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Foraging behaviour of the Great Spotted Woodpecker (*Dendrocopos major*) in the Białowieża National Park: Comparison of breeding and non-breeding seasons

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Although the Great Spotted Woodpecker (*Dendrocopos major*) is the most common of the European woodpecker species, there are no studies detailing its foraging behaviour in the breeding and non-breeding seasons. Our research, conducted in the primeval oak-lime-hornbeam forest of the Białowieża National Park in 1999–2011, compared foraging sites and foraging techniques used by this species in these two seasons. Great Spotted Woodpecker predominantly foraged on standing trees, while lying trees and the ground were occasionally used as foraging sites, but almost exclusively in the breeding season. European hornbeam (*Carpinus betulus*) and small-leaved lime (*Tilia cordata*) were the most frequently used for foraging in the breeding season, whereas Norway spruce (*Picea abies*) and pedunculate oak (*Quercus robur*) were used in the non-breeding season. Great Spotted Woodpecker foraged more frequently on dead and large trees in the non-breeding season. In the breeding season, Great Spotted Woodpecker collected food mainly from living substrates, predominantly sites on large diameter trunks and at low height, while in the non-breeding season it collected food from thin, dead and upper branches. Searching for food and gleaning it from the tree surface was the most common foraging technique used in the breeding season, whereas seed extraction from cones dominated in the non-breeding season. The percentage of foraging time spent on this type of food was positively correlated with the index of Norway spruce seed production. Our study showed that the foraging behaviour of the Great Spotted Woodpecker in the two seasons differs significantly due to changes in food resources.

1. Introduction

The Great Spotted Woodpecker (*Dendrocopos major*) is the most omnivorous of all European woodpecker species with diverse foraging techniques and feeding sites (Michalek & Miettinen 2003). In the breeding season and later in summer its diet consists of invertebrates collected from the surface of trees, while in autumn and winter it feeds on invertebrates living in the wood and seeds of coniferous tree species, mostly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Osiejuk 1994, 1998, Pavlík 1997, Jiao *et al.* 2008, Michalek & Miettinen 2003). Conifer seeds are an important component of the Great Spotted Woodpecker's diet, especially in periods when food of animal origin is limited, for example in winter (Hogstad 1971, Osiejuk 1998). In early spring, this woodpecker may enrich its diet by ringing trees (making holes around the trunk) and drinking the leaking sap or eating invertebrates attracted to it (Turček 1954, Kruszyk 2003). Moreover, it may also depredate bird nests (Kuitunen & Aleknonis 1992, Skwarska *et al.* 2009).

Seasonal changes in the foraging behaviour of woodpeckers are mainly due to changing food types and their amounts, which in a temperate climate is closely correlated with the occurrence of the four seasons. In addition, severe weather conditions such as thick snow cover, can make access to food difficult, forcing woodpeckers to change their foraging techniques or sites where they can find it (Rolstad & Rolstad 2000, Czeszczewik 2009). Moreover, the need to feed nestlings during the breeding season may cause a change in foraging behaviour because food eaten by nestlings may be different from that of adult birds. For example, Pavlík (1997) revealed that the diet of *D. major* nestlings consisted mainly of leaf-eating Lepidoptera larvae, while these larvae constituted only a small part of the diet of adult woodpeckers.

Although the Great Spotted Woodpecker shows large variation in its diet throughout the year, research on seasonal differences in foraging behaviour of this species has rarely been conducted with the same methods in the same site (Jenni 1983, Székely & Moskát 1991). Indeed, studies usually addressed a specific period of the year, such as the breeding season (Török 1990, Pavlík 1997), summer (Osiejuk 1991) or winter (Hogstad 1971, Vanicsek 1988, Osiejuk 1994, 1996, 1998). The foraging behaviour of this woodpecker species in primeval forests is also poorly known. Previous work from the Białowieża Forest focused exclusively on dead trees used by different woodpecker species in deciduous stands, but the characteristics of feeding sites presented in that paper were limited to the species, condition and diameter of the tree trunk (Walankiewicz *et al.* 2002). A more detailed characterisation of foraging sites of *D. major*, in relation to sex, was presented by Stański *et al.* (2020). Another paper by Stański *et al.* (2021a) described anvil placement sites of this woodpecker species. However, none of the above-mentioned papers analysed foraging behaviour in relation to the seasons.

