Factors affecting the occurrence of middle spotted and great spotted woodpeckers in deciduous forests — a case study from Poland

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Based on published data on 117 deciduous forest sites studied in Poland, relationships between habitat factors (size of study plot, type and age of forest stands) and breeding of great spotted and middle spotted woodpeckers were examined. As compared with middle spotted woodpeckers, great spotted woodpeckers occupied twice as large a number of studied plots (97 *vs.* 41) and were characterized by lower area demands. Great spotted woodpeckers avoided young forest stands and residual alluvial forests, preferring oak-dominated forests. Middle spotted woodpeckers selected the oldest, oak-dominated forests. Logistic regression revealed that the presence or absence of great spotted woodpeckers could be predicted from the age of forest stands, and the occurrence of middle spotted woodpeckers was positively correlated with the plot size and type of forest. My results stress the importance of old, sufficiently large (> 15 ha) oak dominated forests conducive to the presence of middle spotted woodpeckers.

Introduction

Selection of a breeding habitat is a key factor in the survival and reproduction of birds (Block & Brennan 1993). It is generally assumed that the habitat use results from a hierarchical decision process associated with decreasing spatial scales (e.g. Hildén 1965, Hutto 1985). The hierarchical nature of this process provides a useful empirical framework for habitat studies and complete descriptions of habitat requirements of birds (e.g. Johnson 1980, Gutzwiller & Anderson 1987, Rolstad *et al.* 2000).

Habitat requirements of the sympatric and taxonomically related great spotted and middle spotted woodpeckers (*Dendrocopos* major and D. medius, respectively) have been widely investigated in different spatial scales and are generally well known (recent review in Michalek & Miettinen 2003, Pasinelli 2003). Interspecific differences refer to patterns of habitat (Spitznagel 1990) and space use (Bachmann & Pasinelli 2000), nest-sites (e.g. Wesołowski & Tomiałojć 1986, Fauvel et al. 2001, Kosiński & Winiecki 2004), foraging behaviour and food items (Jenni 1983, Török 1990, Kruszyk 2003). However, most of these studies have generally been confined to small spatial scales (Johnson 1980). One notable exception is the examination of habitat-use patterns, i.e. "ecological profiles", of breeding bird species, among others woodpeckers Picidae, across habitat types in

central and northern Germany (Flade 1994). However, this study restricted the comparison to showing the frequencies and densities of birds in different habitats. It was found that the breeding occurrence of middle spotted woodpeckers was generally restricted to three forest types (riverine forests, oak-dominated forests and lowland beech forests), while great spotted woodpeckers inhabited all types of forests more evenly.

The patterns of habitat use by woodpeckers might be modified by many different factors connected to structural changes in forest landscape, such as the type and age of forest stands, the patch size and isolation of suitable habitats (e.g. Müller 1982, Pettersson 1985, Angelstam & Mikusiński 1994, Kosenko & Kaygorodova 2001). Such factors may produce variation in patterns of habitat occupancy both within and between species (Wiens 1989). Therefore, identifying factors affecting habitat use is important for effective species and habitat management (e.g. Flade 1994). Moreover, management decisions must be based on reliable, quantitative habitat models (Salwasser 1986, Pasinelli 2000, Angelstam et al. 2004).

Field data on the breeding bird composition and community structure based on territory mapping methods provide high quality data with regard to both the status (presence/absence) of each species and the number of birds holding territory on study plots (Tomiałojć 1980, Bibby *et al.* 2001). Such data could be applied not only to describe and compare the patterns of birds' habitat preferences (Flade 1994) but also to test the habitat requirements of species. In this paper,

Table 1. Distribution of plots according to the type and age of forest stands. The proportion (%) of plots are shown in brackets. ODF = oak-dominated forests, BEF = beech forests, RAF = residual alluvial forests.

