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# Foraging behaviour of the Great Spotted Woodpecker *Dendrocopos major* in relation to sex in primeval stands of the Białowieża National Park

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**Abstract.** The Great Spotted Woodpecker *Dendrocopos major* in spite of its broad food niche may prefer some trees or places on them during foraging. Different preferences for foraging sites can also be found in males and females, which may minimize competition for food between them. The main goal of our study was to define sex-specific use of foraging sites of the Great Spotted Woodpecker, in the primeval oak-hornbeam-lime forest of the Białowieża National Park, E Poland. This forest has never been logged and is distinguished by the structure of great vertical and horizontal diversity, high amount of dead wood and trees which reach large dimensions. Therefore, there are a large number of potential foraging sites, and some trees, due to their species or condition, may be particularly preferred in this respect. Our study revealed that the foraging sessions of woodpeckers were longer on the dead parts of trees than on alive ones which were especially noticeable in the case of females. The longest foraging sessions were found on dead parts of Norway Spruce *Picea abies* for both sexes. The males foraged the longest at high altitudes (> 20 m above the ground) on thin parts of trees (diameter 5–10 cm) whereas females on sites above 15 m and on thicker parts of tree (diameter 10–20 cm). Moreover, the duration of foraging session of females increased with increasing of trunk diameter at breast height, which was not revealed in males.

**Key words:** intersexual competition, niche partitioning, resource partitioning, Białowieża Forest

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## INTRODUCTION

For woodpeckers, which are typically forest birds, the most crucial sites where they collect food are trees. Some woodpecker species are strictly connected with specific tree species or trees with specific characteristics, used as foraging sites. For example, the Middle Spotted Woodpecker *Dendrocopos medius* prefers foraging on large oaks with cracked bark (Pasinelli & Hegelbach 1997), the White-backed Woodpecker *Dendrocopos leucotos* forages chiefly on dead trees or on dead or dying parts of living trees (Czeszczewik 2009), whereas the Three-toed Woodpecker *Picoides tridactylus* collects food mainly on dead Norway Spruces *Picea abies* (Pechacek 2006). In opposite to above mentioned specialized species, the Great Spotted Woodpecker *Dendrocopos major* is an omnivorous bird and the spectrum of its foraging techniques and sites utilized to collect food is very

wide (Michalek & Miettinen 2003). In the breeding season and in the summer a significant part of its food are invertebrates collected from the surface of trunks, branches and leaves, which in winter are replaced by invertebrates living in wood (Pavlík 1997, Jiao et al. 2008). An important component of the diet of this woodpecker is plant food, which mainly consists of seeds of coniferous tree species (e.g. Scots Pine *Pinus silvestris*, Norway Spruce). It may be the main source of food for the Great Spotted Woodpecker, especially in winter and for northern populations (Hogstad 1971a, Alatalo 1978, Osiejuk 1994). However, in spite of its broad food niche, the Great Spotted Woodpecker may also favour some tree species or specific parts of trees as foraging sites. For example, Smith (2007) revealed that this woodpecker very often foraged on dead branches of living trees whereas Kruszyk (2003) showed its strong preference for oaks and hornbeams.

Differential foraging behaviours of particular woodpecker species leading to resource partitioning may reduce competition for food what allow them to coexist in the same habitat (Alatalo 1978, Vanicsek 1988, Török 1990). Resource partitioning is also common between males and females, what is especially important when food resources are limited (Osiejuk 1998, Pechacek 2006). To minimize intersexual competition for food, each sex can: 1) forage on different parts of the trees, 2) use different foraging techniques, or 3) collect food of varying sizes (Selander 1966, Hogstad 1991, Stenberg & Hogstad 2004, Pechacek 2006). Intersexual niche partitioning of woodpeckers may be connected with sexual dimorphism, which is among others, manifested in differences in bill and body size (Hogstad 1978). Size dimorphism allows males and females utilize different feeding niches. For example, males of Hispaniolan Woodpecker *Centurus striatus*, possessing a larger bill than females, are better adapted to excavating in the harder wood or thicker bark (Selander 1966). In the case of woodpeckers where sexual dimorphism is not distinct, competition for food between the sexes may be reduced by utilizing separate feeding territories (Hogstad 1978). Moreover, niche segregation may be associated with dominance of males over females, being expressed by aggressive behaviour (Osiejuk 1998, Pasinelli 2000). However, differences in foraging patterns between the sexes of the Great Spotted Woodpecker were studied relatively rarely and none of these studies was conducted under primeval conditions (Hogstad 1978, Osiejuk 1994, 1998).

The main goal of our study was to identify the parameters of the trees and their parts most commonly used by the Great Spotted Woodpecker during foraging, in relation to the sex. We assumed, that some trees or sites on them can provide more food than others and therefore foraging sessions should be the longest in such places. Our assumption was based on foraging theory, which suggests that generally, animals choose for foraging habitats or patches with the greatest density of prey (Stephens & Krebs 1986). In patchy environments, which is the forest for woodpeckers, the foragers continually assess the quality of a patch (in our case the site on the tree) and make decisions as to when to leave a patch, based on their energy intake (Cowie & Krebs 1979). Moreover, apart prey availability in habitat, prey accessibility is essential for animals, that can be affected by e.g. weather conditions, temperature, time of day (Rolstad & Rolstad 2000, Czeszczewik 2009, Wiebe

& Gow 2013). The decision to choose a feeding place is also influenced by predation risk, therefore, the places with high prey density but with high predator pressure can be avoided (Cresswell 1994, Heithaus 2005). Taking into consideration availability and accessibility of food we hypothesized that dead substrates would be preferred over living substrates and trees with large dimensions (expressed as a trunk diameter at breast height) would be preferred over trees with small dimensions.

