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Wide intersexual niche overlap of the specialized White-backed Woodpecker *Dendrocopos leucotos* under the rich primeval stands in the Białowieża Forest, Poland

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Abstract: Foraging sites and foraging behaviour of the White-backed Woodpecker *Dendrocopos leucotos* females and males were compared within the year in primeval deciduous tree stands of the Białowieża National Park (BNP), NE Poland. The only significant difference was found during winter when females foraged more often on the branches while males used thicker parts of trees (mainly trunks). The strongest niche overlapping of sexes was observed during spring (Schoener's overlap index $OI = 0.87$), while the weakest was in winter ($OI = 0.78$). As a rule females and males foraged separately. Relatively slight differences in foraging behaviour of both sexes could result from weak size dimorphism in this population or from high-quality habitats of BNP or both. Intersexual competition is minimized most likely due to abundant food resources in multispecies tree stands with high amount of dead wood. Habitat quality and possibly climate conditions could influence body size of females and males as well as related foraging behaviour. Differences between females and males of the White-backed Woodpeckers in Białowieża Forest were very small, compared to northern populations. The study showed that this highly specialized woodpecker species could modify its foraging behaviour in response to environmental conditions like food resources and climate.

Pokrywanie się nisz obu płci wyspecjalizowanego dzięcioła białogrzbietego *Dendrocopos leucotos* w drzewostanach pierwotnych Puszczy Białowieskiej. Abstrakt: Porównano miejsca żerowe oraz sposoby żerowania samic i samców dzięcioła białogrzbietego w Białowieskim Parku Narodowym (BPN). Zimą samice żerowały na cieńszych częściach drzew (częściej na gałęziach) niż samce. Największe pokrywanie się nisz obu płci obserwowano wiosną (wskaźnik pokrywania się nisz $OI = 0{,}87$) a najmniejsze zimą ($OI = 0{,}78$). Z reguły samice i samce żerowały osobno. Stosunkowo niewielkie różnice w zachowaniach żerowych samic i samców mogły być związane z niewielkimi różnicami w wymiarach ciała i/lub z wysokiej jakości siedlisk BPN. Prawdopodobnie z powodu obfitych źródeł pokarmu w tych siedliskach konkurencja międzypłciowa jest nieznaczna. Jakość środowiska i warunki klimatyczne mogły wpływać na wielkość ciała samic i samców jak również na ich zachowania żerowe. W porównaniu z populacjami północnymi różnice w żerowaniu samic i samców były nieznaczne. Praca pokazuje, że ten wyspecjalizowany dzięcioł może modyfikować swoje zachowania żerowe w zależności od warunków środowiskowych.

Sexual dimorphism is common at many woodpecker species. It is usually related to differences in foraging behaviour of females and males, and it was explained as leading to reduction of the competition for food (Selander 1966, Ligon 1968, Jackson 1970, Willson 1970, Kisiel 1972, Hogstad 1978). Sexual dimorphism can be expressed in plumage color or/and in body size. Resource division between sexes is usually accompanied by a sexual size dimorphism, especially in bill size (Kilham 1965, Ligon 1968, Kisiel 1972, Austin 1976, Hogstad 1976). Among woodpeckers, usually male is the larger sex and dominates over female (e.g. Peters & Grubb 1983, Hogstad 1991, Osiejuk 1994, Pasinelli 2000, Pechacek 2006). Moreover, intersexual differences in niche utilization could be more clearly expressed during winter (Wallace 1974, Hogstad 1976). The pressure of intersexual competition is usually lower during breeding period, presumably thanks to a better food supply in spring and summer (Hogstad 1977, Pasinelli 2000, Imbeau & Desrochers 2002). To avoid competition, female and male could e.g. partition their territory horizontally and then forage in different parts of it (Hogstad 1976, Sollien et al. 1982). They can also divide the territory vertically (Pechacek 2006).

