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Sexual dimorphism in foraging behaviour of the Great Spotted Woodpecker *Dendrocopos major* during winters with rich crops of Scotch pine cones

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During the winters of 1990–1991 and 1991–1992, when rich crops of Scotch pine cones were observed, the foraging behaviour of male and female Great Spotted Woodpeckers was studied in the Wielkopolski National Park, in western Poland. Fourteen foraging characteristics were distinguished. Aggressive behaviour was observed only rarely. During both winters the exclusive male and female territories probably did not exist, or were very small and close to one another. Both sexes fed mainly on pine cones and microhabitat utilization and foraging behaviour patterns were generally similar. However, significant differences were found in almost all aspects of male and female feeding niches. Males, more than females foraged on cones and their foraging behaviour was more stereotyped. Females used a greater spectrum of microhabitats and techniques, and were more mobile than males. This was probably a consequence of male social dominance, which influenced the females to feed more often on alternative food. These differences are thought to be a result of less defined territories due to a temporarily richer food supply.

1. Introduction

North American (Yeager 1955, Selander & Giller 1959, 1963, Baldwin 1960, Koplin 1969, Willson 1970, Morse 1972, Peters & Grubb 1983) and European (Hogstad 1971, 1976, 1978, Winkler 1973, Aulén & Lundberg 1991) studies of the foraging habits of sympatric woodpeckers have disclosed stratal segregation, as well as behavioural differences. For woodpecker species in which both sexes cohabit a common feeding territory, sexual dimorphism has been related to intraspecific differences in niche utilization (Kilham 1965, 1970, Selander 1965, 1966, Ligon 1968, Jackson 1970, Short 1970, 1971, Willson 1970, Koch et al. 1970, Kisiel 1972, Hogstad 1976, 1978).

Niche partitioning can arise from genetic differences or behavioural plasticity (Werner & Hall 1976). In the first case, intersexual niche partitioning occurs because each sex has a different, genetically determined preferred niche (Jackson 1970, Williams 1980). So, the foraging niche of each sex should not be influenced by the opposite sex. In the second case, niche differences between sexes are the result of social dominance

(Ligon 1968, 1973, Kilham 1970, Glase 1973, Hogstad 1976, 1978). Most often males, by their aggressive behaviour, displace females from a part of the species niche. An experimental analysis of sex-specific foraging in the Downy Woodpecker *Picoides pubescens* (Peters & Grubb 1983) supports the second hypothesis. After removing all males (1) or all females (2) from woodlots, the authors observed a change in foraging behaviour only in case (1), in which females started to forage like males. Therefore, we can make an assumption that the sexes in closely related woodpecker species have different foraging niches, due to female avoidance of the foraging microhabitat of socially dominant males.

The Great Spotted Woodpecker *Dendrocopos major* and the Downy Woodpecker are not strongly dimorphic species. Only the bill-length is significantly greater in males (Selander 1966, Wallace 1974, Hogstad 1978). Hogstad (1976, 1978) hypothesized that weak dimorphism in several *Dendrocopos* species is a consequence of separate feeding territories during the non-breeding season (Pynnönen 1938, 1961). Therefore, stronger dimorphism is a defence against intersexual competition in the species with common territories during the non-breeding season (Hogstad 1976, 1978).

In the present study, the intersexual differences in microhabitat utilization and foraging behaviour of the Great Spotted Woodpecker were investigated during two winters with a relatively high food availability of rich cone crops. The most important questions addressed are:

1. Does higher food availability during winter lead to increased overlapping of male and female foraging niches?
2. Do both sexes of the Great Spotted Woodpecker eat vegetable and animal food in the same proportion?
3. How can we explain the differences in the foraging behaviour between males and females?

2. Materials and methods

The study was conducted during the winters of 1990–1991 and 1991–1992 in an oak-hornbeam forest, partly mixed with pine, near Poznań (Wielkopolski National Park – later WNP, Grabina Reserve and surroundings ca. 30 ha, 52°15′N, 16°50′E). The dominant tree species are *Quercus robur* and *Pinus sylvestris* mixed with less numerous *Carpinus betulus*, *Betula spp.* and *Acer spp.* The fraction of dead trees in the study area vary between 5.4% and 14.9% (mean 12.7%, based on several samples from 1 ha square plot — see Osiejuk 1993). During both winters the Scotch pine had a rich cone crop.