The primary objective of our study was to identify the parameters of trees and sites located therein used by the Great Spotted Woodpecker as feeding grounds with respect to seasons (breeding and non-breeding). We predicted clear preference of foraging on certain tree species and the sites within these trees because they provide more food than others. These include large trees (*i.e.* those with a large trunk diameter at breast height), as they are inhabited by more invertebrates compared to trees with thinner trunks (Lõhmus *et al.* 2010, Sukovata & Jaworski 2010). We hypothesised that the foraging techniques and foraging sites would differ between the two seasons analysed. It was expected that in the breeding season *D. major* is more likely to collect food from the surface of trees, whereas in the non-breeding season it is more likely to extract food from dead parts of trees, as many invertebrates overwinter in dead wood (Lõhmus *et al.* 2010). Moreover, we expected the species to feed primarily on Norway spruce seeds during the non-breeding season, as food of animal origin is limited at this time.

2. Material and methods

2.1. Study area

The Białowieża Forest is located on the border between Poland and Belarus. It is a remnant of the vast lowland forests that covered Europe

hundreds of years ago. The Białowieża National Park (BNP), established in 1921, is located in the Polish part and covers 105 km^2. BNP forest stands, most of which can be classified as primeval forests, are characterised by diverse tree communities of large trees and large amounts of dead wood, including standing snags and fallen, uprooted trees (Tomiałojć 1991, Tomiałojć & Wesołowski 2004). The study plot (about 10 km^2), located in the southern part of the Strictly Protected Area (the best protected zone of the BNP), was covered by an oak-lime-hornbeam stand (*Tilio-Carpinetum*), which is the dominant forest type in the area. It is the most structurally diverse stand, which can be subdivided into five to six layers including three canopy layers. The main tree species growing in the area are small-leaved lime (*Tilia cordata*), European hornbeam (*Carpinus betulus*), Norway spruce, pedunculate oak (*Quercus robur*) and Norway maple (*Acer platanoides*). They are accompanied by many other tree species, such as European ash (*Fraxinus excelsior*), common aspen (*Populus tremula*) and elms (*Ulmus* spp.). The Great Spotted Woodpecker is the most common woodpecker in this area, with up to 2.0 pairs/10 ha (Wesołowski *et al.* 2015a).

2.2. Data collection

Data were collected from 1999 to 2011. Observations were conducted only on days without strong wind (not exceeding 4 on the Beaufort scale), rain or snow to minimise the impact of weather. Observations were usually started one or two hours after sunrise and finished at noon. Great Spotted Woodpecker foraging behaviours were sampled during slow walks in the study area and birds were located using sound (*e.g.* alarm call, drumming) and visual cues. To avoid the observer's influence on the woodpecker's behaviour, we conducted observations from a distance and only when the bird did not show restless behaviour. In addition, to minimise the number of observations of the same individuals in the collected data, after completing a given observation, the researcher started searching for a new foraging woodpecker in a new location several hundred meters away.

Once a foraging woodpecker was located, we recorded the time duration of foraging, foraging substrate, and foraging technique. The time duration of foraging (to the nearest 5 seconds) was measured from the moment the foraging woodpecker was located until the moment it finished foraging (usually leaving the tree). Foraging substrates were classified as a standing tree, fallen tree, or ground. Foraging techniques were classified as: searching and gleaning, wood pecking, bark pecking/scaling, ringing and sap sucking, extracting hornbeam seeds, extracting Norway spruce seeds from cones. If foraging took place on a standing tree, we additionally recorded the following parameters: tree species, tree condition (alive or dead), tree diameter at breast height (DBH), part of a tree (trunk or branch), condition of a foraging spot (alive or dead), diameter at a foraging spot, and height of a foraging spot above the ground. DBH was calculated based on the circumference of the tree trunk, which was measured using a tape measure, whereas the diameter of a foraging spot was estimated from the woodpecker body size as a reference. The height of foraging was assessed using Suunto Height Meter PM-5/1520 or the height of an observer as a reference.

To determine tree preference, we measured tree availability on 82 plots between 1999 and 2003. These plots (0.25 ha each) were randomly selected in the study area, where foraging woodpeckers were observed. For each tree, we recorded its species, condition (alive or dead) and DBH.