White-backed Woodpecker *Dendrocopos leucotos* is one of the rarest European woodpecker species. Due to forest management European populations of this specialist of the dead wood have strongly declined during last century (Cramp 1985, Aulén & Carlson 1990, Virkkala et al. 1993, Czeszczewik & Walankiewicz 2006, Roberge & Angelstam 2006). This species is sexually dimorphic, with male being slightly larger than female. Sexes also differ in plumage: the male has a red crown, the female a black one (Cramp 1985). In north-European populations (60–63°N) males were significantly heavier than females, with longer bill, wing and tarsus and significant intersexual differences in body size were related to distinct separation of foraging niche (Aulén & Lundberg 1991, Stenberg & Hogstad 2004, Hogstad & Stenberg 2005). However, no intersexual difference in body measures which could influence social dominance was found in the Białowieża Forest, central Europe (52°N): females had only significantly shorter bills than males (Wesołowski 1995).

The aim of this study was to look for differences in foraging behaviour and foraging sites between male and female of the White-backed Woodpecker in Białowieża Forest. Due to only slight size dimorphism found in this population (Wesołowski 1995), I expected that foraging behaviour and substrate used by females and males do not differ very much here, as they coexist in lush habitat, rich in dead wood deciduous stands of the Białowieża National Park. Possible differences could perhaps be observed more frequently in winter, when food is limited. In an earlier paper (Czeszczewik 2009a) I analyzed the use of resources and foraging behaviour of the White-backed Woodpecker in respect to season in the Białowieża Forest. Below I analyze whether plentiful food of the Białowieża Forest could minimize differences in foraging behaviour of females and males.

Material and Methods

Study area

The study was conducted within Białowieża National Park (BNP), Poland. This is a part of larger complex of the Białowieża Forest (52°29' – 52°57'N and 23°31'– 24°21'E) which is located in north-eastern Poland and western Belorussia. Central part of BNP (47.47 km^2) has been protected by law since 1921, and is characterized by high degree of naturalness. Most of tree stands have a primeval origin (never logged and never planted) and influence of human activity has been very limited there during the past centuries. Tree stands are multispecies, multilayer and unevenaged, with high amount of dead wood. Almost half of area is covered with lime-hornbeam oak stands (with hornbeam *Carpinus betulus*, lime *Tilia cordata*, oak

Quercus robur, Norway spruce *Picea abies*, maple *Acer platanoides*, elms *Ulmus* spp., ash *Fraxinus excelsior* and some other species) (Faliński 1986). Such species like birches *Betula* spp., aspen *Populus tremula* or sallow *Salix caprea* , regarding as very important species for the White-backed Woodpecker (e.g. Aulén 1988, Stenberg & Hogstad 2004) are very rare in BNP.

Another deciduous tree stands located along forest rivers – ash-alder stands (with ash, alder *Alnus glutinosa* and spruce) – are much less common in BNP. Coniferous spruce-pine forests (with spruce and Scots pine *Pinus sylvestris* and some admixture of broadleaved trees) are located on sandy soils. In this latitude the day from sunrise to sunset lasts 7 hrs 42 min (22 December) to 16 hrs 45 min (21 June). Vegetation season lasts about 200–210 days. Average temperature of the warmest month (July) is 17.9°C and the coldest (January) is –4.3°C. Annual precipitation is on average 594 mm (Faliński 1986).

Data collection

The data were collected in 1999–2007 within strictly protected part of BNP, mainly in hornbeam-lime-oak stands. Foraging White-backed Woodpeckers were observed from sighting until lost through the whole study area. For each foraging bird its sex, foraging behaviour, tree and place on the tree used by woodpecker were recorded. Based on Aulén (1988), seven types of foraging techniques were distinguished: bark-pecking, bark-scaling, superficial woodpecking, deep woodpecking, searching between bark and wood, gleaning, and other (mainly moving i.e. searching of appropriate place for foraging). Tree used by woodpecker was identified to species and its condition was recorded (alive, snag, downed). The diameter of the trunk at the breast height (DBH) was measured. Tree substrate used for foraging was described as a trunk or branch, its diameter (using 7-cm-wide back of White-backed Woodpecker body size as reference), height above the ground and decay stage (alive, dead with or without bark). Woodpeckers were not marked individually and they could be distinguished only by their location. Observations of foraging woodpecker were always marked on the map. Next, based on clusters of observations males and females approximate territories were outlined on the map.

