Exploring Biotic and Abiotic Determinants of Nest Size in Mediterranean Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*)


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Abstract
Standardized long-term multi-plot investigations of variation in nest size in free-ranging model species are rare, despite their value for understanding how the environment influences plastic traits such as nest size. Here, we report the results of an 18-yr descriptive study of nest size in first clutches produced by secondary-cavity nesting great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) in the Mediterranean, whilst also taking individual (lay-date, clutch size, age, species) and environmental characteristics (e.g. weather, oak habitat, region) into account. Nests of both species were built in relatively small standardized boxes erected in habitat patches that differed in the presence of the dominant oak species which was either summergreen deciduous or evergreen sclerophyllous. Nest size showed strong differences between species, and also in relation to environmental factors. Great tits built smaller nests than blue tits, Corsican birds had larger nests than mainland ones, nests tended to be larger in evergreen oak-habitat, and larger nests were built during drier weather. None of the individual-specific traits most often considered in long-term studies (lay-date, clutch size, and female age) were related to nest size in either species. Experimental approaches will be required to identify the underlying mechanisms that caused the observed phenotypic diversity for nest size in our study system.

Introduction

Many animal eggs or offspring develop in a construction, called a nest (Hansell 2000; Schaedelin & Taborsky 2009). Nest building, considered to be an important component of niche construction (Odling-Smee 1988; Laland & Sterelny 2006), is almost universal amongst birds (Hansell 2000). The size and shape of avian nests differ considerably across species but also vary spatiotemporally within species, presumably because nest structures are proximately influenced by resources required for their construction, by the properties of sites where the nest is built or by properties of the nest builders and/or their
reproductive partners (e.g. Hansell 2000; Schaedelin & Taborsky 2009; Mainwaring et al. 2014; Heenan et al. 2015).

Secondary cavity-exploiters build nests in natural tree cavities, unoccupied holes excavated by primary hole-nesters, human constructions (e.g. holes in walls), or man-made boxes designed to attract them for roosting and/or breeding (Lambrechts et al. 2010; Mainwaring 2015). Although man-made boxes are designed so that human visitors can inspect their contents, whole nests or their components were rarely studied compared to other reproductive life-history traits expressed after nest completion (e.g. onset of egg-laying, clutch size, brood size). For instance, <6% of 690 verified published nest-box studies in six hole-nesting passerines (great tit Parus major, blue tit Cyanistes caeruleus, coal tit Periparus ater, marsh tit Poecile palustris, pied flycatcher Ficedula hypoleuca, collared flycatcher F. albicollis) examined nest characteristics quantitatively, such as the size or weight of completed nests (see literature search methods presented in Lambrechts et al. 2010; Mainwaring et al. 2014; Møller et al. 2014a). Field studies of nest size in relation to biotic or abiotic factors in the best-studied model species (great tits, blue tits) have lasted a couple of years at most (e.g. Deeming et al. 2012; Mainwaring et al. 2012; Álvarez et al. 2013; Smith et al. 2013; Kaliński et al. 2014).

