Clutch Size and Breeding Performance of Marsh Tits Parus palustris in Relation to Hole Size in a Primeval Forest

Author: Wesołowski, Tomasz

Clutch size and breeding performance of Marsh Tits *Parus palustris* in relation to hole size in a primeval forest

Tomasz WESOŁOWSKI

Department of Avian Ecology, Wrocław University, Sienkiewicza 21, 50–335 Wrocław, POLAND, e-mail: tomwes@biol.uni.wroc.pl

Abstract. I studied Marsh Tit, a secondary hole nesting bird in an area with superabundant holes (primeval forest in the Białowieża National Park, E Poland), expecting to find no relationship between hole size and, either clutch size, or breeding performance. Analysis of about 350 nest histories collected over 13 years revealed, as expected, no difference between breeding in medium-sized or large holes, but birds using small holes (lowest 25th percentile) laid smaller clutches, fledged marginally fewer young and lost more broods than the birds using the two larger size classes. This variation was not due to differences in timing of laying or the age of females across the hole classes. It is proposed that the use of small holes persisted because of relatively low fitness costs of making such a sub-optimal choice.

INTRODUCTION

Secondary hole nesters, species dependent on the existing supply of tree holes for nesting, may be forced to accept nest sites far from optimal, if these are in short supply. In many managed forests hole availability seems to be limiting (reviews in Newton 1995, 1998), and it is usually assumed that it has always been so, that hole nesting birds have invariably faced chronic hole shortage and fierce competition for holes (reviews in Newton 1995, 1998). Though not corroborated by data from primeval conditions (see below), this conviction led to an expectation that clutch size of hole nesters would often be constrained by hole size (bottom area). Thus, birds breeding in larger holes would lay more eggs and rear more young than the ones forced to use smaller, less than adequate holes. However, attempts to demonstrate a positive relationship between hole/nest box size and clutch size have given equivocal results. Sometimes the predicted relationship was found, sometimes not (review in Wiebe & Swift 2001). These discrepan-

cies could be partially attributable to design problems (e.g. size of nest boxes used outside the range of natural holes used) but they also could reflect real differences across the study sites (Fig. 1).

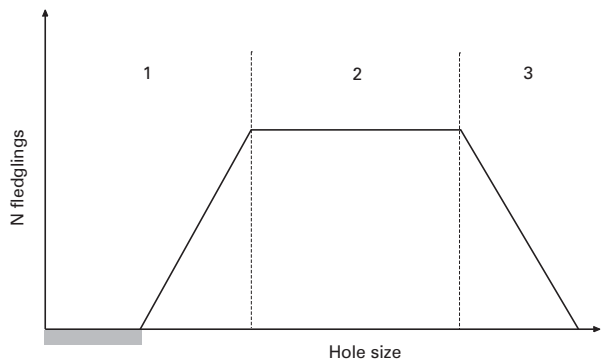Fig. 1. A hypothetical relationship between hole size (cross-section) and breeding productivity in a hole nesting bird: grey area — holes too small to accommodate a bird; 1 — holes useable, clutch size and productivity increase with hole size; 2 — optimum plateau, variation in neither clutch size, nor productivity related to hole size; 3 — holes too large, productivity, but not clutch size, declines with hole size.

One could expect an optimum range of hole sizes, within which the breeding productivity would be highest (Fig. 1). Birds using too small or too large holes would produce fewer young, though for different reasons. There is obviously some minimum size of hole below which birds cannot physically squeeze into. However, above this threshold, there should be a positive correlation between hole size and productivity over the smaller than optimum part of the size range (Fig. 1, section 1), no linear relationship within the optimum range (section 2), and a negative relationship when holes become too large (section 3).

There are several biological reasons behind these expectations. The disadvantages of using too narrow holes could be manifold: brood hyperthermia, high ammonia concentration, trampling of young, increased disease transmission, inadequate nest sanitation or increased predation risk (Löhrl 1973, Slagsvold 1989, Erbelding-Denk & Trillmich 1990, Wiebe & Swift 2001, Wesołowski 2002). Breeding in too large holes, on the other hand, could be costly due to problems with heat loss during incubation/brooding and due to an increased risk of hole loss to stronger competitors (Löhrl 1973, Ludescher 1973). When forced to accept small holes, females could adjust their broods to available space by laying fewer eggs and avoid overcrowding problems. In too large holes this possibility does not exist, laying fewer eggs could make situation even worse.