Data analysis

Presented data concern approximately 18 females and 20 males. Each female was monitored on average 10.9 (range 4–58) times per season in various days, and each male 11.6 (range 4–57) times. In total, 364 observations of females and 423 observations of males were collected. I divided a year into three periods: breeding season (March–June), post-breeding season (July–October) and winter (November–February). If a deep snow cover (>20 cm) occurred in March, observations from such days were classified as winter. Data related to foraging techniques and used substrates were expressed as percentages at the level of observations within each record of a given individual (100% was the total time of the observations of a given foraging individual on one tree during one day). Then, average values from all records of a given bird created one sample point (N), used in subsequent analyses. For more details about methods see Czeszczewik (2009a).

All variables had non-normal distributions and I used the Mann-Whitney U-test (Z) or Kolmogorov-Smirnov test (D) to test for differences between sexes. The Bonferroni correction was used in multiple comparisons. Results are presented as means ± one standard deviation (± SD). Statistical analyses were performed using Statistica version 9.0. The foraging niche breadth *B* was calculated using Simpson's index:

$$B = 1 / \Sigma\, p_i^2$$

where p_i is the proportion of observations falling in the *i*th of *n* categories. *B* can vary from 1 to *n* (Price 1975). The total niche size was calculated by adding *B* values calculated from all

categories. The degree of intersexual overlap in niche utilization was quantitatively determined using Schoener's (1968) overlap index:

$$OI = 1 - 1/2 \Sigma |p_{x.i} - p_{y.i}|$$

where $p_{x.i}$ and $p_{y.i}$ are the frequencies for sexes x and y, respectively, for the *i*th category. *OI* varies from 0 (no overlap), to 1 (complete overlap). The overlap is considered to be significant when the index value exceeds 0.6 (Wallace 1981).

Results

During nine years of study female was observed together with a male foraging on the same tree only 14 time, i.e. 1.8% of all observations. Such observations come predominantly from winter (10 records), three from post-breeding and only one in breeding period. When both sexes foraged on the same tree, females usually foraged slightly higher than males (11.0 ± 4.5 m and 9.4 ± 5.7 m, respectively), but these differences were not significant (Z=0.81, P=0.597). During winter, when females foraged alone, they used slightly higher sites above the ground (13.2 ± 7.0 m, N=129), than when foraged together with a male (11.3 ± 5.6 m, N=7), and these differences were also not significant (Z=0.71, P=0.475). Direct conflicts or other aggressive behaviour between female and male were never recorded.

In all seasons White-backed Woodpeckers of both sexes did not differ significantly in their preference for tree species used for foraging (P>0.05 in all cases, table 1). Most of the tested variables (height of foraging, DBH, condition of used tree and condition of used substrate) did not differ significantly between female and male in neither season. Only during winter females foraged on thinner parts of tree compared to males (P=0.006), what appeared to be a consequence of foraging on the branches (table 2).

Table 1. Tree species used for foraging by females (F) and males (M) of the White-backed Woodpecker during breeding, post-breeding and winter. Numbers represent average frequency of observations on particular tree species. Trees in all condition classes were included, sample sizes are given in parentheses
Tabela 1. *Gatunki drzew, na których żerowały samice (F) i samce (M) dzięciołów białogrzbietych w okresach lęgowym, polęgowym i zimowym. Podano średnią częstość obserwacji na danym gatunku drzewa, uwzględniając wszystkie drzewa (żywe, martwe i przewrócone), wielkości prób podano w nawiasach. (1) – gatunek drzewa, (2) – okres lęgowy, (3) – okres polęgowy, (4) – okres zimowy, (5) – inne*

