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Natural nest sites of Marsh Tit *(Parus palustris)* in a primaeval forest (Białowieża National Park, Poland)

By Tomasz Wesołowski

Abstract. WESOŁOWSKI, T. (1996): Natural nest sites of Marsh Tit *Parus palustris* in a primaeval forest (Białowieża National Park, Poland). Vogelwarte 38: 235–249.

Data on the location of 413 and dimensions of 198 Marsh Tit nesting holes gathered in 1975-95 in a strictly protected forest reserve are analysed. Breeding was confined to deciduous stands. In riverine stands over 96% of the holes were in *Alnus* and *Fraxinus*, in oak-hornbeam stands over 83% in *Tilia* and *Carpinus*. Holes were on average 5.6 m above the ground, in trees with girth at breast height 107 cm, both parameters varied strongly among tree species. Holes were situated mainly in tree trunks (89%), in living trees (92%), and the share of woodpecker-made holes was <2%. Entrances were mostly (74%) in vertical plane. Their minimum diameter was 20 mm in circular openings and 18 mm in elongated ones, median - 30 mm. Openings were usually elongated, in 65% of cases they were <20 cm². Hole bottoms were approximately circular, with median diameter of 9 cm, and minimum diameter of 5.5 cm, median bottom area was 73 cm². Depth of holes (to nest level, median 14 cm) was positively correlated with the least entrance diameter ($r_S = 0.48$).

In comparison with other areas Marsh Tits bred higher, in holes with larger bottoms, the holes having, however, similar depth and entrance diameter. None of the hole dimension variables depended on tree species, thus the observed variation in hole placement was probably to a large extent a by-product of differences in distribution of holes with adequate qualities. Small openings of holes could serve to avoid competition for holes and/ or to evade predators, but non-usage of woodpecker-made holes and nesting in holes in living trees can be best explained as an anti-predator tactic.

Key words: *Parus palustris*, tits, primaeval temperate forest, natural holes, hole dimensions, hole placement, anti-predator tactics.

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1. Introduction

Though secondary hole-nesters belong to the most intensively studied species, our knowledge of their biology is heavily biased - the majority of studies were carried on birds breeding in nest-boxes. Rather scanty data on their biology gathered so far in natural holes (Ludescher 1973, Nilsson 1975, 1984a, 1984b, 1986, van Balen *et al.* 1982, Alatalo *et al.* 1988, 1990, East & Perrins 1988, Walankiewicz 1991, Sändstrom 1992) clearly demonstrate that extrapolation of findings from the nest-box studies to natural holes may be unjustifiable, as numerous aspects of the secondary hole-nesters behaviour and ecology may be dramatically affected. Whereas this needs not necessarily be of importance for answering some questions, it is definitely detrimental when one attempts to pursue functional issues, to pose questions about the adaptive significance of the observed characters. Even the study of birds in natural holes would not remove all difficulties, though. This stems from the fact that in man-transformed managed woods the availability and quality of holes could drastically differ from that found in pristine conditions, and to measure fitness costs and benefits of different actions/characters one has to study birds under approximately the same conditions as those under which the characters have evolved and are maintained (Wesołowski 1983, Tomiałojć *et al.* 1984, Møller 1989, Wesołowski & Stawarczyk 1991).

The existence of the last fragments of primaeval, European lowland forest preserved within Białowieża National Park (hereafter referred to as BNP) has provided a unique opportunity to study patterns of nest-site utilisation by secondary hole-nesters in an area which has offered the birds the

full spectrum of breeding options. Preliminary data on secondary hole-nesters (including some information on Marsh Tit) were already presented in Wesołowski (1989), while Walankiewicz (1991) depicted patterns of hole utilisation in Collared Flycatcher *(Ficedula albicollis)* at BNP.

Here, I document patterns of nest-site utilisation by Marsh Tits in BNP based on data collected during 21 breeding seasons. I provide quantitative data on aspects of nest-hole location at different spatial scales (habitat, tree species, part of tree), as well as their structural parameters. Finally, I discuss the possible adaptive value of the recorded patterns in terms of predator avoidance and interspecific competition.

2. Study area and methods

2.1. Study area

The Białowieża Forest complex is situated at the Polish-Belarussian border. Its western part (580 km², 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, Wesołowski & Tomiałojć 1995).

Though traces of human presence are known from the Neolithic period, intensive timber-cutting did not start there 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 BNP.

The primaeval stands preserved in BNP are distinguishable by a whole array of features: they are multistorey, mixed-species, uneven-aged, composed of trees reaching unusual heights (the tallest Norway spruce *Picea abies* reached 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, 1994), 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. The 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 are about three times more fallen logs there than are 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

Marsh Tit holes were looked for mainly in the course of census work carried out in BNP during the 1975-1995 breeding seasons (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990, Tomiałojć & Wesołowski 1994, unpubl.), but some holes found outside the plots, in other parts of BNP were also included. The studied plots 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). Additionally, special searches for nests, aimed at finding all breeding holes, were made in four deciduous areas in 1987-89 and 1992-1995. These were:

- plot K, corresponding to plot K in Tomiałojć *et al.* (1984); 33 ha, mostly riverine forest of ash-alder type.
- plot C; corresponding to plots CW and CE in Tomiałojć *et al.* (1984) - 48 ha.
- plot M; corresponding to plots MS and MN in Tomiałojć *et al.* (1984) - 54 ha.
- plot W; corresponding to plots WE and WI in Tomiałojć *et al.* (1984) - 50.1 ha.

The latter three areas were all situated in the oak-hornbeam habitat.

Data on the tree species composition in the oak-hornbeam plots were collected in 1989. All living and dead trees with breast height diameter >12 cm were counted within circular (radius 10 m) plots spaced 150 m apart. In the first years of the study the following hole variables were regularly recorded:

- tree species,
- height of entrance from ground level (visually estimated for low situated holes, measured with a clinometer for holes higher than ca. 10 m)
- entrance's orientation (classified to the nearest 1/8 of the wind rose).