As the relationship between hole size and bird productivity could be either positive or negative (Fig. 1), the result of a field study would critically depend on array of hole sizes available within the study area, thus, different studies on the same species may produce apparently contradictory results. Here the relationship between the size of holes used, clutch size and nesting success of Marsh Tits breeding in Białowieża National Park (E Poland) is examined. Holes in this old-growth primeval forest are superabundant and secondary hole-nesters may choose from a large variety of holes (Walankiewicz 1991, Wesołowski 1996, 2001a, 2002). Marsh Tits do select holes — before settling in cavity the females often try two or three holes in a row. Additionally, Marsh Tits are not only passive acceptors, they can both enlarge (by removal of mould and debris) and reduce (by adding more nest material) interiors of their holes (Wesołowski 1996, 1998, 1999). With the ability to choose, and behavioural means to adjust their hole dimensions, all females should be able to procure holes of adequate size. Therefore, I expected to find no relationship between the hole size and, either clutch size, or breeding performance of Marsh Tits nesting in these primeval conditions. In accordance with this expectation, the ectoparasite infestation rates of Marsh Tit broods were independent of hole size (Wesołowski 2001a).

METHODS

Study area and data collection

The Białowieża Forest complex is situated at the Polish-Belarussian border (52°41'N, 23°52'E). The forest represents a remnant of the vast lowland forests that once covered large parts of temperate Europe. Its present unique features result from its considerable size and an exceptionally good state of conservation (Faliński 1986, Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990, Wesołowski & Tomiałojć 1995). Although traces of human presence are known from the Neolithic period, intense timber-cutting did not start before the 20th century. The majority of tree stands in the Polish part are now under management, but a 47.5 km² block of the best preserved primeval stands has been strictly protected within the Białowieża National Park (BNP).

The primeval stands in the strictly protected part of the Park are distinguished by a whole array of features: they are multi-storey, mixed-species, uneven-aged, composed of trees reaching unusual heights and contain a large amount of dead timber and uprooted trees. Detailed descriptions and photographs are given in Tomiałojć et al. (1984), Faliński (1986), Tomiałojć & Wesołowski (1990, 1994), so only a brief review of the study areas is given below.

Data on Marsh Tit nesting and dimensions of their holes were collected in 1987–1989 and in 1992–2001. Intense searches for nests, during which holes of all (except few) breeding pairs were found, were made in four deciduous areas. These were:

— plot K, corresponding to plot K in Tomiałojć et al. (1984) — 33 ha, mostly riverine forest (Ash *Fraxinus excelsior*, Alder *Alnus glutinosa*, Spruce *Picea abies*), at forest edge;

— plot C, corresponding to plots CW and CE in Tomiałojć et al. (1984) — 48 ha, forest interior, dominated by Lime *Tilia cordata*, Hornbeam *Carpinus betulus* and Spruce (forming respectively 46%, 24% and 23% of stands — Wesołowski 1996);

— plot M, corresponding to plots MS and MN in Tomiałojć et al. (1984) — 54 ha, forest interior,

with Hornbeam, Lime, and Spruce as dominant trees (forming respectively 47%, 27% and 13% of stands — Wesołowski 1996).

— plot W, corresponding to plots WE and WI in Tomiałojć et al. (1984) — 50.1 ha, at forest edge, Hornbeam, Lime and Spruce being most numerous (respectively 34%, 28% and 18% of stands — Wesołowski 1996).

The latter three areas were all situated in the oak-hornbeam habitat. The plots were 1–2 km apart. The maximum distance between them amounted to 6 km.

