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Population densities and habitat use of woodpeckers in a Danube floodplain forest in Eastern Austria

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Population densities and habitat use of woodpeckers in a Danube floodplain forest in Eastern Austria

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Abstract

Many characteristics of alluvial forests (e.g. high deadwood availability, structural and species diversity) make them excellent habitat for woodpeckers. A survey of the woodpecker community was conducted in a 1,170 ha study area in floodplain forest in the Donauauen National Park (Eastern Austria) between February and April 2008. Densities of Great Spotted Woodpecker *Dendrocopos major* (5.98 territories/10 ha), Lesser Spotted Woodpecker *D. minor* (0.20-0.24 territories/10 ha), Green Woodpecker *Picus viridis* (0.14-0.15 territories/10 ha) and Black Woodpecker *Dryocopus martius* (0.06 territories/10 ha) were comparatively high, whereas Middle Spotted Woodpecker *Dendrocopos medius* densities (0.28 territories/10 ha) were lower than those reported for many other lowland forests. Based on abundance (*Dendrocopos* species) and occurrence (*D. martius* and *P. viridis*) of the species in 400 x 400 m grid squares, GLMs were performed to test for effects of (1) tree species composition and (2) structural habitat variables. The Great Spotted Woodpecker showed no distinct habitat preferences but selected older stands. Middle Spotted Woodpecker abundance could best be explained by stand age, the proportion of oak and ash, and proximity to sidearms. The Lesser Spotted Woodpecker selected softwoods (alder, willow, white poplar, hybrid poplar) and ash. Its pronounced affinity for sidearms can probably be explained by the association of softwoods with water-ways. The best predictor for the occurrence of the Green Woodpecker was forest edge density. All Green Woodpecker territories were located in less frequently inundated hardwood forest, and hybrid poplars and willows were significantly avoided by this species, possibly due to less favourable foraging opportunities (ants) in wetter habitats. The Black Woodpecker preferred forest rich in oak, maple, hybrid poplar and white poplar and was frequently registered near sidearms. Some overlap in habitat preferences was found for *D. martius* and *D. minor*, which will hardly compete with each other at a microhabitat level, and to some extent for *D. major* and *D. medius*. Nonetheless, the comparatively low densities of *D. medius* are probably not attributable to competition with the Great Spotted Woodpecker but rather to the low stand age (mean 54 years) and the relatively low proportion of oak (10%) in the study area. An analysis of direct observations of the *Dendrocopos* species and *D. martius* showed a

significant preference for dead and dying trees by all species, although stands rich in deadwood were not preferred, possibly because at a volume of 27 m^3 per ha, deadwood may not constitute a limiting factor in the study area.

Key words: woodpecker community, habitat selection, competition, lowland floodplain forest, softwood alluvial forest, hardwood alluvial forest, deadwood, *Dendrocopos major*, *D. medius*, *D. minor*, *Picus viridis, Dyrocopus martius*

Zusammenfassung

Bestandsdichten und Habitatnutzung von Spechten im Nationalpark Donauauen (Niederösterreich)

Für einen großen Teil der europäischen Spechtarten repräsentieren Auwälder, möglicherweise durch ihren oftmals relativ hohen Totholzanteil, einen wichtigen Lebensraum. Im Rahmen dieser Untersuchung wurden Spechte im Nationalpark Donauauen östlich von Wien auf einer 1170 ha großen Probefläche zwischen Februar und April 2008 flächendeckend erfasst. Die Dichten des Buntspechts *Dendrocopos major* (5,98 Reviere/10 ha), des Kleinspechts *D. minor* (0,20-0,24 Reviere/10 ha), des Grünspechts *Picus viridis* (0,14-0,15 Reviere/10 ha) und des Schwarzspechts *Dryocopus martius* (0,06 Reviere/10 ha) waren vergleichsweise hoch; hingegen wurden für den Mittelspecht *Dendrocopos medius* (0,28 Reviere/10 ha) geringere Dichten als in vielen anderen Tieflandwäldern festgestellt. Die Einflüsse verschiedener Habitatparameter auf die Dichten der *Dendrocopos*-Arten bzw. Präsenz/ Absenz von *P. viridis* und *D. martius* in 400 x 400 m großen Rastern wurden mittels Allgemeiner Linearer Modelle (GLMs) analysiert. Der Buntspecht zeigte keine ausgeprägten Habitatpräferenzen, selektierte jedoch Bestände mit einem höheren Bestandesalter. Die Abundanz des Mittelspechts konnte am besten durch das Bestandesalter, den Anteil an Eichen und Eschen, sowie Nähe zu Seitenarmen erklärt werden. Der Kleinspecht selektierte neben Eschen oftmals Altwasserarme begleitende Weichhölzer (Erle, Weide, Silberpappel, Hybridpappel), was die räumliche Konzentration im Uferbereich zu erklären scheint. Das Vorkommen des Grünspechts konnte am besten durch den Grenzlinienanteil (Waldrandbereiche) erklärt werden. Alle Reviere lagen in Hartholzauwald; Hybridpappeln und Weiden wurden signifikant gemieden, möglicherweise aufgrund eines geringeren Nahrungsangebots (Ameisen) an feuchteren Standorten. Der Schwarzspecht bevorzugte Auwaldflächen mit einem hohen Anteil an Eiche, Ahorn, Hybridpappel und Silberpappel und wurde häufig im Bereich von Altwasserarmen festgestellt. Überlappungen in den

Habitatpräferenzen existieren vor allem bei Schwarz- und Kleinspecht, die wohl kaum auf Mikrohabitat-Ebene miteinander konkurrieren, sowie bei Bunt- und Mittelspecht. Die vergleichsweise geringen Dichten des Mittelspechts sind jedoch vermutlich weniger auf Konkurrenz mit dem Buntspecht, als vielmehr auf das geringe Baumalter (durchschnittlich 54 Jahre) sowie den relativ geringen Eichenanteil (10 %) zurückzuführen. Für die *Dendrocopos*-Arten und *D. martius* wurden weiterhin Direktbeobachtungen ausgewertet. Dabei zeigte sich eine signifikante Präferenz für tote und absterbende Bäume, obwohl totholzreichere Standorte nicht bevorzugt aufgesucht wurden, möglicherweise da mit einem Totholzvolumen von 27 m^3 pro ha dieser Faktor im Untersuchungsgebiet generell keine limitierende Habitatvariable darstellt.

INTRODUCTION

Floodplain forests are among the most productive ecosystems in Europe while constituting one of the most endangered habitats (Spitznagel 1990). Most regularly flooded alluvial forests in central Europe have become reduced to tiny fragments as a result of river regulation (Flade 2001). One of the last big unspoilt floodplains in central Europe is found in the Donauauen National Park, which stretches from Vienna to Bratislava. The national park supports a high diversity of animal and plant species, including over 100 species of breeding birds (NP Donauauen 2008). Eight out of the ten European woodpecker species occur here (G. Frank, unpublished data, Wichmann et al. 2009). As habitat specialists (association with old growth forest, deadwood etc.), woodpeckers are suitable as indicator species, enabling inferences about the ecological status and naturalness of forests (Scherzinger 1982, Roberge and Angelstam 2006). Thus, the coexistence of several woodpecker species indicates naturally dynamic forest conditions (e.g. old trees, deadwood and high structural diversity with natural edges and openings; Angelstam and Mikusiński 1994, Mikusiński and Angelstam 1997). Floodplain forests are prime habitat for several species, and *Dendrocopos minor*, *D. medius*, *Picus viridis* and *P. canus* are considered umbrella species for floodplain forests (Flade 1994).

The aim of this study was to analyse population densities and habitat use of woodpeckers in an 11 km^2 study area in the Donauauen National Park, which incorporates both regularly flooded softwood alluvial forest and occasionally to never flooded hardwood forest. Here, up to five woodpecker species may occur within small areas, indicating high quality habitat offering a diversity of resources. One important aspect of habitat quality for woodpeckers is the amount of deadwood (e.g. Olsson 1992, Angelstam and Mikusiński 1994, Pechacek

1995, Pasinelli 2000, Blume 2001, Miranda and Pasinelli 2001, Manton et al. 2005, Roberge et al. 2008). Therefore, deadwood volume and number of snags were recorded at reference points and compared with woodpecker localities.

Furthermore, effects of tree species composition, stand age, and the length of water and forest edges on the occurrence and abundance of woodpeckers were analysed. The five woodpecker species included in this study may differentially respond to these habitat variables. The generalist and ubiquist Great Spotted Woodpecker *Dendrocopos major* (Michalek and Miettinen 2003) occurs at high densities throughout the national park. A total of 5-7% of the Austrian population of the Middle Spotted Woodpecker *D. medius* (Annex 1 of the EU Birds Directive) breed in the IBA (Important Bird Area) "Danube floodplains east of Vienna", making it an area of national importance for this species (Teufelbauer and Frank in prep.). *D. medius* is bound to trees with a rough bark and crevices in which it forages mainly by probing and gleaning (Jenni 1983, Pettersson 1993, Pasinelli and Hegelbach 1997) and reaches its highest densities in oak-dominated broadleaf forests (Michalek et al. 2001). A species of old deciduous woodland rich in deadwood is the Lesser Spotted Woodpecker *D. minor* (e.g. Olsson et al. 1992, Wiktander et al. 1992, Angelstam and Mikusiński 1994, Angelstam et al. 2004, Gorman 2004). Floodplain forests constitute optimal habitat for this species, which shows a preference for softwood trees (Flade 1994, 2001; Spitznagel 1990, Höntsch 2001, Miranda and Pasinelli 2001). The Black Woodpecker *Dryocopus martius* (EU Birds Directive, Annex 1) is widespread in Europe from sea level to the timberline. It shows much flexibility with regard to tree type, tree species composition and tree age and can occur in nearly all forest types with sufficient old-growth stands, interspersed meadows and suitable cavity trees (Glutz von Blotzheim and Bauer 1994; Gorman 2004). The Green Woodpecker *Picus viridis* (SPEC 2) inhabits semi-open habitat mosaics that include old stands and meadows or pastures where it forages predominantly for ants (Flade 1994, Glutz von Blotzheim and Bauer 1994, Gorman 2004). Two additional woodpecker species, *D. syriacus* and *Picus canus*, also occurring in the national park were not included in the study. The first species does not tend to inhabit forest but more open habitat (Glutz von Blotzheim and Bauer 1994); the latter was not recorded in the study area. Another species of the family Picidae, the Wryneck (*Jynx torquatus*), was not considered due to its different life style (migratory; Glutz von Blotzheim and Bauer 1994) and taxonomic affiliation (subfamily Jynginae; Webb and Moore 2005).