2.3. Data analysis

Data from different years were pooled and then analysed by two seasons: breeding and non-breeding. We considered the months of April, May and June as the breeding season, with the remaining months as the non-breeding season (Wesołowski *et al.* 2020). We collected 1001 records of foraging Great Spotted Woodpeckers in total, 507 of which were in the breeding season and 494 in the non-breeding season. The total time of observations of foraging woodpeckers was 993 min in the breeding season and 3602 min in the non-breeding season. However, all analyses involving the determination of the

parameters of trees and sites on these trees used by the Great Spotted Woodpecker included only observations of foraging on standing trees, as foraging on fallen trees was rarely observed. Furthermore, observations where trees were used as anvils (*i.e.* where conifer and hornbeam seeds were extracted by woodpeckers) were excluded from this analysis because time spent hammering hornbeam nuts and conifer cones does not indicate the attractiveness of a given tree or site as a place of food storage, but only its suitability as an anvil. Characteristics of the sites preferred by the Great Spotted Woodpecker as anvil placement sites were presented in Stański *et al.* (2021a). After excluding the above-mentioned observations, 382 records remained in the breeding season and 123 records in the non-breeding season.

To analyse the preference for trees selected as foraging sites, selection indices were calculated according to their species and condition. For this purpose, the proportion of trees representing a specific species and condition status (dead or alive) visited during foraging was divided by the proportion of available trees from a given group in the resources (Manly *et al.* 2002). Available trees were considered those with a DBH of at least 6 cm (the minimum DBH of a tree used for foraging by the Great Spotted Woodpecker). For each selection index, 95% confidence limits were calculated (assuming 0 for results with a negative value) according to the formula given by Manly *et al.* (2002). A selection index was statistically significant if the confidence limits did not contain the value of 1. A tree was considered "preferred" when its selection index was significantly greater than 1, and "avoided" when its selection index was significantly lower than 1 (Manly *et al.* 2002).

The G-tests were used to compare the parameters of foraging sites and foraging techniques between the breeding and non-breeding season. To perform these analyses, the foraging time was converted into percentages, *i.e.* the percentage of foraging time spent on a given tree species, a given height category, etc. was calculated. For the purpose of these analyses trees were categorized according to their DBH into one of the following four classes: <20 cm, 20–40 cm, 40–60 cm, and >60 cm, while the exact foraging spot was divided both according to its diameter (into one of the three classes: <15 cm, 15–30 cm, >30 cm) and its height above the ground (into one of the five classes: <5 m, 5–10 m, 10–15 m, 15–20 m, >20 m).

To check whether the DBH of trees selected for foraging differs between the breeding and non-breeding seasons, a general linear model (GLM) was used. Prior to the analysis the dependent variable - DBH was log-transformed to approach the normality and homoscedasticity of the data. The analysis was performed only for the most frequently used tree species: European hornbeam, small-leaved lime, pedunculate oak, Norway spruce and Norway maple. Tree species (five mentioned above tree species) and season (breeding vs. nonbreeding) were included in the analysis as fixed categorical explanatory variables. Moreover, we also included interactions between variables to find potential differences between DBH in breeding and non-breeding seasons in relation to tree species.

Since foraging on Norway spruce seeds was the dominant method of obtaining food in the non-breeding season, we checked whether the level of seed production by this tree species in a given year affected the percentage contribution of foraging on spruce seeds to the total foraging time of the studied woodpecker. Spearman's rank correlation was used for this purpose. The index of Norway spruce seed production in particular years was correlated with the percentage contribution of foraging on this type of food to the total foraging time in the period from July of a given year to March of the following year (*i.e.* in the non-breeding season). This analysis was conducted for data collected from 2002 to 2010. Data on Norway spruce seed production was derived from the paper by Wesołowski *et al.* (2015b). To assess the level of seed production, the authors of the above-mentioned publication counted cones in the uppermost 5-metre section of the surveyed trees on their southern side in autumn of the current season. Next, based on the number of cones, they determined a crop index from 0 (no cones) to 4 (heavy seed yield). For detailed methodology see Wesołowski *et al.* (2015b). G-tests and calculations of selection indices were carried out using formulas prepared in Excel. Other statistical analyses were performed using Statistica version 12.0.

3. Results

3.1. Trees used for foraging

Great Spotted Woodpecker foraged mainly on standing trees. It used fallen trees very rarely and almost exclusively in the breeding season, and foraging on the ground was observed only during this season (Table 1). The use of foraging sites (ground, fallen trees, standing trees), expressed as a percentage of foraging time, differed significantly between the seasons ($G=9.57$, $df=2$, $p=0.008$).

