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Ecology and Behaviour of White-backed Woodpecker (*Dendrocopos leucotos*) in a Primaeval Temperate Forest (Białowieża National Park, Poland)

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Abstract. Wesołowski, T. (1995) Ecology and behaviour of White-backed Woodpecker (*Dendrocopos leucotos*) in a primaeval temperate forest (Białowieża National Park, Poland). Vogelwarte 38: 61–75.

Data on numbers, habitat distribution, parameters of nest sites, reproduction, and social behaviour collected in 1975–94 in a strictly protected forest reserve are analysed. No signs of decline were found, 28–29 pairs (0.6 pairs/km^2) bred there in 1991. Coniferous stands were avoided, deciduous stands, especially swampy stands with high content of dead wood, were preferred for nesting. All holes excavated in decaying wood, in riverine stands mostly in alders, in drier stands mostly in hornbeams and oaks, on average 17.2 m above the ground. Egg-laying commenced usually in the last days of March-beginning of April, but large temperature-dependent variation occurred. The clutch size was 3–4 eggs, nesting success 36 and 83% in two years. The difference was due to varying predation. Replacement broods after early loss possible. In response to play-backs of drumming both sexes reacted equally often in spring and autumn, indicating persistence of territorial behaviour beyond the breeding period.

Key words: *Dendrocopos leucotos*, primaeval temperate forest, habitat use, nest sites, nesting success, timing of breeding, social behaviour, woodpeckers.

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1. Introduction

The white-backed woodpecker is one of the rarest European woodpeckers and shows evidence of a widespread decline over large parts of central and northern Europe (Cramp 1985, Glutz & Bauer 1980, Tomiałojć 1990). In all parts of Fennoscandia except western Norway its situation is already critical. With their numbers steadily declining, those vestigial populations are on the verge of extinction (Aulén 1988, Carlson & Aulén 1992, Hagvar 1987, Haland & Ugelvik, 1990, Tiainen 1988, 1990, Virkkala *et al.* 1993). The circumstances in Poland seem less serious, though here also its range has shrunk (Tomiałojć 1990, Wesołowski in press a).

The precarious status of White-backed Woodpecker stimulated in the recent years several intensive field studies aimed at elucidation of reasons for decrease and at finding some countermeasures (Aulén 1986, 1988, Aulén & Carlson 1990, Carlson & Aulén 1992, Tiainen 1990, Virkkala *et al.* 1993). Those studies, however, were all carried out in places where the species had been already showing strong declines. There were no reference data from areas with stable, non-declining populations, which could serve as a comparable back-ground. As the Białowieża Forest seemed to harbour such a population (Wesołowski & Tomiałojć 1986, Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990), it was decided in 1990 to carrry out an intensive population study there. For reasons beyond the author's control that study had to be interrupted after two years. Nevertheless, the material collected during that period, along with the data gathered after the appearance of a preliminary publication (Wesołowski & Tomiałojć 1986), within a more extensive monitoring program (Tomjałojć & Wesołowski 1990, 1994) gives sufficient reason for preparation of the current contribution. It presents new information on the numbers, habitat preferences, nest sites, breeding ecology and social behaviour of White-backed Woodpecker living in primaeval conditions.

2. Study area and methods

2.1. Study area

The Białowieża Forest complex is situated at the Polish-Belarussian border. Its western part (580 km^2, ca 45% of the area) belongs to Poland. The Forest represents a remnant of the vast lowland forests that once covered great parts of temperate Europe. Its present unique features result from its considerable size, favourable edge/interior ratio and an exceptionally good state of conservation (Faliński 1986, Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990). Though traces of human presence are known from the Neolithic period, intensive timber-cutting started there not before the beginning of this century. The majority of tree stands in the Polish part are now under management, but a block of the best preserved primaeval stands has been strictly protected within the Białowieża National Park (hereafter referred to as BNP).

The primaeval stands preserved in BNP are distinguishable by a whole array of features: they are multi-storey, mixed-species, uneven-aged, composed of trees reaching unusual heights (the tallest Norway spruce *Picea abies* reach 57 m, and several other species reach 42–45 m) and contain a large amount of dead timber and uprooted trees. Detailed descriptions and photographs are given in Tomiałojć, *et al.* (1984), Tomiałojć & Wesołowski (1990), Faliński (1986), so only a brief review of the most important features of the main habitats present is given below.

Oak-lime-hornbeam stands (*Tilio-Carpinetum*, 44.4% of BNP area) are most structurally diverse. They are composed of a dozen or so species of trees (hornbeam *Carpinus betulus*, lime *Tilia cordata*, pedunculate oak *Quercus robur*, spruce, continental maple *Acer platanoides*), that vary greatly with regard to age and size. In several stands the canopy is formed by trees over 200 years old, and often exceeding 250–400 years. Amount of dead wood intermediate between that found in the swampy and coniferous stands.

Swampy deciduous stands (*Circaeo-Alnetum, Carici elongate-Alnetum*, jointly 21.6% of BNP area) are more uniform, canopy composed mostly of alder *Alnus glutinosa*, ash *Fraxinus excelsior* and spruce. This habitat type is characterised by the highest amount of dead wood; there is about three times more fallen logs there than in the oak-hornbeam stands (Wesołowski 1983).

In the coniferous stands (*Querco-Piceetum, Pineto-Quercetum, Peucedano-Pinetum*, jointly 28.1% of BNP area) the amount of dead timber (mainly broken stumps or logs) is rather moderate, the canopy is composed of spruce and Scotch pine *Pinus sylvestris* with an admixture of birches *Betula spp* and some oaks.

2.2. Methods

Data on White-backed Woodpecker distribution and abundance were collected in the course of census work carried out during the 1975–1994 breeding seasons (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990, Tomiałojć & Wesołowski 1994, unpubl.). The studied plots, 24–33 ha each, were situated in three main types of mature forest stands in BNP. The total area censused ranged from 187.5 ha (7 plots in 1980–1994) to 358.1 ha (14 plots in 1977).