Tree species (1)	Breeding (2)		Post-breeding (3)		Winter (4)	
	F (13)	M (17)	F (9)	M (9)	F (11)	M (11)
Carpinus betulus	45.2±20.3	25.8±29.2	31.9±18.5	41.5±18.2	37.1±25.1	49.7±27.0
Picea abies	8.4±10.4	22.2±22.8	11.0±11.9	9.4±11.7	14.4±15.9	12.2±13.0
Tilia cordata	15.3±14.6	13.6±14.3	16.5±16.7	11.9±13.1	17.6±13.2	5.0±9.2
Quercus robur	11.6±13.8	8.1±10.7	20.0±17.5	10.1±15.0	12.7±21.5	3.0±4.4
Populus tremula	3.2±6.5	7.6±12.2	8.0±16.5	9.7±11.0	1.7±4.0	12.8±21.6
Acer platanoides	4.7±7.6	3.0±6.9	1.3±3.9	1.3±3.1	5.2±8.2	7.4±9.9
Ulmus spp.	2.5±4.8	1.6±4.2	9.4±15.1	1.7±3.3	6.3±12.8	2.0±4.7
Fraxinus excelsior	3.1±7.6	3.9±7.9		10.0±15.9		3.9±12.0
Betula spp.	1.7±4.7	5.9±14.9				2.0±4.6
Alnus glutinosa		7.6±15.7		3.2±5.9		
Other (5)	4.4±7.9	0.7±3.1	1.9±5.6	1.2±2.8	5.0±7.8	2.0±4.7
Kolmogorov--Smirnov test	D=0.103 n.s.		D=0.138 n.s.		D=0.130 n.s.	

Table 2. Comparison of foraging sites used by females (F) and males (M) of the White-backed Woodpecker. After Bonferroni correction, probability was significant at 0.008 level (n.s. means P>0.008, *means P<0.008). Sample sizes in parentheses

Tabela 2. *Porównanie miejsc żerowania samic (F) i samców (M) dzięciołów białogrzbietych. Z poprawką Bonferroniego, wartość prawdopodobieństwa decydująca o istotności różnicy wynosiła 0,008. n.s. – różnica nieistotna statystycznie (P>0,008), * – różnica istotna statystycznie (P<0,008). Wielkości prób podano w nawiasach. (1) – okres lęgowy, (2) – okres potęgowy, (3) – okres zimowy, (4) – wysokość miejsca żerowania, (5) – pierśnica drzewa (cm), (6) – średnica miejsca żerowania (pnia lub gałęzi, cm), (7) – część drzewa, (8) – pień, (9) – gałąź, (10) – inne, (11) – stan używanej części drzewa: (12) – żywa część, (13) – martwa część z korą, (14) – martwa część bez kory, (15) – stan drzewa: (16) – żywe, (17) – martwe stojące, (18) – drzewo przewrócone (leżące)*

		Breeding (1)			Post-breeding (2)			Winter (3)		
		F (13)	M (17)	Test	F (9)	M (9)	Test	F (11)	M (11)	Test
Height (m) (4)		6.9±3.4	6.3±3.2	Z=0.67 n.s.	9.8±3.0	9.2±2.7	Z=0.66 n.s.	13.4±2.9	9.5±4.0	Z=2.20 n.s.
DBH (cm) (5)		42.3±10.4	41.7±8.1	Z=0.56 n.s.	54.2±16.7	53.9±11.9	Z=–0.22 n.s.	56.1±14.7	55.3±13.4	Z=–0.03 n.s.
Substrate diameter (cm) (6)		24.7±11.2	32.5±11.8	Z=–1.95 n.s.	21.2±6.5	28.9±8.2	Z=–2.08 n.s.	13.5±7.2	28.5±7.3	**Z=–3.45***
Part of tree (%) (7)	Trunk (8)	61.3±16.5	72.4±19.3	D=0.11 n.s.	51.1±21.2	56.1±13.0	D=0.05 n.s.	24.3±9.3	61.0±27.2	**D=0.37***
	Branch (9)	37.3±17.2	26.8±19.5		46.4±23.8	41.1±14.1		74.7±9.7	37.7±27.3	
	Other (10)	1.4±3.5	0.7±2.3		2.5±5.0	2.9±8.3		1.0±3.4	1.2±4.1	
Condition of used part (%) (11)	Alive (12)	26.4±15.3	29.3±20.2	D=0.03 n.s.	20.9±13.6	22.9±14.8	D=0.02 n.s.	10.2±8.4	19.7±20.6	D=0.10 n.s.
	Dead/bark (13)	47.3±21.5	40.2±19.5		51.4±21.4	38.8±17.0		59.0±15.4	48.0±20.4	
	Dead/no bark (14)	26.3±16.3	30.5±14.4		27.7±16.9	38.3±27.6		30.8±13.4	32.3±20.5	
Condition of tree (%) (15)	Alive (16)	46.1±18.7	43.4±17.5	D=0.03 n.s.	46.3±20.7	50.8±25.5	D=0.04 n.s.	57.7±23.7	44.2±25.3	D=0.00 n.s.
	Snag (17)	25.6±14.7	31.0±17.8		40.4±11.9	37.4±14.1		38.9±24.3	51.9±23.9	
	Downed (18)	28.3±21.8	25.6±12.4		13.3±24.2	11.8±15.9		3.5±5.9	3.9±8.4	

