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Nest quality in relation to adult bird condition and its impact on reproduction in Great Tits *Parus major*

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Abstract. Birds' nests are special structures built with reproductive aims. Size and structure of the nest can arise from evolutionary trade-offs between benefits such as the insulation from unfavourable conditions, maintenance of eggs or chicks, or security against predation, and costs such as energy spent in construction of the nest and the risk of predation in more visible nests. Therefore, building a good nest is beneficial in terms of reproductive output but expensive in terms of time and energy, so probably only "good" parents would be able to build "good" nests. Our objective was to study possible relationships between the quality of the parents and the quality of the nest, and between the quality of the nest and breeding performance in a Great Tit *Parus major* population. We found positive relationships between different components of the nest quality and components of breeding performance. However, we did not find any significant relationship between quality of the parents and that of the nest. A weak, though significant positive correlation was found between female size and breeding success rate.

Key words: Great Tit, *Parus major*, breeding performance, clutch size, nest size, parental quality

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INTRODUCTION

Birds' nests are more or less elaborated structures built with reproductive aims. They form a receptacle which usually provides protection and an adequate microclimate for the development of eggs and nestlings (Collias & Collias 1984). The size and structure of the nest might arise from an evolutionary trade-off between benefits as the insulation from unfavourable weather conditions or protection of eggs and chicks against predation (Skowron & Kern 1980, Kern 1984, Quader 2006), and costs as the time and energy devoted to its building or the risk of predation in the most visible nests (Withers 1977, Slagsvold 1989b). Overall, nests seem to give important benefits, especially to females (Quader 2006, and references therein), so it might be expected that their characteristics fit adequately the needs for successful incubation and chick caring. For instance, some nest components (hair, feathers) may improve thermal insulation (Hilton et al. 2004), and others may have antiparasitic functions (Clark & Mason 1988). Nevertheless, some authors have stressed that very few studies consider the effects of the nest characteristics on reproductive performance (e.g. Tomás et al. 2006).

In many altricial species, where chicks stay at the nest for some time after hatching, and therefore build more elaborate nests, nest building is an important component of the parental effort. Thus, parents not only allocate a large amount of time and energy to nest building, but also expose themselves to a considerable predation risk (Martin et al. 2000). This effort might be mediated by their health status or their phenotypic quality, since bigger nests are associated to parents in better condition (Lens et al. 1994, Soler et al. 1998a, Tomás et al. 2006). In other words, nest characteristics might be a good indicator of the quality of the parents, and the nest size has been shown to be a sexually selected trait (Moreno et al. 1994, Soler et al. 1998a, b, Møller 2006, Polo & Veiga 2006).

Since the "quality" of the nests is something difficult to define and measure, nest size has been often used as a surrogate of nest quality. Thus, nest size has been shown to be related to the body condition of the parents (Soler et al. 1998a) and with some other estimates of parental quality (Palomino et al. 1998, Soler et al. 1999, De Neve & Soler 2002, De Neve et al. 2004, Mainwaring et al. 2008). Finally, nest size has been shown to be positively related to several fitness related parameters, such as clutch size (Møller 1982, Soler et al. 2001), the total number of eggs laid along the breeding season (Soler et al. 1998a), hatching success (Møller 1982) and breeding success (Slagsvold 1989a). For example, nests with thicker walls and nest bottom are probably better insulated from extreme ambient temperatures, allowing a better embrionic and nestling development (e.g. White & Kinney 1974, Kern 1984). Also, a thicker, soft nest bottom could prevent eggs from breaking during incubation. Sometimes, however, the positive relationship between breeding parameters and nest size is not perfect. For example, Wesołowski (2003) found small clutches in small nests, though the relationship between clutch and nest size disappeared in bigger nests. Furthermore, for hole nesting species, bigger nests might make eggs and nestlings more easy to be preyed upon, since they are closer to the nest entrance (Mazgajski & Rykowska 2008).

In the same sense, the "quality" of a bird is a parameter difficult to define, since many physiological, anatomical or behavioural aspects could influence it. In fact, many different variables have been used as correlates of bird quality when it has been tried to relate it with reproductive performance. Our "quality" measures were related to the age (experience) and size of the birds. Older birds use to be dominants over younger ones and bigger birds over smaller ones (Barluenga et al. 2000, Senar et al. 2001). Social dominance allows a better access to food and nest sites (e.g. Perrins 1979) and dominants use to have better body condition (Carrascal et al. 1998), so we assumed they would be in better condition to face the reproductive demands.