Censuses were carried out with the application of the "combined mapping technique". The method is fully described by Tomiałojć (1980) and Tomiałojć *et al.* (1984). Each plot was checked every 8–10 days during the breeding season (April 10 – June 25). Walking slowly trough the plot a census-taker put on the plan all records of birds, paying special attention to simultaneous records of territorially behaving individuals. When possible, the sex of the observed individuals was noted as well. Drumming was dinstinguished on the plans from other types of vocalisations. All signs of breeding activities, i. e. hole-excavation, copulation, collecting food for young, feeding nestlings, presence of newly fledged young were recorded on the plans as well.

A White-backed Woodpecker census covering the whole area of BNP was carried out only in 1991. Data were gathered between March 15 and May 7, mostly within the first half of this period. Jointly 64 observer/days devoted to that task. Observations started usually early in the morning and continued until midday. Initially, the data were collected by observers walking along standard-routes following the established grid system at sub-compartment intervals. While walking along a transect, an observer followed the division line, stopped at each crossing of sub-compartment lines (every 533 m) to play a tape recording of White-backed Woodpecker drumming (the use of the tape recording increased the detection rate about fivefold – Wesołowski 1995). After "drumming" for up to 5 min the observer prceeded to the next point. Whenever a woodpecker was heard or seen, the observer recorded the position on the field map with the time of day, conditions of detection (whether it was a spontaneous behaviour or a response to the tape), behavioural pattern (drumming, calling, approaching, etc.) and sex of the bird when seen. After completing the first control and obtaining a rough picture of the species distribution, the consecutive visits were less uniformly allocated. The observers were purposefully concentrating on visiting places in which the birds had not earlier been detected to ascertain whether those gaps in local distribution were not artefacts. They used play-backs less regularly, only to make contact with birds. On localising the bird, the observer tried to follow it and map its movements as long as possible to get a picture of the actual location of its home range and to find its hole.

Nest finding is a standard element in the "combined mapping" (Tomiałojć 1980). Thus, holes were looked for during regular mapping work. In 1990–91 a more intensive approach was applied. Holes were searched within the whole area of BNP. The holes found during the census work were checked from the ground on every consecutive visit to the plot (every 8–10 days). Approximate time of fledging at those holes was estimated as follows: if on one visit parents feeding large young had been recorded and on the next no signs of birds presence were detectable, it was assumed that the birds fledged mid-way between the two visits. The exact dates of nest leaving by young woodpeckers were recorded only in 1990 and 1991, when holes with young about to fledge were visited daily.

In 1990–91 observers tried as well to check directly contents of holes in accessible trees. Eggs and nestlings were counted, age and sex of young determined and reasons for nesting failure recorded. Dimensions of holes were taken (diameter of opening, diameter of hole, hole depth and girth of trunk at the height of opening) as well.

At all breeding holes data on their localisation were collected. Initially only tree species, height above the ground and entrance's exposure were recorded. From 1980 on additional aspects of hole localisation were also recorded consistently: tree trunk girth at breast height, tree fragment (trunk vs. limb/branch), state of tree fragment in which the hole was situated (live vs. dead), and slope of structure in which the hole was located (vertical, from above or below of sloping trunk/limb) – Wesołowski (1989).

In 1990–92 catching an colour-ringing of birds were attempted. Three different approaches were applied. 1) Catching at feeders in winter – this method failed to work altogether, as the birds did not use feeders at all (Wesołowski in press c). 2) Attracting birds to mist-nets with dummy birds and play-backs of drumming early in the breeding period. Though the birds usually reacted to the play-backs and approached the source of sound, as a rule, they did not descend low enough to be caught. Only two males were caught that way, and the method was aborted. 3) Catching with a door-trap mounted at hole entrance. It was the only efficient method but with its own limitations. It could be used only for breeding birds nesting in accessible holes (minority in BNP) the broods of which survived long enough to contain nestlings at about two weeks of age.

The birds caught were weighed with a PESOLA spring balance (to the nearest gram) and their wing length (flattened wing), tail length (method of Busse 1974) and bill length (to skull) were measured with a ruler (to the nearest millimetre).

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3. Results

3.1. Numbers, habitat distribution

White-backed Woodpeckers were widely distributed in those parts of BNP occupied by mature deciduous stands, while areas dominated by conifers or by younger regenerating woods (NW corner of BNP) remained to a large extent unoccupied (Fig. 1). The birds encroached on the coniferous areas mostly following larger windfalls. This picture of habitat affiliations is reinforced by the long-term data from the census plots (Table 1). The birds occurred with the highest, (almost 100%) constancy in the riverine stands. The constancy was equally high in some of the oak-hornbeam plots, though other were occupied less regularly. The coniferous plots, on the other hand, were clearly

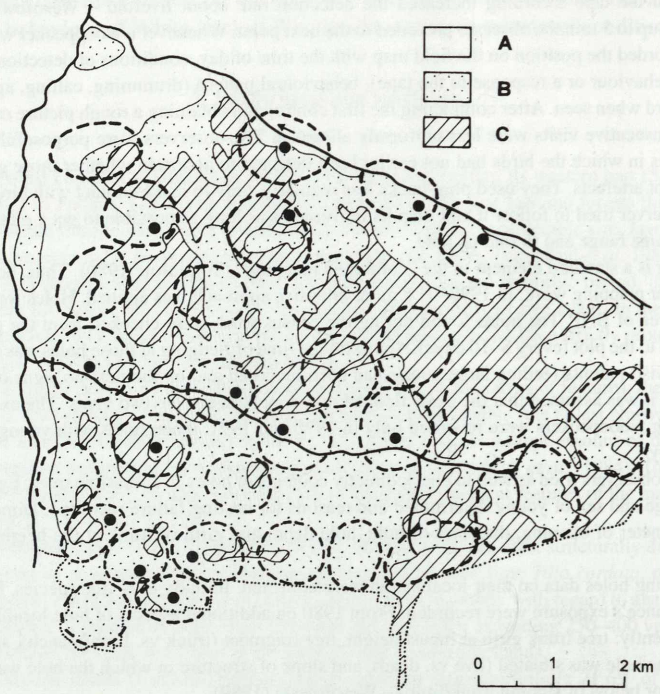

Fig. 1: Breeding territories of White-backed Woodpecker in Białowieża National Park (broken lines) and known holes (black dots) in relation to habitat. Data from 1991. A – bushy formations, young secondary forest; B – mature deciduous stands; C – mature doniferous stands.