Our second objective was to check whether the same parameters of foraging places influence the duration of the foraging sessions for both males and females. We predicted that there are no differences in this respect and both sexes foraged the longest on sites with similar characteristics. Our assumption was based on fact that the Great Spotted Woodpecker is not a strongly dimorphic species (however males have longer bill than females) and therefore it is more likely that in order to minimize the possible intersexual competition, male and female use separate feeding territories, while their foraging behavior remains the same (Hogstad 1978).

## STUDY AREA

The study was conducted in the Białowieża National Park (BNP), located in Polish part of Białowieża Forest — a large forest complex (c. 1500 km<sup>2</sup>) on the border between Poland and Belarus. The BNP is protected since 1921 and after its enlargement in 1996 its area is 105 km<sup>2</sup> at present. Many tree stands of BNP may be classified as primeval forests, which have never been cut. These forests are characterize by a multistorey profile with great vertical and horizontal diversity, high amount of dead wood and trees which reach large dimensions (Tomiałojć 1991). The study was carried out in the primeval oak-hornbeam-lime stands, *Tilio-Carpinetum*, located in the strictly protected part of the BNP. This dominant forest type, covering c. 45% of the total area of BNP, is the most structurally diversified with a variety of tree species and three canopy layers. Small-leaved Lime *Tilia cordata*, Hornbeam *Carpinus betulus*, Norway Spruce, Pedunculate Oak *Quercus robur*, Ash *Fraxinus excelsior* are the most numerous tree species but many other like Norway Maple *Acer platanoides*, Aspen *Populus tremula*, elms *Ulmus* spp. and Great Sallow *Salix caprea* are in admixture.

## MATERIALS AND METHODS

### Data collection

The study was carried out from 1999 to 2011 and data were collected during all months except July, August and September each year. The primeval oak-hornbeam-lime stands of BNP were penetrated, usually between one hour after sunrise to noon, and foraging woodpeckers were searched. To minimize the influence of weather, observations were conducted only on days without strong wind (not exceeded 4 degrees in Beaufort scale), rainfall or snowfall. Foraging birds were searched mainly by the sound (e.g. pecking, alarm call) but to find silent foraging individuals, trees were also scanned through binoculars from time to time. When woodpecker was found, the time of its foraging, its sex and parameters of foraging site were recorded. Foraging time measurements started when the woodpecker was located (and did not show restless behaviour due to observer presence) and stopped when bird finished the foraging, regardless the bird remained in the feeding site or left it, flying to another tree or another place on the same tree. Foraging time of one bird in one site on a tree was considered as a „foraging session”. Only the first foraging session of an observed woodpecker was recorded to avoid the overrepresentation of the records of the same individuals in the collected data. After given observation researcher moved to a new location distant a few hundred meters.

The following variables were recorded for each foraging site: 1) tree species, 2) tree condition (alive or dead), 3) tree diameter at the breast height (dbh), 4) condition of foraging site (alive or dead), 5) diameter of foraging site, and 6) height of foraging site above the ground. Dbh of the tree trunk was measured using a tape measure (the circumference of the tree was measured based on which dbh was calculated). The diameter of foraging site was visually assessed using the woodpecker body size as a reference whereas the height of foraging was measured using altimeter brand Suunto or the height of observer as a reference. In cases where the foraging woodpecker moved over the trunk or branches of the tree, usually, the diameter and height of the foraging site changed, therefore the initial and final size of each these parameters were noted.

### Data analysis

A total of 427 foraging sessions (215 males and 212 females) were included in analysis. We excluded

observations of feeding on spruce and hornbeam seeds, because time spent hammering cones or hornbeam nuts does not indicate the attractiveness of a given place on the tree in terms of food, but only about its usefulness as an anvil. For the purpose of analysis diameter of each foraging place was categorized into one of four classes: to 5 cm, > 5–10 cm, > 10–20 cm, > 20 cm, whereas height of foraging place above the ground was categorized into one of five classes: to 5 m, > 5–10 m, > 10–15 m, > 15–20 m, > 20 m. This was done because both these parameters, firstly, were determined to a certain degree, and secondly, they changed when the woodpecker moved during feeding.

To analyse variables associated with the duration of the foraging session of the Great Spotted Woodpecker two separate generalized linear mixed models (GLMMs) with Poisson error distribution and log-link function were built — one for males and the second for females.

Tree species, foraging height, diameter of foraging site and its condition were included as the fixed categorical explanatory variables whereas dbh as a continuous explanatory variable. In the case of some tree species, sporadically used during foraging, for the purpose of analysis, they were lumped into one group "other", which was one of the categories of the "tree species" variable. Moreover we included also interactions between tree species and condition of foraging place to reveal possible differences between foraging sessions on dead and alive substrates in relation to tree species. Year was included as a random variable. The variable "tree condition" was excluded from the analysis because it was strictly connected with "condition of foraging place" (i.e. all dead trees have only dead foraging places).

