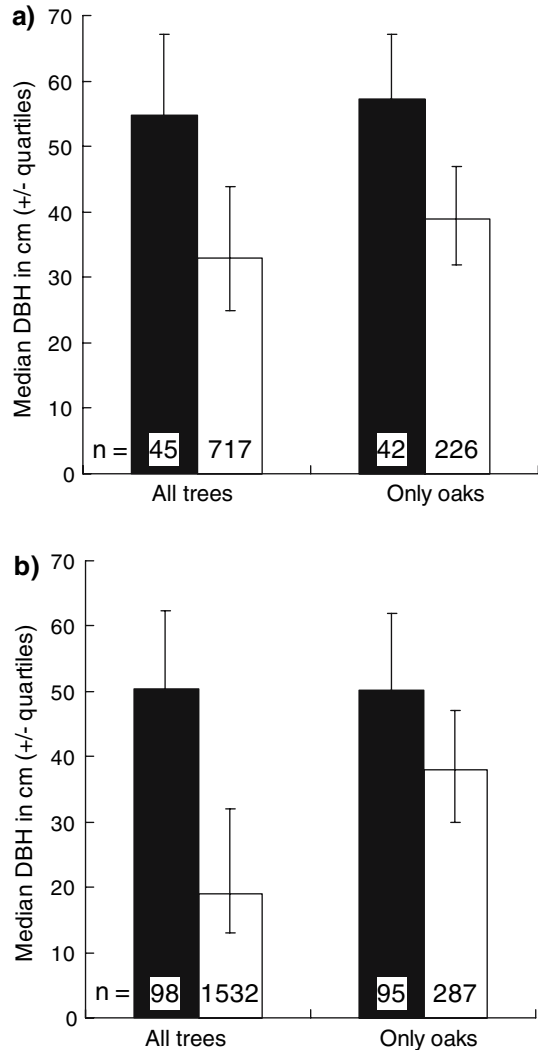
Woodpecker species	Sporophore present	Tree species		Tree condition	
		Oaks	Other	Alive	Dead
MSW	Yes	47	5	40	12
	No	5	0	4	1
GSW	Yes	42	1	40	3
	No	95	1	90	6

Along the same line of arguments, the positive selection of dead trees and of trees with sporophores may not be independent of each other, since dead trees may be more likely than living ones to have sporophores. However, I did not find any relation between the presence of sporophores and the condition of nest trees (Fisher’s exact tests, middle spotted woodpecker:  $P > 0.42$ ,  $n = 57$ ; great spotted woodpecker:  $P > 0.27$ ,  $n = 139$ ; Table 2).

Nest trees of both woodpecker species had on average significantly larger dbhs than available trees (Mann–Whitney  $U$ -tests,  $P < 0.001$  in both species, Fig. 1a). Since oaks were the most often used nest trees (see above), I redid the analyses by considering only oaks as used and available trees. Again, both woodpecker species selected on average larger trees for nesting compared to the available trees (Fig. 1b, Mann–Whitney  $U$ -tests,  $P < 0.001$  in both species).

There was no relation between the presence of sporophores on oaks and dbh (logistic regression, estimate  $\pm$  SE =  $0.013 \pm 0.015$ ,  $\chi^2_1 = 0.81$ ,  $P > 0.36$ ,  $n = 260$  oaks with dbh  $\geq 20$  cm; results identical for dbh  $\geq 15$  cm, data not shown). Because there were many more oaks without ( $n = 234$ ) than with sporophores ( $n = 26$ ), I

**Fig. 1** Median diameter at breast height (dbh) of nest trees (filled bars) compared to available trees (empty bars). **(a)** Middle spotted woodpecker, **(b)** great spotted woodpecker; numbers inside bars indicate sample sizes. Bars indicate 25–75% quartile ranges. Trees used for nesting significantly larger than available trees in all cases (Mann–Whitney *U*-tests,  $P < 0.001$ )



redid the analysis by randomly selecting 26 oaks without sporophores to be used in the logistic regression. Still, I did not find any significant relation between the presence of sporophores and the dbh of an oak ( $0.002 \pm 0.022$ ,  $\chi^2_1 = 0.01$ ,  $P > 0.93$ ,  $n = 52$ ). Thus, the positive selection of large nest trees appeared to be independent of the presence of sporophores.