Other types of information, such as data on hole origin or state of tree decay were noted less consistently. Since 1980 additional aspects of hole localization had been also consistently recorded. These were:

- trunk girth at breast height,
- type of hole (woodpecker-made vs. „natural"),
- tree fragment (trunk vs. limb/branch),
- state of tree fragment in which the hole was situated (live vs. dead),
- slope of structure in which the hole was located (vertical, from above or under sloping trunk/limb),
- shape of entrance (rounded vs. fissural),
- presence of "knotholes" (see Fig. 1).

Dimensions of holes were assessed in 1987-89 and 1992-95. The following variables were measured:

- least/greatest entrance diameter, taken at the narrowest place of the entrance corridor; it could be the entrance's height and width in holes with vertically oriented openings or horizontal depth and breadth in holes with horizontally situated ones (Fig. 1)
- least/greatest hole diameter, measured at the nest rim level
- hole depth, the vertical distance between the lower edge of the entrance and the nest rim level
- "danger distance", the distance between the outer edge of the entrance and the nest centre at the nest rim level (this shows how far a predator has to reach out to touch eggs or nestlings)
- girth of trunk at the entrance height (at nest level in knotholes).

To measure holes, a collapsible ruler and a flashlight bulb, fixed to a bendable wire, were used. As a rule, the measurements were taken during the nestling period, only sometimes after the young had fledged. In the case of pear-shaped holes (Fig. 1B) taking accurate measurements of hole diameter was quite difficult, at times impossible.

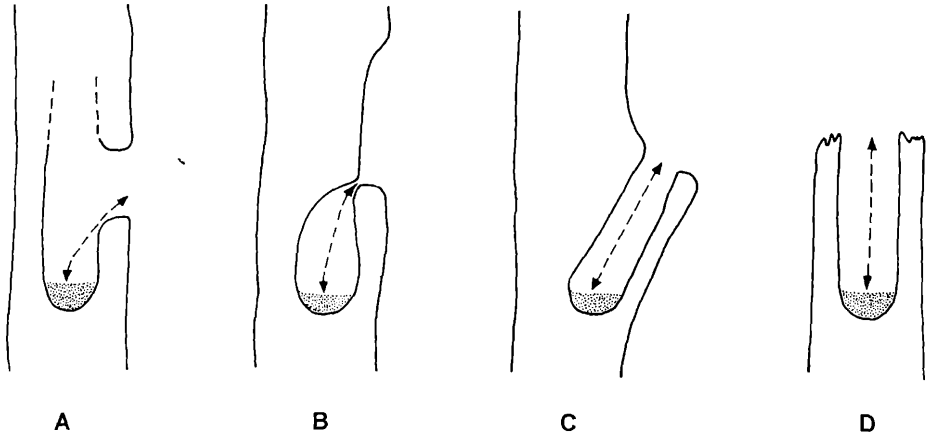

Fig. 1: Longitudinal section through different types of holes used by Marsh Tits in BNP. Slightly simplified drawings of the actual holes, their original proportions maintained. A - trunk hole in rotten sapwood, fissural opening, entrance in the vertical plane; B - as the former, entrance in horizontal plane; C - knothole cavity (formed at the site of a previous limb break), entrance facing diagonally upwards; D - chimney (formed in top of broken trunk), entrance directed upwards. Arrows show the way the measurements of "danger distance" (see text) were taken.

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3. Results

3.1 Location of holes

Marsh Tits bred only in the deciduous stands. Though their territories sometimes included coniferous patches (Tomiałojć & Wesołowski 1994), no breeding hole was found in coniferous stands, so far. In the oak-hornbeam stands the holes were located most often in hornbeams and limes (over 83%), whereas in the riverine stands, in over 96% of cases, they were situated in alders and ashes (Table 1). Thus, sets of tree species used for breeding in the two habitats hardly overlapped. Even within a single habitat type, however, clear differences in patterns of tree species utilisation were visible. The share of hornbeams varied between 31 and 73% while the proportion of limes ranged from 16 to 55% in different plots (Table 2, $\chi^2 = 50.6$, df = 6, $p<0.001$).

Table 1: Tree species used for nesting by Marsh Tits in relation to habitat.

Habitat:	Oak-hornbeam		Riverine		Total	
Tree species	N	%	N	%	N	%
Carpinus betulus - hornbeam	185	55.1	-	-	185	44.8
Tilia cordata - lime	95	28.3	-	-	95	23.0
Alnus glutinosa - alder	-	-	48	62.3	48	11.6
Fraxinus excelsior - ash	3	0.9	26	33.8	29	7.0
Acer platanoides - maple	24	7.1	-	-	24	5.8
Sorbus aucuparia - rowan	14	4.2	-	-	14	3.4
Coryllus avellana - hazel	5	1.5	-	-	5	1.2
Ulmus sp. - elm	2	0.6	2	2.6	4	1.0
Populus tremula - aspen	3	0.9	-	-	3	0.7
Betula sp. - birch	1	0.3	1	1.3	2	0.5
Picea excelsa - spruce	2	0.6	-	-	2	0.5
Quercus robur - oak	1	0.3	-	-	1	0.2
Total	336	100	77	100	413	100

Table 2: Relationships between tree species composition and distribution of tree species utilised by nesting Marsh Tits in the intensively studied oak-hornbeam plots.

Plot	C		W		M	
Percentage of:	Trees	Holes	Trees	Holes	Trees	Holes
Hornbeam	24	31	34	62	47	73
Lime	46	55	28	26	27	17
Spruce	23	1	18	1	13	-
Maple	4	6	8	5	6	9
Other	3	7	12	8	8	1
Sample size (N)	225	83	250	89	329	127

In spite of such versatility Marsh Tits used trees in a non-random fashion. In the riverine habitat alder and spruce constitute about a third of tree stands each (Tomiałojć & Wesołowski 1984). Yet over 60% of Marsh Tits holes were located in alders and none in spruces (Table 1). Spruce was strongly avoided also in the oak-hornbeam habitat. Though it formed 13-23% of stands in different plots in that habitat type, Marsh Tits used it only twice for nesting (Table 2). If we exclude spruce, then among deciduous trees in the oak-hornbeam habitat, hornbeam was overutilized in some areas (plot W - χ^2 =11.0, df = 4, p<0.03; plot M - χ^2 = 17.8, df = 4, p<0.002) but not in others (plot C - χ^2 = 1.5, df = 4, NS) - Table 2.