The size of the cavity nests in great and blue tits is considered to be an adaptive response to various selective factors. For example, nests are predicted to be smaller and thus farther away from the entrance hole when risks of nest predation are higher, larger in colder or wetter environments where eggs or nestlings need to be better insulated, or larger in environments with more food where nests usually also contain a greater number of nestlings (e.g. Nager & van Noordwijk 1992; Wesołowski et al. 2002; Tomás et al. 2006; Mazgajski & Rykowska 2008; Mainwaring & Hartley 2009; Britt & Deeming 2011; Deeming et al. 2012; Lambrechts et al. 2012, 2014; Mainwaring et al. 2012, 2014; Moreno 2012; Smith et al. 2013; Kaliński et al. 2014). Beyond these ultimate causes that might have shaped nest size over evolutionary time scales, the short-term nest-box studies reported that nest size might be proximately influenced by biotic and abiotic factors at ecological time scales. For instance, it is generally accepted that females that are in better physical condition produce larger clutches earlier in the season because of the considerable energetic costs related to the production and incubation of eggs (e.g. Haftorn & Reinertsen 1985; Monaghan & Nager 1997; Visser & Lessells 2001). Builders that are in better physical condition, as reflected in first-egg dates, clutch size or other condition-related traits, are also expected to be physically able to construct bigger cavity nests (e.g. Slagsvold & Lifjeld 1990; Tomás et al. 2006; Álvarez & Barba 2008; Mainwaring & Hartley 2009, 2013; Moreno 2012; Lambrechts et al. 2016). In addition, variation in nest structure components has been associated with variation in ambient temperature within and across breeding seasons (Nager & van Noordwijk 1992; Deeming et al. 2012; Mainwaring et al. 2012). Across field studies, proximate nest-building responses to artificial feeding resulted either in an increase, or a decrease, or no change in nest size when compared to unfed controls (e.g. Mainwaring & Hartley 2009; Smith et al. 2013; also reviewed in Mainwaring & Hartley 2013). Lambrechts et al. (2014, 2015) also argued that different cavity-nesting species perceive the nest-chamber environment in species-specific ways which may explain why in small standardized nest-chambers, larger great tits built significantly smaller nests than smaller blue tits. However, few field studies have investigated the relative simultaneous contribution of different environmental factors in the expression of nest size while controlling for phenotypic characteristics of the nest builders. In addition, nest-chamber size might impose physical constraints on the full expression of nest size in secondary hole-nesting passerines (Lambrechts et al. 2010, 2014; Møller et al. 2014a). Because different studies from different areas of the species’ distribution ranges most often did not use the same box type (Møller et al. 2014a), whilst nest size varies both within and across box types, the relative importance of box size and other environmental factors in the expression of nest size at different spatial scales also remains to be assessed.

In mainland southern France and Corsica, blue tits and great tits that accept standardized man-made boxes for breeding can occupy landscape mosaics where easily identifiable patches of broad-leaved deciduous oak (Quercus pubescens) intermingle with patches of evergreen oak (Q. ilex) (Blondel et al. 1987, 2001, 2006; Lambrechts et al. 2004, 2008). Quantitative measures of caterpillar availability combined with measures of prey delivered to nestlings showed that the deciduous oak habitat is generally much richer in terms of prey abundance than the evergreen oak habitat (e.g. Tremblay et al. 2003). In deciduous oak woods, the peak of availability of caterpillars and other invertebrates used to feed tit nestlings also occurs about one month earlier than in evergreen oak woods. Broad-leaved deciduous oak patches therefore favoured the production of earlier
and larger clutches compared to evergreen oak patches. Four decades of research in the Mediterranean region has revealed phenotypic divergence at different spatial scales for life history, morphological, behavioural, acoustic and plumage colour traits in blue tits (Blondel et al. 2006; Charmantier et al. 2016), which is attributed primarily to oak-related habitat heterogeneity. Female blue tits in these populations display both significant variation and clear individual preferences for some of the nest materials used at these study sites (e.g. aromatic plants, Mennerat et al. 2009). However, the total amount of material brought into the cavity, as reflected in nest size, has been poorly investigated so that very little is known as to how this trait may relate to other biotic and abiotic factors that have been best studied so far (e.g. Lambrechts et al. 2014, 2015).