Age	Т	Total		
of stand	ODF	BEF	RAF	
0–40	3 (2.6)	1 (0.9)	9 (7.7)	13 (11.1)
41–80	3 (2.6)	10 (8.5)	23 (19.7)	36 (30.8)
81–120	12 (10.3)	7 (6.0)	11 (9.4)	30 (25.6)
≥ 121	18 (15.4)	19 (16.2)	1 (0.9)	38 (32.5)
Total	36 (30.8)	37 (31.6)	44 (37.6)	117 (100.0)

I use the data obtained from 117 deciduous forest sites studied in Poland to (1) compare the patterns of habitat use of great spotted and middle spotted woodpeckers according to the three habitat characteristics: type of forest, age of forest stand and plot size; and (2) develop a habitat model describing factors affecting the breeding occurrence of both species.

Material and methods

Source of data

Data on the status (presence/absence) of great spotted and middle spotted woodpeckers and habitats were taken mainly from published data covering the breeding bird communities of 117 plots covering the deciduous forest stands studied in Poland between 1961 and 2000, however, some unpublished data were also included (see Appendix). The term 'presence' means at least the holding of one territory on the study plot during the breeding season. Bird territories which were extended beyond the boundaries of the study areas (marked as "+" in the tables) were not included in the analyses. All of these studies were designed to describe composition and structure of the entire bird communities associated with clearly defined and, in a large majority, homogeneous forest types. Most of these data were obtained with the territory mapping methods as described by Enemar (1959) and improved by Tomiałojć (1980), and 17 were censused using the line transect method. These census techniques involve repeated visits during the breeding season (2-17 in the analysed sample) and seem to provide high quality data considering the status of each species. Only those plots with sufficiently detailed characteristics of habitat (plot size, age, type of forest stand) were included in the analysis. Very small plots (< 4 ha) and large (> 100 ha) heterogeneous plots were omitted. In some cases (Jermaczek 1991) the adjacent small plots covered by the same forest type and age were combined. Since some plots were surveyed for longer than one year (2-25 years), to avoid pseudoreplication (Hurlbert 1984), only one year was randomly sampled for the analysis.



Fig. 1. Distribution of size of study plots (N = 117).

Measured variables

Three habitat variables were extracted from the papers and manuscripts: forest site type (FOR-TYPE), age (AGE) and size of study plot (PLOT SIZE). Unfortunately, it was not possible to extract valuable data on the surroundings of the study plots. The forest types were attributed to one of the five forest classes: beech forests Fagion sylvaticae (BEF), oak-hornbeam forests Carpinion betuli (OHF), acidophilus oak woods Quercetea robori-petraeae (AOF), riverine forests Alno-Ulmion and Salicion albae (RIF) and alder-swamp forests Alnion glutinosae (ASF). However, these forest types were finally grouped into three categories: beech forests (BEF), oakdominated forests (ODF; OHF + AOF) and residual alluvial forests (RAF; RIF + ASF), composed of mostly alder Alnus-dominated stands. The age of the forest stands was determined based on the upper tree layer and divided into four classes: young (≤ 40 years old), middle (41-80 years old), old (81-120 years old) and very old (> 120 years old) (Table 1). However, if age of forest stand was described as a range, e.g. 60-90 years, and there was no other information indicating the age of the upper storey, the median age value was used for the analysis. Within three plots, which were described by the authors as old growth, mature or virgin beech forest, the



Fig. 2. Size of study plot (mean \pm SE) for three types of forest (*N* = 117). ODF = oak-dominated forests, BEF = beech forests, RAF = residual alluvial forests.

age of forest was classified as older than 120 years. In borderline cases or those lacking any information I asked the authors about the age of the forest. The average size of study plot was 17.0 ± 10.3 SD (range 4.0–60.6 ha). The majority of sites (70%, N = 82) were smaller than 20 ha (Fig. 1). The average size of study plots (log transformed) of three types of forest differed significantly ($F_{2,114} = 6.075$, P = 0.003). The average plot size of RAF was significantly smaller than the area of ODF (Tukey test: P = 0.002; Fig. 2).