Table 1: Proportion of study seasons in which White-backed Woodpeckers were recorded breeding in the census plots situated in different habitats. Size of plots varied between 25 and 30 ha, their localisation and detailed descriptions are given in Tomiałojć *et al.* (1984).

Habitat	Plot	N years of censuses	% of seasons with woodpeckers breeding
Riverine	K	20	100
	L	17	94
	H	5	100
Oak-hornbeam	CM	20	90
	MS	20	100
	WW	20	80
	CE	5	80
	MN	5	40
	WE	4	75
	GE	3	100
	GW	3	100
Coniferous	NW	20	5
	NE	20	0
	GB	3	0

Table 2: Tree species used for nesting by White-backed Woodpeckers in relation to habitat.

Habitat	Oak-hornbeam		Riverine		Jointly	
Tree species	N	%	N	%	N	%
Carpinus betulus – hornbeam	15	50	–	–	15	25
Quercus robur – oak	8	27	2	6	10	16
Betula sp. – birch	3	10	–	–	3	5
Acer platanoides – maple	2	7	–	–	2	3
Populus tremula – aspen	1	3	–	–	1	2
Fraxinus excelsior – ash	1	3	4	13	5	8
Alnus glutinosa – alder	–	–	24	77	24	39
Ulmus sp. – elm	–	–	1	3	1	2
Total	30	100	31	100	61	100

avoided, a part of White-backed Woodpecker territory covered such an area only once in 43 plot-years (Table 1) after the area had been struck by a hurricane.

There were 28–29 pairs breeding in BNP in 1991 (Fig. 1) which corresponds to an overall density of 0.6 territories/km². In the most densely populated parts, as in the SW corner of BNP, breeding densities could reach 1 territory/km². There, within an area of 10 km², 8–9 pairs bred in 1990 and 10.5 territories were found in 1991. This result indicates that the standard census plots used in the long-term study, covering only 25–33 ha, were too small (a single pair needed an area of 100 ha) to produce accurate data on White-backed Woodpecker numbers and the species year-to-year numerical variation. The high repeatability of occupation of the same patches from season to season year (Table 1) suggests that the local population remained quasi-stable, and there were no indication of any substantial numerical decline.

3.2. Nest sites

White-backed Woodpeckers excavated new holes each spring. Though the old holes situated within the census plots had been monitored (Wesołowski 1989) not a single case of re-use of the old hole or use of hole made by other woodpecker species was recorded.

The entrance exposures, when recorded in the field, were counted among eight compass directions, but observers tended to overestimate frequency of the main compass directions (N, E, S, W) – Wesołowski (1989). To account for this abserver bias, the data were grouped so as to include bearings from the main direction and the two neighbouring ones, for example all holes described as facing SW, S and SE were treated as the south facing ones in the analysis. Of 58 bearings taken, N and S facing holes occurred equally frequently – 21, while E (16 cases) and W facing holes (15 cases) were less frequent. This difference was not significant (chi² test), though.

Almost 50% of the holes found were situated in swampy stands, the remaining ones being located in oak-hornbeam forest (Table 2). As riverine stands comprised approximately only a third of deciduous stands in BNP, it shows a strong preference (chi² test, chi = 6.90, $p<0.01$) of White-backed Woodpecker towards situating breeding holes in wet places. This preference was also visible in pattern of localisation of holes within oak-hornbeam plots. The birds bred usually in their moistest parts, frequently in the vicinity of permanent pools.

While breeding in different habitats the birds used almost non-overlapping sets of tree species (Table 2). Hornbeams (50%) and oaks (27%) were most frequently used in oak-hornbeam forest, while mainly alders (77%) and ashes (13%) were utilised in riverine stands. As hornbeams constituted only a third and oaks less than a tenth of trees in oak-hornbeam forest (Tomoałojć 1993), it proves that these tree species were clearly preferred. On the other hand, limes, forming about a

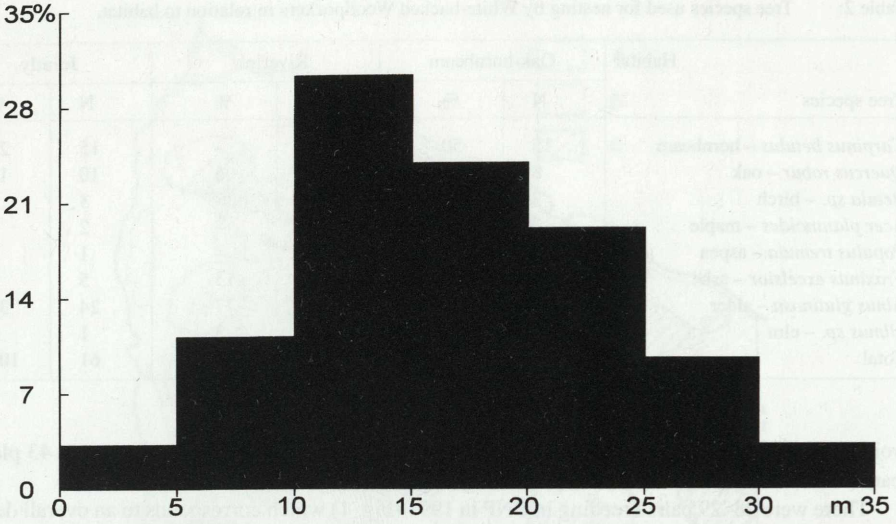

Fig. 2: Distribution (%) of heights of breeding holes above the ground in White-backed Woodpecker (N = 63).

quarter, and spruces, forming about a fifth, of oak-hornbeam stands were clearly avoided – no holes were found in them. In riverine stands spruces were also avoided, whereas alder was a preferred species. It constituted less than 50% of stands there but harboured over three quarters of holes (Table 2).