Here, we report the results of an 18-yr descriptive study of nest size in several study populations of blue and great tits from Mediterranean southern France (mainland, Corsica), whilst also taking into account several life-history traits (first egg date, clutch size, female age) and environmental factors (ambient temperature and rain fall at the time of nest building, dominant oak species, region). These abiotic and biotic factors are usually considered in long-term avian monitoring programs (e.g. Perrins 1979; Blondel et al. 1990, 2006; Møller et al. 2014a,b; Charmantier et al. 2016). The main goal was to explore associations between nest size and several abiotic and biotic factors that can then be further tested with experimental approaches in the future. Based on the literature and the background information available for this study system (see above) that guided our statistical analyses, we examined the following possible associations: (1) Although former studies in local Mediterranean study plots found that great tits build smaller nests than blue tits (Lambrechts et al. 2014, 2015), these studies did not examine whether these interspecific differences remained significant after controlling for abiotic factors related to region or weather. Following the arguments developed in Lambrechts et al. (2014, 2015), we expected to find smaller nests in great tits than in blue tits in analyses that also would take statistically these abiotic factors into account. (2) Lay-date, clutch size and/or female age are often considered as proxies of female quality (Przybylo et al. 2001; Mainwaring et al. 2008; Lambrechts et al. 2014, 2015, 2016). If nest size would reflect female quality, such as the physical ability to build larger nests (e.g. see Álvarez & Barba 2008; Moreno 2012; Lambrechts et al. 2016), we expected at the intra-specific level significant associations between nest size and the other three proxies of female quality indicated above. We thus expected to find larger nests in earlier breeders, in birds being able to produce more eggs and/or in older birds (cf. Lambrechts et al. 2016). (3) Because the physical condition of the nest builders may be better in environments providing more food resources, and where clutches are larger (e.g. Blondel et al. 2006), and based on the results of the long-term monitoring program (Blondel et al. 1999, 2006; Lambrechts et al. 2004; Møller et al. 2014a), we also expected larger nests in deciduous oak patches than in evergreen ones or larger nests on the mainland than in Corsica. (4) If birds from colder or wetter environments require larger, and thus more insulated, nests (cf. Nager & van Noordwijk 1992; Wesołowski et al. 2002; Britt & Deeming 2011; Deeming et al. 2012), we would expect to find significant associations between nest size and weather components (ambient temperature, rainfall). Because colder or wetter environmental conditions are expected to occur more often earlier in the season, we expected to find earlier breeders to build larger nests than later breeders (cf. Lambrechts et al. 2012), which is consistent with expectations (2) and (4). Furthermore, our long-term descriptive studies found that the birds from the mainland or the deciduous oak habitats had significantly earlier lay-dates than the birds from Corsica or the evergreen oak habitats (Blondel et al. 2006). We therefore finally expected to find larger nests on the mainland and in deciduous oak habitats compared to the other environments (Corsica, evergreen oak), which is again consistent with expectations (2) and (4).

Material and Methods

Data from identified nest builders were gathered from two study plots in mainland southern France (broad-leaved deciduous oak plot Rouvière ROU and evergreen oak plot Vic-le-Fesq VIC near Montpellier) and 13 study plots on the island of Corsica (broad-leaved deciduous oak plots Avapessa AVA, Feliceto FEL, Muro MUR, Pietra PIE and Ponte PON near the village of Muro; evergreen oak plots Arinelle ARI, Filagna FIL, Genovesa GEN, Grassa GRA, Murato MRT and Pacciani PAC near the same village of Muro; Pirio PIR and Tuarelli TUA in the Fango valley). The coordinates (latitudes, longitudes) and more detailed descriptions of all the study sites (e.g. altitude, forest age and/or weather) were presented in Blondel (1985; PIR), Blondel et al. (1990; PIR), Dias & Blondel (1996; ROU), Lambrechts et al. (1997a; AVA, MUR, PIR), Doutrelant et al. (2001; ROU, VIC, MUR and PIR), Lambrechts et al. (2004; AVA, FEL, MUR, PIE,
PON, ARI, FIL, GEN, GRA, MRT, PAC), Müller et al. (2006; Vic) and Lambrechts et al. (2008; ROU). Meanwhile, maps indicating the study sites have previously been presented in Blondel et al. (2001), Doutrelant et al. (2001), Blondel et al. (2006), Müller et al. (2006) and Charmantier et al. (2016). Each of the study plots was dominated by a single oak species, either Q. pubescens or Q. ilex (Table 1).

