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Effects of nest characteristics on breeding success of Great Tits *Parus major*

Jagna ALABRUDZIŃSKA[1], Adam KALIŃSKI[1], Robert SŁOMCZYŃSKI[1], Jarosław WAWRZYNIAK[1], Piotr ZIELIŃSKI[2] & Jerzy BAŃBURA[1*]

[1]Department of Experimental Zoology & Evolutionary Biology, University of Łódź, Banacha 12/16, 90–237 Łódź, POLAND
[2]Department of Ecology & Vertebrate Zoology, University of Łódź, Banacha 12/16, 90–237 Łódź, POLAND
[*]corresponding author: e-mail: jbanb@biol.uni.lodz.pl

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Abstract. In this study, nest characteristics (size and proportions of basic components) were not correlated with the timing of breeding. Clutch size was negatively correlated with total nest mass but positively correlated with the proportion of the mass of the lining in the total nest mass. Analyses of hatching and fledging success showed that the quantity and proportion of moss in the nest structure as well as the nest size influenced the performance of eggs and nestlings at the nest. We suggest that variation in nest size and composition may be due to several contradictory pressures associated with the need to keep the moisture and temperature in the nest relatively constant, to protect the brood from predation, and to control sanitary standards.

Key words: Great Tit, *Parus major*, nesting, nest size, hatching, fledging

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INTRODUCTION

The structural part of nests of secondary tree cavity nesters fills the volume of the cavity in order to keep the nest cup in an optimal distance to the cavity entrance (Barnes 1975, Perrins 1979, Gosler 1993, Hansell 2000). This basic part of the nest in tits is typically composed of moss. Depending on the amount of moss, nests may be surprisingly variable in size (depth). The fact that it is usually wet inside tree cavities (Wesołowski 2000, Wesołowski et al. 2002) suggests that protecting eggs and nestlings from too high moisture may be one of the most important roles of big nests of tits.

Large nests may also be a store of the remains of food, fragments of epidermis, non-hatched eggs, dead bodies of nestlings and so on. Thus they also have a sanitary function (Perrins 1979, Gosler 1993, Bańbura et al. 2001). Green plants brought to the nest as repellents (Clark & Mason 1985, Cowie & Hinsley 1988, Bańbura et al. 1995, Lambrechts & Dos Santos 2000, Lafuma et al. 2001) may also be built into the structural layer, thus supporting the sanitary function. On the other hand, it is well known that nest materials provide conditions necessary for many arthropod parasites to live (Hansell 2000, Heeb et al. 2000).

It seems that no single factor can explain why the nests of tits are so variable in size. Because they really are variable, we would like to examine a possibility that this variability influences breeding performance of tits. We were especially interested in potential influences of nest characteristics on hatchability of eggs and survival of nestlings because these measures of breeding performance are most likely to depend on conditions prevailing in nests.

MATERIALS AND METHODS

The study was conducted in the Zoological and Botanic Gardens in Łódź, central Poland, in 2000–2001. About 200 wooden nest boxes were kept at this study area. All the nest boxes were of identical size, with internal dimensions being 13 x 13 x 36 cm and the entrance (diameter 29 mm) located 29 cm from the bottom of the nestbox. The most numerous species of birds occupying the boxes were Great and Blue Tits *Parus caeruleus*. All the nest boxes were cleaned after the breeding season. During the spring, the nest boxes were checked every 5 days to monitor breeding performance. To study effects of nest characteristics, two samples of 15 and 14 nests were randomly chosen in 2000 and 2001, respectively. The following breeding variables were recorded: the date of first egg laying, clutch size, the number of hatchlings, and the number of fledglings.

The depth of nest, following Hansell's (2000) terminology, was measured at the end of the laying stage of the clutch. The nests were collected from the nest boxes after the end of the breeding season, in August. They were placed in a freezer for two weeks in order to kill parasitic and non-parasitic arthropods by deep-freezing — this method proved to be efficient. Then nests were weighed to the nearest 0.1 g and decomposed into the main components: the basic structural part and the lining. Materials composing both these parts were determined and recorded. The lining and constructing materials of the nest were also weighed to the nearest 0.1 g. Some additional variables were derived from the row measurements: the percentage of the lining mass and the percentage of moss mass in the total mass of the nest.

We analyzed effects of nest characteristics on the characteristics of breeding performance: clutch size, the number of hatchlings, the number of fledglings, hatching success (a proportion of eggs which produced hatchlings) and fledging success (a proportion of hatchlings which survived to the moment of fledging).