The foraging behaviour of birds was closely observed between 8:00 and 12:00, from 1 December to 28 February during each winter. To minimize the effect of weather, observations were made only on fine days. One-tree-one-record method was used (1T1R, Matsuoka 1977, Ishida 1990). Eight to ten individuals (Osiejuk 1993) were followed and foraging variables were noted using a tape-recorder. Data for the two years were pooled. Fourteen foraging variables were recorded:

Microhabitat utilization:
Tree species used for foraging,
Tree height (< 10, 10–20, 20 [m]),
Tree diameter at breast height [cm],
Type of tree: dead or alive,
Part of tree used (trunk, branch diameter [cm]: 10, 10–5, 5–3, 3–1, <1),
Height of foraging above the ground (<5, 5–10, 10–15, 15–20, 20 [m]),
Type of the foraging place: dead or alive,
Foraging behaviour:
Foraging technique (gleaning – picking invertebrates from the surface; probing – peering and poking for arthropods on the surface; scaling – scaling the bark of dead branches or trunks for food; excavating – subcambial excavation; picking up cones and husking),
Foraging pattern: stationary or dynamic,
Body position: horizontal – head up, head down, head up and down alternately; vertical – back up, back down, back up and down alternately,
Movement pattern (straight, spiral, sideward around),
Direction of movements (up, down, up and down alternately),
Length of movements [m] (finishing height minus starting height),
Length of flights between trees [m].

Cases of aggressive behaviour between individuals were also noted. The total time of observations were 177 minutes for males and 120 minutes for females (169 and 114 1T1R observation). During the breeding seasons of 1991 and 1992 four territories (pairs) were found on the studied area (Osiejuk 1992, 1993 and unpubl. mat.).

Foraging diversity was calculated using the Shannon-Wiener index $H' = -Sp_i \log p_i$, where H' is the diversity value for the particular observation category (i.e. tree species, foraging technique etc.), p_i is the number of individual observations made within the sub-division of each category i, $i = 1, 2, ..., n$. All values are expressed as the ratio $J' = H' / H_{max}$, where H_{max} is the maximum possible diversity, representing equal utilization of all sub-divisions of the categories used by the species (Pielou 1966).

The degree of intersexual overlap in niche utilization has been quantitatively determined using Horn's (1966) equation

$$R_0 = \frac{\sum(x_i + y_i)\log(x_i + y_i) - \sum x_i \log x_i - \sum y_i \log y_i}{(X + Y)\log(X + Y) - X \log x - Y \log Y}$$

in which X and Y represent the total number of observations (total time) for males and females, respectively, in the particular category; x_i and y_i represent the number of occurrences (fraction of observation time) made in the ith sub-division within each category for X and Y, respectively.

I used the contingency table method (Rosner 1986) to analyse the original numerical data concerning foraging behaviour and microhabitat analysis.

3. Results

3.1. Microhabitat utilization

Generally, the microhabitat utilization pattern was similar in males and females, but some significant differences were found. Males foraged more on Scots pines ($\chi^2 = 3.17$, df = 2, P = 0.2) and on dead trees than females ($\chi^2 = 13.56$, df = 1 , P < 0.001, Table 1). Females preferred slightly higher trees, but the difference was not significant ($\chi^2 = 0.45$, df = 1, P = 0.51, Table 1), and spent more time foraging in the lower part of a tree stand ($\chi^2 = 30.65$, df = 3, P < 0.001, Table 2). Both sexes most often foraged on trunks, but males also used thicker branches than females ($\chi^2 = 20.96$, df = 5, P < 0.001,Table 2). No significant differences were found in the diameter of trees used by

Table 1. Sexual dimorphism in utilization of different tree species, trees with different height, diameter at breast height, and condition.

Tree characteristic	Percentage of feeding time Male	Female
Tree species		
Quercus robur	3.7	11.6
Pinus sylvestris	95.2	88.0
Other	1.1	0.4
Tree height [m]		
< 10	0.0	0.0
10–20	59.5	45.9
< 20	40.5	54.1
Tree diameter at breast height [cm]		
< 20	5.5	8.7
20–40	76.4	78.6
> 40	18.1	12.7
Tree condition		
Alive	21.2	47.7
Dead	78.8	52.3

Table 2. Sexual divergence in selection of place of foraging.