The nest builders used wood-concrete Schwegler B1 boxes (Schorndorf, Germany) or concrete boxes all having circa the same nest-chamber size (ca. 113 cm³). These boxes have a relatively small nest-chamber (Lambrechts et al. 2010; Møller et al. 2006). Daily minimum and maximum ambient temperatures were used to calculate daily average ambient temperatures. Subsequently, we calculated ambient temperatures. Subsequently, we calculated

Table 1: Study years and the number of nest measurements in great tits (P. major) and blue tits (C. caeruleus) from mainland southern France and Corsica and from plots dominated by broad-leaved deciduous oak (Q. pubescens) or evergreen oak (Q. ilex)

<table>
<thead>
<tr>
<th>Study plot</th>
<th>Region</th>
<th>Study years</th>
<th>Great tit measures</th>
<th>Blue tit measures</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rouvière ROU</td>
<td>Mainland</td>
<td>18 yr</td>
<td>1997–2014</td>
<td>229</td>
</tr>
<tr>
<td>Arinelle ARI</td>
<td>Corsica</td>
<td>17 yr</td>
<td>1998–2014</td>
<td>27</td>
</tr>
<tr>
<td>Feliceto FEL</td>
<td>Corsica</td>
<td>17 yr</td>
<td>2000–2014, except 2013</td>
<td>17</td>
</tr>
<tr>
<td>Muro MUR</td>
<td>Corsica</td>
<td>18 yr</td>
<td>1997–2014</td>
<td>47</td>
</tr>
<tr>
<td>Pietra PIE</td>
<td>Corsica</td>
<td>5 yr</td>
<td>1999–2007, except 2006</td>
<td>5</td>
</tr>
<tr>
<td>Ponte PON</td>
<td>Corsica</td>
<td>8 yr</td>
<td>2000–2007, except 2006</td>
<td>8</td>
</tr>
<tr>
<td>Filagna FIL</td>
<td>Corsica</td>
<td>7 yr</td>
<td>2000–2014</td>
<td>4</td>
</tr>
<tr>
<td>Genovesa GEN</td>
<td>Corsica</td>
<td>15 yr</td>
<td>2000–2005</td>
<td>7</td>
</tr>
<tr>
<td>Grassa GRA</td>
<td>Corsica</td>
<td>6 yr</td>
<td>2001–2005</td>
<td>4</td>
</tr>
<tr>
<td>Murato MRT</td>
<td>Corsica</td>
<td>12 yr</td>
<td>2000–2003</td>
<td>5</td>
</tr>
<tr>
<td>Pacciani PAC</td>
<td>Corsica</td>
<td>4 yr</td>
<td>2000–2005</td>
<td>4</td>
</tr>
<tr>
<td>Pirio-Fango PIR</td>
<td>Corsica</td>
<td>6 yr</td>
<td>1997–2014</td>
<td>22</td>
</tr>
<tr>
<td>Tuarelli TUA</td>
<td>Corsica</td>
<td>6 yr</td>
<td>2008–2014, except 2009</td>
<td>–</td>
</tr>
</tbody>
</table>
for each nest during the week preceding the nest size measure the average ambient temperature and the additive amount of rainfall.

When nestings were at least 8 d old, breeders were trapped in the nestbox. The age of the female builders (yearling vs. older) was determined either by using wing plumage colours or, for previously ringed birds, from the monitoring records (cf. Blondel et al. 2006). Breeding attempts for which the female could not be identified were not taken into account.

To investigate the relationships between nest size and environmental factors in first clutches (Table 1), we applied mixed models (proc mixed, Type 3, SAS 9.4, data not transformed; cf. Lambrechts et al. 2014, 2015) and considered the fixed effects of species (great tit vs. blue tit), region (mainland southern France vs. Corsica), oak-habitat type (Q. pubescens vs. Q. ilex), reproductive stage (before vs. during egg-laying), the average weather during the week preceding the nest measurement (average ambient temperature, rainfall), the date when the first egg was laid (lay-date in Julian dates), the size of the incubated clutch and female age (yearling vs. older). Nest-box identity (n = 654), year (1997–2014), female identity (n = 1878) and study site (n = 15) were considered as random factors. None of the interaction terms involving species, region and/or habitat were significant and are therefore not presented.

Results

As concerns the biotic factors, we found that great tits built smaller nests than blue tits (Tables 2 and 3). Despite the strong species effect on nest size, within-species variation in nest size was very large as nest heights in the standardized boxes varied between 1 and 11 cm for great tits and between 1 and 12 cm for blue tits. However, none of the phenotypic traits of the nest builders (lay-date, clutch size, female age) were associated with nest size.