The last two variables were treated as binomial response variables in generalized linear models (Crawley 1993). Standard statistical analyses were applied, with all calculations being performed using STATISTICA for Windows (StatSoft 2000).

RESULTS

Except single nests with no lining, two distinct layers can be distinguished in Great Tit nests: the structural layer and the lining layer. The lining is usually composed of fur, hair, wool, silk, plant and synthetic threads, grass, leaves, moss and many other elements. A dominating component of the structural layer of the nest was moss of the genera *Hypnum*, *Brachyeticum* and *Atrichum* — the mass of moss and its proportion in the mass of the nest were considered as important characteristics of nests. Common additional components of this part were sticks, often constituting a separate sublayer below moss. The structural layer of 10 nests contained Knotgrass *Polygonum aviculare* which was a dominating material in 5 of these cases. In most cases this layer contained also some grass.

Nest size, mass of components and proportions of components were variable (Table 1), with maximum height 15 cm and minimum 4.5 cm, and with maximum mass 93 g and minimum 11 g. There also were marked differences in the amount and proportion of the lining layer and moss as the main component of the nest. The proportion of the lining layer mass in the total nest mass ranged from 0% to 54%, whereas an analogous proportion of moss ranged from 8.5% to 83%.

Table 1. Characteristics of nests studied.

Variable	N	Mean	SD	Median
Nest depth (cm)	27	8.27	2.88	8.00
Nest mass (g)	29	50.80	22.33	49.60
Lining mass (g)	29	15.23	6.69	15.94
Moss mass (g)	29	21.46	14.44	18.15
Lining proportion (%)	29	31.83	15.26	30.17
Moss proportion (%)	29	41.09	19.20	42.55

No nest characteristic was correlated with the timing of breeding. We analyzed some potential effects of nest size and composition on the clutch and brood performance. Clutch size was negatively correlated with the total nest mass ($r = -0.48$, $n = 29$, $p = 0.008$) and positively linked with the proportion of the lining layer mass in the total nest mass ($r = 0.40$, $n = 29$, $p = 0.03$). There was a negative correlation between the number of hatchlings and the proportion of moss in the total nest mass ($r = -0.40$, $n = 28$, $p = 0.03$).

We also analyzed generalized linear models with binomial response variables characterizing hatching and fledging success to test for effects of nest characteristics (Table 2). The binomial hatchability variable was positively affected by both the mass of moss and its proportion in the total nest mass. Thus, mean mass of moss was 24.7 g in 100% hatching success nests, whereas it was 20.2 g in nests with a lower hatching success. Respective values of the moss proportion were 46.4% and 39.1%. Fledging success was positively related to the proportion of moss in the total nest mass and negatively related to the total nest mass. Consequently, the mean proportion of moss was 44.1 % in nests with 100% fledging success

and 36.9% in nests with lower success. Mean mass of complete fledging success nests was 43.2 g, whereas it was 63.6 g in nests with lower fledging success.

Table 2. Effects of Great Tit nest characteristics on binomial hatching an fledging success variables. Wald statistics (W) are given with 1 degree of freedom for each nest variable.

Variable	Hatching success		Fledging success	
	W	p	W	p
Nest depth	0.15	0.703	2.32	0.128
Nest mass	0.97	0.325	7.09	0.008
Lining mass	1.07	0.302	0.47	0.495
Moss mass	11.99	0.000	0.36	0.546
Lining proportion	0.56	0.456	1.76	0.184
Moss proportion	22.14	0.000	9.53	0.002

DISCUSSION

Nest constructing behaviour is specific to most birds (Hansell 2000). Nest sizes, composition and location are important aspects of breeding strategy of birds, which evolved in response to many specific pressures of natural selection. Consequently, many characteristics of nesting are distinctive for particular species (Hansell 2000). Secondary cavity nesters, including tits *Parus* sp., construct their nests inside natural or artificial holes, which saves them from some physical factors and, to some extent, from predatory animals (Martin & Li 1992).

A striking feature of Great Tit (and Blue Tit) nests is their high variation in size and details of construction. Especially, great sizes of many nests are surprising because their constructing has to be very time-consuming, which should be traded-off with other breeding investments (Lessells 1991, Daan & Tinbergen 1997). The depth of a nest decides about the distance between the nest cup and the entrance of the cavity. As natural tree cavities may differ in volume, nests must be adequately flexible in sizes in order to fill the space and keep the nest cup in an optimal distance from the entrance. However, nest boxes have the same standard dimensions and, as a consequence, volume for the nest to fill, but still the nests are greatly variable in depth. If this variability were a result of a kind of misjudgment of the artificial cavity space by females, we would expect no clear influence of nest sizes on the breeding performance. We have shown in this paper that there are some impressive relations between nest traits and breeding characteristics.