To document breeding and the fate of nests, the holes were checked regularly (mostly from the ground). Inspections of the nest contents (using a small bulb on a bendable wire and a small mirror) allowed to estimate fledging dates. Around this time, the holes were observed from a distance c. every 24 hrs, up to the day on which no parents were observed bringing food to the hole. If on the previous day young were at least 18 days old (the youngest age of fledging of undisturbed broods — Wesołowski 2000) and there was no signs of attempted depredation, the nest was considered to be successful. If no feeding was observed at a hole containing young about to fledge (16–17 days old), we searched for parent birds (most of them colour-ringed) to check whether they were collecting food for prematurely-fledged young. If they did, the nest was classified as successful. All other cases of premature cessation of parental activity (no signs of parent presence during an hour observation session) were treated as nest failure.

Unringed adults carrying food for nestlings were caught in door-traps placed at the hole entrance, and colour-ringed. Most of birds (up to 90% of birds in some years) were ringed by the end of the season.

Hole measurements, were taken during the nestling period, but sometimes after the young had fledged. To measure holes, a collapsible ruler and a small bulb on a bendable wire, were used. Several measurements were taken at each hole (Wesołowski 1996, 2002) but the one relevant here is interior diameter of the cavity. It was measured at the nest rim level. Two values — least and greatest interior diameter — were always recorded. Taking accurate measurements of hole diameter in the pear-shaped holes (Wesołowski 1996) was quite difficult, at times impossible.

Analysis

Cross-sections of almost 84% Marsh Tit holes were approximately circular, and most others were

regular, elongated (Wesołowski 1996). Hence, to calculate area of hole cross-section at the nest level, the equation for the area of an ellipse was used.

Sample sizes differ among individual analyses, as gathering of a full set of measurements was not possible in every case. Some holes were used more than once, in different years of the study. This could lead to non-independence of measurements. However, this problem was more apparent than real, as most holes were in living trees (Wesołowski 1996), their characteristics changed with time; the "same" hole measured in various years could have quite different dimensions. Moreover, if the same place was used, it was rarely used by the same birds (Wesołowski 2002).

First egg dates were calculated firstly as absolute (calendar) dates expressed as a number of days passing from the beginning of April, with 1 April = day 1, 2 April = day 2 and so on, and secondly as relative dates. The latter were expressed as deviations of individual laying dates (number of days) from median absolute laying dates (= day 0) of respective years. The relative dates were calculated only for seasons with larger samples of nests; years 1979, 1984, 1986 and 1991 with only 1–2 dates were excluded.

Hatching and fledging dates were usually established by direct observations. The first egg dates, however, were rarely observed directly in the field because in spite of efforts to find nests at building stage, some nests were found only at later stages. Moreover, even in nests found early enough, it was quite difficult to ascertain whether laying already had commenced; nest cups around the laying period were filled with wool, and may have been hidden. Therefore it was necessary to back-calculate the first egg dates. It was assumed that one egg was laid per day, that incubation lasts 15 days, and that nestling age corresponds roughly to stages given in Winkel (1970) for Blue Tits *Parus caeruleus*. When clutch size and/or nestling age were unknown (e.g. holes controlled only from a distance or holes containing only a single nestling) 40 days were subtracted from the fledging date. This corresponded to six days allowed for egg-laying (7 eggs clutch assumed), 15 days for incubation and 19 for nestling stage (Wesołowski 2000).

Individual marking allowed to observe behaviour of individual birds in consecutive seasons and to compare performance of first breeders to older birds. After their first breeding Marsh Tits are extremely sedentary, staying as a rule in the same range (T. Wesołowski, unpublished data). Thus, unringed birds settling in areas previously

used by ringed ones are mostly probably young birds breeding for the first time. Hence, except in the initial ringing seasons, it was justified to treat unringed birds were young, first-time breeders. Older birds which had escaped capture in previous years were treated as young. So the young category may contain some admixture of older birds. The old category, on the other hand, is not biased that way, containing only colour-ringed birds breeding for at least their second time.

All statistical procedures follow the formulae given in STATISTICA for Windows (Anonymous 1996), with two tailed probability values.

RESULTS

The size of Marsh Tits holes in BNP varied from 19 to 314 cm² with median value of 63.6 cm² (mean = 74.6, n = 415). Overall clutch size and number of hatched eggs increased slightly but significantly with hole size (Fig. 2 and 3), whereas the number of fledglings was not related to it (Fig. 4). However, when calculated separately for different parts of the hole size range (Table 1), values of all variables increased significantly with hole size in the lower (r_s = 0.2–0.3), but not in the upper part of the range (r_s = -0.01–0.06, Table 1).