METHODS

Study area

The study was conducted in the Donauauen National Park near Orth an der Donau, Lower Austria, approximately 15 km southeast of Vienna. The area is designated both as Site of Community Interest and as Special Protection Area according to EU law (http://www.umweltdachverband.at/fileadmin/user_upload/pdfs/Natura_2000_Juni_08.pdf). Furthermore, it is considered an Important Bird Area (IBA) by Birdlife (Teufelbauer and Frank in prep.) Following regulation of the Danube in the 19th century, a dyke was constructed between 1882 and 1905, which intersects the forest in an east-westerly direction (Wösendorfer and Leberl 1987). The river's natural flow dynamics are possible up to the dyke, so that frequently flooded riparian forests are still present. Ash *Fraxinus excelsior*, white poplar *Populus alba*, hybrid poplar *P. x canadensis* and oak *Quercus* species are the dominant tree species in 18%, 18%, 14% and 10% the study area, respectively. We differentiate between 'softwood', early-successional forests (composed of *P. alba*, *P. x canadensis*, *P. nigra*, *Salix* sp. and *Alnus* sp.) in areas prone to flooding, and 'hardwood', late-successional forests (*Quercus* sp., *Acer* sp*., Fraxinus excelsior*, *Tilia* sp*., Ulmus* sp*.*) in less frequently flooded areas. In total, 60% of the stands are aged below 60 years, 95% below 90 years; maximum stand age is 160 years (1.3%). Since the national park's foundation in 1996, logging has largely ceased (although timber is still exploited at a small scale). Deadwood is left to remain (unless posing a potential danger along roads), autochthonous vegetation and natural water dynamics are promoted, and some roads have been abandoned (Teufelbauer and Frank in prep., C, Baumgartner pers. comm.). The area lies in the Pannonian climate zone, the warmest and driest region in Austria, with high temperatures in summer (average temperature in July: 19°C) and cold winters (average temperature in January: -1 to -3°C). Evaporation considerably exceeds precipitation (500-700 mm) (PGO 1985).

The study area covers 1,170 ha. A total area of 906 ha (78%) is forested; the rest are meadows, open water, roads and the dyke. Surrounding the study area are agricultural fields, meadows and settlements (Orth an der Donau and Mannsdorf an der Donau).

Woodpecker and habitat survey

Woodpeckers were mapped between 26 February–24 April 2008, which corresponds to the peak of territorial activity for all species studied (Spitznagel 1993, Südbeck et al. 2005). A

rationalised territory mapping approach with three visits was chosen (cf Flade 1994, Frank 2002, Weissmair and Rubenser 2009). The study area was divided into easily recognizable study plots of around 70 ha, based on habitat features such as sidearms and roads. Each plot was visited three times between 26 February and 24 April 2008, following an irregular transect route, with transects around 150 m apart from each other. Study plots in softwood and in hardwood alluivial forest were visited alternately in order to avoid biases stemming from temporal clustering of transect runs in individual habitat types. Woodpecker surveys were carried out when weather conditions were suitable (i.e. no heavy rain or strong wind), starting at sunrise and lasting up to 4.5 hours.

The mapping was based on both visual and acoustic registrations. At each registration, the own location was marked on the GPS device, the direction of the bird determined using a digital compass and the distance estimated. Although recommended by several authors for some of the study species (e.g. Spitznagel 1993, Miranda and Pasinelli 2001, Kosiñski et al. 2004, Südbeck et al. 2005), no playback equipment was used, so as not to bias the data on habitat utilisation and behaviour (Frank and Hochebner 2001).

Data on microhabitat use were only recorded for visually registered birds (*D. major*, *D. medius*, *D. minor*, *D. martius*; sightings of *P. viridis* too infrequent) which spent at least several seconds in a "meaningful" behaviour (e.g. foraging, territorial behaviour, interaction with a mate). Relevant parameters for subsequent analysis are tree condition (living, dying, dead), deadwood volume (lying and standing deadwood of at least 10 cm mid-diameter/DBH) and number of snags (≥10 cm DBH) in a circle of 8 m radius. "Dying" trees were defined as living trees with dead branches.

In addition to the woodpecker survey, habitat data were collected at 119 reference points, which were a subset of reference points used in the 1998/1999 forest inventory by the Austrian Forestry Agency (ÖBF 1999). The reference points were situated in a regular grid at the intersections of 200x400 m. If a reference point was not situated in forest, it was skipped and the next forested point (100 m north or south) was used. Of the habitat data collected, only tree condition, deadwood volume and number of snags were used for analyses. One outlier with exorbitantly high amounts of deadwood (36.94 m^3; mean ± SD: 0.88 ± 3.54 m^3 [corresponding to 1838.17 m^3/ ha; mean ± SD: 44.15 m^3/ ha ± 177.05]) was excluded from the analysis.

Data management and analysis

The waypoints saved on the GPS handheld were transferred to the computer via the Garmin programme MapSource Version 6.10.2, and then converted to ArcMap format. Further map-based analysis was carried out with ESRI ArcMap 9.2. Woodpecker locations were entered manually in ArcMap by measuring distance and direction from the respective waypoints.

Analyses are based on a 400 x 400 m grid (16 ha), enabling relatively detailed information about habitat features. Properties of each grid square were derived from raw data from the 1998/1999 forest inventory (ÖBF 1999), which gives detailed information about dominant tree species and stand age. Based on the prevalent vegetation communities, each grid square was assigned to either softwood (22 grid squares) or hardwood alluvial forest (66 grid squares). Percent cover of the most important dominant tree species (minimum cover 5% of the study area) and of stands aged ≥60 years were calculated for each cell. The lengths of water and forest edges were extracted from an aerial photograph.

Following the recommendations by Südbeck et al. (2005), a territory was assumed when (1) territorial behaviour was observed twice at least seven days apart, (2) territorial behaviour and one adult bird were observed at least seven days apart, or (3) a pair or cavity construction was observed at least once.

Statistical analysis was conducted using Statistica 7.1. Analyses of habitat use are based on the density of individual birds, not on the number of territories. For the three *Dendrocopos* species, the maximum number of individuals of each species observed per grid square in any one of the three visits was used as dependent variable (converted to number of individuals per ha of forest), in order to take account of temporal fluctuations in activity of the different species and to avoid pseudoreplication. Mann-Whitney U tests were used to test for differences in density between softwood and hardwood alluvial forest. Due to their lower densities, presence/absence data were used for *D. martius* and *P. viridis*. Fisher's tests were conducted to test for differences in occurrence between softwood and hardwood forest. The amount of deadwood at woodpecker localities (*D. major*, *D. medius*, *D. minor*, *D. martius*, not sufficient data for *P. viridis*) and at reference points was compared using Kruskal-Wallis tests. Chi^2 tests were used to test for differences in tree vigour (living, dying, dead) between woodpecker localities and reference points.

Generalized linear models (GLMs) were developed using normalised and standardised habitat variables. Loglinear models were calculated to assess the effects of habitat variables

on the abundance of the *Dendrocopos* species. To relate presence-absence data of the rarer larger species, *P. viridis* and *D. martius*, to habitat variables, we used binomial GLMs with logit link. Wald statistics for the GLMs were used to detect univariate effects of habitat variables on abundance and occurrence of the species. Separate analyses were conducted to test for effects of dominant tree species and of structural habitat variables – TreeAge60+ (proportion of stands older than 60 years per grid square), Forest Edge (boundary length between forest and meadows, fields or settlements per grid square), and Water Boundary (boundary length between forest and sidearms, not including the Danube, per grid square). To take account of some intercorrelations between predictor variables, Akaike´s information criterion (AIC) was used to select the best models (lowest AIC). For all models within 4 AIC values of the model with the lowest AIC, AIC weights were calculated as a relative measure of support for the model. The higher the AIC weight, the higher is the relative likelihood of a model compared with competing models (Wagenmakers and Farrell 2004).

RESULTS

Woodpecker abundances in different habitat types

Both abundance and species richness of woodpeckers are very high throughout the study area (Figure 1). On average, 3.0 species per grid square (16 ha) were recorded (for comparison with published data: the mean number of species per 25 ha was 3.47). *D. major* was the most abundant woodpecker species (542 territories), occurring at very high densities of 5.98 territories/10 ha forest (Figure 1a, Table 1). Territory density was higher in hardwood alluvial forest (mean 8 territories/10 ha) than in softwood alluvial forest (4.68 territories/10 ha), but abundance did not differ significantly between the two habitat types (1.2 vs. 1.03 bird registrations per ha forest, Mann Whitney U test: $U = 636.5$, $p = 0.388$). The total density of *D. medius* was much lower (0.28 territories/10 ha) than *D. major* density (Figure 1b). A higher number of territories was found in hardwood forest (0.29 territories/10 ha forest) than in softwood forest (0.10 territories/10 ha forest), although the difference in abundance between the two forest types was not significant (softwood: 0.07 registrations per ha forest, hardwood: 0.13 registrations per ha forest; Mann Whitney U Test: $U = 585$, $p = 0.174$). In contrast, *D. minor* with a total density of 0.20-0.24 territories/10 ha occurred less frequently in hardwood (0.12 territories/10 ha forest) than in softwood alluvial forest (0.36 territories/10 ha forest). An aggregation of *D. minor* observations around water-ways can be seen in Figure 1c. Significantly more Lesser Spotted Woodpecker registrations were in softwood alluvial forest (0.16 registrations per ha forest) than in hardwood forest (0.07 registrations per ha

forest, Mann Whitney U test: U = 391, p = 0.001). All 13 *P. viridis* territories were located in hardwood alluvial forest near meadows, fields or the dyke (Figure 1d). A Fisher's test (two-tailed) comparing the distribution of occupied vs. unoccupied grids in both forest types showed a significant preference for hardwood (p = 0.019). *D. martius* (five territories) equally colonized hardwood as well as softwood forest (Fisher's test two-tailed: p = 0.806; Figure 1e).