Holes were situated between 0.5 and 27 m above the ground (av. 5.6, SD 4.8, N = 411). There were substantial differences in the distribution of nesting heights between tree species, median values varied between 1.4 m in rowan to 12 m in ash (Fig. 2, Median Test, χ^2 = 77.6, df = 5, p<0.001).

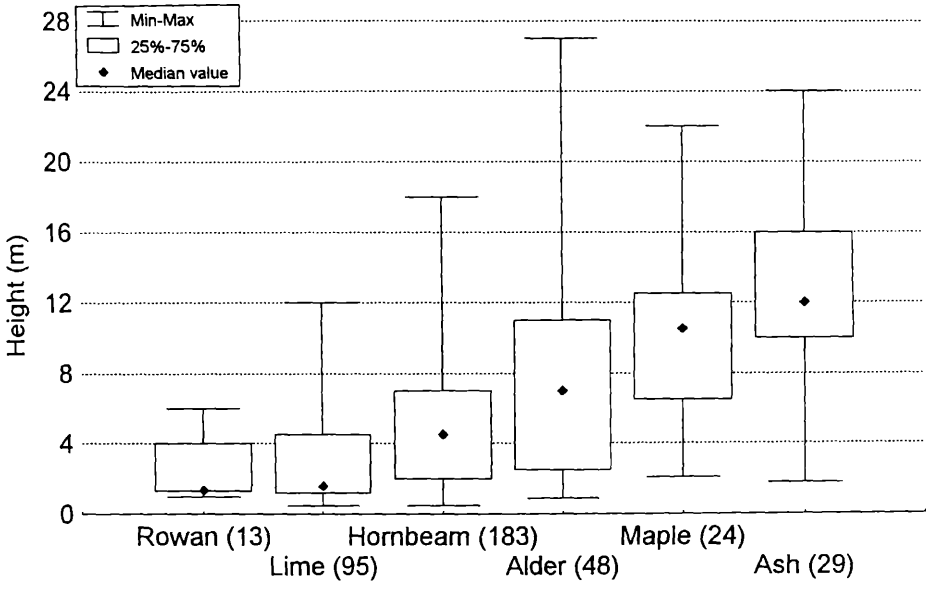

Fig. 2: Distribution of heights above the ground of breeding Marsh Tit holes in relation to tree species. Sample sizes given in parentheses.

Though holes placed below 2 m occurred in all tree species, holes situated below 5 m constituted over 75% of those in rowan or lime and less than 25% of those in maple or ash.

The girth at breast height of Marsh Tit nesting trees varied between 34 and 285 cm (av. 107, SD 45.7, N = 343). It was strongly dependent on tree species (Fig. 3, Median Test, χ^2 = 109.7, df = 5, p<0.001). Holes in rowans and limes were placed in thinnest trees (median = 57 and 87 cm respectively) whereas those in maples and ashes were located in relatively thick ones (median = 117 and 180 cm respectively). Even if lack of large trees in the forest could account for small size of rowans used, this factor could not explain the pattern of girth size distribution in other tree species. Large limes and smaller trees of other species were both available but apparently remained underused.

Holes in trees with larger girth sizes tended to be simultaneously situated higher above the ground. Median girth sizes and median heights in different tree species were positively correlated (cf. Fig. 2 and Fig. 3, r_S =0.82, p<0.05).This was also visible at a species level - in hornbeam (r_S = 0.46,

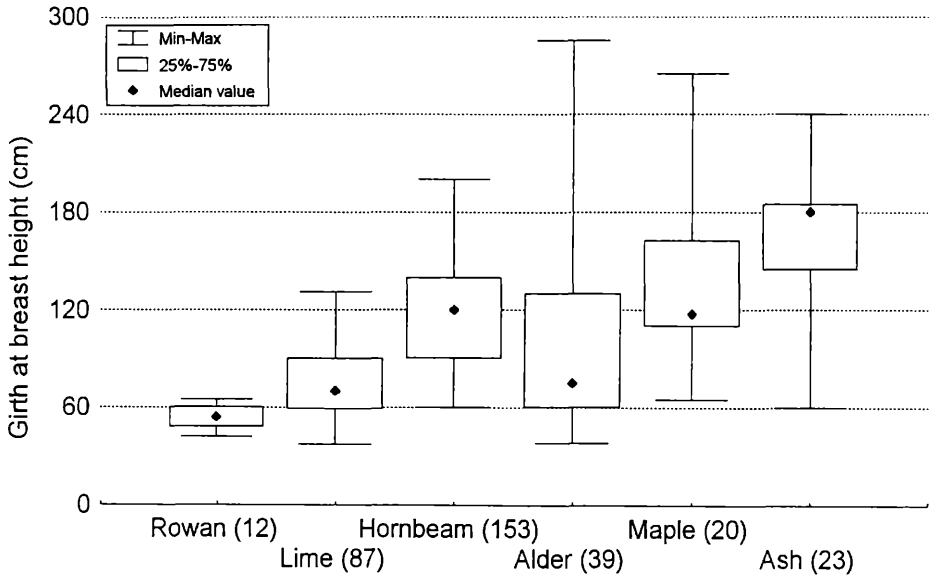

Fig. 3: Distribution of Marsh Tit hole-tree girths in relation to tree species. Sample sizes given in parentheses.

N = 149, p<0.001) and alder (r_S = 0.74, N = 39, p<0.001). In other species either no (lime, r_S = -0.01, N = 87) or only a non-significant relationship occurred.