Data analysis

The size of a study plot, as a continuous variable, was log-transformed to normalise the distribution. The frequency distributions within the categorical variables were tested for homogeneity using two-tailed χ^2 -test, and the *t*-test was used to compare the means of plot sizes among species. To predict the existence of each woodpecker species (dichotomous dependent variable — presence/absence) on the basis of three habitat variables, the backward stepwise logistic regression was used (Trexler & Travis 1993, Kleinbaum & Klein 2002). The significance of each variable included in the models was based on the Wald statistic. To assess the effects of various levels of





Fig. 3. Presence (grey columns) and absence (black columns) of (a) the great spotted and (b) middle spotted woodpecker in different forest types (N = 117; for abbreviations, *see* Fig. 2).

categorical variables the indicator contrasts were computed. This procedure creates the K-1 internal dummy variables and compares them with the reference one (the last one). Since the outliers can significantly affect the results of a logistic regression, at each step of modelling the standardised residuals were checked and outliers (standardised residuals > 2.58) were removed from the data set. The number of cases correctly and incorrectly assigned to each of the presence/ absence group was computed on the basis of the cut value P = 0.5.

The logistic regression analysis was performed using an SPSS statistical package (Norusis 1994). Values reported are means \pm standard errors unless otherwise stated.

Results

Distribution of woodpeckers according to habitat variables

Great spotted woodpeckers occupied twice as large a number of studied plots (84%, N = 97) as compared with middle spotted woodpeckers

Fig. 4. Presence (grey columns) and absence (black columns) of (a) the great spotted and (b) middle spotted woodpecker according to forest age (years). N = 117.

(35%, N = 41), and this difference was statistically significant ($\chi^2 = 56.1$, df = 1, P < 0.001, N = 117).

The average size of a study plot occupied by great spotted woodpeckers (17.8 ± 1.1) was significantly smaller than that occupied by middle spotted woodpeckers (22.2 ± 1.9; $t_{134} = -2.43$, P = 0.02). Great spotted woodpeckers occurred only in plots equal to or larger than 5 ha and middle spotted woodpeckers were absent from areas smaller than 9.4 ha.

The presence of great spotted woodpeckers was significantly associated with both the forest type ($\chi^2 = 10.04$, df = 2, P = 0.007; Fig. 3a) and the age of the forest stand ($\chi^2 = 22.55$, df = 3, P< 0.001; Fig. 4a). This species inhabited RAF less frequently than expected (31 *vs.* 36 plots respectively), and existed more frequently than expected in ODF (35 *vs.* 30 plots). Moreover, great spotted woodpeckers avoided young forest stands (\leq 40 years old).

Middle spotted woodpeckers were associated with both the forest type ($\chi^2 = 41.72$, df = 2, P < 0.001; Fig 3b), and the age of forest ($\chi^2 = 27.74$, df = 3, P < 0.001; Fig 4b). This species selected ODF. Inversely to the BEF and RAF,

this forest type was occupied twice as frequently as expected (28 vs. 13 plots). The middle forest stands (41–80 years old) were inhabited less frequently than expected (4 vs. 13 plots), and the oldest stands (> 120 ha) were preferred (22 vs. 13 plots).

Habitat models describing the presence of woodpeckers

The presence of both woodpeckers was affected by different habitat parameters (Table 2). The occurrence of great spotted woodpeckers was predicted mainly by the age of forest stands. Neither of the constituent dummy variables (age classes) was significant, however, the effect of the youngest forest stand was only slightly insignificant. The forest type was also included in the model, however, its effect was slightly insignificant. The dummy variables suggested that great spotted woodpeckers avoided RAF and BEF. The ability of this logistic model to correctly predict sites where the species was absent was low (Table 3).

The occurrence of middle spotted woodpeckers was positively influenced by the size of the study plot. The chance of finding middle spotted woodpeckers in areas as small as 5 ha of deciduous forest reached 1% and rapidly increased from 37% if the plot size reached 10 ha to 90% if the plot size achieved 16 ha (Fig. 5). Moreover, the forest type significantly affected middle spotted woodpeckers' presence. As shown by the dummy variables, the BEF negatively influenced the breeding presence of this species. The ability of this model to correctly classify plots occupied and unoccupied by middle spotted woodpeckers was very high (Table 3).