If GLMM revealed a significant effect of the fixed explanatory variable paired contrasts were calculated to evaluate differences between levels of a given variable. The presented graphs illustrate statistically significant results presenting mean values with 95% confidence intervals. Statistical analyses were performed in IBM SPSS Statistics ver. 21.0 for Windows.

## RESULTS

GLMM analysis performed for Great Spotted Woodpecker females revealed that the duration of the foraging session was associated with tree species, dbh and the diameter, height and

Table 1. Results of generalised linear mixed model explaining the duration of the foraging sessions of females of the Great Spotted Woodpecker in primeval oak-hornbeam-lime forest.

Variable	df1, df2	F	p
Intercept	21, 190	460.71	< 0.001
Tree species	6, 190	116.10	< 0.001
Condition of foraging site	1, 190	520.90	< 0.001
Tree species × condition of foraging site	6, 190	103.10	< 0.001
Diameter of foraging site	3, 190	766.60	< 0.001
Height of foraging site	4, 190	627.34	< 0.001
Dbh	1, 190	177.38	< 0.001
Random effect	Estimate ± SE	Z	p
Year	0.38 ± 0.16	2.33	0.020

condition of foraging site. Moreover, the interaction between tree species and condition of foraging place was statistically significant (Table 1, 2).

Table 2. Estimates of variables from the model presented in Table 1. Asterisk means the reference category.

Variable	Estimate	SE	p
Intercept	5.18	0.18	< 0.001
Tree species			
aspen	-1.08	0.05	< 0.001
hornbeam	-0.20	0.04	< 0.001
lime	-0.52	0.04	< 0.001
maple	-0.60	0.03	< 0.001
oak	-0.33	0.04	< 0.001
spruce	-0.02	0.04	0.664
other	0*		
Condition of foraging site			
dead	-0.36	0.04	< 0.001
alive	0*		
Tree species × condition of foraging site			
aspen × dead	1.61	0.07	< 0.001
aspen × alive	0*		
hornbeam × dead	0.81	0.05	< 0.001
hornbeam × alive	0*		
lime × dead	0.79	0.06	< 0.001
lime × alive	0*		
maple × dead	0.51	0.09	< 0.001
maple × alive	0*		
oak × dead	0.89	0.05	< 0.001
oak × alive	0*		
spruce × dead	0.83	0.05	< 0.001
spruce × alive	0*		
other × dead	0*		
other × alive	0*		
Diameter of foraging site			
to 5 cm	-0.32	0.03	< 0.001
5–10 cm	-0.02	0.02	0.435
10–20 cm	0.59	0.02	< 0.001
> 20 cm	0*		
Height of foraging site			
to 5 m	-1.12	0.03	< 0.001
5–10 m	-0.70	0.03	< 0.001
10–15 m	-0.66	0.03	< 0.001
15–20 m	0.02	0.02	0.348
> 20 m	0*		
Dbh	0.01	0.00	< 0.001

Table 3. Results of generalised linear mixed model explaining the duration of the foraging sessions of males of the Great Spotted Woodpecker in primeval oak-hornbeam-lime forest.

Variable	df1, df2	F	p
Intercept	21, 193	202.11	< 0.001
Tree species	6, 193	272.51	< 0.001
Condition of foraging site	1, 193	82.58	< 0.001
Tree species × condition of foraging site	6, 193	45.94	< 0.001
Diameter of foraging site	3, 193	302.12	< 0.001
Height of foraging site	4, 193	60.35	< 0.001
Dbh	1, 193	0.22	0.641
Random effect	Estimate ± SE	Z	p
Year	0.16 ± 0.07	2.28	0.022

GLMM for males showed that all above mentioned variables were significant except tree dbh (Table 3, 4).

Table 4. Estimates of variables from the model presented in Table 3. Asterisk means the reference category.

Variable	Estimate	SE	p
Intercept	4.50	0.13	< 0.001
Tree species			
aspen	-0.59	0.05	< 0.001
hornbeam	-0.72	0.42	< 0.001
lime	-0.36	0.04	< 0.001
maple	-0.84	0.05	< 0.001
oak	-0.82	0.46	< 0.001
other	-1.46	0.09	< 0.001
spruce	0*		
Condition of foraging site			
dead	0.15	0.04	< 0.001
alive	0*		
Tree species × condition of foraging site			
aspen × dead	0.14	0.08	0.079
aspen × alive	0*		
hornbeam × dead	-0.49	0.05	< 0.001
hornbeam × alive	0*		
lime × dead	-0.07	0.06	0.212
lime × alive	0*		
maple × dead	0.11	0.09	0.205
maple × alive	0*		
oak × dead	0.27	0.06	< 0.001
oak × alive	0*		
other × dead	0.54	0.11	< 0.001
other × alive	0*		
spruce × dead	0*		
spruce × alive	0*		
Diameter of foraging site			
to 5 cm	0.31	0.03	< 0.001
5–10 cm	0.68	0.02	< 0.001
10–20 cm	0.20	0.03	< 0.001
> 20 cm	0*		
Height of foraging site			
to 5 m	-0.39	0.03	< 0.001
5–10 m	-0.34	0.03	< 0.001
10–15 m	-0.35	0.03	< 0.001
15–20 m	0.39	0.023	< 0.001
20 m	0*		
Dbh	0.00	0.00	0.641



