RESEARCH ARTICLE

Nest size is not closely related to breeding success in Blue Tits: A long-term nest-box study in a Mediterranean oak habitat

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ABSTRACT
Various components of breeding success are predicted to be related to avian nest size because (1) some individuals are physically able to build larger nests than other individuals or (2) larger nests provide more protection in the absence of predation than smaller nests. The results of an 18-yr correlative nest-box study in Blue Tits (Cyanistes caeruleus) show that nest size is not closely related to components that reflect breeding performance, after controlling for other female characteristics (first-egg date, clutch size, and female age) assumed to influence breeding performance in long-term studies. Our results support those of most short-term field studies that have reported weak associations between nest size and breeding performance in cavity-nesting passerines. We suggest that the absence of an association between nest size and breeding performance can be explained by the fact that the vast majority of nest-box studies have used small nest chambers that imposed physical constraints on the full expression of the nest. We recommend using a larger range of nest-chamber sizes that better reflect the characteristics of natural holes exploited by secondary cavity-nesting species.

Keywords: breeding success, cavity-nesting birds, Cyanistes caeruleus, nest boxes, nest size

INTRODUCTION
Animal nests are designed to provide protection against changes in the physical environment (e.g., weather; Skowron and Kern 1980, Slagsvold 1989a, 1989b, Nager and van Noordwijk 1992, Hansell 2002, Deeming et al. 2012, Mainwaring et al. 2012) or the biotic environment (e.g., predators, parasites; Nilsson 1984, Wimberger 1984, Slagsvold 1989a, 1989b, Soler et al. 1998, Wesolowski 2002, Lima 2009, Schaedelin and Taborsky 2009, Stanback et al. 2013a, Mainwaring et al. 2014). If nest building is physically costly, some individuals should be physically able to build larger nests than other individuals (e.g., Lens et al. 1994, Palomino et al. 1998, Tomás et al. 2006, Soler et al. 2007, Moreno et al. 2008, Broggi and Senar 2009, Moreno 2012). Therefore, nest size is often expected to be related to breeding performance or success.

Secondary cavity-exploiting birds build nests within cavities they do not excavate themselves. Hence, they are often limited by the availability of tree cavities in secondary...
forest or other anthropogenically altered habitats (Newton 1994). In the absence of tree cavities, avian secondary cavity-exploiters are willing to breed in artificial boxes that vary in design and that are attached to substrates such as buildings, artificial posts, or trees. Accessible boxes allow the routine monitoring and handling of nests, eggs, breeders, and offspring that facilitates the study of relationships between cavity characteristics, nest design, and breeding performance (Lambrechts et al. 2010). Positive relationships between nest size and breeding performance are expected to be weak in systems with natural or artificial holes where cavity nests are exposed to predation, accepting that large nests are more vulnerable to predation risks than small nests (e.g., Wesołowski 2002, Lima 2009, Wesołowski and Rowiński 2012, Kaliński et al. 2014, Maziarz et al. 2015). Field studies of the best-investigated nest-box breeding passerines in Europe have found, in the vast majority of cases, weak relationships between aspects of nest size and components reflecting breeding performance. For instance, Alabrudzińska et al. (2003) found that total nest mass was not strongly linked to the timing of breeding (laying date) or the hatchability of eggs in Great Tits (Parus major) in Poland. In the same study, fledging success was positively related to nest mass measured after the breeding season, but clutch sizes were smaller in heavier nests and nest size measured before the incubation stage was not related to hatching or fledging success. In Great Tits in Spain, nest weight was not related to aspects reflecting breeding performance (Álvarez and Barba 2008). However, when the various measures of nest design and breeding performance were combined in principal component analyses, Álvarez and Barba (2008) reported a positive relationship between nest size and breeding success. By contrast, in 4 Mediterranean-type study plots, Great Tit nest mass was not related to measures of breeding performance (Álvarez et al. 2013). In Blue Tits (Cyanistes caerulescens), heavier or larger nests did not result in greater breeding success than lighter or smaller nests (Tomás et al. 2006, 2013, Lambrechts et al. 2012). In Blue Tits in Spain, experimental manipulation of nest size and nest components (aromatic plants) did not affect laying date, clutch size, hatching date, hatching success, or brood size on day 6 posthatch and had no detectable influence on breeding success (Tomás et al. 2013). In Blue Tits in southern France, nest size was not significantly related to the number of hatchlings, the number of fledglings, hatching success, fledging success, or nestling mass, after controlling for factors frequently investigated in nest-box studies and known to influence breeding performance (Lambrechts et al. 2012). However, several of the studies cited above reported significant, sometimes unexpected, relationships between size components of nests (e.g., cup dimension, fraction or mass of moss or sticks) and some aspects of reproductive performance. For instance, Great Tit clutches were smaller in nests with more moss (Álvarez et al. 2013), and aspects of parental investment changed after an experimental change in the size or composition of Blue Tit nests (Tomás et al. 2013). The nest-box studies interested in reproductive consequences of nest size usually lasted ~2 yr (see also Lombardo 1994, Rendell and Verbeek 1996). Nest size in relation to breeding success thus remains an underappreciated study topic in most long-term avian life-history studies (Mainwaring et al. 2014, Möller et al. 2014a, 2014b).