#### Comparison of nest sites of middle and great spotted woodpeckers

Of the five models examined (see Methods), two were well supported by the data, as indicated by both  $\Delta AICc$  values and model weights (Table 3). These well-supported models 1 and 2 included the variable tree condition instead of substrate condition and further included either substrate type or substrate position along with all the other explanatory variables (dbh, substrate diameter, cavity height, cavity age,



**Table 3** Differentiation of nest sites between middle and great spotted woodpeckers

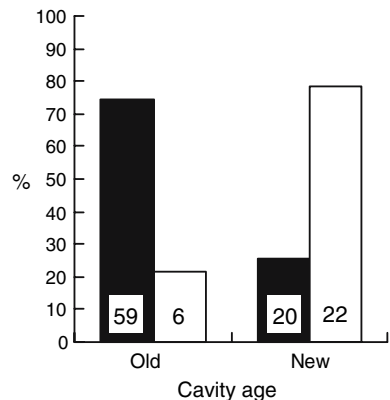
Model	Variables in model	K	-2 Log L	AICc	ΔAICc	Weight
1	Dbh, substrate diameter, cavity height, tree condition, substrate type, cavity age, sporophore	8	74.18	-130.89	0.00	0.50
2	Dbh, substrate diameter, cavity height, tree condition, substrate position, cavity age, sporophore	8	73.95	-130.43	0.46	0.40

Modelled was the probability of a nest cavity having been used by the middle spotted woodpecker. Only models with ΔAICc ≤ 2 are shown. *K* = number of parameters estimated (i.e. variables in the model + intercept); -2 Log L = -2 \* maximum likelihood estimate, derived from SAS; ΔAICc = difference in AICc to the best model; weight = relative support of a particular model compared to the other models, with higher values indicating better support. *N* = 107 cavities (28 middle spotted, 79 great spotted woodpecker).

sporophore, Table 3). Conversely, models 3 and 4 received little support (ΔAICc: 3.91 and 5.34, Akaike weights: 0.07 and 0.03, respectively). These models did not contain tree condition, but substrate condition in both cases, and either substrate type or substrate position along with the other explanatory variables. Together with model-averaged effect sizes and standard errors (SEs, see below), this suggests tree condition to be more important than substrate condition for differentiating between the nest sites of the two woodpecker species. Hardly any support was found for the global model with all the variables (Model 5, ΔAICc = 10.37, weight = 0.003).

Three variables had effect sizes larger than their SEs when considering model-averaged effect sizes and SEs. This suggests that the probability of a nest cavity having been built and used by the middle spotted woodpecker increased with the presence of sporophores next to the cavity (effect size ± S.E. = 1.339 ± 0.647) and decreased with cavities being old (-1.067 ± 0.565) and trees being alive (-0.794 ± 0.627). In other words, cavities of the middle spotted woodpecker were more often freshly excavated and found close to sporophores in dead trees than cavities of the great spotted woodpecker (Table 3, Fig. 2). Model averaged effect sizes ± SE of the other variables were 0.154 ± 0.505 for substrate diameter, -0.111 ± 0.220 for substrate condition, 0.094 ± 0.290 for cavity height, -0.068 ± 0.513 for substrate type, -0.106 ± 0.435 for substrate position, and -0.004 ± 0.166 for dbh

**Fig. 2** Nest cavity age in great spotted woodpeckers (filled bars) and middle spotted woodpeckers (empty bars). Numbers within bars indicate sample size



of nest tree. Apparently, these variables contributed little to the separation of the two species' nest sites.

## Discussion

Trees used for nesting by middle and great spotted woodpeckers were not a random sub-sample of available trees: both species showed preferences for oaks, for dead trees and for trees with large sporophores of polypores close to the cavity entrance. In addition, nest trees were significantly larger in diameter than available trees.

### Middle spotted woodpecker

Very few studies have so far examined nest tree use in relation to availability in the middle spotted woodpecker (Pasinelli 2003). Only one study reported preference for oaks as nest trees in comparison with tree species availability (Mazgajski 1997), while another one found a preference for dead trees, but not for particular tree species (Kosinski and Winiecki 2004). Wesolowski and Tomialojc (1986) suggested selection of cavity tree species to reflect availability. One explanation for the preference of oaks reported here may be that oaks used as nest trees in my study area more often had sporophores than other tree species. However, I did not find such a relation, so the preference for oaks cannot be explained by an increased presence of sporophores. More likely, since the middle spotted woodpecker prefers to nest in large trees, as evidenced by the significantly larger dbh of nest trees compared to available trees in this study, oaks appear to be particularly attractive as nest trees because of their generally large dbh and hence age (also see Fauvel 2001; Kosinski and Winiecki 2004). Presumably, large trees are important resources for nesting in the middle spotted woodpecker, regardless of tree species. The middle spotted woodpecker has been shown to regularly use more than 20 tree species for nesting (Pasinelli 2003) and usually excavates its breeding cavities in large trees, averaging from 39.1 cm to 97.0 cm (Wesolowski 1989; Prill 1991; Mazgajski 1997; Fauvel 2001; Kossenko and Kaygorodova 2003; Kosinski and Winiecki 2004). Although most of these studies did not present data on available trees, these findings support the notion that large trees are important for cavity construction in this woodpecker species, whereas tree species per se is not.