Discussion

The studies in the summarized papers were carried out over four decades. In such a long period some population trends may occur. The population indices suggest that great spotted woodpeckers had the most stable status among European woodpeckers between 1970–1990 and middle spotted woodpeckers showed evidence of a rapid decline and even a local extinction (Mikusiński & Angelstam 1997, Angelstam *et al.* 2004). However, the data from Poland do not suggest any trends, although year-to-year fluctuations in numbers, especially among great spotted woodpeckers occur (Tomiałojć & Stawarczyk 2003, and own data). Therefore, it could be expected that those long-term distributed data

Table 2. Results of logistic regression analyses for the great spotted and middle spotted woodpeckers. Given are coefficients of regression (*B*), their standard errors (SE), Wald statistics, degrees of freedom (df), probabilities (*P*) and logistic regression (*R*) — a measure of the partial correlation between the dependent variable and an independent variable. If the Wald statistic is less than 2, *R* is set to zero. The abbreviations of each variable are given in Material and methods.

Species	Variables	В	SE	Wald test	df	P <	R
D. major	AGE			9.469	3	0.024	0.183
-	AGE (0–40)	-1.833	1.025	3.201	1	0.074	-0.108
	AGE (41–80)	0.708	0.894	0.627	1	0.428	0.000
	AGE (81–120)	8.727	28.538	0.094	1	0.760	0.000
	FORTYPE			5.680	2	0.058	0.128
	FORTYPE (RAF)	-2.912	1.227	5.633	1	0.018	-0.187
	FORTYPE (BEF)	-2.277	1.185	3.695	1	0.055	-0.128
	Constant	3.551	1.141	9.683	1	0.002	
	Model: χ^2 = 32.75, df = 5, p < 0.001						
D. medius	FORTYPE			9.546	2	0.009	0.218
	FORTYPE (RAF)	-15.340	58.608	0.068	1	0.794	0.000
	FORTYPE (BEF)	-8.638	2.800	9.514	1	0.002	-0.253
	PLOT SIZE	5.649	2.083	7.352	1	0.007	0.214
	Constant Model: χ^2 = 96.59, df = 3, <i>p</i> < 0.001	-13.548	5.357	6.396	1	0.011	

probably do not affect the frequency distribution of woodpeckers across habitats.

Data from this study clearly show that great spotted and middle spotted woodpeckers differ in their patterns of habitat use. These patterns generally agree with previously published results (Spitznagel 1990, Michalek & Miettinen 2003, Pasinelli 2003, but *see* Flade 1994). Thus, I will concentrate on those factors that significantly correlate with the presence and absence of both species.

The occurrence of great spotted woodpeckers was affected by the age and type of forest. The negative correlations suggest that this species avoids alluvial and beech forests, as well as young stands (< 40 years old). It was found that trunks constitute an important foraging substrate for great spotted woodpeckers during the breeding season (Jenni 1983). Since the trunk is a relatively unproductive microhabitat (Török 1990), the availability of trees with fissured bark rich in arthropod fauna, e.g. oaks, seems to be important for the occurrence of great spotted woodpeckers. In the case of alluvial and beech forests fissured bark is characteristic of the oldest stands (e.g. Günther & Hellmann 1997, Winter et al. 2005). Moreover, the availability of fallen or standing dead wood enables great spotted woodpeckers to inhabit beech forests (Hertel 2003). Furthermore, older stands support trees with sufficient diameter (diameter at breast height \geq 19 cm) for holeexcavation (e.g. Wesołowski & Tomiałojć 1986, Kosiński & Winiecki 2004). It should be pointed out that the logistic model poorly predicts sites where the species was absent. This result may confirm the high plasticity of this species and the lack of clear habitat factors which limit its existence. However, other factors not included in my analysis might predict the occurrence of great spotted woodpeckers.

It was found that the type of forest and the size of a study plot are the most important factors affecting the occurrence of middle spotted woodpeckers. It is well known that middle spotted woodpeckers prefer mature, oak-dominated forests (e.g. Spitznagel 1990, Pasinelli 2003). However, a recent study has revealed that beech forests might be remarkable as breeding habitats of this species (Flade 1994, Günther & Hellmann 1997, Winter *et al.* 2005). The reluctance



Fig. 5. Probability of middle spotted woodpecker occurrence in relation to the size of study plots (N = 117). Dots signify the theoretical values predicted by the logistic model.

to inhabit this forest type in Poland might be caused by the lack of substrates for foraging, especially in winter (Török 1990). Since middle spotted woodpeckers feed on surface-dwelling arthropods throughout the year, the fissured bark tree species, especially oaks, rich in arthropod fauna constitute an important foraging substrate (Jenni 1983, Török 1990, Pasinelli & Hegelbach 1997, Kruszyk 2003). The arthropod fauna inhabiting the relatively thin and smooth bark of beech trunks may be less abundant than that of mature oaks (*see* Nicolai 1986). Moreover, a bark surface with scratches and clefts is formed

Table 3. Classification matrix of cases assigned to each group for the great spotted and middle spotted woodpeckers. N = number of cases.