We were especially interested in effects of nest characteristics on binomial variables representing hatching success and fledging success, as such variables are expected to be sensitive to conditions for embryonic and post-hatching development, respectively and consequently, to indicate relative breeding performance. We found that the amount of moss and its proportion in total nest mass are variables that positively influence conditions for egg and nestling stages of breeding. On the other hand, the total mass of the nest negatively affects fledging success.

The positive effect of moss may be associated with a sanitary function of the nest structural layer, helping to keep the nest clean, which should be especially important at the nestling stage (Bańbura et al. 2001). In five of the sampled nests we found 6 dead nestlings that were pushed deep into the structural layer. Relatively often single non-hatched eggs were also found in this layer. Fluffing of the nest structure by females that squeeze through the nest materials is also likely to sift parasites, food remains and contaminations down to the bottom of the nest hollow (Bańbura et al. 2001).

Actually, the sanitary function of the nest may be a byproduct of building big nests for some other reasons. Wesołowski (2000) showed that nests located in natural tree cavities undergo a fast process of decomposition, probably by fungi and tree juices. Consequently, the primary function of big nests would be associated with bearing this pressure at least to the moment of fledging. Other functions may be humidity stabilization and temperature insulation (Mertens 1977). Nest humidity must depend on the amount of water which penetrates the cavity. As a consequence, the functional link between nest size/composition variables and humidity/temperature control functions may take different shape in different weather conditions. Moreover, rain interception through tree canopy depends on the species, density and age structure of the forest (Czarnowski & Olszewski 1968). All these relations could potentially cause different selection pressures in different breeding seasons and habitats, which could account for at least some variability in nest characteristics.

Soaking of nests in natural tree cavities studied in the primaeval forest of Białowieża was markedly less important cause of breeding failure than predation, and was observed more often in the early part of the breeding season (Wesołowski et al. 2002). Wesołowski et al. (2002) provide data suggesting that the protection against moisture could be associated with nest sizes. On the other hand predatory mammals, such as Pine Martens *Martes martes* and other mustelids, are known to be able to draw nests out of cavities (Walankiewicz 2002, own unpublished observation), the efficiency of such predation being probably inversely related to nest size. Consequently, two inversely directed selection pressures influencing nest size are likely. The functions of the nest related to the stabilization of nest physical environment and the minimization of nest predation seem likely to combine with the sanitary and anti-parasitic function (Heeb et al. 2000). Under a predicted influence of such different pressures females may construct different nests, which could explain their spectacular variability in size and composition.

However, nest design features may or may not affect breeding performance directly. Hence an alternative explanation of our findings could also be considered that nest traits reflect some aspects of territory and/or individual quality. Territory and individual quality influence breeding performance and thus an indirect correlation between nest traits and breeding performance could appear. To assess a relationship between nest construction features and territory quality, an independent measure of the latter would obviously be needed.

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STRESZCZENIE

[Wpływ cech konstrukcji gniazda na sukces lęgowy bogatki]

W pracy przedstawiono wyniki analizy wpływu rozmiarów i składu materiału gniazda na wielkość zniesienia, wykluwalność jaj i przeżycie piskląt w populacji bogatki zasiedlającej skrzynki lęgowe. Wielkość zniesienia okazała się ujemnie skorelowana z całkowitą masą gniazda (r = -0.48), zaś dodatnio (r = 0.40) z procentowym udziałem mchu w masie gniazda. Cechy gniazd nie były skorelowane z terminami lęgów. Wykluwalność jaj była dodatnio skorelowana z masą mchu i udziałem procentowym mchu w gnieździe. Średnia masa mchu w gniazdach ze 100% wykluwalnością wynosiła 24.7 g (46.4%) — a w gniazdach z mniejszym sukcesem — 20.2 g (39.1%). Proporcja piskląt opuszczających gniazdo była natomiast dodatnio skorelowana z proporcją mchu, a ujemnie z całkowitą masą gniazda.

Dane te wskazują, że rozmiary gniazda i jego cechy konstrukcyjne maja znaczenie przystosowawcze. Główne funkcje gniazd sikor to wypełnianie przestrzeni dziupli, tak aby jaja i pisklęta znajdowały się w bezpiecznej odległości od otworu wlotowego, stabilizacja warunków termicznych i wilgotności (w tym zabezpieczenie przed zatapianiem), a ponadto oddziaływanie sanitarne i anty-pasożytnicze.