The holes were situated between five and 32 m, most often (over 50%) at 10–20 m, above the ground (Fig. 2). The average height being 17.2 m. There was, however, substantial variation dependent on tree species. Holes in oaks were on average situated significantly higher (25.5 m, t = 3.95, p<0.001) than those in alders (17.0 m). These in turn were situated higher than those in hornbeams (10.8 m, t = 4.44, p<0.001) – Table 3. However, these differences in hole height resulted from differences in stature of trees as reflected by their girth size at breast height. The oaks, with an average girth of 320 m, were significantly larger than alders (157 cm) or hornbeams (138 cm) – Table 3 (t test, p<0.001 in both cases).

Over two thirds of the holes in alders were in dead trees or snags while holes in oaks and hornbeams were excavated most frequently in living trees (Table 4). However, even in living trees, with-

Table 3: Girth a breast height of trees containing the breeding holes of White-backed Woodpecker and height of holes above the ground in relation to the species of tree.

Tree species	Girth (cm)			Height (m)		
	Range	Mean (SD)	N	Range	Mean (SD)	N
Hornbeam	82–185	138.4 (29.2)	11	5–16	10.8 (2.8)	14
Alder	85–240	156.8 (46.0)	22	5–28	17.0 (6.0)	26
Oak	190–565	320 (110.9)	9	17–32	25.5 (5.7)	10
Other	105–280	174.4 (52.5)	8	6.5–24	17.9 (5.4)	13
Total	82–565	184.9 (87.7)	50	5–32	17.2 (6.8)	63

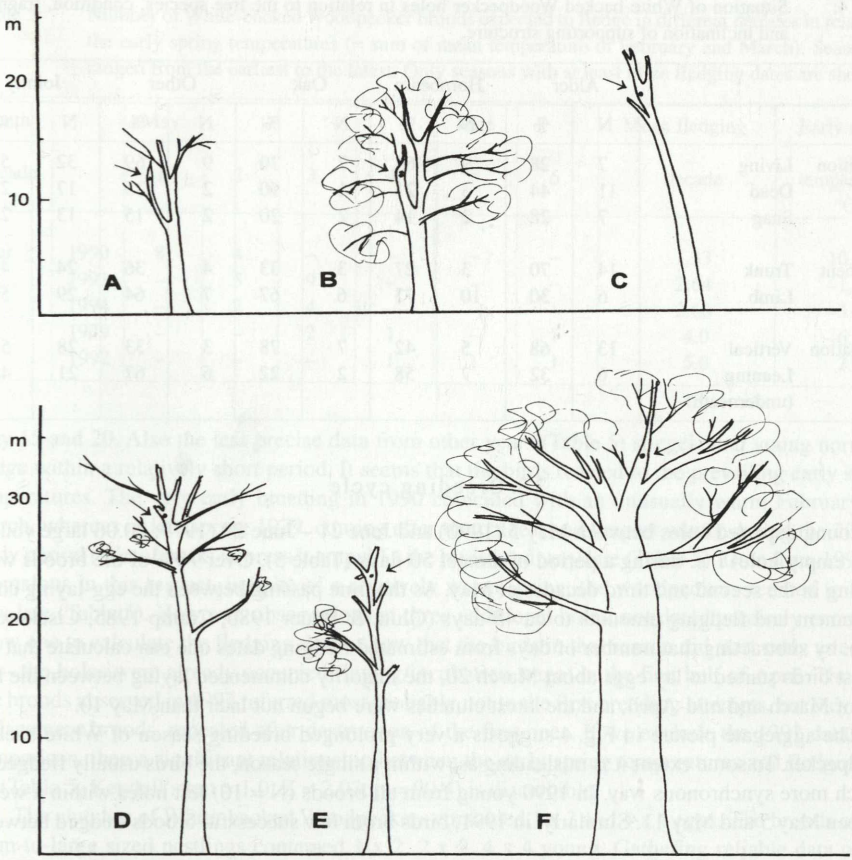

Fig. 3: Characteristic sites of hole positioning (shown by arrows) by White-backed Woodpeckers. A – dead hornbeam, B – living hornbeam, broken vertical limb, C – alder snag, from underside, D – dead top of living birch, E – dead alder, E – oak, decaying limb.

out exception, the holes were situated in places showing signs of decay. 23 of 32 holes in living trees, were in dead limbs, the other ones in dead/decaying fragments of still living trunks/limbs.

The holes in alders were most frequently excavated in the main trunk (70%), whereas in hornbeams and oaks were usually (67–73%) situated in limbs – Table 4, Fig. 3. The difference between localisation of holes in alders and hornbeams was significant (chi = 5.19, $p<0.02$). Most often the holes were made in vertical structures, yet 22–31% of those in alder and oak, and even 58% in hornbeam were located underneath leaning tree fragments (Table 4, Fig. 3).

The holes usually had rounded openings, the opening diameter ranging from 4.5 to 5.5 cm (av. 5.1, SD 0.38, N = 7). The diameter of the holes ranged from 11 to 14 cm (av. 12.4, SD 0.29, N = 9). Their depth was more changeable, varying between 26 and 35 cm (av. 29, SD 2.7, N = 8). The girth of trunk at the entrance level was the most labile variable, as it ranged from 55 to 128 cm (av. 78.2, SD 22.5, N = 8).

Table 4: Situation of White-backed Woodpecker holes in relation to the tree species, condition, fragment and inclination of supporting structure.