Group	Classified as absent (<i>N</i>)	Classified as present (<i>N</i>)	Correctness (%)
D. major			
Absent	7	12	36.8
Present	t 3	94	96.9
Total	10	106	87.1
D. medius	5		
Absent	71	3	96.0
Present	t 3	24	88.9
Total	74	27	94.1

by very old trees (> 200 years old; Günther & Hellmann 1997, Hertel 2003, Winter *et al.* 2005), but stands with such beeches were scarcely represented in my sample (two–three study plots). The relatively high importance of this forest type for middle spotted woodpeckers in central and northern Germany is caused by the admixture of old oaks being related to potential food abundance and serving as nesting trees, and/or high patchiness of forest stands containing different forest types (Flade 1994, Winter *et al.* 2005). It should be pointed out that the majority of plots studied in Poland were rather homogenous and well-selected to characterize the typical form of forest.

Contrary to previous data (Noah 2000, Weiß 2003), my results did not provide evidence for the high frequency of occurrence of middle spotted woodpeckers in alder woods. Patches of alder-dominated forests are generally small in size. Since the home-range size of middle spotted woodpeckers is influenced by the availability of rough-barked trees, it is likely that both the small area of patches and relatively young age of alder stands negatively influenced the occurrence of this species (Pasinelli 2000). Moreover, alder woods are patchily distributed and highly isolated and, in consequence, are less likely to be colonised (Weiß 2003, *see* also Müller 1982).

My analysis shows that the size of a study plot is an important habitat variable affecting the occurrence of middle spotted woodpeckers. Earlier studies have estimated the area requirements of a breeding pair in early spring at 7.2 \pm 3.0 ha (Pasinelli *et al.* 2001). This value is approximately twice as large as that of great spotted woodpeckers (Bachmann & Pasinelli 2002). These results suggest that the middle spotted woodpecker is an area-demanding species. Pasinelli et al. (2001) suggested that the size of areas used by middle spotted woodpeckers could differ between study sites thereby reflecting the differences in habitat quality, e.g. the availability of large oaks and potential cavity trees. My analysis suggests that the probability of the occurrence of middle spotted woodpeckers in plots smaller than 10 ha is very low but rapidly increases up to 90% in plots of 16 ha. However, the 100% probability of the occurrence of the species is reached in an area ≥ 35 ha. I did

not have sufficient data to assess the effect of the surroundings of the study plots on the occurrence of middle spotted woodpeckers, however, these values correspond to the area requirements in Switzerland as reported by Müller (1982), where all forest stands larger than 30 ha were colonized. However, as mentioned above, the area requirements of a pair and, in consequence, the carrying capacity of forest stands could differ as a result of habitat quality (e.g. Pasinelli 2000, Pasinelli et al. 2001, Kosiński & Winiecki 2005) and the degree of isolation of suitable patches of habitat (Müller 1982, Pettersson 1985). Generally, the probability of the occurrence of middle spotted woodpeckers in suitable forest patches smaller than ca. 10 ha is very low or the species is absent (e.g. Müller 1982, Becker & Heyne 1994, Kosenko & Kaygorodova 2001; see also Pasinelli 2003).

Unexpectedly, in the case of middle spotted woodpeckers the logistic model does not include the age of forest stands. Since the oak-dominated forests were represented mainly by the older stands (\geq 81 years old) as compared with the other forest types, especially the alder-dominated stands, it is likely that such age-class distribution results in the nonsignificant effect of this habitat variable in comparison with the variable describing the types of forest.