Here, we reexplore the relationships between the size of nests and the measures of breeding success most frequently quantified in multiyear field investigations that used artificial nest boxes as tools. We present the results of an 18-yr study in Mediterranean Blue Tits in which nest contents have been protected as much as possible against nest predation. If larger nests were beneficial in the absence of predation or were a proximate result of phenotype-related characteristics of the nest builders, we would expect to find significant positive relationships between the size of the cavity nests and other aspects of breeding performance. Because our dataset is so large compared with those of previous studies, we provide especially strong tests.

**METHODS**

In a forest near Montpellier, France (Doutrelant et al. 2008, Lambrechts et al. 2012), we monitored wood-and-concrete Schwegler B1 boxes (Schorndorf, Germany) or concrete boxes with similar external chamber sizes (see appendix 1 in Lambrechts et al. 2010). These boxes have a relatively small internal floor area (~110 cm²) compared with other box types that are accepted by Blue Tits (Lambrechts et al. 2010). Boxes were protected against intrusions of nest predators, most often by using wired cages surrounding the front-plate or the whole box or, in more recent years, by placing boxes in cages on metal posts.

Boxes were usually visited once a week to check the progress of each breeding attempt, the initiation and progress of nest construction, the first egg-laying dates (Julian date), and the numbers of hidden or exposed eggs found in the nest, following basic protocols (Blondel et al. 2006). We measured nest thickness (Hurtrez-Boussès et al. 1999) as the external distance between the internal box floor and the top of the nest rim, following Hansell (2000; his measure “a”, referred to as “nest depth”) and Álvarez and Barba (2008; their measure “B”). Nest volume was estimated as a proxy of nest size by multiplying the nest thickness by the inner surface area of the standardized box floor (cf. Hurtrez-Boussès et al. 1999, Mainwaring et
Table 1. The number of first breeding attempts in Blue Tits per breeding season for which the thickness of nests was measured. Predation or desertion frequently happened before the parents could be trapped. For individual nests that were measured more than once, only one measure per breeding attempt per year is presented.

<table>
<thead>
<tr>
<th>Year</th>
<th>Nests</th>
<th>Deserted (%)</th>
<th>Depredated (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>67</td>
<td>16.4</td>
<td>1.5</td>
</tr>
<tr>
<td>1998</td>
<td>67</td>
<td>14.9</td>
<td>0</td>
</tr>
<tr>
<td>1999</td>
<td>62</td>
<td>14.5</td>
<td>4.8</td>
</tr>
<tr>
<td>2000</td>
<td>63</td>
<td>17.5</td>
<td>0</td>
</tr>
<tr>
<td>2001</td>
<td>73</td>
<td>35.6</td>
<td>13.7</td>
</tr>
<tr>
<td>2002</td>
<td>49</td>
<td>16.3</td>
<td>2.0</td>
</tr>
<tr>
<td>2003</td>
<td>65</td>
<td>10.8</td>
<td>0</td>
</tr>
<tr>
<td>2004</td>
<td>64</td>
<td>7.8</td>
<td>0</td>
</tr>
<tr>
<td>2005</td>
<td>67</td>
<td>1.5</td>
<td>1.5</td>
</tr>
<tr>
<td>2006</td>
<td>68</td>
<td>2.9</td>
<td>17.6</td>
</tr>
<tr>
<td>2007</td>
<td>68</td>
<td>5.9</td>
<td>0</td>
</tr>
<tr>
<td>2008</td>
<td>83</td>
<td>13.2</td>
<td>1.2</td>
</tr>
<tr>
<td>2009</td>
<td>48</td>
<td>2.1</td>
<td>12.5</td>
</tr>
<tr>
<td>2010</td>
<td>92</td>
<td>9.8</td>
<td>15.2</td>
</tr>
<tr>
<td>2011</td>
<td>103</td>
<td>14.6</td>
<td>0</td>
</tr>
<tr>
<td>2012</td>
<td>95</td>
<td>40.0</td>
<td>0</td>
</tr>
<tr>
<td>2013</td>
<td>62</td>
<td>24.2</td>
<td>1.6</td>
</tr>
<tr>
<td>2014</td>
<td>87</td>
<td>20.7</td>
<td>1.1</td>
</tr>
</tbody>
</table>