Table 1. Estimated total number of territories in the study area and breeding density per 10 ha calculated for all five recorded woodpecker species separately for total study area (1,170 ha, including open land, water-ways etc.) and total forest area (906 ha).
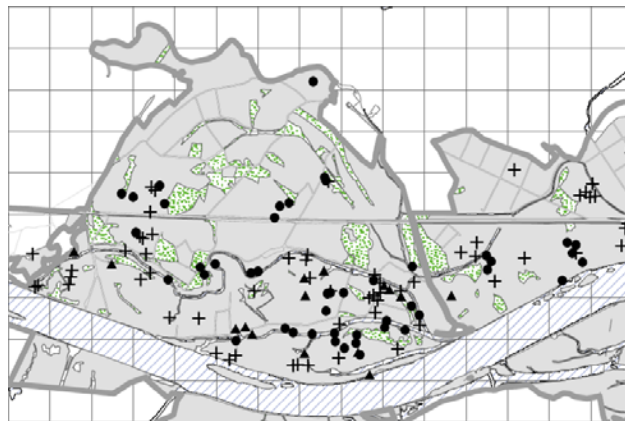
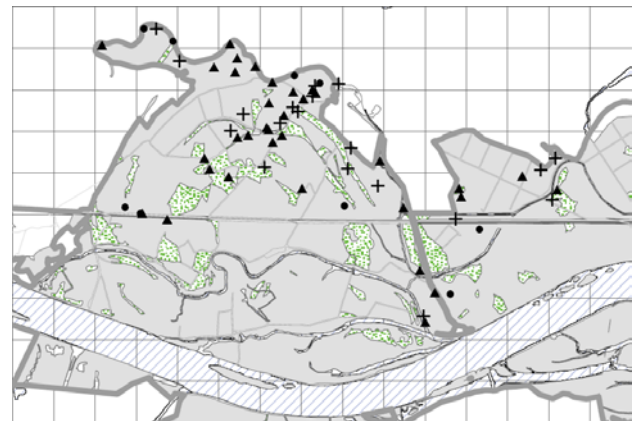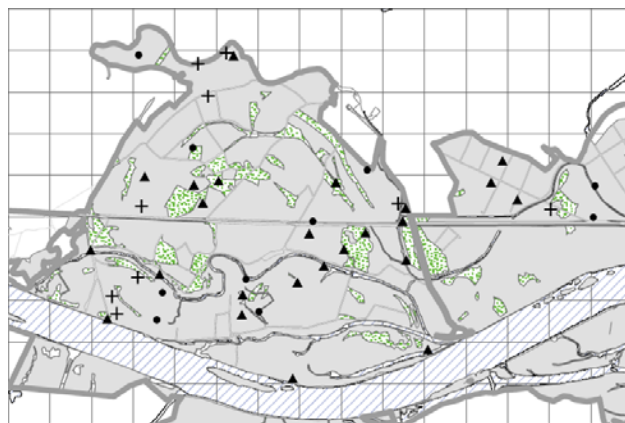| Species	Total number of territories	Territories/10 ha	Territories/10 ha forest
D. major	542	4.67	5.98
D. medius	25	0.22	0.28
D. minor	19(-23)	0.16-0.20	0.20-0.24
D. martius	5	0.04	0.06
P. viridis	13(-14)	0.11-0.12	0.14-0.15
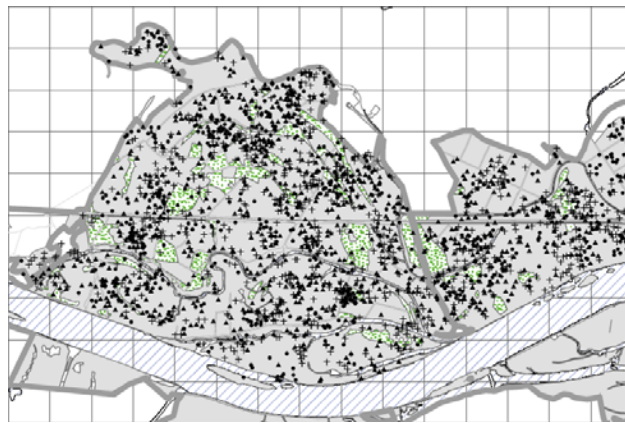
(a) *D. major*
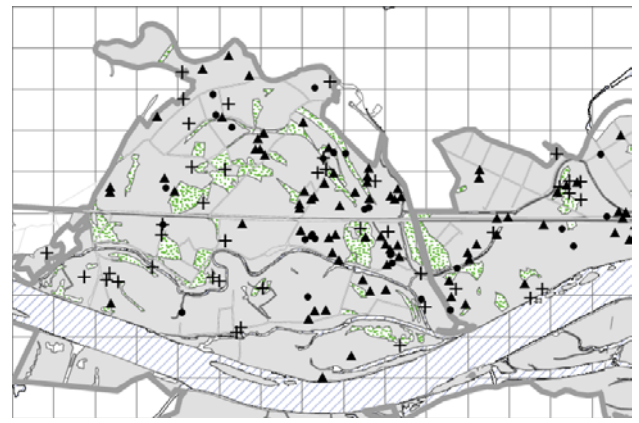
(b) *D. medius*

(c) *D. minor*

(d) *P. viridis*

(e) *D. martius*

Habitat types in study area

- forest
- meadow
- water
- National Park boundary
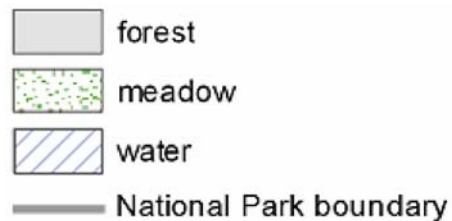
Figure 1. All registrations of *Dendrocopos major* (a), *D. medius* (b), *D. minor* (c), *Picus viridis* (d) and *Dryocopus martius* (e). Survey rounds are indicated by different symbols: 26 February–18 March 2008 (triangular), 19 March–4 April 2008 (cross) and 5 April–24 April 2008 (dot).

Deadwood

The average volume of deadwood in the study area was 27.84 m^3/ha; the mean number of snags (≥10cm DBH) was 15.17 per ha. In softwood alluvial forest, the mean deadwood

volume was 40.66 m³/ha, in hardwood forest it was 22.35 m³/ha. The difference between the two forest types was almost significant (Mann Whitney U test: U = 987, p = 0.064). The mean number of snags per ha did not differ significantly between softwood and hardwood alluvial forests (12.1 and 16.5 snags/ha, respectively; Mann-Whitney U test: U = 1206, p = 0.673).

Chi² tests comparing the proportion of living, dying and dead trees used by woodpeckers to availability showed that dead and dying trees are highly selected by all species (Chi² tests: *D. major*: χ^2 = 257.8, p < 0.001; *D. medius*: χ^2 = 86.9, p < 0.001; *D. minor*: χ^2 = 102.4, p < 0.001; *D. martius*: χ^2 = 103.5, p < 0.001; Figure 2; no observation data for *P. viridis*). In spite of that, Kruskal Wallis Tests showed no significant difference between woodpecker localities and reference points regarding deadwood volume (H = 6.85, p = 0.144) or number of snags (H = 5.23, p = 0.236) in a circle of 8 m radius.
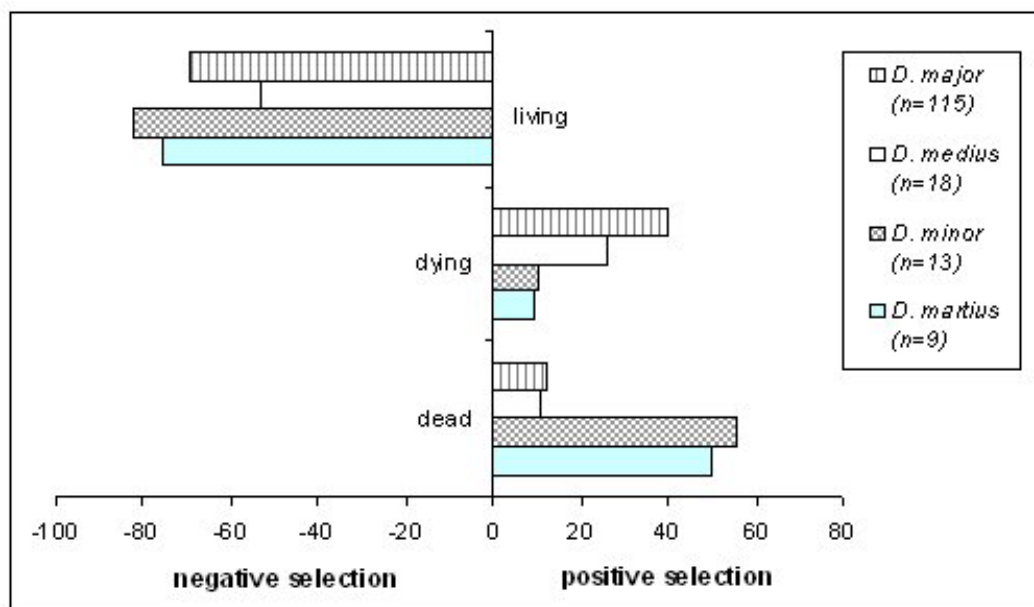

Figure 2. Selection of living, dying and dead trees by woodpeckers and percent deviance from availability.

Univariate results from Wald statistics in the GLMs to test for effects of structural habitat variables and of tree species on abundance and occurrence of the species are presented in Table 2; results from AIC model selection in Tables 3-11.

Table 2. Wald statistics from univariate analyses of predictors in the GLMs. Significant effects at a level of α = 0.05 are indicated by one asterisk (*); at a level of α = 0.001 by three asterisks (***). Positive and negative effects are indicated by (+) and (-), respectively.

Habitat variables	Woodpecker species				
	D. major	*D. medius*	*D. minor*	*P. viridis*	*D. martius*
Maple	5.87	1.79	0.65	1.82	4.61* (+)
Oak	0.05	26.13*** (+)	3.42	1.39	4.41* (+)
Ash	0.37	14.83*** (+)	19.10*** (+)	3.35	0.09
Alder	0.10* (+)	3.07	21.43*** (+)	0.40	0.24
Hybrid Poplar	4.62	0.07	4.13* (+)	7.79*** (-)	5.04* (+)
Willow	1.96	0.70	15.49*** (+)	4.25* (-)	0.40
White Poplar	1.03	1.54	25.84*** (+)	0.49	3.94* (+)
Water Boundary	0.31	3.88*	10.58*** (+)	0.96	4.55* (+)
Forest Edge	1.98	0.10	3.13	5.34* (+)	0.45
TreeAge60+	9.37*** (+)	44.63*** (+)	3.56	2.11	0.95

The Great Spotted Woodpecker significantly selected forest stands older than 60 years. TreeAge60+ was the only structural habitat variable significantly affecting abundance in univariate analyses (Table 2) and was included in all of the best models according to AIC (Table 3). A model including only TreeAge60+ had an AIC Weight of 0.22, indicating that the model has a 22% chance of being the best model in the model set. This is only 1% lower than the maximum AIC Weight (0.23) of a model including Forest Edge in addition to TreeAge60+.