The differing degrees of importance of forest types for middle spotted woodpeckers is not only affected by the presence of trees related to potential food abundance and nest-hole excavation but also by the spatial distribution, area covered by each forest type, as well as the cutting age. As regards the generally small area of alder-dominated forests in Poland (ca. 520 km²; see Matuszkiewicz 2001), high isolation and relatively small area of individual patches, this forest type most probably plays an inessential role in maintaining the viable population of middle spotted woodpeckers on a national scale. However, in some regions, e.g. in northeastern Poland, this forest type could locally play an important role for this (Tomiałojć & Stawarczyk 2003, A. Sikora pers. comm.) and other woodpecker species due to its larger share in the forest landscape and its less intensive management (e.g. Wesołowski 1995) but the data are scarce. Moreover, it was found that pairs might occupy

a mosaic of different deciduous forest types (A. Sikora pers. comm., own data). Furthermore, during breeding the shift from old-growth oak forests to smaller-sized, marginal patches of other deciduous stands, e.g. willow-poplar and alder-swamp forest, was observed (own data). Such forest stands usually provide a number of sites suitable for hole excavation. In this way, even small patches of alluvial forest bordering with rough-barked stands may play a decisive role in creating habitats for middle spotted woodpeckers. Hitherto, the difference in the levels of cutting age for particular tree species in Poland (60-80 years for alder, 100-140 for beech and 120-180 and occasionally 240 for oak; Anonymous 2004) restrict the availability of alder and beech forests for woodpeckers. These tree stands do not reach a sufficient age to form substrates for hole-excavation and foraging (Hertel 2003, Weiß 2003, Winter et al. 2005).

The results of my own and other studies imply that forest management should focus mainly on the age of forest stands and availability of dead wood to support great spotted and particularly middle spotted woodpeckers in the long-term. The maintenance of valuable populations of middle spotted woodpeckers requires the protection of oak-dominated forest older than 80 or even 120 years (e.g. Pasinelli 2000, Kosiński & Winiecki 2005). In the case of lowland beech forests, very old stands (> 200 years) could provide suitable conditions for both species (Hertel 2003, Winter et al. 2005). Moreover, contiguous alder forest tracts with live alders with a diameter at breast height larger than 22-25 cm and with standing dead trees > 35 cm at breast height should be suitable habitats for middle spotted woodpeckers (Weiß 2003). In addition, forest management should promote an uneven-aged structure to provide for a continuous supply of trees suitable for foraging and hole excavation in the future (Pasinelli 2000) and continuity of the most suitable forest stands (Müller 1982, Kosenko & Kaygorodova 2001).

This study has demonstrated the differences in patterns of habitat use by two taxonomically related, sympatric woodpecker species. In spite of some differences in habitat selection, older and fissured bark tree stands seem to be important for both species, especially for middle spotted woodpeckers. This species was generally restricted to mature, oak-dominated forests and avoided smooth-barked or young stands (< 80 years old). Moreover, my study supports evidence that the middle spotted woodpecker is an area-demanding species compared to great spotted woodpeckers. These results may have important management implications for the creation of habitats suitable for the endangered middle spotted woodpecker.