Nest thickness and nest volume have been used as proxies of nest size in studies that compared investment in nest building across individuals that occupied the same box type (e.g., Hurtrez-Boussès et al. 1999, Lambrechts et al. 2012, 2014). Nests were not always measured during the same reproductive stage; in some years nests were measured only before the onset of egg laying, whereas in other years they were also measured during the period of egg laying or, occasionally, during the period of incubation. Reproductive stage was therefore divided into 3 study periods during which the nests were measured: (1) up to 1 wk before the initiation of egg laying, (2) during egg laying, and (3) after egg laying and prior to hatching (cf. Lambrechts et al. 2014).

In the vast majority of the cases, females were captured within the nest chamber with nest-box traps when the nestlings were ≥8 days old. Occasionally, females were trapped with mist nets placed next to the occupied nest box. All captured females were ringed (with rings provided by the CRBPO in Paris). Body parts were measured following protocols established in a long-term monitoring program (e.g., Blondel et al. 2006, Doutrelant et al. 2008, Lambrechts et al. 2012). Nestlings normally reach the body size of the adults from 13 days posthatch onward (Gibb 1950, Neub 1979, Perrins 1979). In all years, nestling body mass was measured mostly at 14–16 days posthatch, rarely younger (11–13 days posthatch) or older (>16 days posthatch) (cf. Doutrelant et al. 2008, Lambrechts et al. 2012). On a given date, nestlings from the same brood could differ in age, so plumage development was scored and used as a reliable estimate of nestling age, following Gibb (1950). In some years, eggs or whole clutches were removed for the purposes of other studies (e.g., Lambrechts et al. 2012). Boxes with removed eggs or clutches were not considered in the analyses that related nest size to breeding success. Because of time or logistic constraints or difficulties in monitoring nests, not all the factors considered in the present study were quantified for all the nests measured. For instance, some nests were lost before the nestlings fledged (Table 1) and some female parents, for unknown reasons, could not be trapped.

We analyzed relationships between the thickness of nests and 3 measures of breeding performance from first clutches: brood size at hatching, brood size at fledging, and average nestling body mass per brood when the oldest nestlings in a brood stopped growing at ≥13 days posthatch. We classified nests into breeding attempts with at least 1 fledgling versus breeding attempts that did not result in fledglings. Two types of breeding failure were defined: (1) depredated nests, from which eggs or nestlings disappeared well before the expected fledging date and/or where clear signs of predation were noticed; and (2) deserted nests, where unhatched clutches or dead broods without signs of predation were found.

To investigate the relationships between nest size and measures of breeding performance in first clutches (Table 1), after controlling for other characteristics of the nest builders known to influence breeding performance in long-term field studies, we applied mixed models (proc mixed, Type 3, SAS 9.4, data not transformed) and considered the fixed effects of nest thickness as a proxy of nest size (cm), reproductive stage (nest thickness measured before vs. during vs. after egg laying), the Julian date when the first egg was laid (first-egg date), the size of the incubated clutch, and female age (yearling vs. older). First-egg date and clutch size were used as proxies of female quality or territory quality following Przybylo et al. (2001), Mainwaring et al. (2008), or Álvarez and Barba (2008). We first took into account the nests with at least 1 fledgling and compared them with deserted and depredated nests, considering box identity (n = 227) and year (1997–2014) as random factors. Female identity was not taken into account in this analysis because nests often failed before the parents could be trapped. We then analyzed only the nests with at least 1 fledgling, considering box identity (n = 212), year (1997–2014, except 2009), and female identity (n = 524) as random factors.
Table 2. Average (± SD) thickness of Blue Tit nests that had different outcomes (n = number of nest measures taken).