The Great Spotted Woodpecker collected food on trees representing 11 species during the breeding season and nine species during the non-breeding season. The distribution of the recorded foraging time per specific tree species differed between the seasons ($G=47.65$, $df=10$, $p<0.001$). In the breeding season, woodpeckers foraged mostly on European hornbeams and small-leaved limes, whereas during the non-breeding season – on Norway spruces and pedunculate oaks (Fig. 1). The selection indices showed statistically significant preferences for oaks, maples and aspens in the breeding season and for oaks, maples and spruces in the non-breeding season. Lime and hornbeam, although the most abundant in the study area, were used below the levels predicted based on their availability (Table 2).

Live trees were used more often during foraging than dead trees, but selection indices indicated a preference for the latter in both analysed seasons (Table 2). The proportion of foraging time spent on live and dead trees differed in both seasons ($G=8.82$, $df=1$, $p=0.003$). In the non-breeding season, the use of dead trees increased more than twice compared to the breeding season (Table 3). The use of trees in each thickness class differed between the seasons ($G=30.33$, $df=3$, $p<0.001$). The foraging time on trees in all thickness classes, except the thinnest one, was similar in the breeding season,

Type of foraging site	Breeding season		Non-breeding season	
	n	% time	n	% time
Standing trees	472	93.05	493	99.97
Fallen trees	18	3.75	1	0.03
Ground	17	3.20	0	0

Table 1. Percentage distribution of foraging time in particular foraging sites in the breeding and the non-breeding seasons. All observations were included. N = number of sample size.

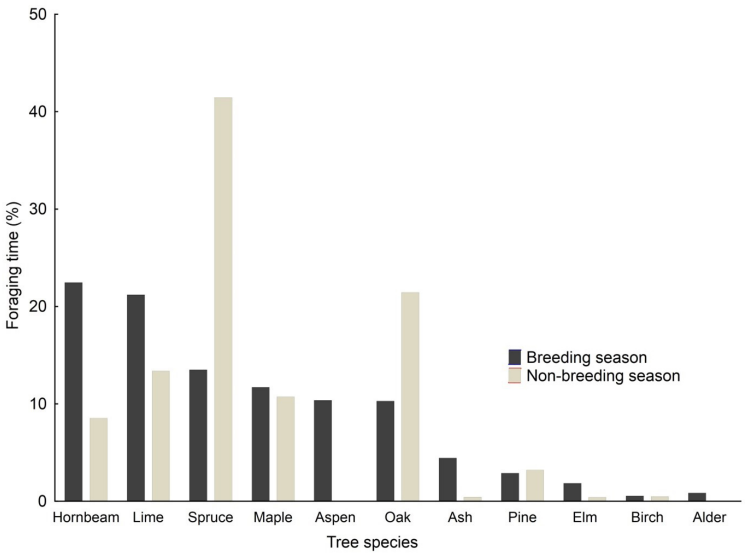

Fig. 1. Percentage of foraging time of the Great Spotted Woodpecker on particular tree species in breeding and non-breeding seasons. Sample size is 382 for breeding season and 123 for non-breeding season. Only observations on standing trees were included whereas observations of foraging on hornbeam and conifer seeds were excluded.

Table 2. Tree species used during foraging by the Great Spotted Woodpecker in relation to their availability. Only observations on standing trees were included whereas observations of foraging on hornbeam seeds and conifer seeds were excluded. A tree is "preferred" when its selection index is significantly greater than 1, and "avoided" when its selection index is significantly lower than 1. A selection index is statistically significant if the confidence limits (CL) do not contain the value of 1.

Tree species	Resources (no. of trees)	Breeding season		Non-breeding season	
		No. of visits	Selection index with 95% CL	No. of visits	Selection index with 95% CL
Hornbeam	4004	101	0.73 (0.57–0.90)	23	0.52 (0.27–0.77)
Lime	4299	86	0.58 (0.44–0.73)	10	0.21 (0.05–0.37)
Spruce	1270	48	1.10 (0.71–1.49)	42	2.99 (2.04–3.94)
Oak	208	42	5.88 (3.65–8.12)	27	11.74 (6.67–16.82)
Maple	342	45	3.83 (2.43–5.23)	13	3.44 (1.15–5.73)
Ash	93	5	1.57 (0.00–3.38)	2	1.95 (0.00–5.41)
Elm	298	17	1.66 (0.63–2.69)	2	0.61 (0.00–1.69)
Aspen	54	30	16.19 (8.78–23.59)	–	
Birch	24	2	2.43 (0.00–6.90)	1	3.77 (0.00–13.31)
Alder	7	4	16.65 (0.00–38.26)	–	
Pine	43	2	1.36 (0.00–3.85)	3	6.31 (0.00–15.46)
Other	487				
Alive	10439	327	0.91 (0.88–0.95)	79	0.68 (0.59–0.78)
Dead	690	55	2.32 (1.75–2.89)	44	5.77 (4.40–7.14)

whereas in the non-breeding season the woodpecker foraged most of the time on the thickest trees (Table 3). Generally, trees selected during foraging in the non-breeding season had a larger DBH compared to trees used in the breeding season, however, no differences were found between both seasons in the case of individual tree species (Table 4, Fig. 2).