The aim of this work was to study the relationship between parental quality, nest quality and breeding performance in Great Tits *Parus major*. Since this species quickly accepts nestboxes for breeding, it is a good model to study variation in nest size, since all the individuals start from a cavity of the same size and general characteristics. Also, Great Tit nests are compact structures, so they can be removed from the nestbox to measure and weight them without damaging the nest. This allows measuring the nest at the early stages of incubation, avoiding the changes in nest characteristics that incubation and chick rearing might cause (e.g. Palomino et al. 1998). Overall, we expected a positive relationship both between parental and nest quality, and between nest quality and breeding success.

STUDY AREA AND METHODS

The study was performed within extensive orange plantations in Sagunto, eastern Spain (39° 42'N, 0° 15'W, 30 m a.s.l.) in 2006. Nestboxes have been available in this area since 1986, and studies on Great Tits have been being carried on since then (e.g. Andreu & Barba 2006, Greño et al. 2007).

All nestboxes were visited at least once a week since late February. When a Great Tit nest was found, we visited the nestbox as frequently as necessary (daily in some periods) to estimate the parameters of interest (e.g. Barba et al. 1995). Thus, laying date of the first egg (laying date hereafter), clutch size, number of eggs hatched and number of fledglings were recorded. From these, we estimated hatching success (proportion of eggs hatched), fledging success (proportion of nestlings which fledged), and breeding success (proportion of eggs producing fledglings). These percentages were arcsin square root transformed for analyses (Zar 1996). Laying dates (earlier nests considered better), clutch size, and hatching, fledging and breeding success were considered as indicators of breeding performance. We used 47 nests, though sample sizes differed for different studied parameters as nests failed along the nesting period.

All nests were measured and weighed by the same author (EA) 2–3 days after incubation was started. Basal area was limited by the size of the nestbox. Nestboxes used, which proceed from different suppliers, measured between 110.5 and 116.5 mm long and between 106.2 and 121.2 mm wide, so the length and width of each nest was measured. The distance between the entrance hole and the nestbox bottom varied between 83.80 and 104.02 mm. After measuring the basal area, we took the nest out of the nestbox to take other measurements (see Fig. 1) and its weight. We used a digital calliper for linear measurements and a digital balance (accuracy 0.1 g) for weighing.

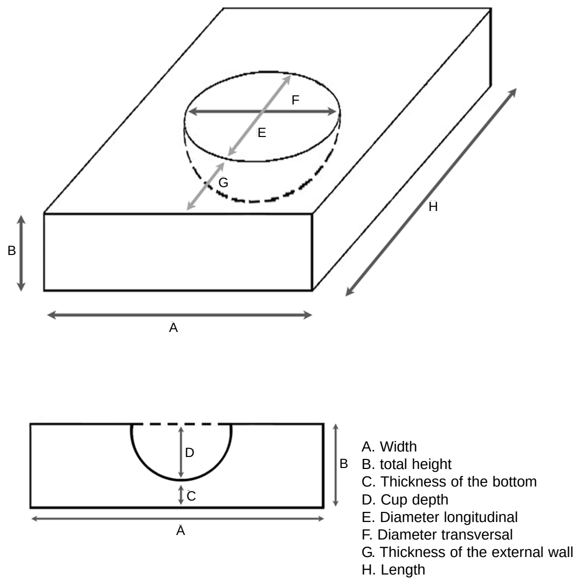

Fig. 1. Detail of the linear measurements taken from each nest. The bottom of the nest is always equal to the bottom of the nestbox.

Parents were captured at the nest, using traps, or around it, using mist nets, when nestlings were 12–14 days old. They were ringed with individually numbered metal rings, and their sex and age class (first year or older breeders) determined (Svensson 1992). Wing and tarsus length and weight were measured, and an index of body condition (weight/tarsus length) was computed. Most birds were measured by the authors using standardized protocols.

Our approach to cope with the difficulties in defining nest and parent "quality" has been taking into account several parameters measured on nests or birds and perform Principal Component Analyses to reduce the number of variables to a few components which might be better indicators of overall nest or bird quality. This is the same approach as the one used, for example, to estimate "body size" from a set of morphological parameters (e.g. Freeman & Jackson 1990, Wiebe & Swift 2001). We also followed this approach to extract the principal components of breeding performance from parameters generally used to define it. Factor scores were computed from factor loadings of the varimax rotation of the axes. We arbitrarily selected eigenvalues above 1, also taking into account that the selected components explained a large percentage of the variance. Each resulting component was regressed against the original variables to explore which were more related to each particular component.