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Year of Name of plot Size (ha) of Age of Type of Source study study plot stand forest 1971 ASF 11.0 15-75 Bednorz (1983) 1971 28.0 10-60 ASF __ " __ 1973 10.0 170-200 AOF _ " _ 1961 Buki by Lutomskie lake NR 32.0 ca. 300 BEF Bednorz & Bogucki (1964) 1961 14.0 ca. 100 RIF Debina NR 1968 23.0 ca. 300 OHF Bogucki (1977) 10.0 50-60 ASF Bukaciński & Jabłoński (1992) 1983 O-I 1969 Chojnik 8.5 90-180 BEF Dyrcz (1973) BEF 1977 | + ||10.0 100-150 Głowacińska & Głowaciński (1981) 1977 IV 8-10 BFF Głowacińska & Głowaciński (1981) 4.0 1967 25.0 OHF G 95 Głowaciński (1975) 1967 GS 25.0 > 120 OHF ___ " ___ 1971 ŁΟ 8.0 50 ASF __ " ___ 1971 GM 5.0 25 - 35OHF _ " _ 1988 18.0 >150 BFF Głowaciński (1990) A 10.0 100-200 1981 BFF Głowaciński & Profus (1992) Т 1993 _ 12.5 old arowth BEF Głowaciński & Profus (1996) 1973 BJ 10.0 ca. 140 BEF Gradziel (1992) 1973 BM 10.0 ca. 120 BEF ___ ,, ___ BS BFF 1973 10.0 ca. 140 ___ " ___ ΒZ ca. 150 1973 10.0 BEF ___ " ___ 1975 15.0 95 AOF Górski (1976) _ 1975 23.0 65 ASF __ " __ BEF near Wola Rokietnicka 50-70 1986 10.0 BEF Hordowski (1993) 1988 OHF near Żurawica 14.0 100 OHF __ " __ **RIF** near Kosienice RIF 1988 9.5 30 - 40__ " __ 1990 **BEF** near Hołubla 10.0 60-80 BEF __ " ___ **BEF** near Hołubla 13.0 50-80 BEF 1990 __ " __ 1992 **BEF** near Tuligłowy 10.0 60-80 BEF __ " __ 1992 BEF near Wola Maćkowska 10.0 60-90 BEF __ " __ 1992 BEF near Maćkowice 10.5 70-80 BEF __ " __ BEF on Turnica Mountain range 40-60 BEF __ " __ 1992 11.0 1992 40-50 RIF RIF on the Krzeczkowski stream valley 21.0 ___ " ___ 1992 RIF on the Turnica stream vallev 22.0 40-50 RIF __ " __ 1992 Beech-fir forest between Cisowa and Krzeczkowa 22.0 60-80 BEF __ ,, __ 1992 Beech-fir forest on the Turnica 17.0 60-80 BFF Mountain range ___ " ___ 1992 Oak forest between Ciemierzowice 30-50 and Wacławice 15.0 OHF __ " __ 1992 Oak forest near Wacławice 7.8 > 100 OHF __ " ___ 1992 **RIF** in Starzawa 17.0 41-80 RIF __ " __ 1992 **RIF** near Starzawa 15.0 70-100 RIF ___ " ___ 1992 RIF on the Turnica Mountain range 81-120 RIF __ " __ 8.0 RIF 1998 Dolina Mirachowskiej Strugi NR 26.0 41-80 Jakubas (1999) 1967 Muszkowicki Las Bukowy NR 11.2 140-150 BEF Jakubiec (1972) 10.0 41-60 RIF 1983 ŁOJ III/KG + KH Jermaczek (1991) 1983 ŁOJ IV/KC 5.0 61-80 RIF __ " __ 1983 ŁOJ IV/KE 5.0 61-80 RIF __ " __ > 80 1983 ŁOJ V/KA 5.0 RIF __ " __ 1983 ŁOJ V/KD 20.0 > 80 RIF __ " __ 1983 ŁOJ/KI + KJ 10.0 61-80 RIF __ " __ 1984 GRD/CB + CC 10.0 110-120 OHF ___ ,, ____ 1984 GRD/GA + GB + GC 15.0 110-120 OHF __ " __ ŁOJ V/LD + LE 1984 10.0 > 80 RIF __ " __ > 100 RIF 1984 ŁWZ/LB + LC 10.0 __ " __ 1985 BCZ/JA + JB 10.0 100-110 BEF __ " __ 1985 BCZ/ŁA + ŁB 10.0 100-110 BEF ___ ,, __

5.0

0-20

RIF

__ " __

1986

ŁOJ I/BA

Appendix. Sources of the data used in the analysis. Year of the study was randomly sampled. For abbreviations of the forest types *see* Material and methods; NR = nature reserve.