3.2. Foraging spots on trees

In the breeding season, live parts of trees were used about twice as often as dead parts, while the result was the opposite for the non-breeding season (Table 3), and the difference between the seasons was significant ($G=34.55$, $df=1$, $p<0.001$). During the breeding season, *D. major* used tree trunks more often than branches, in contrast to the non-breeding season when branches were the dominant foraging sites (Table 3). The seasons differed significantly in this respect ($G=57.35$, $df=1$, $p<0.001$). In the breeding season, foraging sites on different thickness classes were used with similar intensity, whereas in the non-breeding season, more than 75% of the foraging time was spent on sites of < 15 cm thick, and the thickest spot was used for a very short time (Table 3). The distribution of the observed foraging time across diameter classes differed between the seasons ($G=35.44$, $df=2$, $p<0.001$). The foraging time of *D. major* was quite evenly distributed among the sites in different height classes in the breeding season, whereas the percentage of foraging time in the non-breeding season increased with increasing height of foraging sites (Table 3). The difference between the seasons was significant in this respect ($G=68.29$, $df=4$, $p<0.001$).

3.3. Foraging techniques

Searching for food and gleaning it from the tree surface or ground was the most common foraging technique in the breeding season. However, the most time-consuming foraging technique of

woodpeckers was the extraction of seeds from Norway spruce cones (about 36% of their total foraging time). In the non-breeding season, these seeds became the primary food and the foraging time spent on them doubled. Hornbeam seeds were another important component of the woodpecker's diet in the non-breeding season (Table 5). Foraging techniques significantly differed between the seasons ($G=60.62$, $df=5$, $p<0.001$).

We also found that the percentage of foraging time spent on Norway spruce seeds in the non-breeding season was significantly positively correlated with the index of spruce seed production (Spearman rank correlation $r=0.93$, $p<0.001$, $n=9$). During periods when spruce trees produced many cones, the woodpecker foraged exclusively or almost exclusively on seeds of this tree species (Fig. 3).

4. Discussion

Our results showed that both foraging sites as well as foraging techniques of the Great Spotted Woodpecker differed during the breeding and non-breeding seasons. In the breeding season, this woodpecker mainly collected food of animal origin, however, food of plant origin also contributed to its diet. In the non-breeding season, however, the proportion of time spent collecting food of plant origin more than doubled, with the woodpecker feeding mainly on Norway spruce seeds. It is well documented in the literature that seeds of coniferous trees, mainly Scots pine and Norway spruce are an important component of this woodpecker's diet in winter (Hogstad 1971, Alatalo 1978, Osiejuk 1994, Michalek & Miettinen 2003). Our research showed that the spruce seeds

Table 3. Percentage distribution of foraging time in relation to tree condition, its DBH, condition of used site, part of tree, diameter of used site, and height of foraging above the ground. N = number of sample size. Only observations on standing trees were included whereas observations of foraging on hornbeam seeds and conifer seeds were excluded.

Variable	Breeding season (n=382)	Non-breeding season (n=123)
Tree condition		
Alive	82.20	63.69
Dead	17.80	36.31
Tree size class (DBH)		
<20 cm	7.16	0.59
20-40 cm	33.96	10.19
40-60 cm	28.56	28.66
>60 cm	30.32	60.56
Condition of foraging site		
Alive	67.65	26.77
Dead	32.35	73.23
Part of tree		
Trunk	62.57	12.41
Branch	37.43	87.59
Diameter of foraging site		
<15 cm	39.08	75.14
15-30 cm	33.31	21.35
>30 cm	27.60	3.51
Height of foraging		
<5 m	22.27	0.59
5-10 m	22.16	3.88
10-15 m	20.98	17.40
15-20 m	22.64	25.79
>20 m	11.94	52.33

Table 4. Results of general linear model assessing the effect of tree species (European hornbeam, small-leaved lime, pedunculate oak, Norway spruce and Norway maple) and season (breeding vs. nonbreeding) on the DBH trees used during foraging by the Great Spotted Woodpecker.