Throughout its range, the middle spotted woodpecker excavates nest cavities in decaying or dead parts of living, decaying or dead trees (Pasinelli 2003), very often close to a sporophore of a polypore (e.g. *Fomes fomentarius*, *Laetiporus sulphureus*, *Phellinus* sp.), an old cavity, a limb hole or below a dead limb (Pettersson 1984; Dubreuil et al. 1998; Pasinelli 2000a; Fauvel 2001; Spitznagel 2001; Kosinski and Winiecki 2004). Fungus-infected wood is softer than healthy wood, which decreases the effort of excavating a cavity, and this may explain the positive selection for nest trees with sporophores found in this study. Furthermore, neck muscles and bill are relatively weak in the middle spotted woodpecker, hampering extensive excavation into hard, living substrates (Rüger 1972; Jenni 1981). This is also reflected by the species' foraging behaviour consisting mainly of probing into bark crevices rather than pecking for arthropods in the bark (Jenni 1983; Pettersson 1983; Pasinelli and Hegelbach 1997; Pasinelli 2000b). The preference for nest trees with sporophores was not a by-product of the positive selection of old oaks, because there was neither

an association between trees with sporophores and tree species nor any relation between dbh of oaks and the presence of sporophores.

Besides trees with sporophores, dead trees were also preferred despite their striking rarity in the study forest (below 0.7% of all trees, Table 1). Dead trees have been reported as nest substrates earlier, although comparisons with availability are lacking (Pasinelli 2003; exception: Kosinski and Winiiecki 2004). The soft wood of decaying parts of dead trees likely offer similar conditions for cavity excavation as living trees with polypores, not least because dead trees are probably always infected by fungi (even if no fruit body is visible). The prevalence of sporophores on both living and dead nest trees (Table 2) suggests, however, that condition of trees (alive or dead) used for nesting is of secondary importance with respect to nest site selection. This is supported by the lacking association between nest tree condition and the presence of sporophores (although the generality of this independence should be examined with data including more dead nest trees than in this study). Thus, the middle spotted woodpecker appears to use the sporophores of polypores, rather than tree condition, as a cue for selecting suitable sites for cavity excavation.

### Great spotted woodpecker

The great spotted woodpecker is the most flexible *Dendrocopos* species in Europe, both in terms of its foraging and nesting ecology (Michalek and Miettinen 2003). This flexibility is reflected in this study: despite significant preferences for trees with sporophores and dead trees for nesting, great spotted woodpeckers regularly excavated their nests also in trees without sporophores and in living trees (cf. Table 1). Although this does not rule out the possibility that nest sites may have been built in places of rotten wood, my findings agree with previous studies indicating that the great spotted woodpecker is much less dependent ‘on sites such as rotten, dead, broken, stump, under bracket fungus as other woodpeckers’ (Michalek and Miettinen 2003; but see Smith 1997; Kosinski and Winiiecki 2004). In terms of tree species, oaks were positively selected, but as in the middle spotted woodpecker, this selection likely reflects the preference for large trees rather than for oaks per se (Fig. 1). Similarly, Michalek and Miettinen (2003) found no evidence for associations of nest cavities with particular tree species. In contrast to my findings, Smith (1997) did not demonstrate any marked selection for nests to be in trees with large diameter, although the majority of cavities were in trees with 28 cm dbh or above. On the other hand, Smith (1997) found strong selection for dead trees or dead parts of trees as in this study, but depending on tree species. In contrast, Kosinski and Winiiecki (2004) found positive selection for oak and alder, but not for dead trees. Overall, these contradictory results suggest that the great spotted woodpecker is much more able to adjust resource use for nesting to local availability than perhaps any other European woodpecker species.