Place of foraging characteristic	Percentage of feeding time Male	Female
Place of foraging		
Trunk	37.0	32.2
Branches ∅ > 10 cm	12.9	24.3
Branches ∅ 5–10cm	31.1	8.4
Branches ∅ 3–5 cm	0.7	1.1
Branches ∅ 1–3 cm	13.4	25.7
Branches ∅ < 1 cm	4.9	5.3
Place of foraging condition		
Alive	19.7	36.0
Dead	80.3	64.0
Height of place of foraging [m]		
< 5	–	–
5–10	–	2.2
10–15	1.4	14.5
15–20	72.4	60.6
> 20	26.2	22.6

both sexes ($\chi^2 = 2.68$, df = 2, P = 0.26). Females fed more than males on living substrates ($\chi^2 = 8.83$, df = 1, P = 0.003, Table 2). In other aspects of microhabitat utilization the differences between the sexes of the Great Spotted Woodpecker were smaller (Tables 1 & 2).

3.2. Foraging behaviour

Foraging behaviour of males and females was more similar than microhabitat utilization. The variables connected with locomotion on trees (foraging pattern ($\chi^2 = 0.004$, df = 1, P = 0.95), movement direction, body position ($\chi^2 = 4.30$, df = 2, P = 0.12), and movement patterns) were nearly the same or identical (Table 3). Greater differences were found only in the preference of foraging techniques ($\chi^2 = 15.16$, df = 4, P = 0.004). Males fed mainly on cones – 87.9% of feeding time (husking and picking, Table 3); females – 80.1%. Males picked up cones faster, therefore, the picking up time / husking time ratio was higher for males (males – 0.08, females – 0.18). This difference explains why males foraged on branches with a diameter of 5–10 cm almost four times more often than females and two times less frequently on branches of 1–3 cm in diameter (husking places were located on branches 5–10 cm, cones were picked up from twigs with diameter < 1 cm). Males did not use scaling at all and females used it to a very small extent (Table 3).

Table 3. Sexual differences in foraging behaviour of Great Spotted Woodpecker.

Foraging behaviour characteristic	Percentage of feeding time Male	Female
Foraging pattern		
Stationary	96.9	93.3
Dynamic	3.1	6.7
Movement direction		
Up	89.2	73.2
Up & down	10.8	26.8
Body position		
Horizontal with head up	93.4	93.1
Vertical with back down	6.6	6.9
Foraging technique		
Gleaning	4.0	2.2
Probing	–	–
Scaling	–	4.9
Excavating	8.1	12.8
Husking	81.7	68.0
Picking up cones	6.2	12.1

The greatest intersexual differences concerned the velocity of movements on trees and flights between trees. Females were markedly more active than males, spending twice as much time on feeding with a dynamic foraging pattern, however, this difference was not significant (Table 3). Since the fraction of feeding time with dynamic foraging pattern was low in both sexes (3% and 7%) no detailed analysis was made. Both observations of mean length of flights between the place of foraging (male 12 m, female 19 m; t = –3.16, df = 172, P = 0.002) and the average time of observation (male 133 and female 179 seconds; t = 2.63, df = 281, P = 0.009) support the hypothesis that females are more mobile than males (Table 4).

3.3. Aggressive and territorial behaviour

Aggressive behaviour was observed four times during 297 minutes of total observation time. All of these observations concern a male attacking a female. Aggressive behaviour was initiated when females fed too close to males (0.5–2 m). Many times I observed a few individuals feeding within 10–30 m of each other without any aggressive behaviour.

3.4. Foraging diversity and intersexual niche overlap

In my study I found that the females scored higher values of foraging diversity in nine cat-

Table 4. Characteristic of the flights between places of foraging – intersexual divergence.

Characteristic of the fligths	Male	Female
The total lenght of the flights during 1 our of observation [m/h]	288	589
Number of fligths during 1 hour of observation	24	31
Average length of the flight [m]	12.3	18.8
Number of observations	96	78

egories (except the categories: tree species, tree diameter, and movement pattern) (Table 5, Wilcoxon matched-pairs signed-ranks test, z = –2.31, P = 0.0208). These results indicate that the foraging behaviour of males in WNP was more stereotyped than that of the females. The degree of intersexual overlap, R_0, ranged from 0.92 to 1. Overlap in niche utilization between the sexes were lowest in places of foraging, tree condition, and height of foraging (Table 5).