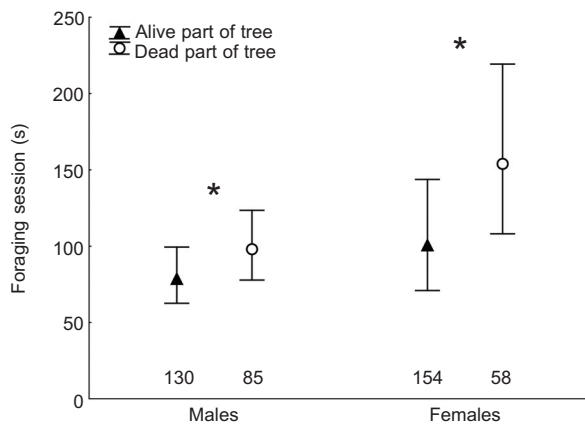


Fig. 1. Mean duration of the foraging session (with 95% confidence limits) of Great Spotted Woodpecker males and females on dead and alive foraging sites. Asterisk indicate significant differences between dead and alive substrates. Numbers indicate sample size.

Generally, the longest foraging sessions were found on Norway Spruce for both sexes whereas the shortest ones on hornbeam in the case of males and maple and aspen in the case of females. Foraging session was longer on dead tree parts than on alive ones which was especially noticeable in the case of females (Fig. 1). This phenomenon was found for all tree species except hornbeam and lime in the case of males (Fig. 2) and maple in the case of females (Fig. 3). The longest foraging was revealed on dead parts of Norway Spruces for both sexes (Fig. 2, 3). Males foraged the longest on sites located above 20 m (Fig. 4) and having a diameter 5–10 cm (Fig. 5) whereas

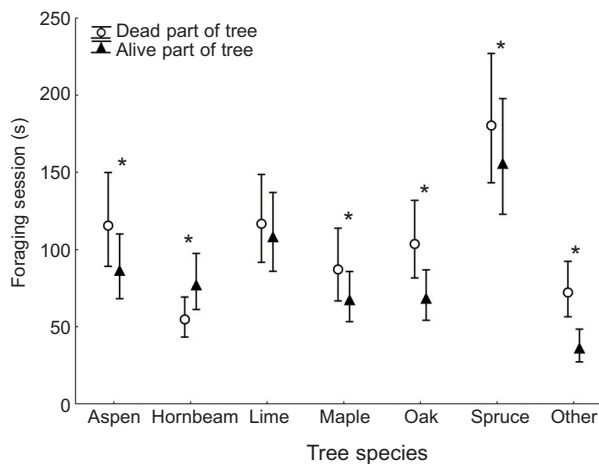


Fig. 2. Mean duration of the foraging session (with 95% confidence limits) of Great Spotted Woodpecker males on particular tree species in relation to substrate condition. Asterisk indicate significant differences between dead and alive substrates. Other: Alder *Alnus glutinosa*, Ash, birches *Betula* spp., elms.

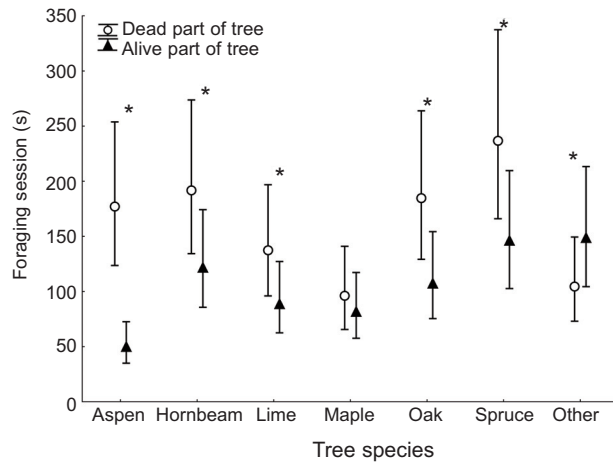


Fig. 3. Mean duration of the foraging session (with 95% confidence limits) of Great Spotted Woodpecker females on particular tree species in relation to substrate condition. Asterisk indicate significant differences between dead and alive substrates. Other: Alder, Ash, birches, Scots Pine, elms.

females on sites above 15 m (Fig. 6) and having a diameter 10–20 cm (Fig. 7). The duration of the foraging session of females increased with increasing of tree dbh which was not observed in the case of males (Fig. 8).

The random effect “year” was significant in both analysed models (Table 1, 3).