<table>
<thead>
<tr>
<th>Outcome of nest</th>
<th>Nest thickness (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deserted (no visible signs of predation)</td>
<td>5.55 ± 1.23 (range: 3–10) n = 303</td>
</tr>
<tr>
<td>Depredated (eggs or nestlings suddenly disappeared or there were clear signs of predation)</td>
<td>5.40 ± 1.27 (range: 2–8) n = 78</td>
</tr>
<tr>
<td>At least 1 fledgling</td>
<td>5.65 ± 1.42 (range: 1–11.5) n = 1,208</td>
</tr>
</tbody>
</table>

RESULTS

During the 18-yr study period, 1,280 measures of nest thickness from first clutches were taken. In some breeding seasons, nests were measured more than once before the eggs hatched. Several females were also monitored during more than one breeding season. In this sample, the thickness of the nests varied between 1 and 11.5 cm; thus, nest volumes varied between approximately 110 and 1,300 cm³ when nest thickness was multiplied by the internal bottom surface of the boxes.

Despite our efforts to protect nests against predation, nests were occasionally deserted or depredated (Table 1). Deserted or depredated nests were slightly thinner than nests with at least 1 fledgling (Table 2), but the differences in nest thickness were not significant (P = 0.174; Table 3). Females that produced no fledglings tended to have larger clutches than females that produced at least 1 fledgling (P = 0.044; Table 3).

In nests with at least 1 fledgling, the 3 measures of breeding performance were not related to nest thickness (all P > 0.20, Table 3). As expected, females with larger clutches produced more hatchlings (P < 0.0001) and more fledglings (P < 0.0001). Nestlings were also heavier in smaller broods (P < 0.0001) and in broods produced by older females (P < 0.0001).

DISCUSSION

In a nest-box breeding population of Mediterranean Blue Tits that was protected as much as possible against nest predation, we found no strong association between the size of the cavity nest and 4 components of breeding performance. Our study controlled for other female traits assumed to influence breeding performance in long-term field studies (first-egg date, clutch size, and female age; Lambrechts et al. 2012). Our findings therefore support the results of short-term nest-box studies that used substantially smaller data sets (see above; Rendell and Verbeek 1996).

Failed Nests and Their Size

Nest boxes are usually designed to protect bird occupants, which may explain why avian breeding success is often substantially lower in tree cavities accessible to nest predators than in artificial boxes protected against nest predation (e.g., Wesolowski 2002, Wesolowski et al. 2002, Lambrechts et al. 2010, Kalinski et al. 2014). Despite our efforts to protect the cavity nests against predation, some nests were either deserted or depredated and hence did not produce fledglings. In some years, a weasel (Mustela nivalis) was noticed inside boxes that contained destroyed eggs or was seen close to boxes with traces of killed parents or nestlings (M. M. Lambrechts et al. personal observation). Occasionally, front-plates of boxes were found on the ground, combined with evident traces of predation. We observed that nest predation occurred most frequently in 4 study years (Table 1) when the boxes were

Table 3. The mixed procedure (Type 3 tests of fixed effects, data not transformed) using failure level (depredated vs. deserted vs. at least 1 fledgling), number of hatchlings, number of fledglings, or average full-grown nesting mass when the oldest nesting in a brood stopped growing (>13 days posthatch) as the dependent variable, and nest thickness (as a proxy of nest size), reproductive stage (nests height measured before vs. during vs. after egg laying), onset of the first clutch (first-egg date in Julian dates), size of the incubated clutch (number of eggs), and female age (yearling vs. older) as fixed effects. Box identity, year, and/or female identity (ring number) were considered as random factors (for details, see text).