		Alder		Hornbeam		Oak		Other		Jointly	
		N	%	N	%	N	%	N	%	N	%
Condition	Living	7	28	9	64	7	70	9	69	32	52
	Dead	11	44	3	21	1	10	2	15	17	27
	Snag	7	28	2	14	2	20	2	15	13	21
Fragment	Trunk	14	70	3	27	3	33	4	36	24	45
	Limb	6	30	10	73	6	67	7	64	29	55
Inclination	Vertical	13	68	5	42	7	78	3	33	28	57
	Leaning (underneath)	6	32	7	58	2	22	6	67	21	43

3.3. Breeding cycle

The young departed holes between May 5 (1990) and June 21 – June 24 (1979: 20.06 large young, 24.06 empty hole) i. e. during a period of almost 50 days (Table 5). Over 70% of the broods were fledging in the second and third decades of May. As the time passing between the egg-laying commencement and fledging amounts to ca 45 days (Glutz & Bauer 1980, Cramp 1985, Cisakowski 1992), by subtracting that number of days from estimated fledging dates one can calculate that the earliest birds started to lay eggs about March 20, the majority commenced laying between the last days of March and mid-April, and the latest clutches were begun not later than May 10.

The aggregate picture in Fig. 4 suggests a very prolonged breeding season of White-backed Woodpecker. To some extent it is misleading as, within a single season, the birds usually fledged in a much more synchronous way. In 1990 young from all broods (N = 10) left holes within a week, between May 5 and May 11. Similarly, in 1991, birds brom few successful broods fledged between

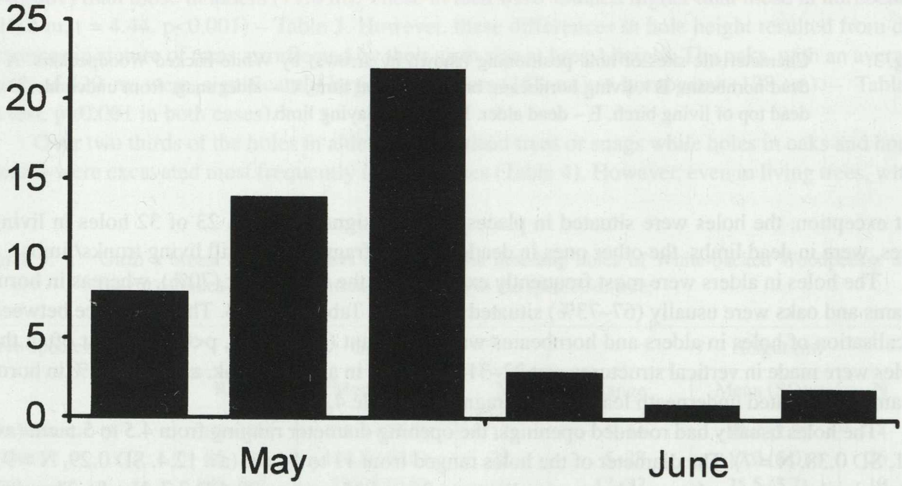

Fig. 4: The distribution of estimated fledging dates of White-backed Woodpecker in the consecutive ten-day periods. All years data, N = 50.

Table 5: Number of White-backed Woodpecker broods expected to fledge in different decades in relation to the early spring temperatures (= sum of mean temperature of February and March). Seasons arranged from the earliest to the latest. Only seasons with at least three fledging dates are shown.

Month		May				June		Mean fledging	Early spring
Decade		1	2	3	4	5	6	decade	temperature °C
Year	1990	8	4	–	–	–	–	1.33	10.0
	1991	–	5	9	–	–	–	2.64	–1.5
	1994	–	2	4	–	–	–	2.66	–3.0
	1979	–	–	2	1	–	1	4.0	–6.5
	1992	–	–	–	1	1	1	5.0	2.7

May 15 and 20. Also the less precise data from other years (Table 5) suggest that young normally fledge within a relatively short period. It seems that the birds reacted to the prevailing early spring temperatures. The very early breeding in 1990 coincided with an unusually warm February and March, whereas in late spring 1979, coming after the coldest and longest winter during the 20 year study period (Wesołowski in press b, unpubl.) the birds bred very late (Table 5). Data from 1992 are anomalous in this respect, in spite of a relatively warm spring, the woodpeckers seemed to breed very late (Table 5). However, observations at three additional holes, not dated precisely enough to allow one to calculate the fledging dates, show that the birds in that season did start early as expected – the holes were already occupied (laying/incubation stage) in the first half of April. Thus, the late broods abserved in 1992 referred most probably not to the first breeding attempts, but they were replacement broods, repeated after destruction of the first ones. If we exclude the 1992 data from comparison, then a significant relationship between the early spring temperatures and fledging dates (Table 5, Kendall's tau = 1.0, Z = 2.03, p = 00.4) is discernible.

The clutches of White-backed Woodpeckers contained 1 x 3 and 4 x 4 eggs. The broods of medium-to-large sized nestlings contained 1 x 2, 2 x 3, 4 x 4 young. Gathering reliable data on the number of fledglings proved impossible.

Ten of 12 nests were successful in 1990, whereas only five of 14 broods produced young in 1991. The difference was statistically significant (p = 0.02, Fisher exact probability test). All nest failures occurred at the nestling stage. They were due to mammalian predation (bitten off quills or feathers under the tree with hole) – 3, woodpecker predation (enlarged hole opening) –1, unspecified predation – 3, desertion (death of adult?) – 1, overexposure due to soaking of hole – 1.

Otherwise, brood loss due to female death was observed in 1985 (apparently uninjured dead female clung to the trunk of a neighbouring tree) and two instances of usurpation of freshly excavated holes by Starlings *Sturnus vulgaris* were detected. It is unknown, though, whether the holes overtaken by Starlings had already contained clutches or not.