## DISCUSSION

Our study revealed that foraging sessions of the Great Spotted Woodpecker were the longest in places having a moderate diameter, located

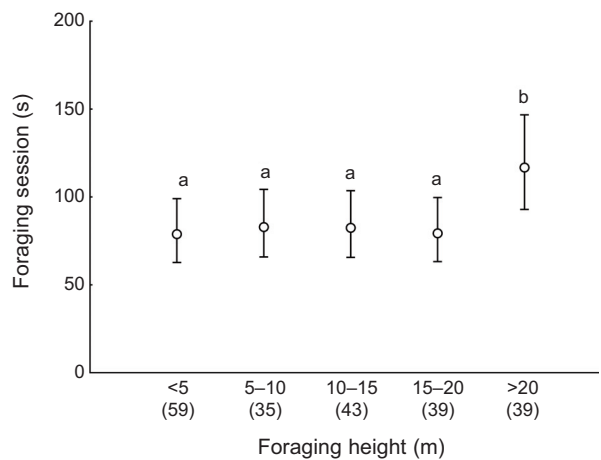


Fig. 4. Mean duration of the foraging session (with 95% confidence limits) of Great Spotted Woodpecker males at different heights. Different letters indicate significant differences between particular categories of foraging height. Numbers in brackets indicate sample size.

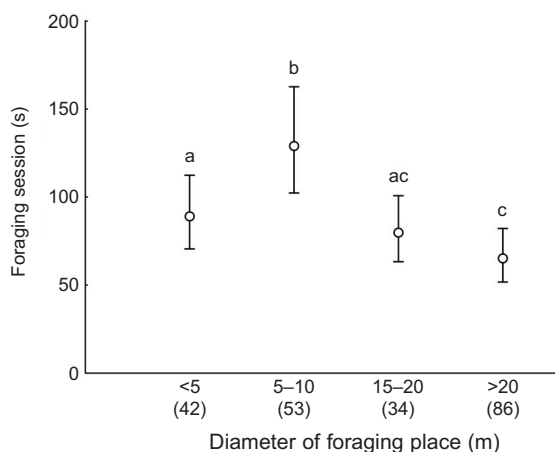


Fig. 5. Mean duration of the foraging session (with 95% confidence limits) of Great Spotted Woodpecker males in sites of different diameter. Different letters indicate significant differences between particular categories of foraging places. Numbers in brackets indicate sample size.

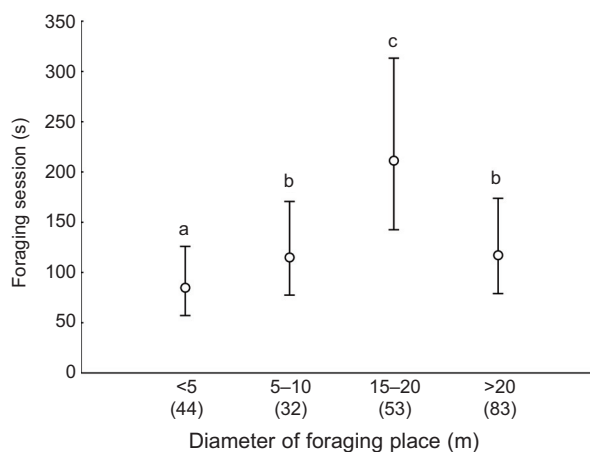


Fig. 7. Mean duration of the foraging session (with 95% confidence limits) of Great Spotted Woodpecker females in sites of different diameter. Different letters indicate significant differences between particular categories of foraging places. Numbers in brackets indicate sample size.

higher up in trees, and being dead what was especially noticeable in the case of females. Thus our assumption that dead substrates would be preferred over living substrates was confirmed.

The longest foraging sessions of both sexes were revealed on dead parts of Norway Spruce what suggests that this tree species is an important site of foraging for the Great Spotted Woodpecker, where it collects food not only in the form of seeds but also invertebrates.

Spruces, especially dead ones, are inhabited by many organisms, mainly insects (e.g. beetles), which also overwinter inside the wood

(Hilszczański 2008, Löhmus et al. 2010). The study by Hogstad (1970), who observed foraging of the Three-toed Woodpeckers on only one dead spruce for a few days, confirms that this tree species can be excellent storage of food. Dead spruce can also be a frequent place of foraging for the White-backed and Middle Spotted Woodpeckers, which was observed in BPN (Czeszczewik 2009, Stański 2014). However, foraging of the Great Spotted Woodpecker on spruces apart from picking out cones, which are then hammered in the anvils, is uncommonly reported, and if such behaviour is observed this is only a small percentage of observations (Alatalo 1978).

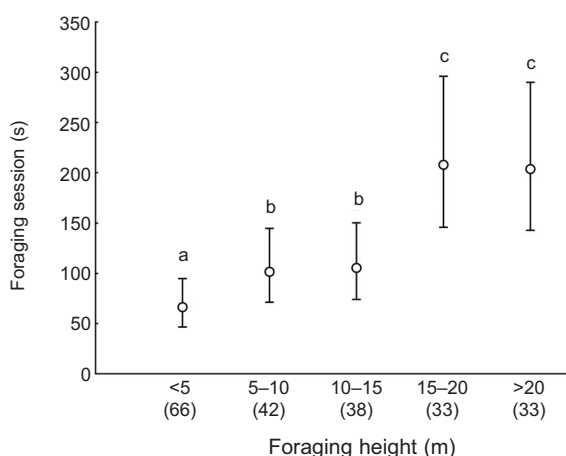


Fig. 6. Mean duration of the foraging session (with 95% confidence limits) of Great Spotted Woodpecker females at different heights. Different letters indicate significant differences between particular categories of foraging height. Numbers in brackets indicate sample size.