Effect	df	F	p
Intercept	1	18383.68	<0.001
Tree species	4	34.71	<0.001
Season	1	29.65	<0.001
Tree species x season	4	1.96	0.100
Error	427		

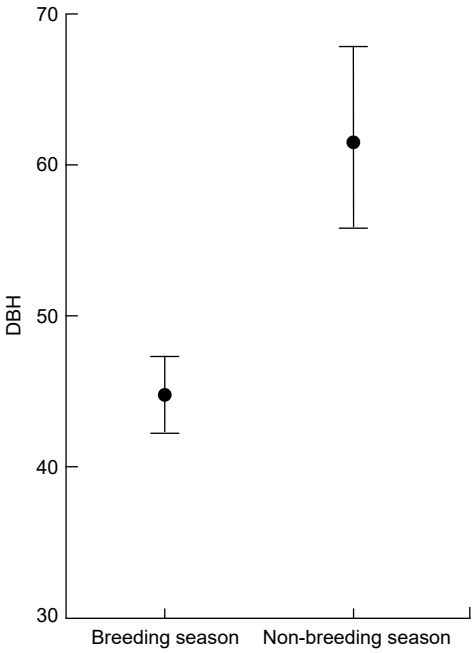

Fig. 2. Diameter at breast height (DBH) of trees used by the Great Spotted Woodpecker during foraging in breeding and non-breeding seasons. Whiskers indicate 95% confidence limits. Only observations on standing trees were included whereas observations of foraging on hornbeam and conifer seeds were excluded.

play a key role for the Great Spotted Woodpecker also in the primeval oak-lime-hornbeam stand of the Białowieża National Park, despite the fact that potential food resources are very diverse due to the high diversity of tree species in this area, supporting a rich invertebrate fauna (Gutowski & Jaroszewicz 2001). In contrast, seeds of Scots pine are rare food of this woodpecker in the study area due to the low abundance of this tree species in oak-lime-hornbeam forest (see Table 2).

Our results further revealed that Norway spruce are also important foraging sites for food of animal origin. Dead wood of Norway spruce is inhabited by many organisms, mainly insects (*e.g.* beetles), which also overwinter in it (Hilszczański 2008, Lõhmus *et al.* 2010). This is the reason why some woodpecker species, such as Three-toed Woodpecker (*Picoides tridactylus*) (Hogstad 1970, Pechacek 2006) or White-backed Woodpecker (*Dendrocopos leucotos*) (Czeszczewik 2009), frequently forage on spruce, but such information is rarely reported for the Great Spotted Woodpecker (Alatalo 1978, Stański 2020).

Searching and gleaning, which were common in the breeding season, were replaced in the non-breeding season by pecking at wood or bark, which resulted in a change of foraging sites. In some periods of the year, usually the colder ones, the number of invertebrates living on the surface of trees becomes low or access to them is difficult (Nicolai 1986, Rolstad & Rolstad 2000, Stańska *et al.* 2018). This forces woodpeckers to change their foraging technique and to search for new sites to collect food. Searching and gleaning are the most effective techniques on parts of trees with cracks and crevices, which provide a suitable habitat for a rich invertebrate fauna (Nicolai 1986). This may explain why, in the breeding season, woodpeckers foraged more frequently on trunks, at low height and at sites with a large diameter. In the non-breeding season, woodpeckers searched for food on higher and mostly dead, not very thick branches, suggesting that such places are rich in invertebrates that live inside the wood. The attractiveness of dead branches for the Great Spotted Woodpecker as foraging sites was also demonstrated by Smith (2007) in forests of England. The significant preference for oak trees by woodpeckers throughout the year can also be explained by the presence of many dead branches, which, combined with their large size and rough bark, makes them an excellent habitat for invertebrates that live both on their surface and inside them (Southwood 1961, Nicolai 1986, Izdebska 2010).

European hornbeam was the most frequently visited tree species by the Great Spotted Woodpecker in the breeding season, which suggests its important role as a site providing food. The low selection index, indicating avoidance of hornbeams, resulted mainly from the high availability of small DBH hornbeam trees. Young, thin hornbeams in BNP oak-lime-hornbeam stands are very abundant, but their smooth bark and hard wood do not make them suitable foraging sites. Older trees, on the other hand, are characterised by thick bark, full of cracks and the presence of branches that break quite easily, resulting in damaged places where the wood is susceptible to rot and decay (Walankiewicz & Czeszczewik 2006). In addition, the number of dead branches

Table 5. Foraging techniques used by the Great Spotted Woodpecker in the breeding and the non-breeding seasons. All observations were included. N = number of sample size.