We explored the relationships between selected components using multiple regressions with stepwise selection of variables, since at least two components were selected to describe each of the three aspects (see Results). We only show the final model which included significant variables. When no variables were entered into the model we report it as non-significant. We also explored the relationships between some original variables in those cases where previous studies (e.g. Slagsvold 1989a, Palomino et al. 1998, Alabrudzińska et al. 2003, Tomás et al. 2006) suggested a possible cause-effect relationship. Finally, we tested possible effects of parental age class on nest quality or breeding performance using General Lineal Models. Linear and quadratic relationships were explored in all cases, though quadratic relationships are only presented if they improved the linear ones. The SPSS 15.0 statistical package was used for all the analyses.

RESULTS

The four variables used to define parental quality were reduced to two principal components. The first component explained 44% of the variance, and was related to the condition of the birds, while the second one explained a 43% of the variance and was related to the size of the birds (Table 1).

The nine variables used to define nest quality were reduced to three principal components. The first one explained 27% of the variance, and was related to the overall size of the nest (Table 2). The second one explained 25% of the variance and was related to the size of the nest cup. The third one explained 22% of the variance and was mostly related to the basal area of the nest. Since this last component was virtually fixed for all the nests

Table 1. Results of principal component analyses performed on four morphological variables measured on 33 female and 28 male Great Tits. Correlation coefficients between the components and the original variables are also shown. * — $p < 0.05$, ** — $p < 0.01$, *** — $p < 0.001$.

	Female		Male	
	PC1	PC2	PC1	PC2
Wing length	0.15	0.63**	0.24	0.78***
Tarsus length	0.15	0.90***	0.13	0.90***
Weight	0.87***	0.42*	0.92***	0.33
Condition	0.97***	0.26	0.99***	0.17
Eigenvalue	1.74	1.46	1.89	1.56
% variance accounted for	43.45	36.37	47.35	38.89

Table 2. Results of the principal component analysis performed on 9 variables measured on 43 Great Tit's nests. Presentation as in Table 1.

	PC1	PC2
Total height	0.95***	0.09
Width	0.04	0.04
Length	0.19	0.25
Cup depth	0.62***	0.04
Thickness of the external wall	0.08	0.82***
Thickness of the bottom	0.73***	0.09
Diameter longitudinal	0.03	0.93***
Diameter transversal	0.04	0.77***
Weight	0.76***	0.09
Eigenvalue	2.42	2.21
% variance accounted for	26.94	24.55

(it was the basal area of the nestboxes), we did not consider it in further analyses.

The five variables used to define reproductive performance were reduced to two principal components. The first component explained 50% of the variance and was related to the three estimated success rates (Table 3). The second one explained 27% of the variance and was related to laying date and clutch size.

We found no significant relationship between the quality of the parents or their age (both for males and females) and the quality of the nest they build ($p > 0.05$ in all cases). On the other hand, the success rate of a nest was positively related to the size of the female ($F_{2,29} = 3.44$, $p = 0.046$) (Fig. 2), though this relationship was weak and disappeared when removing two outlying points. All the other relationship between parental quality and breeding performance were non-significant.

The success rate of the nest increased as the overall size of the nest increased ($F_{1,36} = 7.907$, $p = 0.008$) (Fig. 3). Also, nests with larger nest cup held clutches which started earlier and were larger ($F_{1,36} = 7.014$, $p = 0.012$) (Fig. 4). Success rate also tended to be higher in these nests, though the relationship was only marginally non-significant ($p = 0.067$).

Concerning the original variables, we explicitly tested some hypotheses based on results of previous studies (see Introduction). Thus, we found no significant relationship between laying date and nest weight ($r = 0.19$, $p = 0.21$, $n = 47$). Clutch size was not related to nest weight ($r = 0.18$, $p = 0.22$, $n = 47$), but it was positively related with the transversal diameter or the nest cup ($r = 0.36$, $p = 0.012$, $n = 47$). Neither nest weight ($r = 0.09$, $p = 0.62$, $n = 37$) nor the thickness of the nest bottom ($r = 0.05$, $p = 0.78$, $n = 37$) were related to hatching success. Finally, there was no significant relationship between nest weight and the number of fledglings ($r = 0.20$, $p = 0.20$, $n = 40$).

Table 3. Results of the principal component analysis performed on 5 variables of the breeding performance measured on 43 Great Tit's nests. Presentation as in Table 1.