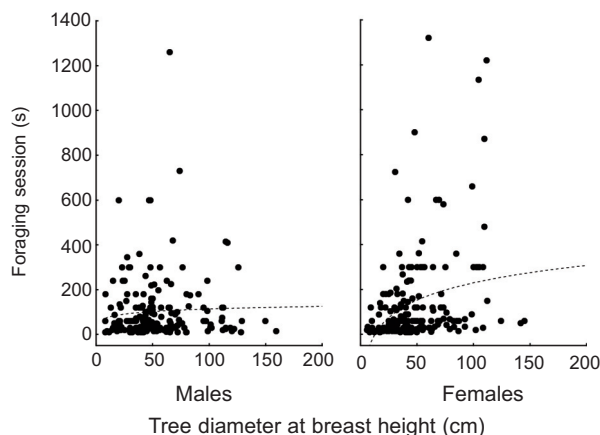


Fig. 8. Relationship between tree trunk diameter at breast height and the duration of the foraging session of Great Spotted Woodpecker males and females.

Our second hypothesis assumed that trees with large dimensions should be preferred over trees with small dimensions. It was based on the fact that trees with large dbh are characterized by a higher number of invertebrates compare to trees with smaller dbh, as demonstrated by studies of two species of butterfly caterpillars (Sukovata & Jaworski 2010). The abundance of insects e.g. beetles living in or below the bark also increased significantly with tree diameter (Löhmus et al. 2010). However, we revealed that duration of foraging session increased with increasing tree dbh only in the case of females. It was not observed in the case of males. Both this phenomenon, as well as much longer foraging on dead tree fragments compare to alive ones in females than in the case of males, may be due to the fact that the former are based more on animal food. Similar results to ours were obtained by Osiejuk (1998), who found that females foraged much more often on dead parts of trees and on thicker trees (taking into account only animal food). However, he stated this only during winter with poor availability of Scots Pine cones, which is when the competition for food was strong. Another study of Osiejuk (1994) showed, that males due to social dominance, expressed by aggressive behaviour, influenced females to feed more often on animal food than on seeds excavated from cones.

Our study showed that woodpeckers foraged longer in places having a moderate diameter and located higher up in trees. This phenomenon may be explain by the fact that the number of potential places rich in food and suitable for foraging is likely to increase with height, which could have been influenced, among others, by their better sun exposure compared to lower situated sites. More insolated trees or their fragments have richer invertebrate fauna, thus may cause the woodpeckers forage there longer (Nicolai 1986). Such places are attractive for woodpecker species that collect food from the surface like the Middle Spotted Woodpecker (Pasinelli & Hegelbach 1997).

Selection of specific foraging places by the Great Spotted Woodpecker could also result from the competition and thus, resource partitioning between different woodpecker species. In order to minimize competition, individual species of woodpeckers inhabiting the same habitat firstly use different feeding techniques, which allows them to obtain different types of food, and secondly, they use places on trees of different

diameter or located on different heights (Hogstad 1971b, Alatalo 1978, Török 1988, 1990, Kruszyk 2003). For example, Hogstad (1971b) showed that the Great Spotted Woodpecker preferred to feed on thinner parts of trees and at higher heights than the Three-toed Woodpecker. Such resource partitioning is also apparently present in BPN, where all species of woodpeckers breed, with the exception of the Syrian Woodpecker *Dendrocopos syriacus*, which means that competition for food could be potentially strong here. For example, spruces, being a great storage of food in BPN, are used not only by the Three-toed Woodpecker, but also by the Great Spotted, the Middle Spotted and the White-backed Woodpeckers (Czeszczewik 2009, Stański 2014). However, particular woodpecker species collect food in different way or in different sites to minimize competition. For example, the Great Spotted Woodpeckers foraged high and on moderate parts of trees, as was shown in this work, while the White-backed woodpecker low and on substrates above 20 cm of diameter (Czeszczewik 2009). On the other hand, Wesołowski (2003) suggests that competition for food does not seem to play an important role in the BPN. His statement was based on data from breeding season, when food resources are usually superabundant here. However, in the non-breeding season, when food resources are less, competition for food may play a greater role (Czeszczewik 2010).

The length of the foraging session was also influenced by the year which may be related to the change of foraging behaviour resulting mainly from the change in the composition of available food. In the BPN, the availability of animal food as well as the degree of fruiting of spruce and hornbeam, which are an important food resource for the Great Spotted Woodpeckers in the non-breeding period, were subject to considerable fluctuations in individual years (Wesołowski & Rowiński 2006, Stański 2014, Wesołowski et al. 2015).

In conclusion, foraging sessions of the Great Spotted Woodpecker were longer in sites located higher, having a moderate diameter, and being dead what was especially noticeable in the case of females. It may suggest that these are attractive places for collecting food. Norway Spruces, in particular, their dead parts, are an important source of food for studied woodpecker species not only in the form of cones but also as invertebrates collected there.