None of the GLMs testing for effects of tree species on *D. major* abundance was significant. A very large number of models (64) were within the range of the threshold of 4 AIC values, with a variable composition of predictor variables, indicating that none of the tree species had a major effect on *D. major* distribution. Only a slight positive effect of alder was found, which featured in most of the "best" models and was significant in univariate analyses (Table. 2).

Table 3. Summary of Akaike model selection for the effects of structural habitat variables on the abundance of *D. major* (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Forest Edge, TreeAge60+	156.5	0.23	0.002
TreeAge60+	156.6	0.22	0.001
Water Boundary, Forest Edge, TreeAge60+	158.2	0.10	0.006
Water Boundary, TreeAge60+	158.5	0.08	0.006

The best structural habitat model for *D. medius* abundance (AIC Weight = 0.23) includes TreeAge60+ and Water Boundary (Table 4), both of which were positively associated with *D. medius* density. The Middle Spotted Woodpecker exhibited a positive selection for oak and ash, which are included in all of the "best" models of tree species selection. The highest AIC Weight (0.23) was obtained for a model including oak, ash and maple, but the AIC Weight was only little lower for a model including only oak and ash (0.20; Table 5).

Table 4. Summary of Akaike model selection for the effects of structural habitat variables on the abundance of *D. medius* (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Water Boundary, TreeAge60+	-89.6	0.23	<0.001
Water Boundary, Forest Edge, TreeAge60+	-87.7	0.09	<0.001
TreeAge60+	-87.2	0.07	<0.001

Table 5. Summary of Akaike model selection for the effects of tree species on the abundance of *D. medius* (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Maple, Oak, Ash	-86.1	0.23	<0.001
Oak, Ash	-85.9	0.20	<0.001
Maple, Oak, Ash, Alder	-85.7	0.18	<0.001
Maple, Oak, Ash, Alder, White Poplar	-85.4	0.16	<0.001
Oak, Ash, White Poplar	-85.2	0.15	<0.001
Oak, Ash, Alder	-85.2	0.14	<0.001
Oak, Ash, Alder, White Poplar	-85.1	0.14	<0.001
Maple, Oak, Ash, White Poplar	-85.0	0.13	0.001
Oak, Ash, Hybrid Poplar	-84.9	0.13	<0.001
Maple, Oak, Ash, Hybrid Poplar	-84.9	0.13	0.001
Maple, Oak, Ash, Willow	-84.3	0.10	0.001
Maple, Oak, Ash, Alder, Willow	-84.3	0.09	0.001
Oak. Ash, Willow	-84.1	0.08	0.001
Maple, Oak, Ash, Alder, Hybrid Poplar	-84.1	0.08	0.001
Maple, Oak, Ash, Alder, Willow, White Poplar	-84.0	0.08	0.001

Oak, Ash, Alder, Hybrid Poplar	-84.0	0.08	0.001
Oak, Ash, Alder, Willow	-83.8	0.07	0.001
Oak, Ash, Hybrid Poplar, White Poplar	-83.6	0.07	0.001
Oak, Ash, Alder, Willow, White Poplar	-83.6	0.07	0.001
Maple, Oak, Ash, Alder, Hybrid Poplar, White Poplar	-83.4	0.06	0.001
Maple, Oak, Ash, Hybrid Poplar, White Poplar	-83.4	0.06	0.001
Oak, Ash, Alder, Hybrid Poplar, White Poplar	-83.4	0.06	0.001
Oak, Ash, Willow, White Poplar	-83.3	0.06	0.001
Maple, Oak, Ash, Willow, White Poplar	-83.3	0.06	0.001
Maple, Oak, Ash, Hybrid Poplar ,Willow	-83.1	0.05	0.001
Oak, Ash, Hybrid Poplar, Willow	-83.1	0.05	0.001
Maple, Oak, Ash, Alder, Hybrid Poplar, Willow	-82.6	0.04	0.001
Oak, Ash, Alder, Hybrid Poplar, Willow	-82.5	0.04	0.002

For *D. minor*, a model including Water Boundary, Forest Edge and TreeAge60+ had the strongest support, with an AIC Weight more than twice as high as that of a model containing only Water Boundary (0.23 and 0.11, respectively; Table 6). In univariate analyses, Water Boundary was the only significant variable, but significance was only just missed by the variables Forest Edge (p = 0.076) and TreeAge60+ (p = 0.059; Table 2). While *D. minor* abundance was clearly positively related to the length of the water boundary, there was a slight negative relationship with forest edge density. *D. minor* tended to select stands younger than 60 years.

Table 6. Summary of Akaike model selection for the effects of structural habitat variables on the abundance of *D. minor* (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Water Boundary, Forest Edge, TreeAge60+	-111.5	0.23	0.002
Water Boundary	-110.2	0.11	0.002
Water Boundary, TreeAge60+	-110.0	0.11	0.003
Water Boundary, Forest Edge	-109.4	0.08	0.004
TreeAge60+	-100.8	0.00	0.550
Forest Edge	-100.4	0.00	0.887
Forest Edge, TreeAge60+	-98.8	0.00	0.833

Regarding tree species selection, *D. minor* significantly selected ash, alder, willow and white poplar, which were included in all of the best AIC models, as well as hybrid poplar (Tables 2 and 7). The highest explanatory power (AIC Weight = 0.23) was achieved by a model including ash, alder, willow, white poplar, hybrid poplar and oak, but support was nearly as strong for a model without oak (AIC Weight = 0.21).

Table 7. Summary of Akaike model selection for the effects of tree species on the abundance of *D. minor* (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Oak, Ash, Alder, Hybrid Poplar, Willow, White Poplar	-134.4	0.23	<0.001
Ash, Alder, Hybrid Poplar, Willow, White Poplar	-134.2	0.21	<0.001
Maple, Ash, Alder, Hybrid Poplar, Willow, White Poplar	-133.4	0.14	<0.001
Maple, Ash, Alder, Willow, White Poplar	-133.3	0.13	<0.001
Maple,Oak, Ash, Alder, Hybrid Poplar, Willow,White Poplar	-132.9	0.11	<0.001
Maple, Oak, Ash, Alder, Willow, White Poplar	-131.3	0.05	<0.001
Ash, Alder, Willow, White Poplar	-131.2	0.05	<0.001

Forest edge density is the most influential factor affecting *P. viridis* occurrence. A model that contained only Forest Edge (AIC Weight = 0.22) was nearly as well supported as a model including Forest Edge and TreeAge60+ (AIC Weight = 0.23; Table 8), the latter factor exerting a positive, but non-significant influence.

Table 8. Summary of Akaike model selection for the effects of structural habitat variables on *P. viridis* occurrence (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Forest Edge, TreeAge60+	113.1	0.23	0.004
Forest Edge	113.2	0.22	0.003
Water Boundary, Forest Edge, TreeAge60+	114.2	0.13	0.007
Water Boundary, Forest Edge	114.4	0.12	0.007

P. viridis did not show clear preferences for tree species, with a large number of variables in numerous "best" models (Table 9). Hybrid poplar and willow, the variables in the most likely model according to AIC Weights (0.23), were significantly avoided by *P. viridis* (Table 2).

Table 9. Summary of Akaike model selection for the effects of tree species on *P. viridis* occurrence (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Hybrid Poplar, Willow	109.6	0.23	0.001
Ash, Hybrid Poplar, Willow	109.8	0.20	0.001
Hybrid Poplar	110.2	0.17	0.001
Maple, Ash, Hybrid Poplar, Willow	110.3	0.16	0.001
Maple, Hybrid Poplar, Willow	110.8	0.13	0.001
Oak, Ash, Hybrid Poplar, Willow	111.1	0.11	0.002
Maple, Oak, Ash, Hybrid Poplar, Willow	111.4	0.09	0.002

Ash, Hybrid Poplar	111.4	0.09	0.002
Alder, Hybrid Poplar, Willow	111.4	0.09	0.002
Oak, Hybrid Poplar, Willow	111.4	0.09	0.002
Hybrid Poplar, Willow, White Poplar	111.6	0.09	0.002
Ash, Alder, Hybrid Poplar, Willow	111.7	0.08	0.002
Maple, Hybrid Poplar	111.8	0.08	0.002
Ash, Hybrid Poplar, Willow, White Poplar	111.8	0.08	0.002
Alder, Hybrid Poplar	111.9	0.07	0.002
Hybrid Poplar, White Poplar	112.0	0.07	0.002
Oak, Hybrid Poplar	112.1	0.06	0.002
Maple, Ash, Alder, Hybrid Poplar, Willow	112.2	0.06	0.003
Maple, Ash, Hybrid Poplar, Willow, White Poplar	112.2	0.06	0.003
Maple, Oak, Hybrid Poplar, Willow	112.6	0.05	0.003
Maple, Alder, Hybrid Poplar, Willow	112.6	0.05	0.003
Oak, Ash, Alder, Hybrid Poplar, Willow	112.7	0.05	0.004
Maple, Hybrid Poplar, Willow, White Poplar	112.7	0.05	0.004
Maple, Ash, Hybrid Poplar	112.8	0.05	0.004
Oak, Ash, Hybrid Poplar, Willow, White Poplar	112.9	0.04	0.004
Maple, Oak, Ash, Hybrid Poplar, Willow, White Poplar	113.0	0.04	0.004
Ash, Alder, Hybrid Poplar	113.1	0.04	0.004
Maple, Oak, Ash, Alder, Hybrid Poplar, Willow	113.1	0.04	0.004
Oak, Alder, Hybrid Poplar, Willow	113.1	0.04	0.004
Oak, Ash, Hybrid Poplar	113.2	0.04	0.004
Ash, Hybrid Poplar, White Poplar	113.4	0.03	0.005
Alder, Hybrid Poplar, Willow, White Poplar	113.4	0.03	0.005
Oak, Hybrid Poplar, Willow, White Poplar	113.4	0.03	0.005
Maple, Alder, Hybrid Poplar	113.5	0.03	0.005
Ash, Alder, Hybrid Poplar, Willow, White Poplar	113.6	0.03	0.005

The best-supported model of structural habitat variables (AIC Weight = 0.23) for *D. martius* included only Water Boundary (Table 10), which had a positive effect on the occurrence of the species.