The girth of trees at hole-entrance level ranged from 34 to 170 cm (av. 86 cm, SD 29.3, N = 138). In thinner trees both measures were strongly positively correlated (r_S = 0.94, N = 87, girth at breast height <=100 cm) and the two variables did not differ by more than 10%. In larger trees, however, the two measures varied totally independently of each other (r = 0.07, N = 50, girth at breast height >100 cm).

Exposures of hole entrances were counted among eight compass directions (Fig. 4). The picture shows that holes exposed to the main compass directions were more frequent (χ^2 = 43.7, df = 7, p<0.001) than holes exposed to the intermediate directions (NE, NW, SW, SE). Such a result suggested the existence of a systematic error in data collection. To avoid this bias, it was decided to pool the data and re-analyse them broken down only into four main categories. The samples of holes with intermediate exposures were halved and added to the samples from the two neighbouring main directions. The transformed distribution of entrance exposures did not significantly deviate from uniform (χ^2 = 2.0, df = 3, NS), i.e. Marsh Tits did not show any clear-cut preferences with respect to opening orientation.

The majority of hole entrances, constituting over 74% (N = 341) of all (Table 3), were situated in vertical plane, 12% of entrances (in holes underneath leaning tree fragments) were down facing, and 14% of openings were directed obliquely upwards. In extreme cases entrances were facing directly upwards. This was the case in chimney-type holes (Fig. 1D, 6 x lime, 1 x ash) and in holes situated in wedges in trunk/limb bifurcations (5 x lime, 5 x alder, 1 x hornbeam). Overall there was no significant differences in the distribution of vertical, up or down facing holes among various tree species (Table 3; χ^2 test, 3. df., NS).

As a rule Marsh Tit used holes formed by processes of tree decay, located in live parts of trees. Only less than 2% of 359 holes were made by woodpeckers and about 8% of 359 holes were localised in dead substrate (Table 4). Holes in dead wood were found ca 3 times less frequently in horn

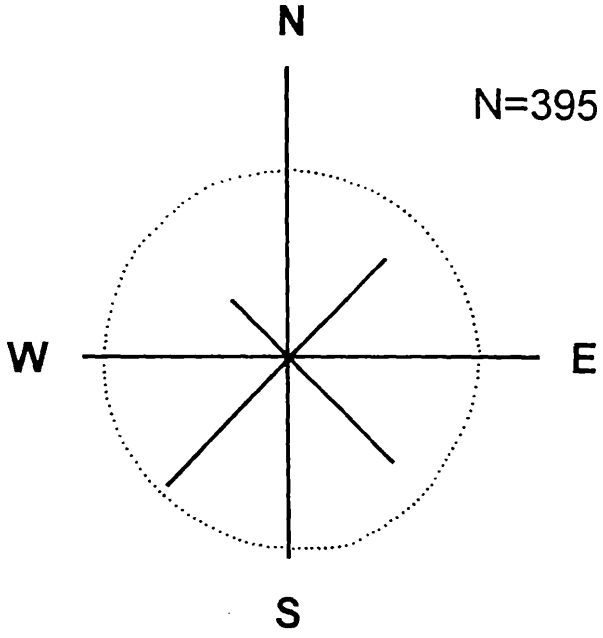

Fig. 4: Distribution of entrance exposures of Marsh Tit holes in BNP in the horizontal plane. Length of solid lines is proportional to the number of holes facing in a given direction.

Table 3: Distribution of entrance orientation of Marsh Tit holes in BNP in the vertical plane.

	Plane							
	Up		Vertical		Down		Total	
Tree species	N	%	N	%	N	%	N	%
Hornbeam	18	37	112	45	22	54	152	45
Lime	9	18	68	27	9	22	86	25
Alder	9	18	27	11	2	5	38	11
Ash	4	8	16	6	1	2	21	6
Maple	5	10	12	5	3	7	20	6
Other	4	8	16	6	4	10	24	7
All	49	100	251	100	41	100	341	100

beams and twice more frequently in alders than could be expected from the overall frequency of holes in those tree species (cf. Table 1 and Table 4, $\chi^2 = 18.0$, 3. df., $p < 0.001$). All holes in birches and spruces (Table 1) were in snags.

Holes were situated mainly in trunks, only 11% (N =362) were found in limbs. Holes in limbs were underrepresented in limes and alders and overrepresented in ashes and maples (cf. Table 1 and Table 4, $\chi^2 = 61.2$, 5. df., $p < 0.001$). These differences were to some extent reflected in the distribution of hole heights above the ground (Fig. 2). Holes in maples and ashes, being frequently in limbs, were simultaneously high above the ground but holes in alders, in spite of being placed relatively high (Fig. 2) were still placed in the main trunk.

Table 4: Placement of Marsh Tit holes in BNP in relation to hole origin, tree condition, and tree fragment.

Placement aspect		Tree species						
		Horn beam	Lime	Alder	Ash	Maple	Other	All
Woodpecker	N	1	2	3	-	-	-	6
	%	17	33	50	-	-	-	100
Dead part	N	5	5	8	3	3	6	30
	%	17	17	27	10	10	30	100
Limb	N	16	1	2	12	9	1	41
	%	39	2	5	29	22	2	100
Knothole	N	15	1	10	12	11	4	53
	%	28	2	19	23	21	7	100

Knotholes (Fig. 1C) formed 13% of all holes (N =413). Such holes were almost non-existent in limes and underrepresented in hornbeams but three-four times more frequent than expected in maples and ashes (cf. Table 1 and Table 4, χ^2 =54.7, 5. df., p< 0.001).

3.2. Dimensions of holes

Marsh Tits at BNP relied totally on the already existing holes, but they could adjust their internal dimensions to some extent. They were frequently observed to remove mould and debris from their holes' bottoms before starting bringing the nest material, but no case of a bird flying out with wood chips (which could indicate known from other areas - Ludescher 1973 - enlargement of hole by pecking) was recorded.