## REFERENCES

- Alatalo R. V. 1978. Resource partitioning in Finnish woodpeckers. *Ornis Fennica* 55: 49–59.
- Cowie R. J., Krebs J. R. 1979. Optimal foraging in patchy environments. In: Anderson R. M., Turner E. D., Taylor R. L. (eds). *Population dynamics*. Blackwell, Oxford, pp. 183–205.
- Cresswell W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: Profitability or risk? *J. Anim. Ecol.* 63: 589–600.
- Czeszczewik D. 2009. Foraging behaviour of White-backed Woodpeckers *Dendrocopos leucotos* in a primeval forest (Białowieża National Park, NE Poland): dependence on habitat resources and season. *Acta Ornithol.* 44: 109–118.
- Czeszczewik D. 2010. Wide intersexual niche overlap of the specialized White-backed Woodpecker *Dendrocopos leucotos* under the rich primeval stands in the Białowieża Forest, Poland. *Ornis Polonica* 51: 241–251.
- Heithaus M. R. 2005. Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. *Mar. Biol.* 147: 27–35.
- Hilszczański J. 2008. [Bark of dead infested spruce trees as an overwintering site of insect predators associated with bark and wood boring beetles]. *Leśne Prace Badawcze* 69: 15–19.
- Hogstad O. 1970. On the ecology of the three-toed woodpecker *Picoides tridactylus* (L.) outside the breeding season. *Nytt Magasin for Zoologi* 18: 221–227.
- Hogstad O. 1971a. Notes on the winter food of the Great Spotted Woodpecker, *Dendrocopos major*. *Sterna* 10: 233–241.
- Hogstad O. 1971b. Stratification in winter feeding of the Great Spotted Woodpecker *Dendrocopos major* and the Three-toed Woodpecker *Picoides tridactylus*. *Ornis Scand.* 2: 143–146.
- Hogstad O. 1978. Sexual dimorphism in relation to winter foraging and territorial behaviour of the Three-toed woodpecker *Picoides tridactylus* and three *Dendrocopos* species. *Ibis* 120: 198–203.
- Hogstad O. 1991. The effect of social dominance on foraging by the Three-toed Woodpecker *Picoides tridactylus*. *Ibis* 133: 271–276.
- Jiao Z. B., Wan T., Wen J. B., Hu J. F., Luo Y. Q., Fu L. J. Zhang L. S. 2008. Seasonal diet of the Great Spotted Woodpecker (*Picoides major*) in shelterwood plantations of Wulate Qianqi County, Inner Mongolia. *Forestry Studies in China* 10: 119–124.
- Kruszyk R. 2003. [Population density and foraging habits of the Middle Spotted Woodpecker *Dendrocopos medius* and Great Spotted Woodpecker *D. major* in the Odra valley near Wrocław]. *Notatki Ornitolologiczne* 44: 75–88.
- Lõhmus A., Kinks R., Soon M. 2010. The importance of dead-wood supply for woodpeckers in Estonia. *Baltic Forestry* 16: 76–86.
- Michalek K. G., Miettinen J. 2003. *Dendrocopos major* Great Spotted Woodpecker. *BWP Update*, Vol. 5, No. 2. Oxford Univ. Press.
- Nicolai V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69: 148–160.
- Osiejuk T. 1994. Sexual dimorphism in foraging behaviour of the Great Spotted Woodpecker *Dendrocopos major* during winters with rich crops of Scotch pine cones. *Ornis Fennica* 71: 144–150.
- Osiejuk T. 1998. Study on the intersexual differentiation of foraging niche in relation to abundance of winter food in Great Spotted Woodpecker *Dendrocopos major*. *Acta Ornithol.* 33: 135–141.
- Pasinelli G. 2000. Sexual dimorphism and foraging niche partitioning in the Middle Spotted Woodpecker *Dendrocopos medius*. *Ibis* 142: 635–644.
- Pasinelli G., Hegelbach J. 1997. Characteristics of trees preferred by foraging Middle Spotted Woodpecker *Dendrocopos medius* in northern Switzerland. *Ardea* 85: 203–209.
- Pavlik S. 1997. [Woodpeckers as predators of leaf-eating lepidopterus larvae in oak forests]. *Tichodroma* 10: 127–137.
- Pechacek P. 2006. Foraging behavior of Eurasian Three-toed Woodpeckers (*Picoides tridactylus alpinus*) in relation to sex and season in Germany. *Auk* 123: 235–246.
- Rolstad J., Rolstad E. 2000. Influence of large snow depths on Black Woodpecker *Dryocopus martius* foraging behavior. *Ornis Fennica*: 77: 65–70.
- Selander R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113–151.
- Smith K. W. 2007. The utilization of dead wood resources by woodpeckers in Britain. *Ibis* 149: 183–192.
- Stański T. 2014. [Comparison of foraging and nesting sites between the Middle Spotted Woodpecker *Dendrocopos medius* (L., 1758) and the Great Spotted Woodpecker *Dendrocopos major* (L., 1758) in a primeval lime-oak-hornbeam forest of Białowieża National Park]. Ph.D. Thesis, Siedlce University of Natural Sciences and Humanities.
- Stenberg L., Hogstad O. 2004. Sexual dimorphism in relation to winter foraging in the white-backed woodpecker (*Dendrocopos leucotos*). *J. Ornithol.* 145: 321–326.
- Stephens D. W., Krebs J. R. (eds). 1986. *Foraging theory*. Princeton Univ. Press.
- Sukovata L., Jaworski T. 2010. [The abundance of the nun moth and lappet moth larvae on trees of different trunk thickness in Scots pine stands in the Noteć forest complex]. *Leśne Prace Badawcze* 71: 231–237.
- Tomiałojć L. 1991. Characteristics of old growth in the Białowieża Forest, Poland. *Nat. Areas J.* 11: 7–18.
- Török J. 1988. Food resource partitioning between two *Dendrocopos* species during the breeding season. *Opuscula Zoologica* 23: 197–202.
- Török J. 1990. Resource partitioning among three woodpecker species *Dendrocopos* spp. during the breeding season. *Holarctic Ecol.* 13: 257–264.
- Vanicsek L. 1988. The study of bird species foraging on the bark. *Aquila* 95: 83–96.
- Wesołowski T. 2003. Bird community dynamics in a primeval forest — is interspecific competition important? *Ornis Hung.* 12–13: 51–62.
- Wesołowski T., Rowiński P. 2006. Tree defoliation by winter moth *Operophtera brumata* L. during an outbreak affected by structure of forest landscape. *For. Ecol. Manage.* 221: 299–305.
- Wesołowski T., Rowiński P., Maziarz M. 2015. Interannual variation in tree seed production in a primeval temperate forest: does masting prevail? *Eur. J. Forest Res.* 134: 99–112.
- Wiebe K. L., Gow E. A. 2013. Choice of foraging habitat by northern flickers reflects changes in availability of their ant prey linked to ambient temperature. *Ecoscience* 20: 122–130.