3.4. Social behaviour

There was no intersexual difference in body measures which could influence social dominance. Wing length, tail length and body mass were similar in both sexes (Table 6). Only females had significantly (t test, t = 3.03, p<0.01) shorter bills than males. This, however, could be of more importance in foraging (unstudied) rather than in social interactions.

Reactions of birds to simulated territorial intrusions were gathered in a systematic fashion in the early spring of 1991. Birds reacting to the play-backs were either calling/drumming from a distance (ca 36%) or flew towards the source of sound (ca 61%). Only ca 20% of birds detected with-

Table 6: Biometry of White-backed Woodpecker in Białowieża National Park.

	Females			Males		
	Range	Mean (s)	N	Range	Mean (s)	N
Wing length (mm)	142–148	144.8 (3.2)	4	143–149	145.4 (2.0)	7
Tail length (mm)	87–100	95.0 (5.6)	4	95–101	97.3 (2.2)	6
Bill length (mm)	35–39	36.9 (1.7)	5	38–42	39.6 (1.3)	8
Body mass (g)	101–110	105 (3.3)	5	100-108	104.8 (3.1)	5

out vocal stimulation, i. e. birds seen or heard by observers moving between the consecutive play-back stations, did respond to the drumming played-back from the point immediately following place of their spotting – Table 7, category „without". In 10 cases of non-response the observers were able to prove that the birds were within the audibility range. In the majority of cases, however, (category of no details) there was simply no sign of bird presence. Obviously not all those events could be attributed to the birds' failure to respond, yet the claim that substantial fraction of the birds failed to react to the play-backs seems justifiable.

The birds attracted by the play-backs usually flew towards the source of voice uttering no calls. Having landed, they looked out and tried to spot the "rival". Then they often flew short distances, back and forth over the source of sound, with noisy, clearly audible wing beats. About a third of the birds stays quiet throughout the whole observation session, the remaining ones uttering calls or drumming (Table 8). It seems that females were even slightly more frequently attracted to the tape-recorder and drummed more often than males (35 vs. 25%), but those differences were not significant.

The intensity of the reaction to play-backs declined in the course of the breeding season, paralleling the general decline in spontaneous drumming activity. Parents feeding young did not usually respond to the play-backs. In some cases, however, a resurgence of intense drumming activity was observed in May. The birds behaved like early in the spring – very aroused, they drummed frequently, displayed in flight, chased other birds, even attempted to peck holes (female

Table 7: Differences in reactions to play-backs of White-backed Woodpeckers detected with and without help of the drumming play-backs. Category of "No details given" refers to situations in which an observer had only noted woodpecker's presence and did not give any information on its behaviour. "No reaction" – a bird had been spotted before play-back session commenced, was observed throughout the session, neither responded acoustically nor approached the source of sound. "Calling or drumming from a distance" – bird responded only acoustically, did not move toward the source of sound. "Approaching tape recorder" – the bird moved towards the source of sound.

	With		Without	
Type of reaction	N	%	N	%
No details given	8	3.7	55	66.2
No reaction			10	12.0
Calling or drumming from a distance	78	35.8	8	9.6
Approaching tape recorder	132	60.6	10	12.0
Total	218	100.0	83	100.0

pecking a hole on May 16, 1991; male pecking a hole on May, 10, 1992). These were probably the birds attempting to re-nest after nest loss.

The bird reacted to drumming play-backs also in the autumn, as revealed by observations carried out on October 8–10, 1990. Of 28 places in which drumming was presented, White-backed Woodpeckers approached the tape recorder in eleven, i. e. a positive reaction in almost 40%. This was the same level of response one observed in the early spring (Wesołowski 1995). The responding birds were females in seven cases and males in four cases. On each occasion, only a single bird approached the source of sound, which suggests that White-backed Woodpeckers possessed individual territories at that time. Though spontaneous drumming was not heard then, some of the approaching birds did drum in reaction to the tape recorded.

Observations on displacements and/or site-tenacity of colour-ringed birds are limited to the most intensively controlled area, plot W of Tomiałojć & Wesołowski (1995), situated in the SW part of BNP. A male caught at the beginning of April 1990 in a village park (ca 1 km S from the forest edge) by mid-April established a territory in the plot W, got paired but did not breed. In 1991 another male occupying a territory in this area was caught and colour-ringed along with his female at nest hole. The female was observed in the same plot in 1992 and again in 1994 (data for 1993 missing). She was paired in 1994 with the male ringed in 1990. These results indicate that at least some individuals may be quite mobile and change their home ranges form year to year.

4. Discussion

White-backed Woodpeckers in BNP did not show sign of any large-scale decline during the twenty-year study period, thus the expectation of obtaining data from a non-decreasing population has been fulfilled. The birds seemed to saturate the available habitat but, due to their considerable spatial requirements, even in this primaeval forest, their densities remained quite low, on avarage about 100 ha being necessary to support a pair. This result corresponds well with findings from Norway – 70–150 ha (Sternberg 1990) but lies below values obtained by Bernoni (1994) for southern subspecies *D. l. lilfordi* in Italy. In the Apennines he found densities reaching 2 pairs/100 ha.

White-backed Woodpeckers showed a strong preference for breeding in deciduous, especially swampy deciduous, stands in BNP. This reflected, to a large extent, the species preference for breeding in places that contain a large amount of dead wood constituting an indispensable nesting (see below) and foraging substrate (Matsuoka 1979, Glutz & Bauer 1980, Aulén 1988, Sternberg 1990, Bernoni 1994). Amount of soft decomposing wood in the deciduous stands of BNP exceeded that found in the coniferous stands (Wesołowski 1995) and the most preferred riverine stands contained, in turn, about three times more dead wood than the oak-hornbeam ones (Wesołowski 1983). The increased safety from predators in the riverine stands (Wesołowski & Tomiałojć in press) could be another factor influencing the bird preference for swampy woods.