Table 10. Summary of Akaike model selection for the effects of structural habitat variables on *D. martius* occurrence (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Water Boundary	119.6	0.23	0.017
Water Boundary, TreeAge60+	120.4	0.15	0.032
Water Boundary, Forest Edge	120.9	0.12	0.041
Water Boundary, Forest Edge, TreeAge60+	121.9	0.07	0.061
Forest Edge	123.5	0.03	0.180

Maple, oak, hybrid poplar and white poplar were significantly selected by *D. martius* (Table 2)*,* and all four tree species were included in the model that had the most support (AIC weight = 0.23; Table 11).

Table 11. Summary of Akaike model selection for the effects of tree species on *D. martius* occurrence (all models within 4 AIC values of the model with the lowest AIC values presented).

Variables	AIC	AIC Weight	p
Maple, Oak, Hybrid Poplar, White Poplar	118.1	0.23	0.011
Maple, Oak, Hybrid Poplar, Willow, White Poplar	119.9	0.10	0.020
Maple, Oak, Alder, Hybrid Poplar, White Poplar	120.0	0.09	0.021
Maple, Oak, Ash, Hybrid Poplar, White Poplar	120.1	0.08	0.022
Maple, Oak, Hybrid Poplar	120.2	0.08	0.029
Maple, Hybrid Poplar, White Poplar	120.7	0.06	0.035
Oak, Hybrid Poplar, White Poplar	120.7	0.06	0.036
Maple, Oak, Alder, Hybrid Poplar, Willow, White Poplar	121.7	0.04	0.035
Maple, Oak, Ash, Hybrid Poplar, Willow, White Poplar	121.8	0.04	0.036
Maple, Oak, Ash, Hybrid Poplar	121.9	0.04	0.052
Maple, Oak, Ash, Alder, Hybrid Poplar, White Poplar	122.0	0.03	0.039
Maple, Hybrid Poplar	122.0	0.03	0.071

DISCUSSION

In our study area with up to five co-occurring species per 16 ha grid square (mean: 3 species per 16 ha; 3.47 species per 25 ha), high woodpecker species richness is supported within small areas, indicating high habitat diversity and habitat quality (Angelstam and Mikusiński 1994, Mikusiński and Angelstam 1997). For comparison, in a floodplain forest along the Upper Rhine, the mean number of woodpecker species per 25 ha was 2.7 (Spitznagel 1990); in mountain forests in the Bavarian Forest National Park, it was only 1.5 (Scherzinger 1982). Considering the large size of the study area (11.7 km^2), densities of *D. major*, *D. minor*, *D. martius* and *P. viridis* are remarkably high, as it is a well-known phenomenon that estimated densities are affected by the size of the sample area (Spitznagel 1993, Gaston et al. 1999). Generally, higher densities tend to be reported from studies in smaller areas (Gaston et al. 1999). Due to the large home ranges of woodpeckers, densities are often overestimated when only small study areas are considered (Spitznagel 1993, Kosiñski and Winiecki 2005). Thus, to assess variability in abundance of woodpeckers, data from medium-sized (1-15 km^2 of woodland) and very large study areas (over 15 km^2) should be more taken into account (Spitznagel 1993). As comparability with small-scale studies is poor, a comparison of our results with published data will focus on those with similarly large study areas.

A further aspect leading to differences between studies is the mode of calculating density, which may be based on the total area surveyed (crude density) or only on suitable habitat for the species (ecological density, e.g. Gaston et al. 1999, Weiß 2003, Kosiñski and Winiecki 2005). In this paper, we provide estimates of crude and ecological densities (referring to total forested area) for all woodpecker species.

Great Spotted Woodpecker

The recorded ecological density of *D. major* (5.98 territories per 10 ha of forest) was close to maximum densities reported (e.g. between 5.1 and 6.6. breeding pairs/10 ha in alluvial ash/elm forests, ancient alder forests, oak-hornbeam forests or parks; Cramp 1985, Glutz von Blotzheim and Bauer 1994, Pavlik 1999). The density of Great Spotted Woodpeckers is considered to be a good indicator of habitat quality in forests (Weiss 1998). Densities above 1.3 pairs/10 ha normally only occur in very favourable habitat with old growth forest and dead and decaying trees (Glutz von Blotzheim and Bauer 1994); typical maxima in Switzerland and Germany lie at around 2 pairs/10 ha (Cramp 1985). In alluvial forest in the Traun-Donau-Auen in Upper Austria, densities of 1.8-2 territories/10 ha were found (Weissmair and Rubenser 2009); in wet deciduous forest at the Innere Unterspreewald (Germany) density was 0.67 pairs/10 ha forest (Noah 2000). Extremely high *D. major* densities were reported from small study areas, e.g. 5.5-7.8 territorries/10 ha in mixed oak stands in the Vienna Woods (Michalek et al. 2001) and 7.2-7.6 territories/10 ha in parks or denser park-like forests in Berlin and Vienna (Winkler et al. 1995).

The high population density throughout the study area indicates ideal conditions for *D. major*. However, as estimates are based on suspected breeding (territorial behaviour) only, it cannot be ruled out that breeding density is overestimated, as unpaired Great Spotted Woodpeckers also drum (Blume 1961). Also, *D. major* density may vary greatly between years (Pavlik 1999). Large scale studies from old deciduous riverine forest in Poland found densities of 1.2 and 2.4 pairs/10 ha in two consecutive years (Kosiñski and Kempa 2007).

Due to the high adaptability of *D. major*, habitat selection of this species cannot be generalised for its entire range, and diet depends to a large part on availability (Cramp 1985). Our results emphasise the generalist lifestyle of *D. major* (Michalek and Miettinen 2003). In accordance with results by Wesolowski and Tomialojc (1986), Spitznagel (1990) and Noah (2000), the species occupied all forest types in the study area. The single significant predictor of *D. major* density was the proportion of forest stands aged ≥60 years. Availability of old trees, which possess a richly fissured bark and harbour a rich arthropod fauna

(Kosiñski 2006), as well as being sufficiently large for cavity construction (e.g. Kosiñski and Winiecki 2004), is one of the key elements determining *D. major* abundance (Spitznagel 1990, Miranda Botello-Gut 2006, Kosiñski 2006, Kosiñski and Kempa 2007). Possibly, one factor contributing to the high densities in our study area might be winter food supplies. Walnuts, hornbeam seeds and hazel nuts, which are abundant in the study area, are staple winter diet for *D. major* in many regions (Cramp 1985, Winkler et al. 1995, Michalek and Miettinen 2003). In contrast, *D. medius*, which occurred at relatively low densities compared to its larger congener, is mainly insectivorous also in winter (Jenni 1983, Glutz von Blotzheim and Bauer 1994).

D. major is a generalistic species with respect to habitat selection, prey utilisation and foraging behaviour. Therefore, it has been suggested that the distribution of Great Spotted Woodpeckers may be affected mainly by the availability of nest sites rather than by food (Kosiñski and Winiecki 2004). Given the high amounts of dead and dying trees, suitable cavity trees may not be severely limiting in the study area. Deadwood volume and number of snags did not differ between woodpecker localities and reference points, although at a microhabitat level *D. major* was selecting dead and dying trees to a much greater proportion than relative to availability.

Several authors have pointed out the importance of dead wood on living trees for *D. major* (Jenni 1983, Michalek and Miettinen 2003, Miranda Botello-Gut 2006). In the Niderholz forest in the Swiss lowlands, the amount of dead wood on living trees (before foliation) and the availability of old trees ≥36cm DBH (after foliation) were found to be the best predictors of *D. major* habitat use (Miranda Botello-Gut 2006). While the amount of dead branches could not be quantified for our entire study area and was thus not included in the models, our results also point to high importance of dead branches on living trees for the species in early spring. While 18% of trees used by *D. major* were dead, 53% were living with dead branches, and almost two thirds of branches and twigs utilized for foraging or drumming were dead.

It can be speculated that the carrying capacity for *D. major* in the study area has been reached not so much due to a lack of resources but due to intraspecific competition (Kosiñski and Kempa 2007). For instance, it has been found that early paired males have larger territories than unpaired or late paired males and try to enlarge their territories (Michalek unpublished, cited by Michalek and Miettinen 2003). In a forest in north-eastern Switzerland, non-overlapping core areas of Great Spotted Woodpeckers had median sizes of 3.4 ha (Bachmann and Pasinelli 2002), which is twice as large as if the forested area in our study area was equally partitioned between all males.

Middle Spotted Woodpecker

At 0.28 territories/10 ha forest, *D. medius* density was similar to that reported from a 3,873 ha area in the Lobau, the Viennese part of the Donauauen National Park (0.30 territories/10 ha, Wichmann and Frank 2005). This is considerably lower than densities in typical lowland forests, where the majority of density estimates for *D. medius* lie at around 0.7-1.4 territories/10 ha (references in Pasinelli 2003, Jenni 1977); absolute maxima for small areas are 3.9 territories/10 ha in the Vienna Woods (Michalek et al. 2001). Flade (1994) and Weiß (2003) indicate average densities of 0.44-0.46 territories/10 ha for comparatively large study areas in hardwood alluvial forests and ash-alder forests, respectively. In ash-alder forest in the Nature Protection Area Innerer Unterspreewald, density ranged from 0.69-0.8 territories/10 ha forest (Noah 2000). In the Upper Rhine floodplains, *D. medius* density was 0.68 territories/10 ha forest (Spitznagel 1990). Even lower densities than in our study were found in floodplain forest in the Traun-Donauauen in Upper Austria (0.16 territories/10 ha; Weissmair and Rubenser 2009).

Methodologically, one explanation for the comparatively low density of *D. medius* in our study area may be the fact that no playback equipment was used as has been recommended by several authors for this species (Spitznagel 1993, Noah 2000, Kosiñski et al. 2004, Südbeck et al. 2005). Ecologically, the low density can be explained by the young age of the stands (mean: 54 years) and the relatively low proportion of oak-dominated stands (10%). The Middle Spotted Woodpecker is a habitat specialist restricted to mature deciduous forests with rough-barked tree species (Winkler et al. 1995, Pasinelli 2000, Pasinelli 2003). In line with previous studies (Spitznagel 1990, Miranda Botello-Gut 2006, Kosiñski 2006, Müller et al. 2009), oak cover and the proportion of old trees had a major influence on *D. medius* abundance, with significantly higher densities in grid squares with a high proportion of oak and forest stands aged 60 years and above. Furthermore, *D. medius* density was positively affected by the proportion of ash.