Table 3. Comparison of foraging techniques used by females (F) and males (M) of the White-backed Woodpecker. Sample sizes in parentheses
Tabela 3. *Porównanie technik żerowania samic (F) i samców (M) dzięciołów białogrzbietych. Wielkości prób podano w nawiasach. (2) – okres lęgowy, (3) – okres polęgowy, (4) – okres zimowy, (4) – kucie kory, (5) – płytkie kucie drewna, (6) – łuskanie, (7) – zbieranie z powierzchni, (8) – głębokie kucie drewna, (9) – żerowanie między korą a drewnem, (10) – inne*

	Breeding (1)		Post-breeding (2)		Winter (3)	
	F (13)	M (17)	F (9)	M (9)	F (11)	M (11)
Bark-pecking (4)	21.9±21.8	29.8±20.0	43.9±31.6	34.3±19.1	33.5±17.0	31.6±10.5
Superficial woodpecking (5)	9.1±12.4	17.7±17.0	16.6±12.4	26.3±21.3	27.3±9.9	26.7±15.0
Scaling (6)	8.4±10.8	3.8±12.1	2.2±6.7	0	3.8±6.7	1.9±6.2
Gleaning (7)	24.6±20.0	13.1±17.1	14.1±20.7	14.9±13.3	3.9±12.0	3±5.7
Deep woodpecking (8)	14.7±9.9	15.2±13.8	13.1±9.9	10.9±13.6	14.7±12.4	21.9±13.0
Searching of bark or wood (9)	8.4±10.8	3.0±8.3	6.2±8.6	3.4±5.2	12.3±7.7	9.9±9.6
Other (10)	12.9±17.3	17.4±19.9	3.9±6.4	10.3±27.4	4.4±7.4	5.1±12.0

The rate of used foraging techniques did not differ significantly between sexes (all seasons pooled, table 3). The niche breadth was similar for female and male and they also overlapped significantly ($OI>0.6$ in all cases; only diameter of tree substrate in winter had lower OI value, 0.56). The total foraging niches overlapped most during breeding season ($OI=0.87$), while the least overlapping was found in winter ($OI=0.78$). During winter and breeding time male's niche was on average broader compare female's niche (table 4).

Table 4. Niche breadth (Simpson's index) of both sexes of the White-backed Woodpecker and overlap (overlap index) in breeding (B), post-breeding (P) and winter (W) seasons
Tabela 4. *Szerokość niszy samców i samic dzięcioła białogrzbietego oraz pokrywanie się nisz w okresie lęgowym (B), polęgowym (P) i zimą (W). (1) – okres, (2) – szerokość niszy (indeks Simpsona), (3) – wskaźnik pokrywania się nisz, (4) – typ żerowania, (5) – samica, (6) – samiec, (7) – gatunek drzewa, (8) – pierśnica drzewa, (9) – stan drzewa, (10) – miejsce żerowania (pień lub gałąź), (11) – stan miejsca żerowania, (12) – średnica miejsca żerowania, (13) – wysokość miejsca żerowania, (14) – technika żerowania, (15) – razem*

Period (1)	Niche breadth (2)						Niche overlap (3)		
	B		P		W		B	P	W
Foraging category (4)	Female (5)	Male (6)	Female	Male	Female	Male	F/M	F/M	F/M
Tree species (7)	3.92	6.55	5.09	4.44	4.67	3.45	0.73	0.77	0.69
DBH (8)	2.84	2.68	2.47	1.84	1.78	1.63	0.88	0.85	0.95
Tree condition (9)	2.79	2.86	2.53	2.43	2.06	2.15	0.95	0.96	0.86
Used substrate (10)	1.94	1.68	2.10	2.06	1.62	1.94	0.89	0.95	0.63
Condition of substrate (11)	2.76	2.94	2.60	2.86	2.20	2.68	0.93	0.87	0.89
Diameter of substrate (12)	2.88	2.27	3.00	2.26	2.03	2.62	0.83	0.74	0.56
Foraging height (13)	2.14	2.16	2.68	2.94	1.89	2.91	0.98	0.86	0.71
Foraging technique (14)	5.91	5.19	3.80	4.30	4.37	4.30	0.79	0.83	0.92