Foraging technique	Breeding season		Non-breeding season	
	N	% time	N	% time
Searching and gleaning	238	26.75	20	1.00
Pecking of wood	48	10.68	38	5.65
Pecking and scaling of bark	119	20.98	64	7.29
Ringing and sap sucking	10	2.57	2	0.14
Extracting hornbeam seeds	5	2.61	90	12.22
Extracting seeds from cones	87	36.41	280	73.70

increases with increasing DBH of hornbeam trees (Michałowska 2010). Great Spotted Woodpeckers foraged mostly on old, thick hornbeam trees with an average DBH of more than 40 cm, trees which, although quite common, are not as numerous as young trees in BNP primeval stands. Moreover, we found that hornbeam seeds were an important component of the Great Spotted Woodpecker's diet in the non-breeding season, which is rarely reported from other areas (Löhrl 1972, Jenni 1983). The comparison of trees selected for foraging with trees selected for cavity excavation in the BNP oak-lime-hornbeam forest showed some similarity. *D. major* most often excavated nesting holes in aspen, hornbeam and pedunculated oak (Hebda *et al.* 2017). Two of the latter tree species were also frequently used during foraging, while foraging on aspen was less frequent, but given its low abundance in the stand it was a species strongly preferred as a foraging site. On the other hand, nesting holes were rarely found in Norway spruce and small-leaved lime, which are frequent foraging sites (Hebda *et al.* 2017).

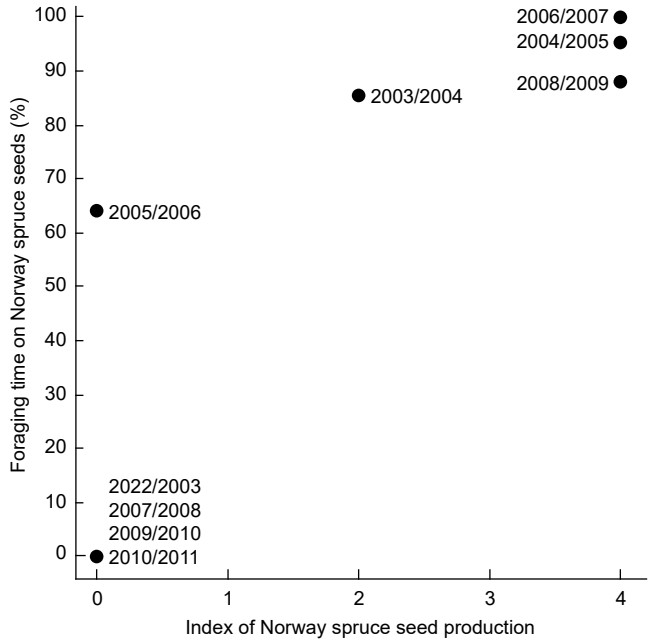

Fig. 3. Percentage of foraging time of the Great Spotted Woodpecker on Norway spruce seeds in non-breeding seasons in relation to index of Norway spruce seeds production. The numbers next to the points represent particular non-breeding seasons. Indices of Norway spruce seeds production based on Wesołowski *et al.* (2015b).

Our results largely agree with those obtained by Jenni (1983), who conducted his study in oak-hornbeam forest near Basel in Switzerland. He found that in winter, the Great Spotted Woodpecker foraged mainly on dead parts of trees (70% of the foraging time) and in upper tree strata, whereas in April, May and June it foraged on lower levels and the use of dead substrates decreased to 40%. The similarity also applied to the foraging techniques used – pecking was used throughout the year, while gleaning was used only in warmer months. The author also revealed

a strong preference by woodpeckers for oaks in winter. However, in contrast to our results, tree seeds in his research were not important to *D. major* in winter.

In the same area, Stański *et al.* (2021b) conducted analogous studies on the Middle Spotted Woodpecker (*Leiopicus medius*), which allows us to compare the foraging sites selected by both woodpecker species. In general, they foraged on specific tree species with similar intensity – hornbeam was the most visited tree species in the breeding season, but in the non-breeding season the use of this tree species decreased, while the use of Norway spruce increased. Moreover, the most preferred tree species by both woodpecker species as foraging sites in both seasons was pedunculate oak. In addition, both the Middle- and the Great Spotted Woodpecker in the non-breeding season clearly preferred foraging on trees with a large diameter. However, unlike *D. major*, parameters of foraging spots and foraging techniques used by *L. medius* were similar in both seasons (Stański *et al.* 2021b).