4. Discussion

During the two winters studied both sexes of the Great Spotted Woodpecker foraged mainly on Scots pine cones. The differences in the use of almost all categories show that female foraging behaviour was more diverse (Tables 1 to 5). Because females foraged on animal food during 20% of their feeding time (males only 12%), they used a greater spectrum of microhabitat, techniques and other factors.

In winters with low food availability males and females of the Great Spotted Woodpecker hold exclusive territories, so the microgeografic allopatry is reduced by intersexual competition for food. Consequently, both sexes show similar foraging patterns and do not waste energy in conflict over foraging sites (Hogstad 1978).

Table 5. Indices of intersexual overlap in foraging behaviour and foraging diversity of males and females of Great Spotted Woodpecker.

Variables of micro-habitat utilisation and foraging behaviour	Indices of intesexual overlap (R_0)	Foraging diversity (J') *	
		Male	Female
Tree species	0.98	0.38	0.35
Tree height	0.99	0.70	0 99
Tree diameter	0.98	0.66	0.60
Tree condition	0.94	0.69	1
Place of foraging	0.91	0.81	0.82
Place condition	0.98	0.72	0.94
Height of foraging	0.94	0.46	0.72
Foraging pattern	0.99	0.20	0.36
Movement direction	0.97	0.49	0.84
Body position	1	0.35	0.36
Movement pattern	1	0	0
Foraging technique	0.96	0.42	0.62
Mean	0.97	0.49	0.63

During the two winters I studied the food availability was high, because of rich crops of Scots pine cones. Aggressive behaviour was rarely observed except for individuals feeding too close to each other. Birds frequently fed within 10–30 m of each other without any aggressive behaviour. This suggests that during my studies exclusive male and female territories did not exist or they were very small. Pynnönen (1939) noticed that Great Spotted Woodpeckers, especially when populations are high take up such clearly defined territories that the boundaries can be drawn to the exact trees. Pulliainen (1963) made a similar observation. Because the observed individuals were not marked, it is hard to recognize which situation I found in WPN (i.e. no exclusive territories or territories are very small). However, the analysis of the flights of observed birds support the first hypothesis.

Based on the results obtained we can assume that both sexes tried to maximize energy income by feeding on the 'easiest food' (Stephen & Krebs 1986, see also Pulliainen 1963, Osiejuk 1991). But females, as a social sub-dominant (Ligon 1968), were sometimes forced to resign temporarily from this kind of food. This probably happens only if they come too close to a male. Some facts support the conclusion that niche differences between the sexes may arise from male dominance. (1) Female has to shift to a less preferred niche in the presence of a male (only when distance between the male and female is very short). (2) While females were more mobile than males during foraging, they — suprisingly — spent more time on husking and picking. So, cones were a relatively worse kind of food for females (lower ratio energy income / time of foraging, Stephens & Krebs 1986). My observations suggest that it might be caused by the females' behaviour to avoid energy-wasting combats (see Skoczylas 1961, Kilham 1962, 1970, Ligon 1968, Williams & Batzli 1979, Peters & Grubb 1983). Maybe, during foraging on competetive food, females have to keep an eye on males, so they needed more time for husking and picking up.

Because of a difference between the habitats and a difference in methodology, it is hard to make a comparison between my results and

Hogstad's (1978) in a straightforward way. There are, however, some basic differences between these two studies:

1. Hogstad (1978)
   a) low food availability,
   b) exclusive male and female territories,
   c) similar foraging behaviour of male and female,
   d) intersexual competition for food reduced by microgeografic allopatry.
2. Wielkopolski National Park
   a) high food availability,
   b) probably no exclusive territories (or very small territories),
   c) significant differences in foraging behaviour of male and female,
   d) intersexual competition for food reduced by female shift to a less preferred niche in the presence of males.

The conclusion is that the differences between feeding niches of the male and female of the Great Spotted Woodpecker were related to a less territorial system, in my study, due to a temporarily richer food supply.

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Selostus: **Puolalaisten käpytikkojen talviruokailu**

Wielkopolskin kansallispuistossa tutkituilla käpytikkakoirailla ja -naarailla havaittiin erilaiset ruokailutavat. Koiraat söivät enemmän käpyjä kuin naaraat, jotka olivat ruokailussaan monipuolisempia ja liikkuvampia. Kirjoittaja arvelee erojen syyksi koiraan sosiaalista ylivaltaa.

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