Hole dimensions were not significantly dependent on tree species, probability values were 0.08 (hole depth - Kruskal-Wallis ANOVA by Ranks, $H_{4,174}$ = 8.34, NS) or higher. Hence all data were pooled and analysed jointly, irrespective of tree species.

Minimum values of entrance diameter amounted to 18 mm (Table 5). All holes with least entrance diameter <20 mm (N = 7) had very elongated openings, the greatest diameter exceeded that

Table 5: Dimensions of Marsh Tit holes in BNP. Entrances and bottoms were assumed to be elliptical in outline, hence the equation for the area of an ellipse was used to calculate their areas.

	Variable		N	Statistics		
				Mean ± SD	Median	Range
Entrance	least diameter	(cm)	189	3.2 ± 1.2	3	1.8-8
	greatest diameter	(cm)	189	8.1 ± 6.6	6.5	2-44
	area	(cm^2)	189	20.2 ± 16.9	14	3-104
Bottom	least diameter	(cm)	174	9.5 ± 2.4	9	5-16
	greatest diameter	(cm)	174	10.0 ± 2.5	10	5.5-18
	area	(cm^2)	174	78.5 ± 38.4	73	24-201
Cavity	depth	(cm)	187	14.4 ± 5.8	14	2-53
Danger	distance	(cm)	146	18.1 ± 5.8	17	9-56

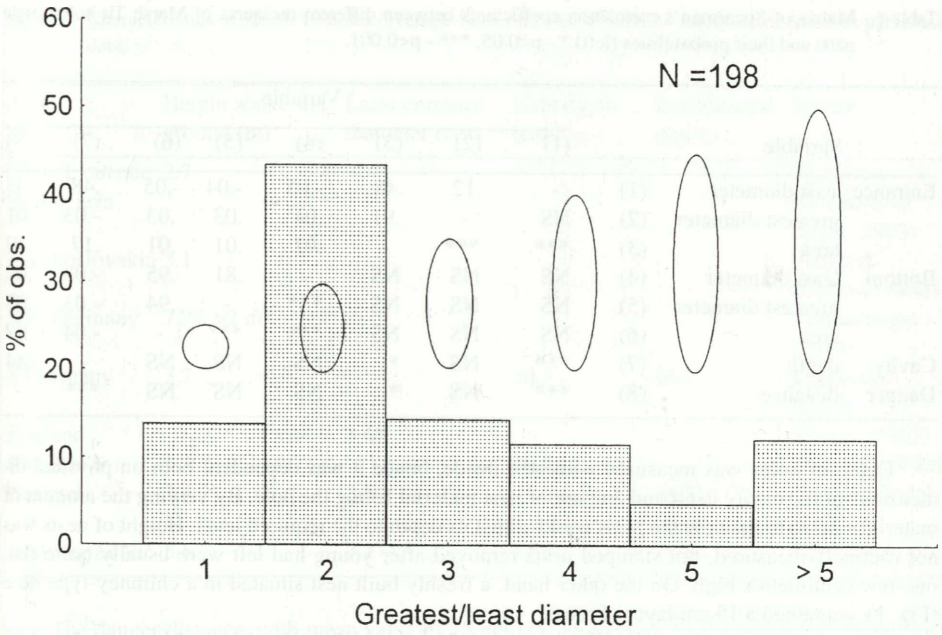

Fig. 5: Frequency distribution of entrance shapes of Marsh Tit holes in BNP. Numbers below x-axis refer to upper boundaries of individual categories. Approximate shapes of different categories of openings are shown above the columns.

of the least by three or more times. The birds could enter holes with such narrow openings only with difficulties, they had had to turn sideways before entering and then had to literally squeeze through the entrance. The least diameter of smallest circular opening equalled 20 mm. This was probably the narrowest entrance passable for Marsh Tits. Holes with rather narrow openings (median 3 cm) were most often used but the least opening diameter could be up to 8 cm (Table 5).

Openings were usually elongated, most often only moderately, their greatest diameter exceeding the least by a factor two-three (Fig. 5), but in the extremely elongated, fissural openings the difference could be twentyfold. Overall the entrance greatest diameter was much more variable than the least, but 75% of measurements were below 10 cm and median value - 6.5 cm (Table 5).

Entrance's area varied most, from 3 to 104 cm^2, but in 65% of the cases it remained below 20 cm^2 and median value equalled 14 cm^2. Variation in both the least and greatest hole diameter contributed significantly to the variation in entrance area, but the influence of the longer measurement was much stronger (Table 6).

Bottom's least diameter ranged from 5 to 16 cm, with median value of 9 cm (Table 5). Almost 84% of the holes had approximately circular cross-sections, thus greatest diameter of the bottom was quite similar to the least one, its median value amounted to 10 cm. The diameter of smallest circular holes amounted to 5.5 and the largest ones to 16 cm. Only 16% of the holes were elongated, the most elongated ones had bottom measurements of 5 x 14, 5 x 11 and 8 x 16 cm.

Bottom area varied over almost a 12-fold range but 58% of the holes had bottom area within the range of 50-99 cm^2, with median value of 73 cm^2 (Table 5). Both least and greatest bottom diameters contributed very strongly to variation in the bottom area. There was, however, no correlation among any of the hole-bottom variables and any of the entrance measurements (Table 6).

Table 6: Matrix of Spearman's correlation coefficients between different measures of Marsh Tit holes (right part) and their probabilities (left) * - p<0.05, *** - p<0.001.

	Variable		Variable							
			(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Entrance	least diameter	(1)	-	.12	.48	-.05	-.04	-.05	.48	.41
	greatest diameter	(2)	NS	-	.91	.04	.03	.03	-.03	.01
	area	(3)	***	***	-	.02	.01	.01	.17	.19
Bottom	least diameter	(4)	NS	NS	NS	-	.81	.95	-.03	.07
	greatest diameter	(5)	NS	NS	NS	***	-	.94	-.03	.07
	area	(6)	NS	NS	NS	***	***	-	-.04	.07
Cavity	depth	(7)	***	NS	*	NS	NS	NS	-	.84
Danger	distance	(8)	***	NS	*	NS	NS	NS	***	-

Depth of holes was measured with nest inside, hence it was dependent both on physical dimensions of the cavity itself and amount of nest material filling the hole. By varying the amount of material carried to the hole the birds could adjust its depth to the required level. Height of nests was not routinely measured, but stamped nests removed after young had left were usually quite flat, one-few centimetres high. On the other hand, a freshly built nest situated in a chimney-type hole (Fig. 1), contained a 15 cm layer of moss.