Year of	Name of plot	Size (ha) of	Age of	Type of	Source
study		study plot	stand	forest	
1986	ŁOJ I/BG	5.0	0–20	RIF	<u> </u>
1986	ŁOJ II/BB	5.0	21-40	RIF	<u> </u>
1986	ŁOJ II/BF	5.0	21-40	RIF	<u> </u>
1986	ŁOJ II/KB	5.0	21-40	RIF	<u> </u>
1986	ŁOJ II/KF	5.0	21-40	RIF	<u> </u>
1986	ŁOJ III/BC	5.0	41–60	RIF	<u> </u>
1986	ŁOJ IV/BD + BE	10.0	61-80	RIF	<u> </u>
1998	Radecin I	19.0	ca. 300	BEF	Jermaczek & Gawroński (2003)
1998	Radecin II	26.24	ca. 130	BEF	» (` ` ` `
1987	Las Piwnicki	34.15	> 240	OHF	Kartanas (1995)
1989	_	12.0	120-250	BEF	Kieś (1991)
1992–1995	VI (Straszykowa)	24.0	100	BEF	Kieś <i>et al.</i> (1997)
1992–1993	VII (Pazurek)	18.5	ca. 110	BEF	»
1994–1995	VIII (Bukowica NR)	20.0	old growth	BEF	<u>"</u>
1988	=	29.75	145-155	AOF	Kosiński (1993)
1994	Ruska Kepa NR	17.0	ca. 40	RIF	Kowalski (1997)
1968	Turbacz NR	20.0	old growth	BEF	Kozłowski (1974)
1994	Krępak NR	10.0	ca. 70–80	BEF	Kunysz (1994)
1995	Turnica		a. 80 (100–120)	BEF	Kunysz (1995)
1977	Las Pilczycki	20.0	>120	OHF	Lontkowski (1989)
1981	Błogie NR	60.6	ca. 140	OHF	Markowski (1995)
1980	Gaik NR	35.36	150-170	OHF	_ "
1966	ASF near Niezgoda	11.04	62-72	ASF	Mrugasiewicz (1974)
1966	ASF near Radziądz	17.71	67	ASF	— » —
1966	BF near Borowina	45.74	115–150	BEF	"
1967	-	23.5	ca. 70–100	OHF	Ranoszek (1969)
1993	_	14.8	20-40	ASF	Rowiński (1997)
1995	 Rezerwat im. Króla	14.0	20-40	AOI	
1990	Jana Sobieskiego	55.0	50-150	OHF	Rowiński <i>et al</i> . (1998)
1984	1	10.38	40	AOF	Stawowy (1987)
1984	2	11.25	70	AOF	"
1984 1984	3	13.72		AOF	
	4		110	AOF	
1984	4 L.P.	9.42	250		<u> </u>
1965			a. 85–130 (260)	OHF	Tomiałojć (1974)
1965	L.NO.	14.9	>160	OHF	
1965	L.G.	11.09	70-80	OHF	"
1965	L.O.	9.94	ca. 45	ASF	
1970		20.6	70-80 (100)	OHF	Tomiałojć & Profus (1977)
1970	IV	13.7	130	OHF	"
1970	V	17.1	180	OHF	— " <u>—</u>
1976	Н	25.0	≥100	RIF	Tomiałojć <i>et al.</i> (1984)
1994	CM	24.0	170-200	OHF	Tomiałojć & Wesołowski (1996)
1994	ĸ	33.0	120-140	RIF	"
1994	L	25.0	100-130	ASF	<u>"</u>
1994	MS	30.0	170-200	OHF	"
1994	W	25.5	170-200	OHF	"
1976	MN	24.0	160–230	OHF	Tomiałojć <i>et al</i> . (1984)
1998	Konewka NR (KON)	16.0	120-200	OHF	Topolski (2002)
1998	Spała NR (SPA)	16.0	up to 230	OHF	"
1973	Urbanowo NR	10.0	ca. 70–80	RIF	Urbaniak (1974)
1981	-	16.5	40–60	ASF	Wesołowski (1985)
1978	A	32.7	65–80	AOF	Witkowski <i>et al</i> . (1995)
1991	Wzgórze Joanny NR	24.2	120–160	BEF	"
1994	В	23.1	115–120	AOF	"
1994	-	22.0	120–140	BEF	"
1994	-	22.0	60–85	ASF	<u> </u>
1993	-	14.0	60	RIF	Wysocki (1997a)
1993	Bukowe Zdroje NR	50.04	100–140	BEF	Wysocki (1997b)
1993	Kołowskie Parowy NR		90-130 (140)	BEF	
	A	16.0	90	RIF	Zieliński & Studziński (1996)
1987–1989					
1987–1989 1987–1989	В	20.0	70	RIF	»

Appendix. Continued.

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