<table>
<thead>
<tr>
<th>Nest thickness</th>
<th>Reproductive stage</th>
<th>First-egg date</th>
<th>Clutch size</th>
<th>Female age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Failure level</td>
<td>F = 1.85</td>
<td>F = 0.70</td>
<td>F = 0.29</td>
<td>F = 4.05</td>
</tr>
<tr>
<td>Hatchlings</td>
<td>df = 1 and 1,037</td>
<td>df = 2 and 1,037</td>
<td>df = 1 and 1,037</td>
<td>df = 1 and 1,037</td>
</tr>
<tr>
<td>P = 0.174</td>
<td>P = 0.494</td>
<td>P = 0.592</td>
<td>P = 0.44</td>
<td>P = 0.138</td>
</tr>
<tr>
<td>Fledglings</td>
<td>F = 0.23</td>
<td>F = 0.11</td>
<td>F = 0.17</td>
<td>F = 1.356</td>
</tr>
<tr>
<td>df = 1 and 475</td>
<td>df = 2 and 475</td>
<td>df = 1 and 475</td>
<td>df = 1 and 475</td>
<td>df = 1 and 475</td>
</tr>
<tr>
<td>P = 0.602</td>
<td>P = 0.899</td>
<td>P = 0.676</td>
<td>P &lt; 0.001</td>
<td>P = 0.859</td>
</tr>
<tr>
<td>Nestling mass</td>
<td>F = 1.22</td>
<td>F = 0.73</td>
<td>F = 1.89</td>
<td>F = 55.17</td>
</tr>
<tr>
<td>df = 1 and 466</td>
<td>df = 2 and 466</td>
<td>df = 1 and 466</td>
<td>df = 1 and 466</td>
<td>df = 1 and 466</td>
</tr>
<tr>
<td>P = 0.269</td>
<td>P = 0.484</td>
<td>P = 0.17</td>
<td>P &lt; 0.0001</td>
<td>P &lt; 0.0001</td>
</tr>
</tbody>
</table>
attached to the trunks of trees. Since 2011, boxes were protected by metal cages placed on metal posts, which substantially reduced the number of depredated nests in the study area. Kaliński et al. (2014) found that any nests in small chambers could suffer from predation when predators had access to the chamber contents via the entrance hole; however, they also explained that in larger chambers, the thicker (i.e., higher) nests suffered more from predation than the thinner ones. Perhaps reduction in nest size might be an efficient strategy against predation when front-plates cannot be removed by predators (e.g., Kaliński et al. 2014). In the present study, however, successful nests were somewhat thicker than depredated nests (Table 2), which indicates that even the thickest nests were not depredated in our study area when nest boxes were protected.

Successful Nests and Their Size

If nest size reflects the physical ability to build a nest without paying predator-related costs, we predicted greater breeding success in larger nests than in smaller nests, which was not supported by our results. For nests that produced at least 1 fledgling, we found that nest size was not closely related to breeding success when the breeding performance of different individuals was compared. However, the birds might have been able to adjust the size or design of the nest to perceived spatiotemporal variation in the environment to keep hatching success, fledging success, or the physical condition of nestlings at similar high levels. For instance, we do not exclude the possibility that nest components (e.g., moss or animal-based lining material) might be related to aspects of breeding performance when nest design would be adjusted to abiotic factors such as weather (e.g., Hansell 2000, Mainwaring et al. 2012, 2014) or to biotic factors such as nest parasites (e.g., Heeb et al. 2000, Gentes et al. 2007, Mennerat et al. 2009). In addition, most studies worked with 1 box type, exceptionally 2 or more (Møller et al. 2014a, 2014b). Nest size is adjusted to the size of the box chamber (e.g., Lombardo 1994, Mazgajski and Rykowska 2008, Stanback et al. 2013b, Møller et al. 2014a, 2014b; M. M. Lambrechts et al. personal observation), imposing physical constraints on the full expression of the nest (Lambrechts et al. 2010). We observed that Great Tits and Blue Tits are able to double or triple the nest volume in larger box types (Møller et al. 2014b; M. M. Lambrechts et al. personal observation). Perhaps the relationships between nest size and aspects of breeding success might become stronger when the data from large and small boxes are compared (e.g., van Balen 1984, Kaliński et al. 2014, Møller et al. 2014a, 2014b; but see Lombardo 1994) or in open-nesting species in which nest size is not physically constrained by the size of the nest chamber (e.g., Soler et al. 1998, Hansell 2000, Moreno 2012). Reproductive consequences of nest building have been investigated with field experiments that imposed nest designs that might have been counter-selected in the past (e.g., Gwinner et al. 2000, Remes and Krist 2005, Moreno et al. 2008). Future studies could investigate nest building and its biological consequences in relation to imposed changes in the architecture or properties of nest chambers that reflect the characteristics of natural holes (Lambrechts et al. 2010, Kaliński et al. 2014, Møller et al. 2014a, 2014b). Multiyear experiments could also manipulate the size or composition of nests while controlling for nest-chamber characteristics (cf. Moreno et al. 2010, Tomás et al. 2013).

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Author contributions: M.M.L., A.G., and C.D. conceived the study (based on Lambrechts et al. 2012) and supervised the research. P.P., C.D., A.G., and M.M.L. developed the methods. All the authors collected data and conducted the research. M.M.L., P.M., A.C., and A.G. analyzed the data. M.M.L. wrote the manuscript.

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