Except for a single exceptionally deep hole (53 cm), the hole depth varied between 2 and 30 cm. In over two thirds of the cases the hole depth fell within 10-20 cm range, with median value being 14 cm (Table 5). It was significantly positively correlated with the least entrance diameter (Table 6) i.e. holes with wider openings tended to be deeper (Fig. 6).

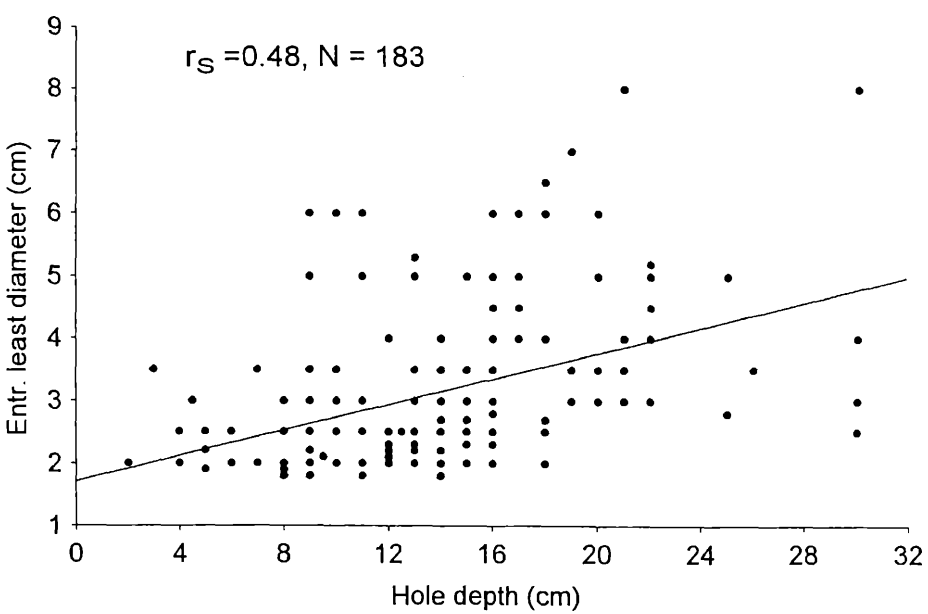

Fig. 6: Relationship between the minimum entrance diameter and hole depth in Marsh Tit holes in BNP.

Table 7: Characteristics of Marsh Tit holes (average values) in various areas. * recalculated from the published data.

Area	Height above the ground (m)	Least entrance diameter (cm)	Hole depth (cm^2)	Bottom area (cm^2)	Source
Poland, outside Białowieża	2.7				Glutz von Blotzheim & Bauer (1993)
Czechoslovakia	3.1				Pikula & Beklová (1980)
NW Germany	72% >2 m				Mildenberger (1984)
S Germany	3.7		20.1	44.7	Ludescher (1973)
England		3.6*			Morley (1953)
Sweden	1.1		16.2		Nilsson (1984b)
Holland	3.4	3.6		38.7	van Balen et al. (1984)
Białowieża NP	5.6	3.2	14.4	78.5	This study

The danger distance, with mean value of 18 cm was on average ca 4 cm larger than the hole depth (Table 5), and in over two thirds of the cases the difference fell within 2-6 cm. Both variables were very strongly positively correlated. The danger distance was also positively correlated with the least entrance diameter, but there was no correlation with the bottom diameter (Table 6).

4. Discussion

There are only few quantitative data on Marsh Tit natural holes available for comparison with the Białowieża findings. Data on height of holes above the ground are most frequently given. They clearly show that Marsh Tits at BNP - 5.6 m bred much higher than that in the other areas (Table 7). This could be a by-product of unusual stature of tree stands in BNP (see "Study area"), owing to which suitable holes could be situated relatively higher there than in other areas. In spite of this, and in contrast to Nilsson's (1984b) statement, it seems that the Białowiża birds choose to breed rather low (Fig. 2), in small trees (Fig. 3). That they could breed in larger trees and much higher is demonstrated by the distribution of mean nesting heights of other hole-nesters at BNP, which without exception are larger than in Marsh Tit (Wesołowski & Tomiałojć 1986, Wesołowski 1989, 1995 Walankiewicz 1991). For example, the most numerous secondary hole-nester of BNP - Collared Flycatcher *Ficedula albicollis* - breeds most often in hornbeams (70-80%) at average height of 7.5 m (Wesołowski 1989, Walankiewicz 1991), whereas average height of Marsh Tit holes in this tree species was only 4.9 m (Fig. 2). Nilsson (1984b) suggested that the low nesting of Marsh Tits was due to avoidance of competition with other, behaviourally dominant, hole-nesters. This explanation, though, could hardly be applied to the Białowieża situation, where densities of other tits are usually severalfold lower than in Western Europe (Tomiałojć *et al.* 1984, Wesołowski *et al.* 1987) and hole-nesters are not limited by availability of nest-sites, as even the latest breeding Collared Flycatchers have a substantial excess of holes at their disposal (Walankiewicz 1991).

Only Mildenberger's (1984) study from NW Germany contains some comparable data on species of trees used for nesting. These were mostly birches (24x), alders (8x) limes and willows *Salix spp.* (4x each), i.e. species used also at BNP, but at different proportions (Table 1).