Depending on forest type, majority of holes in BNP were placed either in hornbeams or in alders. Overall, there was very little overlap between the sets of species used in these two habitats. The same pattern is visible when one compares data from different parts of the species range. Aspens, alders and birches prevail in Norway and Sweden (Haland & Toft 1983, Aulén 1988, Sternberg 1990), beeches *Fagus silvatica* in Italy (Bernoni 1994), beeches and sycamores *Acer platanoides* in the Alps and the Bayerischer Wald (Ruge & Weber 1974, Scherzinger 1982). This demonstrates that the birds are versatile, they can accept a wide spectrum of tree species provided that they supply the bird with a necessary resource, namely soft decaying wood. This is clearly demonstrated by the Białowieża data – there was no single case of a White-backed Woodpecker hole excavated in healthy intact wood in BNP. This requirement is underlined by all the above mentioned authors, too.

Also differences in hole placement between various tree species visible in BNP were best accounted for by varying location of dead fragments and varying tree architecture. The holes in alders were mostly situated in trunks, as small crowns of this tree species did not usually have limbs large enough to support a hole. On the other hand frequently bifurcating trunks and limbs of hornbeams, and large dead limbs in the crowns of oaks provided the birds with an ample opportunity to situate a cavity. To support a hole, trunsk/limbs had to be above some threshold diameter. The minimum trunk diameter at hole entrance level recorded in BNP amounted to 17.5 cm, on average it was 25 cm. Data from other areas (Matsuoka 1979, Aulén 1988, Bernoni 1994) give similar values. 23.5–27.5 cm. This sets a minimum set of requirements for a White-backed Woodpecker nesting place: it has to be a snag or dead tree fragment with at least 20 cm diameter. A forest without such structures will not provide adequate nesting substrate. Moreover, as the birds excavate new holes every year, there must be enough such trees within a single range to provide a steady supply of nesting substrate for making new holes.

The choice of a tree species and location of a hole within the tree were, to a large extent, a function of availability of decaying wood, the height of holes above the ground constituted an additional variable. White-backed Woodpeckers preferred breeding high above the ground. They bred higher than any other woodpecker species both in BNP (Tomiałojć & Wesołowski 1986) and in other areas (Matsuoka 1979, Aulén 1988). The absolute height of holes above the ground differed among various study areas, following differences in tree stature among them. As a consequence of unusual tree heights in BNP (Faliński 1986, Tomiałojć & Wesołowski 1990) White-backed Woodpecker bred much higher there than in any other region (Matsuoka 1979, Cramp 1985, Aulén 1988, Sternberg 1990, Bernoni 1994).

The pressure of predators on nesting birds in the Białowieża primaeval forest is unusually high, comparable to that found in the tropical rain forest (Tomiałojć & Wesołowski 1990, Wesołowski & Tomiałojć in press). Thus one would expect to find in BNP nesting birds some means of avoiding predation, ways to hinder detection of nests and/or to make them less accessible. This should be especially important for such an early nesting species, young of which appear at the time when alternative food sources for predators are scarce (see below). Several peculiarities of the White-backed Woodpecker holes location can be interpreted in this way – by choosing trees in swampy places, excavating holes in snags or dead tree fragments, placing them high above the ground, often from underside of sloping structures, the holes were made difficult to access, especially for mammalian predators. This was combined with an extremely shy conduct of adults at holes and very quiet behaviour of nestlings making detection of holes very difficult.

Compared to other woodpeckers White-backed Woodpeckers commenced breeding unusually early. They were the earliest breeding woodpecker species in BNP (Wesołowski & Tomiałojć 1986). This phenomenon is known also from other parts of the bird's extensive range (Italy – Bernoni 1994, Alps – Ruge & Weber 1974, Finland – Pynönen 1939, NW Russia – Maltchevskiy & Pukinskiy 1983, Japan – Matsuoka 1979). As suggested by Matsuoka, this early breeding may costitute an adaptation to the peak availability of wood-boring coleopteran larvae, one of the main food types fed to the nestlings (Matsuoka 1979, Aulén 1988, Sternberg 1990, Bernoni 1994).

The earliest White-backed Woodpecker in BNP commenced laying about March 20 but the majority started egg-laying in the first half of April. These are the earliest breeding dates of all given in the literature so far. In other areas usually the birds commence breeding in the second half of April (Glutz & Bauer 1980, Cramp 1985) what can be to some extent explained by harsher climatic conditions – further North or in the mountains. The exceptionally early start of nesting secured the Białowieża birds time of attempt replacement broods, a possibility so far not reported for this species. Laying the replacement clutches could be additionally facilitated by tree defoliation caused by leaf-eating caterpillars in some years, as it happened in 1992 (L. Tomiałojć unpubl.). In such years trees of the forest at the beginning of May looked like it would normally have looked at a much earlier date. The birds could be thus deceived as to real time of season, and so induced to lay late replacement clutches.

Table 8: Vocal reactions of birds approaching a "drumming" tape recorder.

Type of vocalisation	Females N	Females %	Males N	Males %	All N	All %
No	22	42	14	36	42	32
Calls	13	25	16	41	45	34
Drum	18	34	9	23	45	34
Total	53	100	39	100	132	100

White-backed Woodpeckers bred very successfully in 1990, some young fledged from 80% of nests, but rather poorly in 1991 – only about one third of the pairs produced young. The main reason behind these differences was predation. The high nesting success in 1990 coincided with a outbreak of bank voles *Clethrionomys glareolus* in BNP, which reached then the highest numbers in a twenty year period. In 1991, on the other hand, rodents were over 300-fold less abundant (Pucek *et al.* 1993). Predators concentrated mostly on voles in 1990 and switched to birds in 1991, the proportion of birds in pine marten *Martes martes* diet increasing from 16% in 1990 to 46% in 1991 (Jędrzejewski *et al.* 1993). The woodpecker broods became apparently more attractive for predators in the year in which the rodent population crashed.