Holes size differed significantly across years (Fig. 5; Kruskal-Wallis ANOVA H $_{9,386}$ = 24.27, p = 0.0039). This was related to the timing of breeding; the median hole size increased with the median laying dates r_s = 0.87, p = 0.001, n = 10 (Wesołowski 1998, 2001b). Two groups of years were distinguishable: those years with the median

Fig. 3. Number of eggs hatching in relation to hole size (r_s = 0.20, p = 0.0003, n = 324). Dot size — frequency of individual values, from 1 (smallest dots) to > 10 (largest dots).

Fig. 4. Number of young fledging in relation to hole size (r_s = 0.01, p = 0.85, n = 224). Dot size reflects frequency of individual values, from 1 (smallest dots) to > 8 (largest dots).
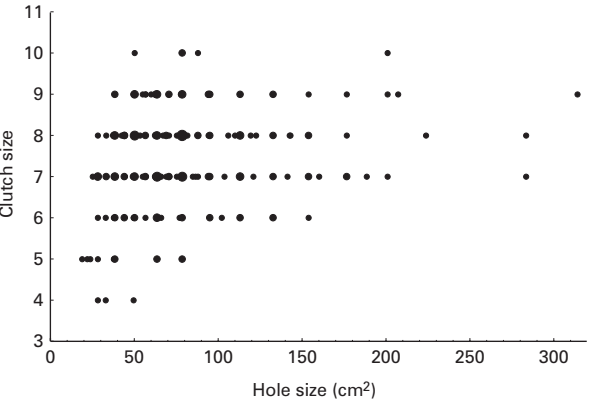

Fig. 2. Clutch size in relation to hole size (r_s = 0.18, p = 0.0005, n = 366). Dot size —frequency of individual values, from 1 (smallest dots) to > 18 (largest dots).
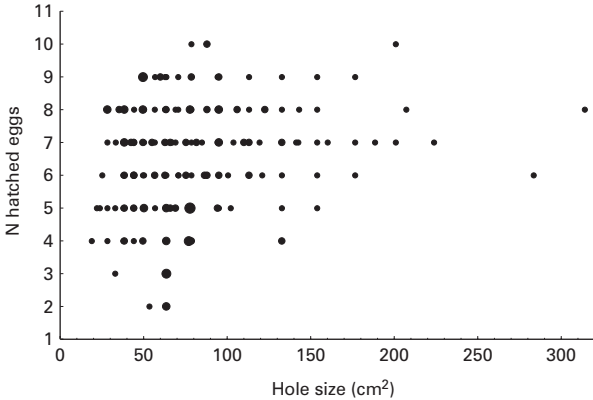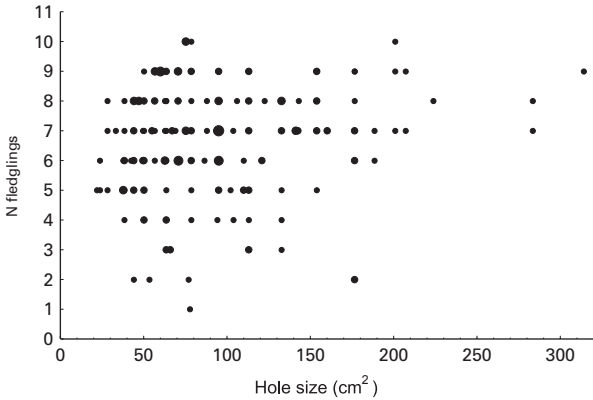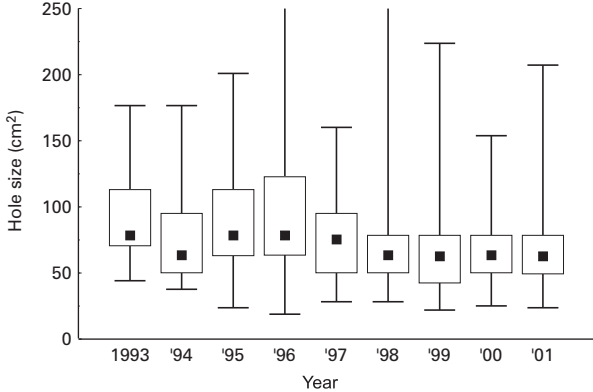