Though Marsh Tits at BNP avoided some tree species and used others out of their share (Tables 1 & 2), it is doubtful whether they really selected tree species, whether they actually chose between e.g. nesting in hornbeam or lime. Utilisation of almost completely non-overlapping sets of tree species in different habitats (Table 1), large variation in proportion of various species used in different patches within the same habitat type (Table 2) and, foremost, the lack of significant variation in dimensions of holes among individual tree species strongly suggest that the birds selected holes of appropriate quality and the observed variation in the tree species used and location of holes within the trees (Tables 1-4, Figs 1-4) was to a large extent an incidental consequence of a non-uniform distribution of holes with the required qualities.

This conclusion notwithstanding, the knowledge of which tree species are used with highest frequency can be very useful for management purposes. Even if our knowledge of processes of hole formation and dynamics is very limited (see Sändstrom 1992, Wesołowski 1995b), using findings of this study we can still predict that limes, alders and hornbeams will be „good" species, easily providing birds with holes.

There was one aspect of hole location which seemed to be relevant, irrespectively of hole dimensions, namely the bird strongly avoided to breed in dead substrate, only 8% of their holes were located in such places. Though snags were plentiful and living trees with dead parts were common and contained numerous holes (Wesołowski & Tomiałojć 1986, Wesołowski 1995b), they were rejected. This remains in sharp contrast with data from Germany (Ludescher 1973, Mildenberger 1984), where Marsh Tits most frequently located holes in dead wood, often enlarging them by pecking, habitually used old holes of Willow Tits *Parus montanus*. Ludescher (1973) even concluded that Marsh Tits preferred nesting in dead wood and only secondarily, due to lack of dead wood in managed forests, they were forced to accept holes in living trees. This explanation could not hold good for the Białowiża situation, thus, the question is whether these discrepancies were really due to geographical differences in preferred nest sites or rather the birds in Germany used the "best-of-bad choices" approach to adjust to local conditions in managed woods. It is impossible to check if Marsh Tits at BNP would re-use the Willow Tit holes, though, as the two species occur locally in non-overlapping habitats.

Avoidance of nesting in dead (= soft) wood and keeping away from woodpecker-made holes (Table 4) by Marsh Tits at BNP could be seen as means of avoiding predators. Woodpeckers are reported to be an important nest mortality factor in this (Ludescher 1973, Mildenberger 1984, Nilsson 1984b) and other secondary hole-nesting species (Rendell & Robertson 1989, Walankiewicz 1991). As woodpeckers at BNP peck holes mostly in dead wood (Wesołowski 1995b, Wesołowski & Tomiałojć 1995), thus, the best method to evade their predation is to place one's nest in a hole with small entrance (see below) surrounded by hard "defensive walls" provided by a living tree.

Values of the least entrance diameter recorded at BNP were similar to those found elsewhere, similarly the entrance areas of holes did not differ substantially from those presented in the literature (Table 7). However, the minimum measurements of opening given by Nilsson (1984b) - 15 and 16 mm - are at variance with the Białowieża observations, where the birds could not enter holes with diameter less than 18 mm. How the Swedish birds, which are no smaller than the Białowieża ones (Nilsson J-A. 1992, Cramp & Perrins 1993, Glutz von Blotzheim & Bauer 1993), could squeeze through such a narrow opening remains a puzzle.

Holes in other areas were on average slightly deeper than those at BNP (Table 7). This difference could be partially due to different measurement techniques, to the nest level at BNP and to the cavity bottom without nest in other areas. After accounting for this, it can be said that the hole depth did not vary substantially among the areas. There were, however, large differences in the size of hole bottoms. Mean values given in S Germany and Holland were almost twice smaller than those recorded at BNP (Table 7). Values of trunk diameter at hole height in England (av. 9.1 cm, recalculated from Morley 1953) imply that holes must have much smaller bottoms there as well. One could

argue that birds breeding in managed stands had no choice, large holes were lacking, so they had to accept breeding in small ones. This possibility can be ruled out at least in the case of the Dutch study, as it is known that there were plenty of larger holes available (van Balen *et al.* 1982). As the authors suggest, Marsh Tits may have been forced to breed in very narrow holes to avoid interference from stronger competitors. By the same token one would have to conclude that the usage of relatively spacious holes at BNP (their bottom areas equalled those used by Collared flycatchers there - Walankiewicz 1991) would be indicative of much relaxed interspecific competition for holes at BNP, which seemed to be indeed the case (see above).

If one accounts for different measurement techniques (to nest level in Marsh Tits vs. holes without nests in Collared Flycatcher), holes of both species at BNP had also similar danger distances - av. 18.1 (Table 5) vs. 25.2 cm (Walankiewicz 1991). They differed though in the least entrance diameter - it was much smaller (av. 3.2 cm, Table 5) in the Marsh Tit holes than in the Collared Flycatchers ones (av. 4.4 cm, Walankiewicz 1991).

The question of "why Marsh Tits breed in holes with small openings" cannot be answered unequivocally. On one hand, as the smallest species in the secondary hole-nester guild, Marsh Tits can avoid interspecific competition for holes by choosing holes inaccessible for larger species. As already discussed (see above), in these primaeval conditions, with excess of holes, there was presumably no strong selection pressure to do so. On the other hand, nesting in holes with small openings non-passable for larger animals could serve as an efficient anti-predator device (Walankiewicz 1991). The need for effective means of avoiding predation was especially acute in this primaeval situation, with the diversified set of would-be predators and endemic high nest-predation rates (Tomiałojć et al. 1984, Walankiewicz 1991, Wesołowski & Tomiałojć 1995). Looking from this perspective, Marsh Tits apparently managed to hinder, if not to deny completely, access to their holes for some larger enemies, such as Great Spotted woodpeckers *Dendrocopos major* and pine martens *Martes martes,* both species known to be important predators of Collared Flycatchers holes (Walankiewicz 1991). However, by nesting in holes with small openings they could not avoid Weasels *Mustela nivalis,* another important predator of hole-nesters (Dunn 1977, Järvinen 1989) commonly occurring at BNP (Jędrzejewski *et al.* 1995). This predator is so small (Schmidt 1992) that it could penetrate all, even the narrowest Marsh Tit holes.