Our study had some limitations. Firstly, data from the whole study period were pooled and analysed only in the seasonal aspect (breeding and non-breeding seasons). The aspect of year-to-year variation in foraging sites and techniques used was omitted from the analysis due to the small number of records collected in some years. The availability of food that the Great Spotted Woodpecker feeds on varies considerably from year to year (Wesołowski & Rowiński 2006, Wesołowski *et al.* 2015b), so both preferred sites and foraging techniques can differ every year. In addition, weather conditions can also vary from year to year which can affect how and where woodpeckers forage (*e.g.* snow cover can make access to food difficult). We suggest that future studies should include the aspect of year-to-year variation in *D. major* foraging, taking both food abundance and weather conditions into account.

Many previous studies have shown the strict positive relationship between dead wood resources and the abundance of bird communities including woodpeckers (Kouki & Väänänen 2000, Walankiewicz *et al.* 2002, Lõhmus *et al.* 2010, Czeszczewik *et al.* 2013). However, intensive forest management, including the removal of dead or decaying trees caused dead wood to become a highly limited resource, which translated to the decline both in the number of woodpeckers and their species richness in many areas (Angelstam & Mikusiński 1994, Bütler *et al.* 2004, Czeszczewik & Walankiewicz 2006). In spite of the great role of dead trees and dead branches, studies highlighting their role as foraging sites usually involve specialized woodpecker species such as the White-backed woodpecker and the Three-toed woodpecker (*e.g.* Pechacek 2006, Czeszczewik 2009). In contrast, our finding clearly showed that dead wood is important as a foraging site even for such a common and omnivorous species as the Great Spotted Woodpecker, which proves the necessity of maintaining sufficient amounts of dead wood in commercial forests rather than removing it, as is usually done. Furthermore, the seasonal variation in foraging sites and foraging techniques of *D. major* suggests that a diverse stand structure may be potentially beneficial not only for the species studied, but also for other woodpecker species. The results of our study can be applied in forest management carried out both in the Białowieża Forest and other forests.

In conclusion, our study showed, that the foraging behaviour of the Great Spotted Woodpecker differed significantly between the two seasons in all the analysed aspects. Although the food of animal origin dominated in the woodpeckers' diet in the breeding season, food of plant origin also had a substantial share. In the non-breeding season, Norway spruce was the most important tree species, where *D. major* obtained food, mainly in the form of seeds, extracted from cones. When considering food of animal origin, large-diameter sites located on trunks and at low height were used most frequently in the breeding season. In the non-breeding season, on the other hand, the studied woodpecker most often collected food on upper dead branches.

Födosöksbeteende hos större hackspett (*Dendrocopos major*) i Białowieża National Park under och mellan häckningssäsongerna

Trots att den större hackspetten är den vanligaste hackspetten i Europa finns det inga studier om dess födosöksbeteende under och mellan häcknings-säsongerna. I vår undersökning, som utfördes

i en orörd ek-lind-avenbok skog i Bialowieża nationalpark under 1999–2011, studerade vi födosöksplatser och -tekniker som arten använder under och mellan häckningssäsongerna. Större hackspetten sökte sin föda främst i stående träd medan de använde liggande träd endast sporadiskt och uteslutande under häckningssäsongen. Avenbok (*Carpinus betulus*) och lind (*Tilia cordata*) användes mest vid födosök under häckningssäsongen, medan gran (*Picea abies*) och ek (*Quescus robur*) användes mest mellan häckningssäsongerna. Hackspettarna sökte oftare föda i stora döda träd utanför häckningssäsongen. Under häckningssäsongen samlade hackspettarna föda främst från levande substrat på grova stammar på låg höjd, medan de främst använde kvistar högre upp på tunnare, döda träd mellan häckningssäsongerna. Födosökande och samlande av föda från trädens ytor användes främst som teknik under häckningssäsongen, medan dissekering av kottar dominerade mellan häckningssäsongerna. Födosökstiden som hackspettarna använde för att dissekera kottar korrelerade positivt med granens fröproduktionsindex. Vår undersökning visar att födosöksbeteende hos större hackspett skiljer sig märkbart på grund av förändringar i födoresursernas tillgänglighet.

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