Fig. 5. Sizes of Marsh Tit holes in different years (medians, 25–75% values, and the ranges of values). Only seasons with > 10 holes are shown.

hole size within 62.8–63.6 cm^2, and those with hole size exceeding 75 cm^2 (Fig. 5). To remove a possible confounding influence of this inter-year variation, years were grouped into two classes: 1) „small" seasons — median hole size < 75 cm^2 and, 2) „large" seasons — median hole size > 75 cm^2. All analyses were run both separately for each year class + the pooled data from all years. To check whether breeding in very large or very small holes had any effect on reproduction the data within each group were divided into three classes: 1) small (25th percentile), 2) medium — 25th–75th percentile, and 3) large holes — 75th percentile. In the large seasons these corresponded to hole size < 63.6, > 63.5 and < 95.0, and > 95.0 cm^2, respectively. In the small seasons the border values amounted to < 50.0, > 50 and < 79.0, and > 79.0 cm^2. All holes of identical size were put into a single category, this sometimes resulted in slightly smaller or larger samples in individual categories. The respective classes of holes from both types of seasons were then pooled to make totals for each class.

The standardised clutch size of Marsh Tit was significantly smaller, by 0.7 eggs, in small holes than in medium or large ones, this difference being less pronounced in the "large" seasons (Table 2). As young Marsh Tit females lay smaller clutches than older ones and their clutch size strongly declines with season (Wesołowski

1998, 2000), this could confound the relationship. However, the egg laying dates were not related to hole size, the difference in the relative laying dates among hole size classes being less than a day (Kruskall-Wallis ANOVA (H $_{2,413}$ = 4.02, p = 0.13). Similarly, there was no consistent difference in size of holes used by younger and older females (Table 3). Thus, the effect of hole size on clutch size seems genuine.

Hatching success in successful nests did not depend on the hole size and the type of season, in every category all eggs hatched in 46–59% of cases (χ^2 = 0.15–0.74, df=2, p = 0.69–0.93). Equally, the fledging success showed no relationship, all young fledged from 67–85% of nests in individual categories (χ^2 = 0.50–2.43, df=2, p = 0.30–0.77). Overall, the number of young fledging from small holes was only marginally less (by 0.5 young) than fledging from the medium sized holes (Table 4). This difference could be totally explained by the smaller clutches laid in small holes (Table 2).

Hole size, however, was related to the total failure rate. Broods in small holes had about 50% higher chance of total failure than nests in the medium or large holes. This tendency was detectable in both types of seasons, but the difference was significant only in the pooled sample (Table 5). Due to this and their lower clutch size, birds breeding in small holes produced 20–25%

Table 1. Correlations (Spearman's rank) between hole size and Marsh Tit reproduction.

Variable	Hole cross-section								
	≤ median			> median			All groups		
	n	r	p	n	r	p	n	r	p
Clutch size (n eggs)	199	0.19	0.006	167	0.04	0.612	366	0.18	<0.001
n hatching eggs	168	0.30	> 0.001	156	0.06	0.491	324	0.20	<0.001
n fledglings	120	0.22	0.015	104	-0.01	0.907	224	0.01	0.853

Table 2. Standardised Marsh Tit clutch size in relation to hole size and type of season (see the text for definitions). Hole size classes: small — 25th, medium — 25th–75th, large — 75th percentiles.