## STRESZCZENIE

**[Behawior żerowiskowy dzięcioła dużego w zależności od płci w pierwotnych drzewostanach Białowieskiego Parku Narodowego]**

Głównym celem badań było poznanie miejsc preferowanych podczas żerowania przez dzięcioła dużego w pierwotnych łąkach Białowieskiego Parku Narodowego. Założono, że niektóre drzewa i określone miejsca znajdujące się na nich, bardziej niż inne obfitują w pokarm, co sprawia, że średni czas sesji żerowania (zdefiniowanej jako czas żerowania dzięcioła w jednym miejscu na jednym drzewie) będzie na nich dłuższy niż w pozostałych miejscach. Przyjęto hipotezę, że dzięcioły najdłużej żerować będą na martwych częściach drzew oraz na drzewach o znacznych rozmiarach (wyrażonych w ich pierśnicy). Ponadto założono, że najdłuższe sesje żerowania zarówno samców jak i samic dzięcioła dużego odbywać się będą w miejscach o podobnych parametrach.

W latach 1999–2011 teren badań był penetrowany w celu wyszukania żerujących dzięciołów dużych. Po znalezieniu żerującego ptaka mierzono czas jego żerowania oraz notowano jego płć i parametry miejsca żerowania: gatunek i pierśnicę drzewa, średnicę, stan (żywe/martwe) i wysokość miejsca żerowania nad ziemią.

Ogółem do analizy włączono 215 sesji żerowania samców i 212 sesji żerowania samic, wykluczając obserwacje żerowania na nasionach świerka i grabu, ponieważ nie świadczą one o atrakcyjności danego miejsca jako źródła pokarmu, a tylko o jego użyteczności jako kuźni.

Wykazano, że na długość sesji żerowania samic wpływały: gatunek drzewa, pierśnica oraz

średnica, wysokość i stan części, na której odbywało się żerowanie, a także rok, który został uwzględniony w analizie jako czynnik losowy (Tab. 1, 2). Natomiast na długość sesji żerowania samców wpływały wszystkie wymienione czynniki z wyjątkiem pierśnicy drzewa, na którym odbywało się żerowanie (Tab. 3, 4). Obie płcie żerowały dłużej na martwych częściach drzew niż na żywych, co było szczególnie widoczne w przypadku samic (Fig. 1). Najdłuższe sesje żerowania stwierdzono na martwych częściach świerków zarówno w przypadku samców jak i samic (Fig. 2, 3). Samce żerowały najdłuższej na wysokości powyżej 20 m (Fig. 4) i na częściach drzew o grubości 5–10 cm (Fig. 5) natomiast samice na wysokości powyżej 15 m (Fig. 6) i na częściach o średnicy 10–20 cm (Fig. 7). Czas sesji żerowania samic zwiększał się wraz ze wzrostem pierśnicy drzewa czego nie zaobserwowano u samców (Fig. 8).

Dłuższe sesje żerowania na częściach drzew, które były martwe, położone wysoko nad ziemią i o przeciętnej grubości sugerują, że takie miejsca są atrakcyjne pod względem pozyskiwania pokarmu przez dzięcioły duże. Badania ponadto dowiodły, że świerki, a w szczególności ich martwe fragmenty, są dla dzięciołów dużych istotnym źródłem pokarmu w postaci zasiedlających je bezkręgowców. Wpływ roku na długość sesji żerowania może być związany ze zmianami w składzie i ilości dostępnego pokarmu. W Białowieskim Parku Narodowym występują znaczne fluktuacje w ilości pokarmu, który jest ważnym składnikiem diety dzięcioła dużego, zarówno zwierzęcego (np. gąsienice) jak i roślinnego (nasiona grabu i świerka).