	PC1	PC2
Laying date	0.04	0.82***
Clutch size	0.09	0.79***
Hatching success	0.83***	0.09
Fledging success	0.95***	0.18
Breeding success	0.95***	0.19
Eigenvalue	2.50	1.36
% variance accounted for	49.99	27.27

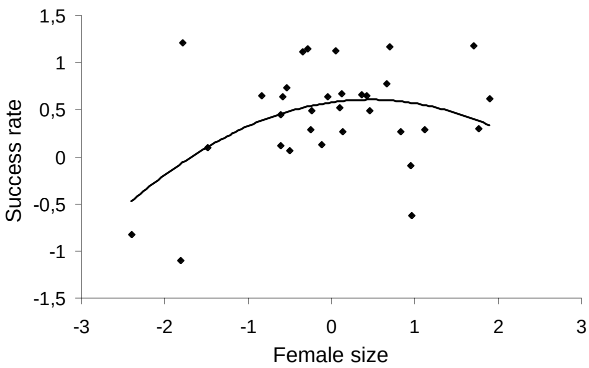

Fig. 2. Relationship between female size (PC 2 of bird quality) and success rate (PC 1 of reproductive performance, a variable including hatching, fledging and breeding success). The relationship disappeared when the two outlying points (lower success rate) were removed.

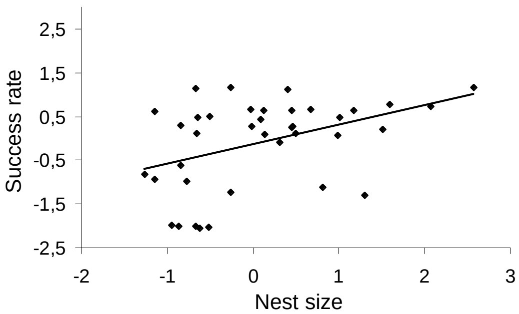

Fig. 3. Relationship between nest size (PC 1 of nest quality) and success rate (PC 1 of reproductive performance, a variable including hatching, fledging and breeding success).

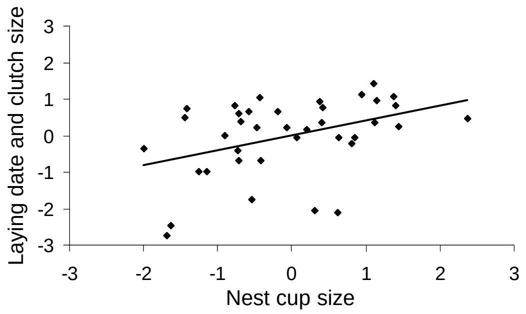

Fig. 4. Relationship between nest cup size (PC 2 of nest quality) and laying date and clutch size (PC 2 of reproductive performance).

DISCUSSION

A clear conclusion of our work was that better quality nests were related with better breeding performance. We have shown that the success rate of the nest (a variable including hatching, fledging and breeding success) increased as the overall size of the nest increased. The original variables more related to "overall size" were the weight of the nest and its height, the later related to a thicker nest bottom and a deeper nest cup. A related result was that nests with larger nest cups (wider cups) and with the cup farther from the nest entrance (thicker external wall) held larger clutches, started laying earlier and tended to have more success. Thus, the overall conclusion is that those nests in which the parents invested more effort were more successful.

An open question, not solved by our work, is whether nest characteristics themselves were important for success, or was the quality of the parents the important variable behind this relationship. What we could say is that none of the quality measures of the parents was positively related to the quality of the nest. On one hand, this might only reflect that we have not measured the adequate parental characteristics. For example, Tomás et al. (2006) found that age and size of the parents were not related to nest weight in Blue Tits *Cyanistes cyaneus*, while some measures of the health status, as prevalence of blood parasites or immunoglobulin levels were related to nest weight. However, this relationship was found only one out of two years, indicating that nest quality is not always clearly related to parental quality. Similar results were reported by Mainwaring et al. (2008), since they did not find significant relationships between parental age or size (except for head-bill length in females) and nest weight, while it was feather mite load of females the parameter positively related to nest weight. Second, the timing of measuring some characteristics might not have been the most appropriate. For example, parents were weighed by the end of the nestling period, when most effort was already done. On the other hand, the lack of relationship between parental quality and nest quality, while breeding success was positively related to nest quality, suggests that the nest itself might be directly affecting breeding success. The relative importance of this effect should be determined through experimental studies breaking the possible relationship between parental and nest quality.