Habitats considered suitable for *D. medius* are oak-dominated forests with a minimum age of 60-100 years (Jöbges and König 2001, Pasinelli 2003, Angelstam et al. 2004, Kosiñski and Winiecki 2005), or alder-dominated forest with a minimum age of 60 years (Noah 2000). In oak forests in Germany, the probability of occurrence of *D. medius* was greatest in forest stands older than 94.75 years (Müller et al. 2009). Stands <40 years old tend to be avoided by Middle Spotted Woodpeckers (Kosiñski and Winiecki 2005), and density has also been found to be slightly negatively correlated with middle-aged forest stands (40-80 years, Kosiñski and Winiecki 2005, Kosiñski 2006). Older forests (>120 years, Pasinelli and

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Hegelbach 1997, Kosiñski and Winiecki 2005, Kosiñski 2006; >180 years, Jöbges and König 2001) are strongly preferred; however, in our study area, only 2.4% of stands were 120 years old or older; 19.7% were 80 years or older.

Oak-dominated stands were highly selected by *D. medius*, although oak is the dominant tree species in only about 10% of our study area. Numerous authors have shown a very strong association of the species with oaks (Pasinelli and Hegelbach 1997, Pasinelli 2000, Jöbges and König 2001, Michalek et al. 2001, Pasinelli 2003 and references therein, Steverding 2003, Kosiñski 2006, Müller et al. 2009). Their structural features (rough bark, thick branches, many dead limbs) and the high abundance of arthropods and their larvae make oaks ideal foraging habitat for *D. medius* (Pasinelli and Hegelbach 1997, Michalek et al. 2001). Some authors noted that the abundance of *D. medius* can also be influenced by other typically rough-barked tree species such as black alder, elm, willow and ash (Noah 2000, Zuna-Kratky et al. 2000, Weiß 2003, Pasinelli 2003, Roberge et al. 2008) and may even occur in beech forests without oaks when they are old enough to provide suitable structures and associated arthropod fauna for foraging (Hertel 2003). All deciduous tree species may develop the structures required by *D. medius* for foraging; however, while beeches do not develop these structures until 250-300 years old, this is the case much earlier in oaks, ash, black alder, lime, willow and elm (Jöbges and König 2001).

According to Müller (1982), other tree species do not influence *D. medius* density as long as the density of oaks is sufficient. In our study area, oak density is relatively low and the Middle Spotted Woodpecker additionally exhibited a significant preference for ash, which has been found to be a preferred nesting tree for *D. medius* along with oak in Poland (Kosiñski and Winiecki 2004) and was the second most preferred foraging tree after oak in Switzerland (Jenni 1983). Pasinelli (2000) suggested that rough-barked tree species other than oak play a role only if they are of the right age and occur at high enough densities to provide high arthropod abundances. This may have been the case for ash, which was the most common tree species in the study area. Furthermore, ash cover was positively correlated with tree age, whereas the rough-barked softwoods (willow, alder, poplar) were generally younger than the hardwood stands. An important role of ash has also been found in Switzerland, where *D. medius* was reported from ash-dominated forests with few oaks (Jenni 1977) and in Germany, where similarly high densities as in oak stands were found in alder-ash forest and in homogenous wet alder forest (though most territories also contained old oaks; Noah 2000).

It has been suggested that stands with a low proportion of oaks can be suitable only if deadwood or non-vital trees are available to provide sufficient food (Liesen 1994). Although there is generally a positive association of *D. medius* density with deadwood (e.g. Südbeck and Flade 2004, Weiss 1998, Hertel 2003), the species is not necessarily dependent on deadwood for foraging (Pasinelli and Hegelbach 1997, König 1998, Steverding 2003) and has even been reported breeding in habitat with no or very little standing deadwood (Jöbges and König 2001). However, in our study area, with its young forest age and a relatively low density of oaks, deadwood is probably important by compensating for the lack of old rough-barked trees for foraging (Liesen 1994, Hertel 2003, Pasinelli 2003). Dead and dying trees were highly selected by foraging Middle Spotted Woodpeckers. This concurs with findings from beech forests (Hertel 2003) and alder forests (Weiß 2003) in Germany. Despite selection of dead wood when foraging, *D. medius* did not select stands with higher amounts of deadwood, as deadwood is apparently not limiting in the study area. Similarly, no preference of stands rich in deadwood was found in the Lobau and in the Vienna Woods, which was attributed to the high availability of dead branches in living trees (Wichmann and Frank 2005).

An affinity of Middle Spotted Woodpeckers to forest edge has been shown (Liesen 1994, Angelstam et al. 2004, Kosiñski and Winiecki 2004), which can be explained by higher sun exposure and a related higher availability or accessibility of arthropods (Pasinelli and Hegelbach 1997). In our study, *D. medius* density was not significantly affected by edge density; neither was an effect of light availability found in the Lobau or in the Vienna Woods (Wichmann and Frank 2005). Possibly this plays a greater role in areas with harsher climates. In our study area, we found a weak positive relationship between *D. medius* abundance and the length of water edge. While some authors have found the species to be indifferent to proximity to water (Cramp 1985, references in Pasinelli 2003), others suggested an influence (references in Pasinelli 2003), although as Pasinelli (2003) points out, this may stem from the presence of suitable forest types rather than the water-ways per se.

Lesser Spotted Woodpecker

Several studies have shown that *D. minor* is highly dependent on deciduous trees for foraging and nesting (Alatalo 1978, Cramp 1985, Wesolowski and Tomialojc 1986, Olsson et al. 1992, Wiktander et al. 2001, Mörtberg and Wallentinus 2000). The highest *D. minor* densities have been found in riparian and broad-leaved deciduous forests (Wesolowski and Tomialojc 1986, Spitznagel 1990, Wiktander et al. 1992). At 0.20-0.24 territories/10 ha, Lesser Spotted Woodpecker density is extremely high in our study area. Over large areas,

densities normally do not exceed 0.1 pairs/10 ha (Glutz von Blotzheim and Bauer 1994, Winkler et al 1995), and apart from small-scale studies (<120 ha), higher densities have been reported only from floodplain forest in the Upper Austrian Traun-Donauauen (0.4 territories/10 ha; Weissmair and Rubenser 2009) and from ash-alder stands in the Polish Bialowieza primeval forest (0.3 pairs/10 ha; Wesolowski and Tomialojc 1986). In willow, alder and oak-elm woods in the Rhine floodplains in south-west Germany, densities of 0.16 pairs/10 ha forest were reached (Spitznagel 1990), in swampy forest at the Spreewald, reported densities are 0.16-0.17 pairs/10 ha (Glutz von Blotzheim and Bauer 1994, Noah 2000). A rough estimate of breeding density at the Lower Inn lies at 0.1 pairs/10 ha (Reichholf and Utschick 1972); in the Lüneburger Heide and other forests in Niedersachsen (Germany), density ranged from 0.01 to 0.04 pairs/10 ha (Glutz von Blotzheim and Bauer 1994).

The majority of *D. minor* registrations were near sidearms, where the species occurred mainly in softwood stands (alder, willow, white poplar, hybrid poplar) and ash. The preference for softwoods is in accordance with the literature (e.g. Spitznagel 1990, Flade 1994, 2001, Winkler et al. 1995, Miranda and Pasinelli 2001, Höntsch 2001). A preference for oak and hornbeam stands as reported by other authors (Cramp 1985, Steverding 2003) could not be found. It has been pointed out, however, that prey density on different tree species can vary between years and that the birds' preferences for particular tree species may change accordingly (Wiktander et al. 2001).

Several studies have shown a preference of *D. minor* for riparian sites and wet forest (Spitznagel 1990, Wiktander et al. 1992, Noah 2000, Höntsch 2001, Miranda and Pasinelli 2001). Riparian woods may be preferred because they are often left unmanaged and thus contain high amounts of deadwood (Wiktander et al. 1992). In Germany, orchards and riparian sites were found to be used for cavity construction 2.5-6.5 times as frequent as expected in relation to their area, compared to deciduous forest. This was attributed to both quantity and quality of deadwood at these sites (Höntsch 2001). In non-riverine forests in north-eastern Switzerland, the distribution of *D. minor* could best be predicted by the presence of softwoods, small distances to lakes or rivers, and low elevation, while snags had a negative effect (Miranda and Pasinelli 2001).

Although our models evaluating the importance of habitat variables on the abundance of *D. minor* showed a significant selection of sidearms and softwood trees, they do not support a positive effect of water-ways per se. In the model including only structural habitat variables (Forest Edge, Water Boundary, TreeAge60+) but not tree species, the length of water-ways

was a highly significant predictor of *D. minor* abundance. However, when tree species were included in the model, Water Boundary did not turn out to be significant (results not shown). This lends support to the notion that the association of *D. minor* with water-ways may be an artefact because its favoured tree species are typically associated with water-ways and because of the often good supply of deadwood in the vicinity of water-ways.

A dependence of *D. minor* on deadwood has been reported by numerous authors (Cramp 1985, Olsson et al. 1992, Petterson 1993, Winkler et al. 1995, Wiktander et al. 2001, Kosiñski and Kempa 2007, Roberge et al. 2008). While noting a preference for older forests, Olsson et al. (1992) found that young forests are populated if they contain many snags while old forests lacking snags are not used. Thus, one key element of Lesser Spotted Woodpecker habitats appears to be a good supply of deadwood (Olsson 1992, Miranda and Pasinelli 2001, Wiktander et al. 2001). The commonly reported preference of older forests (Spitznagel 1990, Olsson 1992, Angelstam et al. 2004, Kosiñski and Kempa 2007) could be explained by the fact that old woods generally harbour higher amounts of deadwood. Contradictory, some authors did not find an effect of the presence of old trees on *D. minor* occurrence (Miranda and Pasinelli 2001) or even report a higher number of occurrences in stands <80 years than in 80-140-year-old forest (Spitznagel 1990). We found a negative trend with increasing tree age, which can be explained by the fact that stands of the preferred softwood trees were generally younger than hardwood stands. The data indicate that in our study area tree species composition is a primary determinant of habitat use. No doubt deadwood supply is one key factor (e.g. Olsson 1992, Angelstam and Mikusiński 1994, Manton et al. 2005). Deadwood availability in our study area tended to be higher in the preferred softwood stands, whereby the difference between the softwood and hardwood forest was almost significant. Nonetheless, a comparison of woodpecker localities and reference points showed that stands with higher amounts of deadwood were not significantly selected.