Apart from the agents already discussed, there could be other factors potentially influencing the choice of holes of different dimensions, such as e.g. lighting conditions, insulation, hole ventilation, economy of movement inside a hole etc. However, consideration of these possibilities has to be postponed till proper data are gathered in the future studies.

5. Summary

This paper offers an analysis of data on location of 413 and dimensions of 198 Marsh Tit holes gathered in 1975-95 in the strictly protected forest reserve. Breeding was confined to deciduous stands. In riverine stands over 96% of the holes were in *Alnus* and *Fraxinus,* in oak-hornbeam stands over 83% in *Tilia* and *Carpinus* (Table 1) but relative share of the latter two species varied locally (Table 2). Holes were on average 5.6 m above the ground with large interspecific variation - from median 1.4 m in *Sorbus* to 12 m in *Fraxinus* (Fig. 2). Girth at breast height (av. 107 cm) strongly depended on tree species, medians ranged from 57 cm in *Sorbus* to 180 cm in *Fraxinus* (Fig. 3). Entrances were mostly (74%) in vertical plane (Table 3), directions of entrance's exposures in horizontal plane did not vary significantly (Fig. 4). Holes were situated mainly in tree trunks (89%), in living trees (92%) and the share of woodpecker-made holes was <2% (Table 4). Their minimum diameter was 20 mm in circular openings and 18 mm in elongated ones, median 30 mm (Table 5). Openings were usually elongated (Fig. 5), median of greatest diameter 6.5 cm, 75% of the values below 10 cm. Minimum entrance's area was 3, median 14 cm^2, in 65% of the cases entrances were <20 cm^2. Hole bottoms were approximately circular (84%), with median diameter of 9 cm, and minimum diameter of 5.5 cm. Median bottom area was 73 cm^2, 58% of the values were within 50-99 cm^2 range (Table 5). Depth of holes (to nest level) was positively correlated with the least entrance diameter (Fig. 6, Table 6), two thirds of the holes were 10-20 cm deep, median 14 cm.

In comparison to other studies, Marsh Tits bred higher, in holes with larger bottoms but holes had similar depth and entrance diameter. None of the hole dimension variables depended on tree species, thus the observed variation in hole placement was probably to a large extent, a by-product of differences in distribution of holes with adequate qualities. Small openings of holes could serve to avoid competition for holes and/or to evade predators, but non-usage of woodpecker-made holes and nesting in holes in living trees can be best explained as an anti-predator tactic.

6. Zusammenfassung

Natürliche Neststandorte der Sumpfmeise (*Parus palustris*) in einem Urwald (Białowieża Nationalpark, Polen).

In der vorliegenden Arbeit werden Daten von 413 Neststandorten und Maße von 198 Nisthöhlen der Sumpfmeise behandelt, die von 1975–1995 in dem vollkommen geschützten Urwaldgebiet gesammelt wurden. Die Neststandorte lagen durchweg in Laubholzbeständen. In Feuchtgebieten befanden sich 96% der Nisthöhlen in Alnus und Fraxinus, im Eichenmischwald über 83% in Tilia und Carpinus (Tab. 1), aber der relative Anteil dieser beiden Baumarten variierte lokal (Tab. 2). Die Nisthöhlen lagen im Mittel 5,6 m über dem Erdboden, mit großer Variation bei den verschiedenen Baumarten – bei Sorbus betrug der Median 1,4 m, bei Fraxinus 12 m (Fig. 2). Der Brustumfang der Nistbäume (Durchschnitt 107 cm) hing stark von der Baumart ab, und Medianwerte variierten von 57 cm bei Sorbus bis 180 cm bei Fraxinus (Fig. 3). Die Höhleneingänge lagen meistens (74%) in vertikaler Ebene (Tab. 3), und im Hinblick auf die gewählte Himmelsrichtung ergaben sich keine signifikanten Unterschiede (Fig. 4). Die meisten Nisthöhlen befanden sich in Baumstämmen (89%), in lebenden Bäumen (92%), und weniger als 2% der Höhen waren ehemalige Spechthöhlen (Tab. 4). Der Median des Höhleneingangs betrug 30 mm (Tab. 5) und betrug im Minimum 20 mm bei kreisrunden und 18 mm bei ovalen Eingängen. Die meisten Eingänge waren oval (Abb. 5). 75% der Höhlendurchmesser lagen unter 10 cm, der Medianwert betrug 6,5 cm. Der Median des Eingangsbereichs betrug 14 cm^2 und betrug bei 65% der Höhlen weniger als 20 cm^2. Die Höhlenböden waren ungefähr kreisrund (84%), der Medianwert ihres Durchmessers betrug 9 cm, minimale Druchmesser lagen bei 5,5 cm. Der Median der Bodenfläche betrug 73 cm^2, wobei 58% der Werte zwischen 50 und 99 cm^2 betrugen (Tab. 5). Der Medianwert der Tiefe der Nesthöhlen betrug 14 cm, wobei zwei Drittel der Höhlen 10–20 cm tief waren, und die Tiefe der Höhlen war positiv korreliert mit dem Durchmesser des Eingangs (Abb. 6, Tab. 6). Im Vergleich zu anderen Studien brüteten die Sumpfmeisen höher und in Höhlen mit größeren Höhlenböden aber in Höhlen mit ähnlicher Tiefe und entsprechenden Eingangsdurchmesser. Die beobachtete Nisthöhlenvariation hing nicht von den verschiedenen Baumarten ab, sondern ergab sich wohl zufällig vor allem aus dem zur Verfügung stehenden Substrat. Enge Höhlenöffnungen dürften Nestfeinde abhalten und die Nisthöhlenkonkurrenz vermindern, und das Meiden von Spechthöhlen und die Anlage von Höhlen in lebenden Bäumen lassen sich am besten als ein Feind-Abwehrverhalten interpretieren.

7. References

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