### Interspecific comparison

The comparison of nest site characteristics between the two woodpecker species revealed differentiation of their nesting niches mainly in terms of tree condition, the presence of sporophores and cavity age. Middle spotted woodpeckers more frequently nested in freshly excavated cavities close to sporophores of tree fungi in dead trees than did great spotted woodpeckers. In contrast to my study, the middle

spotted woodpecker has been found to excavate its cavities higher up in trees (Wesolowski and Tomialojc 1986; Prill 1991; Günther 1993; but see Fauvel 2001), to use substrates with smaller diameters at cavity entrance (Günther 1993) and to use limbs more often (Fauvel 2001) than the great spotted woodpecker. The two woodpecker species differ in some morphological traits important for cavity excavation and cavity location, for example in bill size, neck muscles and body size (Rüger 1972; Jenni 1981), and therefore, some differences in nesting niches are to be expected (also see Kosinski and Winięcki 2004). Further, it is likely that habitat structure of forests differed among studies, which may explain differences in niche differentiation observed (although note that all studies were done in oak-dominated habitats comparable to the one in my study). Nevertheless, regardless of habitat, all studies suggested nesting niches of the two species to be differentiated, which may indicate the presence of interspecific competition for nest sites. If the nest niches were ‘fixed’ properties of each species, determined primarily by morphology, but not influenced by nest site selection of the other species, we would expect to find similar niche differentiation in all the studies, which is not the case.

### Management implications

This study has shown that nest trees of middle and great spotted woodpeckers are large and thus old and show characteristics of trees usually found in primeval forests. Specifically, the presence of sporophores of polypores in living trees indicates rotten wood usually in advanced stage of decay, which dramatically lowers the economic value of the trees. Such trees, along with completely dead trees, are quickly removed by forestry to improve growing conditions for healthy and economically more promising trees, and to prevent infestation of neighbouring trees. Yet, the removal of such economically unimportant trees reduces the ecological quality of forests that are otherwise suitable for the highly specialised middle spotted woodpecker. This may reduce carrying capacities in those forests, because home range size of the middle spotted woodpecker is inversely related to the densities of potential cavity trees (i.e. trees with sporophores, limb holes, or old cavities) and old oaks (Pasinelli 2000a). In terms of management of middle spotted woodpecker habitats, oaks with large dbh and with sporophores as well as dead trees should be retained and can serve both as future cavity trees and as foraging trees. It is important to note though that densities of trees suitable for cavity construction and for foraging can be fairly high, averaging 26 potential cavity trees per ha in my study site (Pasinelli 2000a) and ranging from 15–80 large oaks (potential foraging trees) per ha (Pettersson 1984; Bühlmann and Pasinelli 1996; Coch 1997; Pasinelli 2000a; Michalek et al. 2001).

Retention of currently existing potential cavity trees may not suffice to meet current and future requirements of the middle spotted woodpecker. Because nest cavities are preferentially built in decaying wood, their re-usability is very poor. In fact, not one of the breeding cavities and only four (7%) of 57 nest trees in this study had been used more than once for nesting by the middle spotted woodpecker (own unpublished data). Forest management may therefore be required to actively recruit potential cavity trees, particularly in forests with low availability of such trees. Several methods have been proposed for producing decaying and dead trees, for example girdling (Aulén 1991) or topping of trees (Bull and Partridge 1986; Filip et al. 2004). Girdling may be most promising when applied at a tree height of 5–15 m above ground, where cavities of the middle spotted woodpecker are usually found

(Pasinelli 2003). Inoculating parts of living trees with (naturally occurring) wood-decaying fungi may also hold promise (Parks et al. 1995; but see Filip et al. 2004).

The use of artificial cavities has been a very successful management tool for the red-cockaded woodpecker in the south-eastern United States (Walters et al. 1992; Conner et al. 2001). Unlike the middle spotted woodpecker, however, red-cockaded woodpeckers continue to use the cavities (both natural and artificial ones) for several years (Conner et al. 2001), and thus, providing artificial cavities for middle spotted woodpeckers may be only of temporally limited use.

Increasing the availability of dying and dead trees may also be important to reduce impacts of potential interspecific competition for nest sites between the two *Dendrocopos* species studied. In addition, although the great spotted woodpecker is currently the most numerous and widespread woodpecker species throughout Europe, this study and others (reviewed by Michalek and Miettinen 2003) suggest that the species will benefit as well if old and dead trees are retained. Given the potential role of the great spotted woodpecker as a key stone species in managed forests, increasing the availability of old trees and of dying and dead trees may be the best way to also benefit the whole community of secondary cavity nesters. The importance of old and dead trees for biodiversity and forest ecosystem functioning is generally accepted (e.g. Harmon et al. 1986; Aulén 1991; McComb and Lindenmayer 1999), but the implications of this for forest management and conservation still lags behind.

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