The only data on breeding success in other areas originate from Finland where no nest predation was recorded – all pairs produced fledglings in 1990–91, young in two holes died (disease?) in the earlier years (Virkkala et al. 1993). The Finish birds produced 2.6–2.7 fledglings/pair (Virkkala et a. 1993). Also Norwegian data 2.8–3.1 young/pair (Sternberg 1990) – show that nesting losses could not be high. Only Swedish observations show low productivity – (1.5 fledglings/pair, Aulén & Carlson 1990). The latter result is partially explained by a lower clutch size in this declining population (very few four-egg clutches observed). It remains unknown, however, whether nest predation played any role in lowering the productivity there.

It was impossible to count directly the number of young fledged under the Białowieża conditions. Nevertheless, if we assume that data on average clutch size (3.8) and brood size (3.4) were representative for the local conditions we would arrive at approximate value of three fledglings/successful nest. Multiplying this figure by the proportion of successful broods would give 2.4 fledglings/breeding pair in 1990 and only 1.1 fledgings/pair in 1991. As years with low rodents densities prevailed (11 of 20 seasons – Pucek et al. 1993), the nesting success of White-backed Woodpecker in BNP most of the time probably remained quite poor, closer to the 1991 than the 1990 level, thus productivity stayed probably below two fledgings/pair most of the time. If low productivity was rather a norm in a primaeval forest, then the woodpeckers should be adapted to cope with it. Other things being equal, low productivity itself should not lead to population decline. Thus, contrary to the opinion of Aulén & Carlson (1990), it seems that factors other than the insufficient production of young have to be the crucial factors causing populations of White-backed Woodpeckers to decline. A very thin scattering of birds over large areas, being consequence of habitat fragmentation, combined with limited dispersal abilities of this species, result in low juvenile survival and difficulties with recruitment of young birds into the breeding population (Carlson & Aulén 1992, Virkkala et al. 1993). In other words, even if the remaining habitat patches were perfect for White-backed Woodpecker survival and reproduction, their very isolation would end up in the population extinction. Thus, to safeguard the survival of this species one has to protect large contiguous areas enabling a viable population to exist. Provided that the whole area of the Białowieża Forest should become a national park, this forest complex could fulfil this condition (Wesołowski 1995).

In the breeding season White-backed Woodpecker females in BNP aggressively reacted to simulated territorial intrusions, play-backs of drumming: they approached the source of sound equally often as males (Wesołowski 1995) and drummed as frequently as the did (Table 8). Also in the autumn birds of both sexes reacted aggressively to play-backs of drumming, their reaction seemed to be equally vigorous as in the spring. These findings are in variance with handbook descriptions (Glutz & Bauer 1980, Cramp 1985). They demonstrate that in this species both sexes participate in territory defence, and that territorial behaviour is not limited to the breeding season.

5, Summary

Observations were collected in Białowieża National Park (E Poland) a strictly protected nature reserve. The park preserves the last fragments of the primaeveal temperate European forest. White-backed Woodpeckers were distributed over the whole area of the Park with preference to mature deciduous areas (Fig. 1). There was no observable decline in 1975–1994, 28–29 pairs bred there at a density of 0.6 p/km^2 in 1991. Coniferous stands were avoided by the birds, deciduous stands, especially swampy ones, with high content of dead wood, preferred for nesting (Table 1). The birds excavated new holes each year. In riverine stands holes were located mostly in alders, in drier stands mostly in hornbeams and oaks (Table 2), on average 17.2 m above the ground (Table 3), always in dead trees or dead tree fragments (Table 4, Fig. 3). Egg-laying commenced usually in the last days of March-beginning of April, but large temperature-dependent variation occurred (Table 5). Young fledged most often in the second half of May (Fig. 4). The woodpeckers laid 3–4 eggs, their nesting success amounted to 36 and 83% in two years, the difference was due to varying predation. In 1992 the birds laid probably replacement clutches after early loss of the first ones. In response to play-backs of drumming both sexes react equally often in the spring (Table 8) and autumn, indicating persistence of territorial behaviour beyond the breeding period and strong female territoriality.

6. Zusammenfassung

Die vorliegenden Beobachtungen wurden im Bialowieza-Nationalpark in Ostpolen gemacht. Dieser vollständig geschützte Park umfaßt das letzte Stück Urwald der gemäßigten Zone Europas. Weißrückenspechte sind im gesamten Park verbreitet unter Bevorzugung alter Laufholzbestände (Ab. 1). 1991 brüteten 28–29 Paare in einer Dichte von 0,6 Brutpaaren/km^2,.und von 1975–1994 ließ sich keine Bestandsabnahme beobachten. Zum Brüten werden besonders sumpfige Laubwaldbestände mit hohem Anteil an toten Bäumen bevorzugt (Tab. 1), Nadelholzbestände werden gemieden. Die Vögel zimmern jedes Jahr neue Nisthöhlen. An Flußläufen befanden sich die meisten Nisthöhlen in Erlen, auf trockeneren Standorten meistens in Hainbuchen und Eichen (Tab. 2), durchschnittlich 17,2 m über dem Boden (Tab. 3), stets in toten Bäumen oder abgestorbenen Ästen (Tab. 4, Abb. 3). Die Eiablage begann gewöhnlich in den letzten März- oder ersten Apriltagen und war stark temperaturabhängig (Tab. 5). Die Jungvögel flogen meist in der zweiten Maihälfte aus (Abb. 4). Die Spechte legten 3–4 Eier, und der Nesterfolg betrug in 2 Jahren 36 bzw. 83%, wobei der Unterschied auf verschieden starken Feinddruck zurückging. 1992 kam es wahrscheinlich zu Ersatzgelegen, nachdem die Erstgelege verloren gegangen waren. Auf vorgespieltes Trommeln reagieren beide Geschlechter gleich stark im Frühjahr und im Herbst (Tab. 8), was auf ganzjährige Territorialität hinweist, die auch bei den Weibchen stark ausgeprägt ist.

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