Hole size class	Type of season					
	Small		Large		All	
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Small	-0.5 (1.04)	61	-0.3 (1.40)	25	-0.5 (1.16)	86
Medium	0.1 (1.0)	137	0.2 (1.14)	58	0.1 (1.07)	195
Large	0.2 (0.84)	58	0.2 (0.99)	26	0.2 (0.89)	84
Kruskal-Wallis ANOVA	H = 20.50, p <0.0001		H = 3.59, p = 0.166		H = 23.82, p <0.0001	

Table 3. Size of holes used by Marsh Tit females of different age in relation to type of season (see the text for definitions). Age classes: 1 — year of ringing, in most cases probably the first breeding season, 2 — the following year, > 3 — combined data, 4th–8th seasons after ringing.

| Age class | Type of season | | | | | |
| | Small | | Large | | All | |
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
1	68.4 (30.98)	113	85.9 (37.78)	49	73.7 (34.04)	162
2	79.7 (54.06)	40	92.3 (39.05)	26	84.7 (48.77)	66
3	81.8 (53.32)	30	99.3 (46.34)	11	86.5 (51.58)	41
> 3	74.3 (27.37)	13	69.9 (28.62)	13	72.1 (27.53)	26
Kruskal-Wallis ANOVA	H = 1.63, p = 0.65		H = 4.48, p = 0.21		H = 2.64, p = 0.45	

Table 4. Frequency of Marsh Tit total nest failure in relation to hole type and season (see the text for definitions). Probability values refer to χ^2 test, 2df. Hole size classes: small — 25th, medium — 25th–75th, large — 75th percentiles.

| Hole size class | Type of season | | | | | |
| | Small | | Large | | All | |
	n	%	n	%	n	%
Small	67	34.3	30	30.0	97	33.0
Medium	146	21.2	70	20.0	216	20.8
Large	61	24.6	32	12.5	93	20.4
Probability	0.12		0.23		0.046	

fewer young than the ones using the medium and large holes (ca 4.2 vs. 5.4 or 5.3 fledglings/nesting attempt respectively).

DISCUSSION

Contrary to expectations, both clutch size and productivity of Marsh Tits in BNP did depend on hole size, but this relationship was visible only in the lower part of the hole range. Birds breeding in large holes did not show any signs of lowered pro-ductivity. Overall there was a weak positive relationship between clutch and hole size (r_s = 0.18). Clutch size of other secondary hole nesters in BNP showed either no (r = 0.1, Pied Flycatcher *Ficedula hypoleuca,* Czeszczewik 2001) or a weak positive (r = 0.17, Collared Flycatcher *Ficedula albicollis*, Walankiewicz 1991) correlation with the hole bottom area. On the other hand, clutch size of Marsh Tits in other areas very strongly correlated with hole size: r = 0.95 in a German study (SW Germany, recalculated from Fig. 12 in Ludescher 1973) and r = 0.74 in a Russian study (Courish Spit, Baltic Coast, Markovets 2001). The strong relationship found in Ludescher's study could be due to shortage of adequate nest sites, avoidance of strong competitors, and clutch size limitation in narrow holes — Marsh Tits there used much smaller holes ($mean_{30}$ = 45 cm^2) than at BNP and bred often in old Willow Tit *Parus montanus* holes. The Russian results are more difficult to explain. Marsh Tits on the Courish Spit had plenty of choice (up to 57 useable holes in a single territory), bred in almost as large holes as the birds at BNP (mean hole size 69 cm^2), and laid similar number of eggs (6–10, mean 7.7) — recalculated from Markovets & Visotsky (1993), Markovets

Table 5. Standardised number of Marsh Tit fledglings in relation to hole size and type of season (see the text for definitions). Hole size classes: small — 25th, medium —25th–75th, large — 75th percentiles.

| Hole size class | Type of season | | | | | |
| | Small | | Large | | All | |
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Small	-0.2 (1.34)	37	-0.2 (1.14)	13	-0.2 (1.28)	50
Medium	0.3 (1.54)	95	0.1 (1.05)	25	0.3 (1.45)	120
Large	0.2 (1.64)	36	-0.2 (1.91)	13	0.1 (1.70)	49
Kruskal-Wallis ANOVA	H = 4.26, p = 0.119		H = 0.84, p = 0.658		H = 5.07, p < 0.079	

(2001). Despite these apparent similarities, the relationship between clutch and hole size was much stronger on the Courish Spit than at BNP.

Why did birds at BNP choose to breed in too small holes? Were they just making mistakes? Was hole supply really limited? Or do females knowing their eventual clutch size select the hole size best fitting the pre-selected clutch size? Whatever the mechanisms responsible for setting clutch size in Marsh Tits, the latter explanation cannot be true. Young or late commencing birds, which were laying smaller clutches (Wesołowski 1998), did not favour small holes. Additionally, the birds in small holes not only laid fewer eggs, but also lost broods more frequently, so by choosing larger holes they would probably increase their chance of nest success.