Competition between Great Spotted, Middle Spotted and Lesser Spotted Woodpeckers

Generally, the study area is so densely populated by Great Spotted Woodpeckers that overlap with territories of other species can hardly be avoided. As a result, all Middle and Lesser Spotted Woodpecker territories seem to overlap with some Greater Spotted Woodpecker territories. In contrast, there is little overlap between Middle and Lesser Spotted Woodpecker territories. Reports of interference competition between the similar-sized *D. major* and *D. medius* are rare (Jenni 1983, Bachmann and Pasinelli 2002), even though the two species exhibit similar habitat preferences, reaching their highest densities in old stands

with many oaks (Jenni 1977, Jenni 1983, Michalek et al. 2001, Steverding 2003) and preferring old trees with fissured bark (Jenni 1983, Kosiñski 2006, Michalek et al. 2001). Territories of the two species often overlap (e.g. Jenni 1977, Bachmann and Pasinelli 2002), and space use patterns, home range sizes and breeding densities of Great Spotted and Middle Spotted Woodpeckers are typically independent of one another (Pasinelli 2000, 2003, Wesolowski 2003, Miranda Botello-Gut 2006). The species normally coexist without disputes throughout the year (Jenni 1983).

In our study area, individual observations showed that *D. major* and *D. medius* exhibited very similar preferences for tree species, but tree strata (trunk versus branches) and preferred foraging techniques differed between the species (S. Riemer, unpublished data). Generally, niche differentiation is greater during the winter months (Jenni 1983, Kosiñski and Ksit 2006, Miranda Botello-Gut 2006), when the species deviate more in their use of strata, diameters of branches used, and foraging techniques (*D. major* mainly pecking, *D. medius* mostly gleaning; Jenni 1983). Furthermore, despite similar preferences for tree species and dead branches, the main prey differs between the species, with *D. medius* feeding mainly on trunk- and bark-dwelling arthropods and *D. major* on xylophagous Coleopterans and ants (Jenni 1983). While there appears to be little competition for food, disputes for potential or already used nesting cavities have been observed (Jenni 1983, Bachmann and Pasinelli 2002, Michalek and Miettinen 2003). Kosiñski and Ksit (2007) found distinct nest site characteristics of Great and Middle Spotted Woodpeckers in near-natural riverine forests but convergence in structurally less diverse managed stands, with Middle Spotted Woodpeckers apparently losing out to Great Spotted Woodpeckers during the nest-building phase (Kosiñski and Ksit 2007). Even in very old but structurally simplified managed oak stands, lower *D. medius* densities could in part be explained by interspecific competition for nest sites (Kosiñski and Ksit 2007). Our data do not allow drawing conclusions about nest competition in the study area, although the structurally diverse habitat and high supply of deadwood may make it only a minor issue.

There is little information regarding competition of *D. minor* with the other two *Dendrocopos* species. We found that habitat preferences of *D. minor* differ from those of *D. major* and *D. medius*, which could indicate a lack of competition between the species or competition leading to niche differentiation. Although in optimal habitat, *D. minor* frequently occurs syntopically with *D. major* and *D. medius*, it has been suggested that the distribution of *D. minor* may be affected by *D. major* and *D. medius* distribution due to foraging and nesting competition (Noah 2000). Noah (2000) suggested that competition with *D. major* and *D. medius* may have played a role in a slight decline of the Lesser Spotted Woodpecker at the

Innere Unterspreewald while noting that forestry changes had most likely been a main influence. In our study area, *D. minor* territories overlapped with those of *D. major*, but there was very little overlap with *D. medius* territories. *D. medius* is considered to be ecologically intermediate between the other two species. With regard to feeding guilds, *D. major* is an omnivore while *D. medius* and *D. minor* are both classified as arboreal insect eaters, feeding mainly on surface-living insects (Mikusiński and Angelstam 1997, Gorman 2004). Although *D. minor* was using a wider array of habitat types than *D. medius*, specialising on softwood trees, and used dead trees to a much greater proportion than the other *Dendrocopos* species, it can be surmised that the spatial segregation of *D. medius* and *D. minor* territories might serve to avoid competition between the species. Besides potential competition, it should be considered that the Great Spotted Woodpecker is one of the most common predators on *D. minor* nests (Blume and Tiefenbach 1997, Rossmanith et al. 2007). It has even been suggested that the dominance of *D. major* is a major factor keeping *D. minor* populations at low levels (Blume and Tiefenbach 1997).

Grey-headed woodpecker

Historically a common breeding bird in the Danube floodplains, *P. canus* is now rare, following population declines during the last decades (Teufelbauer and Frank in prep.). Occurrences are still reported from several parts of the Donauauen National Park with richly structured old growth stands (G. Frank, unpublished data; N. Teufelbauer, unpublished data, Birdlife, unpublished data). It was somewhat unexpected that no Grey-headed Woodpecker could be recorded in our study area. Generally, the habitat does not appear to be unsuitable for the species, which has been classified as typical breeding bird of floodplain forests and softwood riparian forests along rivers and lakes (Scherzinger 1982). However, old growth stands are paramount for the Grey-headed Woodpecker (Weiss 1998), which is usually found in older, more closed forests than *P. viridis* (Spitznagel 1990). Thus, one possible explanation for the absence of the species in our study area may lie in the relatively low stand age.

Declines of the species have been noted in many European regions (Snow et al 1998) such as the Traun-Danube floodplains in Upper Austria (Weissmair and Rubenser 2009). Causes for the decline are still unclear; processes of habitat deterioration such as destruction of old natural woodland, agricultural intensification, and removal of deadwood have been suggested (Snow et al 1998, Weissmair and Rubenser 2009). Another issue is competition with its ecologically similar congener *P. viridis*. Although both species may breed in close vicinity in richly structured landscapes (Flade and Miech 1986, Glutz von Blotzheim and

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Bauer 1994), syntopic occurrence is rare despite largely overlapping ranges (e.g. Svärdson 1949, Scherzinger 1982). Svärdson (1949) suggested that the southern limit of *P. canus* in Sweden, like in Finland, is determined by competition with *P. viridis*, and in several regions, the Grey-headed Woodpecker seemed to benefit from declines of the Green Woodpecker (Reichholf and Utschick 1972, Glutz von Blotzheim and Bauer 1994). Also, some competition for roosting cavities between *P. canus*, *P. viridis* and *D. martius* has been reported (Blume 1996). Whether interference competition or interspecific avoidance leads to regional separation of the two *Picus* species is still unclear (Scherzinger 1982, Cramp 1985). According to Glutz von Blotzheim and Bauer (1994), *P. canus* is much influenced by landscape structure and by the distribution of *P. viridis*. Perhaps the Green Woodpecker is indeed more competitive in lowlands, benefiting from the milder climate (Scherzinger 1982), as well as from the high deadwood supply and the numerous open spaces.

Green Woodpecker

The density of *P. viridis* in our study area was 0.14-0.15 territories/10 ha. This is comparable to density in the Upper Austrian Traun-Donau-Auen (0.11-0.16 territories/10 ha; Weissmair and Rubenser 2009). Over large areas, *P. viridis* abundances rarely reach more than 0.025 pairs/10 ha, although at smaller scales higher densities have been reported for old beech forests (0.6 pairs/10 ha) and mixed deciduous forests (0.6-1.2 pairs/10 ha, with maxima of 1.3 pairs/10 ha; Glutz von Blotzheim and Bauer 1994). In the Rhine Floodplains, densities reached 0.051 pairs/10 ha of woodland (Spitznagel 1990); at the Innere Unterspreewald, densities ranged from 0.044 to 0.049 pairs/10 ha (Noah 2000).

All *P. viridis* territories in our study were found in hardwood forest around meadows, fields, settlements and, in one case, the dyke. Dykes are regularly frequented by foraging Green Woodpeckers (G. Frank, unpublished data, Noah 2000). In an Upper Rhine floodplain forest, all but one territory of Green Woodpeckers incorporated dykes (Spitznagel 1990).

Typical *P. viridis* biotope is forest intersected by meadows. Today, the species is found mostly in extensive cultural landscapes, parks and forest pastures. Forest edges and forest roads, hedges, gardens and settlements are regularly frequented (Scherzinger 1982). The Green Woodpecker is considered to be a typical edge species (Mikusiński 1997, Weiss 1998), requiring trees for nesting and open areas for foraging (Mikusiński 1997, Mikusiński 1997). Moreover, biotopes rich in edges such as open areas with shrubs, hedges or forest edges offer much structural diversity and thus harbour the highest species richness of ants (Muschketat and Raque 1993), the primary prey of *P. viridis* (Glutz von Blotzheim and Bauer

1994, Cramp 1985, Blume 1996). Thus, space requirements of the species are determined by edge density rather than by area (Blume 1996). Accordingly, Forest Edge was the only structural habitat variable significantly affecting *P. viridis* occurrence in our study area. All Green Woodpecker territories were in hardwood alluvial forest, and 11 out of 13 territories were located north of the dyke. Areas south of the dyke, both those containing hardwood and softwood forest seemed to be avoided despite the presence of meadows and clearings, which may also explain why edge density was only just significant.

The significant avoidance of hybrid poplar and willow could be explained by the fact that the majority of regularly flooded alluvial forest south of the dyke was made up by these species. A possible explanation for the avoidance of habitats south of the dyke may be the availability of ants. Resistance to flooding might play a major role for habitat preferences and spatial distribution of ants in floodplains, with lower species richness in frequently inundated regions (Lude et al. 1999). In the Donauauen National Park, species richness has been found to be negatively associated with wetness of the habitat (M. Tista, unpublished data), and an analysis of the ant communities north and south of the dyke found significantly more species in the northern sections (T. Fellner, unpublished data). Thus, the distribution of *P. viridis* might reflect differences in foraging opportunities.

Concurring with results from Scandinavia (Rolstad et al. 2000), *P. viridis* did not exhibit any significant preferences for particular tree species. This confirms the notion that the openness of the forest is much more important than tree species composition for this species (Spitznagel 1990). Like in Scandinavia (Rolstad et al. 2000), there was no effect of stand age on *P. viridis* distribution. Probably, the Green Woodpecker is more dependent on open areas and on ant availability than on old growth stands.

P. viridis is known for showing an affinity for cultivated land, using meadows, orchards, vineyards or village lawns for foraging (Cramp 1985, Flade and Miech 1986, Mikusiński 1997, Rolstad et al. 2000). Interestingly, five out of the 15 *P. viridis* territories apparently incorporated intensive agricultural fields. Declines of *P. viridis* in Europe have been attributed to the intensification of agriculture and habitat loss due to the conversion of meadows and pastures to intensively cultivated fields (Mikusiński 1997). Nonetheless, the species may use agricultural areas when high trees are available e.g. in hedges or isolated stands (Glutz von Blotzheim and Bauer 1994, Blume 1996). Although the Green Woodpecker's main prey, ants, are scarcer or less accessible in intensively managed meadows (Weissmair and Rubenser 2009), our data indicate that agricultural fields may satisfy the Green Woodpecker's need for open spaces.