Discussion

Woodpecker species with some size dimorphism usually exhibit significant differences in foraging patterns, and usually it is explained by a dominance of the larger sex over the smaller one (Kilham 1970, Hogstad 1978, Osiejuk 1994, Pasinelli 2000, Pechacek 2006). Northern populations of the White-backed Woodpecker showed this pattern as well (Aulén & Lundberg 1991, Stenberg & Hogstad 2004). However, in the present study, differences between females and males in foraging patterns were relatively small in accordance with the small differences in body size showed by Wesołowski (1995): female had significantly shorter bill while the other size features were similar (table 5). Populations of the White-backed Woodpeckers around the Baltic Sea (including Białowieża population) are genetically similar (Ellegren et al. 1999), so it seems likely that different factors (e.g. food resources, climate conditions) could shape their body size and foraging behaviour on different areas.

Some authors suggest that females are forced by males (a socially dominant sex) to forage on suboptimal zones (e.g. higher on the tree), while males use "high-quality" zones of tree (Jackson 1970, Hogstad 1991, Pechacek 2006). This explanation does not seem likely in the studied population in BNP. Rather, the study confirms the idea of Aulén and Lundberg (1991) that foraging differences may result from size dimorphism. Female, with her shorter bill could be better fit to forage in more delicate and thin branches, or softer substrate. Male could more often utilize lower zones of a tree, on a trunk where bark is thicker than on the higher zones or/and on the branches. Similar result was recorded by Newell et al. (2009): male Pileated Woodpeckers *Dryocopus pileatus* foraged on thicker substrate than female did, and it was the only difference in their foraging behaviour.

Woodpeckers' populations may not be uniform in habits throughout its continental range but may consist of local populations or demes adapted to particular climates, types of woodland, insect populations, and sets of avian and other competitors, that together make up their immediate environments (Kilham 1965). In more diverse plant communities, segregation is possible due to a greater diversity of available foraging sites, a lack of competition from other species or a wide variety of resources on several species of plants (Austin 1976).

Some species like e.g. the Eurasian Three-toed Woodpecker *Picoides tridactylus* or White-backed Woodpecker partitioned their breeding territories horizontally to avoid com-

Table 5. Comparison of size and weight differences between sexes in three populations of the White-backed Woodpecker. Sample sizes ($N_{♀}$, $N_{♂}$) vary according to traits compared. * $P<0.05$, ** $P<0.01$, *** $P<0.001$, n.s. – $P>0.05$

Tabela 5. *Porównanie dymorfizmu wielkości i masy ciała w trzech populacjach dzięcioła białogrzbietego. Wielkości prób ($N_{♀}$, $N_{♂}$) w poszczególnych grupach były różne w zależności od porównywanych cech. (1) – ciężar ciała, (2) – długość skrzydła, (3) – długość ogona, (4) – długość dzioba, (5) – szerokość dzioba, (6) – skok, (7) – długość czaszki*

	Norway 63°N (Stenberg & Hogstad 2004) N♀= 47–56, N♂=46–58	Sweden 60°N (Aulén & Lundberg 1991) N♀= 11–20, N♂=15–23	Poland 52°N (Wesołowski 1995) N♀= 4–5, N♂=5–8
Body weight (1)	***	*	n.s.
Wing length (2)	***	n.s.	n.s.
Tail length (3)	n.s.	n.s.	n.s.
Bill length (4)	***	*	**
Bill depth (5)	***	n.s.	no data
Tarsus (6)	**	no data	no data
Skull length (7)	***	no data	no data