The idea that Marsh Tits may have been forced to breed in very narrow holes to avoid interference from stronger competitors may be also refuted. The birds used relatively spacious holes at BNP (their bottom areas equalled those used by very numerous Collared Flycatchers there — Walankiewicz 1991), despite this overlap, the interspecific competition for holes at BNP was almost non-existent (Wesołowski 1989, in press, Walankiewicz 1991).

Though Marsh Tit holes were generally in excess, it is still possible that in some cases local shortages occurred and that some pairs with access only to small holes on their territories were forced to accept them. Unfortunately it is impossible to address this issue directly, as finding all possible holes in this primeval forest has been impossible. However, as Marsh Tits could enlarge the existing holes (Ludescher 1973, Wesołowski 1999) such no-choice situations were probably rare.

The possibility that birds were making mistakes by choosing sub-optimal nesting places should also be considered. Natural selection for avoiding small holes may be weak, if costs of selecting them were not very high. This could be the case with Marsh Tits at BNP, where eight of each ten birds breeding in large and seven of ten breeding in small holes produced young. So only every tenth bird choosing small hole was really severely punished. Perhaps this has not been strong enough difference, to make Marsh Tits avoid small holes entirely. Similarly, Wiebe & Swift (2001) proposed the low fitness costs as an explanation for the lack of relationship between the hole and clutch size in a primary hole nester, Northern Flicker *Colaptes auratus*.

Breeding in small holes was disadvantageous for Marsh Tits at BNP, but breeding in large holes

had no detectable detrimental effects. This notwithstanding, the birds clearly avoided nesting in very large holes. Numerous empty Nuthatch *Sitta europaea* holes (mean bottom area 325 cm², Wesołowski & Rowiński in review) in the study areas were almost never used by nesting Marsh Tits. However, as the Nuthatch holes usually simultaneously possessed several features (spacious bottoms, large entrances, conical knotholes, high above the ground) making them unattractive for Marsh Tits (Wesołowski 1996, 2002), it is difficult to decide whether the birds avoided them because of their size or for some other reason.

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STRESZCZENIE

[Wielkość zniesienia i udatność lęgów sikor ubogich w zależności od rozmiarów dziupli w lesie pierwotnym]

W ściśle chronionej części Białowieskiego Parku Narodowego dziuplaki wtórne dysponują nadmiarem dziupli, mogą więc wybierać do gnieżdżenia dziuple optymalnych rozmiarów. W tych warunkach oczekiwano, że wielkość zniesienia, liczba wyklutych młodych, liczba podlotów i poziom strat w lęgach nie będą zależeć od wielkości dziupli (powierzchni dna, Fig. 1). To przypuszczenie sprawdzano na danych z ponad 350 lęgów zebranych w ciągu 13 lat. Zgodnie z oczekiwaniami, w dziuplach dużych i średniej wielkości nie obserwowano związku między powierzchnią dna a którąkolwiek z analizowanych cech reprodukcji. Natomiast w dziuplach najmniejszych (dolne 25%) wielkość lęgu zwiększała się z powierzchnią dna (Fig. 2–4). W najmniejszych dziuplach ptaki składały mniej jaj (Tab. 2), wyprowadzały nieznacznie mniej młodych (o 0.4 podlota, Tab. 5), a lęgi w nich częściej ulegały zniszczeniu (Tab. 4). Ponieważ ani wiek ptaków (Tab. 3), ani pora składania jaj nie były związane z wielkością używanej dziupli, mniejsze zniesienia w małych dziuplach były prawdopodobnie wynikiem dopasowywania przez ptaki liczby składanych jaj do wielkości dziupli. Przypuszczalnie gnieżdżenie w małych, wąskich dziuplach mogło się utrzymywać w tej populacji ze względu na stosunkowo niski koszt dostosowania, stosunkowo niewielką obniżkę dostosowania ptaków dokonujących suboptymalnego wyboru.