Black Woodpecker

In most forest habitats, *D. martius* density usually does not exceed 0.025 pairs/10 ha (Glutz von Blotzheim and Bauer 1994). Thus, the determined density of 0.06 pairs/10 ha in our study area is very high, especially for deciduous woodland (Spitznagel 1990). Extremely high densities of 0.18 pairs/10 ha were reported from managed mixed forest in Poland (Kosiñski and Kempa 2007). In floodplain forest along the Upper Rhine, density was 0.02 pairs/10 ha (Spitznagel 1990); at the Innere Unterspreewald, it was 0.127 pairs/10 ha (Noah 2000), indicating optimal conditions for the species.

All *D. martius* territories in our study area contained previously mapped nesting cavities (F. Werba, unpublished data). Densities may have been underestimated, as it has been shown by satellite tracking that territory mapping can fail to identify all breeding pairs (Bocca et al. 2007). Black woodpeckers are generally only weakly territorial and territory ranges may overlap by 27% in the breeding period (Bocca et al. 2007). Despite the high density in our study area, lowland floodplain forest cannot be considered typical habitat for *D. martius* (Spitznagel 1990). Originally a bird of mixed and coniferous forests of montane and boreal ecosystems, it reaches its highest densities in montane mixed forests and in oak-pine forests (Pechacek 1995). Changes in forestry practice and the introduction of beech have enabled the colonisation also of floodplain forests in the 20th century (Spitznagel 1990, Blume 1996). In central Europe, the distribution of *D. martius* is contiguous with that of beech, which is a favoured nesting tree (Pechacek 1995). Nonetheless, the high densities in our study area devoid of beech show that *D. martius* is not necessarily dependent on beech. While smooth-barked, high beech trees are preferred for nesting in most habitats in central Europe, at least 20 other species have been reported as cavity trees (Ruge and Bretzendorfer 1981, Scherzinger 1982, Blume 1996). In the Donauauen National Park, *D. martius* constructs its nesting cavities primarily in white poplars (G. Frank, unpublished data).

D. martius is no biotope specialist, but requires old growth forest interspersed with gaps. Although able to utilise a broad range of habitats, both continuous and highly fragmented, it has nonetheless high demands in terms of habitat quality (Ruge 1993, Mikusiński 1995). A combination of old growth forest and free-standing large-diameter trees for nesting, as well as clearances and open forest with decaying trees for foraging are required, ideally in natural forest of different successional stages (Scherzinger 1981, Mikusiński 1995, Winkler et al. 1995, Blume 1996). Habitat selection of the Black Woodpecker largely depends on the distribution of its main food source, wood-living ants (Rolstad et al. 1998). It uses a variety of strata for foraging, picking up ants from the ground, pecking for wood-boring insects in rotten

branches or dead and dying trunks, less frequently also searching for bark- and wood-dwelling arthropods in the upper trunk region and on large branches (Weiss 1998). In our study area, *D. martius* was most often observed foraging at low heights in dead trees. Certainly, the species benefits from the high availability of snags and rotten wood, where ants are generally most abundant (Rolstad et al. 1998).

The frequent registrations of *D. martius* near sidearms could be explained by the quantity or quality of deadwood in the vicinity of water-ways. Forest edge density and stand age had no effect on the species; some other habitat properties that have been found to be important for *D. martius* (e.g. availability of tall trees, stand density, canopy closure; Rolstad et al. 1998, Bocca et al. 2007) could not be recorded at a level detailed enough for inclusion in our models. Overall, *D. martius* is highly flexible with regard to habitat selection, and there is considerable variability in habitat choice between years and between individuals (Bocca et al. 2007).

Although a positive association with tree age has been noted in regularly managed forest in Germany (Scherzinger 1982), concurring with results from the Rhine Floodplains (Spitznagel 1990) and from managed forest in Scandinavia (Rolstad et al. 1998), *D. martius* did not exhibit a significant preference for older woods in our study area. The Black Woodpecker may use both young stands and older stands for foraging (Mikusiñski 1995, 1997, Rolstad et al. 1998, Spitznagel 1999, Angelstam et al. 2004). In floodplains of the Upper Rhine, the highest frequency of occurrence was found in those grid squares where old woodland and younger forest stands were mixed in equal proportion (Spitznagel 1999). It has been suggested that foraging habitat is selected mainly on the basis of ant availability, while the age of the forest stand only plays a minor role (Rolstad et al. 1998). An additional factor affecting habitat selection may be predation risk. For instance, in Scandinavia, young (denser) plantations appear to provide better cover from goshawks (*Accipiter gentilis*), the main predator of *D. martius* (Rolstad et al 1998).

As a great diversity of forest types can be used by Black Woodpeckers, tree species composition appears to be of minor importance for the species (Ruge and Bretzendorfer 1981). In the March-Thaya floodplains, where *D. martius* primarily inhabits old growth stands rich in deadwood, regularly flooded softwood forests have been found to be of particular importance (Zuna-Kratky et al. 2000). In our study area, softwood and hardwood alluvial forests were equally used and *D. martius* selected stands of both softwood species (hybrid poplar and white poplar) and hardwoods (oak and maple).

Conclusions

The number of woodpecker species has been found to be positively associated not only with forest naturalness (Roberge et al. 2008), but also with bird species richness in general (e.g. Europe: Mikusiński et al. 2001, Roberge and Angelstam 2006; Canada: Drever et al. 2008). High population densities and the co-occurrence of up to five woodpecker species within small areas – such as in our study – indicate high habitat quality and resource diversity (Scherzinger 1982, Mikusiński and Angelstam 1997, Roberge and Angelstam 2006), suggesting favourable conditions for a variety of forest-dwelling bird species. Conditions will likely improve further in the future, with the natural ageing of trees, further accumulation of deadwood and (through management) replacement of hybrid poplars and other neophytes with native trees.

Hybrid poplars are unpopular with conservationists, having been associated with declines in bird populations in floodplains in Western Europe (Archaux and Martin 2009). Our data do not point to a negative impact of hybrid poplars on all species. *D. major* and *D. medius* neither significantly selected nor avoided hybrid poplar stands. However, the observation data showed that while both species used hybrid poplars, proportionate use was lower than availability. *D. minor* and *D. martius* selected hybrid poplars both at stand level and at the level of individual trees (along with preferences for several other tree species), whereas the Green Woodpecker significantly avoided hybrid poplar stands. All four species for which observation data were available showed pronounced preferences for black poplars. Thus, while woodpeckers can utilise hybrid poplars, they would probably benefit more from native black poplars.

Woodpecker densities were very high in both softwood and hardwood alluvial forest, though preferences differed between species. Although bird species richness and breeding densities can be extremely high in softwood alluvial forest (Flade 1994, 2001), hole-nesting birds tend to be rare compared to most other forest types (Flade 2001). Of the woodpecker species included in our study, only the Lesser Spotted Woodpecker, which is considered an umbrella species for this habitat type (Flade 2001), showed a preference for softwood forest. The other species were indifferent to forest type (*D. major*, *D. martius*) or preferred hardwood forest (*P. viridis*; positive trend of *D. medius* densities).

Deadwood is one key resource for woodpeckers. A comparison of trees used by woodpeckers and trees at reference points shows that dead and dying trees are highly selected by all four species where sufficient data were available; nonetheless there was no

significant difference between the amount of deadwood at woodpecker localities and at reference points. This may indicate that at over 27 m^3 per ha, the amount of deadwood is not limiting in the study area. Similarly, at 34 m^3/ha, deadwood volume was apparently not limiting for the Three-toed Woodpecker (*Picoides tridactylus*) in montane forest in southern Germany (Pechacek and d'Oleire-Oltmanns 2004).

Interspecific competition can cause or maintain differentiation of ecological niches of competing species (Townsend et al. 2002). In our study area, habitat preferences were largely distinct between woodpecker species. Some similarities were found for *D. martius* and *D. minor*, the largest and the smallest guild member, which have very different ecologies and will hardly compete with each other at a microhabitat level. Similarly, in Finland, *D. martius* and *D. minor* could not be separated by habitat, but by tree and foraging technique (Alatalo 1978). *D. major* and *D. medius* also exhibited similarity in habitat preferences. Competition between the two species is probably avoided mainly by differential use of foraging structures and foraging behaviour. Our supplementary observations showed some differentiation with respect to microhabitat choice (regarding tree condition, parts of trees used, foraging substrate, and foraging modes), but also some convergence (no differences in DBH of trees or width of structure used). The data do not suggest that it is competition by its larger congener that keeps *D. medius* densities at a relatively low level. Competition between *D. medius* and *D. minor* might be avoided by spatial segregation.

Overall, there appeared to be more differentiation in choice of macrohabitat than in the Bavarian Forest National Park (Scherzinger 1982), or in the Bialowieza National Park (Wesolowski and Tomialojc 1986). In Bialowieza, woodpeckers most likely were more influenced by seasonal and spatial distribution of food resources and safety from predators than by interspecific competition (Wesolowski and Tomialojc 1986). Our diverging results from findings from the Bavarian Forest could be attributed to the higher population densities in our study area, promoting greater divergence in niche dimensions. Also, the overall harsher conditions in the Bavarian forest may have caused all species to concentrate in high quality patches.

As pointed out by Alatalo (1978), niche differentiation should be studied at different scales. Our study focused on macrohabitat and tree species composition, which are the most important niche dimensions according to Alatalo (1978). However, a more complete picture would have emerged if other abiotic and biotic factors had been included. In Finland, these were (in decreasing order of importance) foraging technique, geographic region, relative foraging height and position within the tree. Integral to the coexistence of various species is

the diversity of resources available (Alatalo 1978). The presence of different tree species, various successional stages, living and dead wood, open and densely overgrown forest parts, i.e. habitat with several layers, high edge density, and species and structural diversity in a natural forest can fulfil the various requirements of the different species (Scherzinger 1982).

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Ausbildung

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Sprachkenntnisse

Deutsch (Muttersprache), Englisch (ausgezeichnet), Französisch (fortgeschritten, Diplôme d'Études en Langue Française 1), Spanisch (fortgeschritten)