petition i.e. by foraging in different parts of their territory (Hogstad 1976, Sollien et al. 1982, Stenberg & Hogstad 2004). In winter, most of the White-backed Woodpecker pairs in BNP were also observed within their breeding territories (birds were observed in the same area during each season frequently). Among some other woodpecker species females and males occupy separate territories during winter (e.g. Ligon 1968, Hogstad 1978), especially under harsh winter conditions when food supply is strongly limited (Osiejuk 1998). In species of which both sexes cohabit a common feeding territory, sexual dimorphism was related to intersexual differences in niche utilization (e.g. Kilham 1965, Selander 1966, Ligon 1968, Kisiel 1972). Species with stronger sexual dimorphism are also more dimorphic in foraging behaviour. Therefore, niche segregation is vertical while at less dimorphic species horizontal (female and male forage in other parts of territory; Hogstad 1978). Peters and Grubb (1983) showed that behavioural plasticity is the mechanism of niche partitioning between the sexes. In the Białowieża Forest pairs foraging together (or both sexes foraging close to each other) were observed rarely and such cases happened mainly winter. So, it seems that females and males shared their niches horizontally – by foraging in different part of territory at the same time.

Differences between foraging habits of the sexes occupying the same territory should be stronger than in the case of microgeographical allopatry (Hogstad 1976, 1978). According to this theory, niche overlap of the Middle Spotted Woodpecker *Dendrocopos medius* was smaller during the pre-breeding period when the shared by both female and male area was used more intensively than in breeding period (Pasinelli 2000). Also Willson (1971) reported for three woodpecker species, that overlapping in foraging height increases in spring. Although most of studies mentioned above found a decrease in overlap as food became less abundant, this might be the case only when demand for food is greater than the supply, i.e. in a competitive situation (Weatherly 1963, Wiens 1977, Conner 1981). Similarly, overlap of the White-backed Woodpecker female and male niches in BNP was the smallest in winter and the highest in breeding period, however it was always significant (0.78–0.87). Such high overlap is probably possible because the Białowieża Forest is food-rich (over 9,000 insect species including c. 1000 species of saproxylic beetles, Gutowski & Jaroszewicz 2001; a lot of dead and dying trees available, Czeszczewik 2009b).

Male as a dominant sex should be more specialized having narrower niche comparing to female (Ligon 1968, Pechacek 2006). More conventional foraging of male was explained by reflecting its dominance over female in optimal feeding sites (Hogstad 1976, 1978, 1991, Williams 1980, Peters & Grubb 1983, Aulén & Lundberg 1991, Osiejuk 1994, Pasinelli 2000). Some authors however, showed that males of some species tended to be more generalistic (Austin 1976). In BNP male's foraging niche was broader comparing to female both during breeding season and during winter. This result could rather suggest the dominance of female; however presence of the male did not influence her behaviour. No conflicts or aggressive behaviour between sexes, or significant changing of foraging habits were observed when they foraged close to each other. In other studies, female when unaccompanied by male modified her foraging behaviour by using male's niche (Peters & Grubb 1983, Hogstad 1991). So, present study confirms my assumption that morphological differences in body size could be related to both foraging behaviour and habitat quality. The exceptional habitat richness of the BNP regarding insects was shown before (Gutowski & Jaroszewicz 2001, Wesołowski & Rowiński 2006). It seems that females and males of the White-backed Woodpecker in BNP forage according their own skills of foraging and do not affect behaviour of each other, because richness of their habitat allows that (Czeszczewik 2009b).

Northern populations of the White-backed Woodpecker showed sexual dimorphism in body size and foraging behaviour (Aulén & Lundberg 1991, Stenberg & Hogstad 2004), while more southern woodpeckers from the BNP showed only slight differentiation both in body size (Wesołowski 1995) and in foraging manner. Two contradicting explanations of that are possible. First, only in the northern parts of range males of the White-backed Woodpecker being dominant over females force them to forage in different sites. Second, in the north both sexes forage in different sites according their inherited skills which express their different bill or body sizes. This might result from a long term adaptation to harsh winter conditions. Under milder conditions of lush habitat of the BNP no such strong selective pressure acts. Therefore, male's dominance over female is non-existing, as there is no reason to compete for food in this rich forest. This also shows that the White-backed Woodpecker could adjust its foraging behaviour in response to regional habitat conditions.

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