The relationship between nest cup size and clutch size has been scarcely explored at an intraspecific level. Palomino et al. (1998) did not find a relationship between nest cup volume and clutch size in Rufous Bush Robins *Cercothichas galactotes*, while Møller (1982) found a positive relationship in Barn Swallows *Hirundo rustica*. At an interspecific level Slagsvold (1989b) showed that clutch size was related to the inner size of the nest cup. We found a positive relationship both between nest cup size and clutch size (using PCA) and, more explicitly, between the transversal diameter of the nest cup and clutch size, thus confirming this relationship at an intraspecific level. Slagsvold et al. (1989b) suggested that clutch size might therefore be limited by nest size. An alternative is that females build a nest big enough to hold the number of eggs they are going to lay (Møller 1982). Since, for the present study, all pairs had nestboxes of virtually the same bottom area, the positive relationship between nest cup size and clutch size support this later hypothesis, i.e. females are able to shape the nest cup to accommodate the eggs they are going to lay.

It is also noticeable the negative relationship between nest size and laying date, laying starting earlier in bigger nests. At least two studies have failed to find this relationship in cavity-nesting species, including the Great Tit (Alabrudzińska et al. 2003, Tomás et al. 2006). It is difficult to think about a direct cause-effect relationship, so this should be mediated by the quality of the parents. Though we found no relationship between our measures of parental quality and laying date, some relationship between laying date and parental quality might exist. Larger clutches are usually laid early in the season (probably by "better" parents), so the positive relationship between clutch size and nest size could be mediating also here.

One of the characteristics of the nest which might be important for thermoregulation is the thickness of the walls and bottom (Palomino et al. 1998). The thickness of nest bottom might be also important to prevent egg breakage during incubation — we have observed that the eggs of some nests in our population are directly laid on the nestbox bottom without any nest material in between. However, neither Palomino et al. (1998) nor ourselves found a positive relationship between thickness of the bottom and hatching success.

In hole-nesting species, bigger nests had more risk of being preyed upon (Wesołowski 2002, Mazgajski & Rykowska 2008). This was because, by putting more material into the nestbox, eggs and nestlings were more easily accessible to predators which take the nest content from outside the nestbox. Main predators in our study area (Black Rats *Rattus rattus*, Montpellier Snake *Malpolon monspessulanus*, Garden dormouse *Eliomys quercinus*) are able to pass through the entrance hole, so the distance between eggs or nestlings and the hole is not so important in terms of pre-dation risk.

In conclusion, there is a positive relationship between nest quality and breeding success in Great Tits. It remains to be solved to which extent this relationship is due to nest characteristics and which is the parental contribution independently of nest quality. An experimental approach would be needed to answer this. Also, taking into account other components of parental quality (i.e. health status, plumage coloration), of nest characteristics (i.e. nest composition) and reproductive performance (i.e. weight and health status of the fledglings), would aid to clarify the relative importance of nest characteristics in the reproductive performance of birds.

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STRESZCZENIE

[Wielkość gniazd bogatki — jej związek z kondycją ptaków dorosłych i wpływ na reprodukcję]

Wielkość i struktura gniazd ptaków wynika z ewolucyjnego kompromisu między korzyściami takimi jak m. in. izolacja jaj oraz piskląt od niekorzystnych warunków i bezpieczeństwo lęgu a kosztami, np. czasem i energią poświęconymi na jego budowę i ryzyko drapieżnictwa w przypadku większych, bardziej widocznych gniazd. Stąd budowa gniazd jest korzystna dla reprodukcji, ale kosztowna z punktu widzenia poświęcanego czasu i energii. Można więc zakładać, że tylko "dobre" ptaki mogą budować "dobre" gniazda. Celem pracy było określenie związku między jakością ptaków dorosłych i charakterystykami gniazda oraz między charakterystykami gniazda a wynikami lęgu u bogatki.

Badania prowadzono we wschodniej Hiszpanii. Kontrolowano skrzynki lęgowe określając czas przystępowania do lęgów, wielkość zniesienia, liczbę wyklutych i opuszczających gniazdo piskląt. Gniazda były mierzone (Fig. 1) i ważone w pierwszych dniach wysiadywania jaj. Ptaki dorosłe były łapane podczas karmienia piskląt (ok. 12-14 dnia ich życia), określano ich płeć i wiek, mierzono długość skoku i skrzydła oraz ważono.

"Jakość" ptaków dorosłych jak i gniazd oraz wyniki lęgu opisywano grupując opisane cechy przy pomocy analizy składowych głównych (Tab. 1, 2, 3).

Nie stwierdzono związku między kondycją ("jakością") ptaków dorosłych a charakterystykami gniazda. Słaba, ale istotna pozytywna korelacja została stwierdzona między wielkością samic a sukcesem reprodukcyjnym (Fig. 2). Wykazano pozytywny związek między wielkością gniazda a sukcesem reprodukcyjnym (Fig. 3) oraz wielkością czary gniazdowej a składową łączącą termin przystępowania do lęgu i wielkość zniesienia (Fig. 4).