As concerns the environmental factors, we observed larger nests in Corsica than on the mainland, larger nests in evergreen oak patches than in broad-leaved deciduous oak patches, smaller nests during periods with more rain (Fig. 1), but no significant association between nest size and ambient temperature (Tables 2 and 3).

Discussion

Here, we report the results of a long-term descriptive study in two model species with the aim to explore the existence of associations between nest size and a number of biotic and abiotic factors, possibly to be taken into account in future field experiments. Nest size, as other phenotypic traits, is expected to be proximately influenced by a combination of species-specific, individual-specific and environmental factors (e.g. Hansell 2000). As concerns differences between species, we found that in relatively small standardized nesting boxes the smaller blue tits (ca. 10 g) built bigger nests than the larger great tits (ca. 17 g) also taking several abiotic and biotic factors into account. Different species varying in body size and life-history strategies might respond differently to the same set of environmental factors, which could subsequently be reflected in how the nest is built. For instance, several studies have proposed that in nests inside tree cavities and other protected places, parents, eggs or nestlings should be placed beyond the predator’s reach (e.g. Wesołowski 2002; Mazgajski & Rykowska 2008; Kaliński et al. 2014). If species differing in body size

<table>
<thead>
<tr>
<th>Tit species</th>
<th>Region oak habitat</th>
<th>Nest height (cm)</th>
<th>Ambient T (°C)</th>
<th>Rain (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great tit</td>
<td>Mainland</td>
<td>5.1 ± 1.4</td>
<td>12.6 ± 2.1</td>
<td>5.7 ± 10.0</td>
</tr>
<tr>
<td>229 nest measures</td>
<td>Q. pubescens</td>
<td>1–8.5</td>
<td>8.2–22.3</td>
<td>0–60.0</td>
</tr>
<tr>
<td>Great tit</td>
<td>Corsica</td>
<td>5.2 ± 1.6</td>
<td>13.0 ± 1.4</td>
<td>19.0 ± 18.7</td>
</tr>
<tr>
<td>92 nest measures</td>
<td>Q. pubescens</td>
<td>2–10</td>
<td>9.5–15.7</td>
<td>0–60.2</td>
</tr>
<tr>
<td>Great tit</td>
<td>Corsica</td>
<td>5.4 ± 1.8</td>
<td>14.8 ± 1.7</td>
<td>16.0 ± 18.3</td>
</tr>
<tr>
<td>73 nest measures</td>
<td>Q. ilex</td>
<td>2–11</td>
<td>11.2–18.5</td>
<td>0–57.8</td>
</tr>
<tr>
<td>Blue tit</td>
<td>Mainland</td>
<td>5.6 ± 1.4</td>
<td>12.5 ± 2.0</td>
<td>8.7 ± 15.4</td>
</tr>
<tr>
<td>1414 nest measures</td>
<td>Q. pubescens</td>
<td>1–11.5</td>
<td>8.2–18.8</td>
<td>0–83.7</td>
</tr>
<tr>
<td>Blue tit</td>
<td>Mainland</td>
<td>6.4 ± 2.0</td>
<td>10.3 ± 1.9</td>
<td>32.4 ± 22.0</td>
</tr>
<tr>
<td>24 nest measures</td>
<td>Q. ilex</td>
<td>3–10</td>
<td>8.0–14.2</td>
<td>0–57.8</td>
</tr>
<tr>
<td>Blue tit</td>
<td>Corsica</td>
<td>6.3 ± 1.7</td>
<td>12.8 ± 1.7</td>
<td>14.7 ± 17.7</td>
</tr>
<tr>
<td>731 nest measures</td>
<td>Q. pubescens</td>
<td>2–12</td>
<td>7.4–18.2</td>
<td>0–78.4</td>
</tr>
<tr>
<td>Blue tit</td>
<td>Corsica</td>
<td>6.1 ± 1.7</td>
<td>15.0 ± 1.8</td>
<td>13.6 ± 19.4</td>
</tr>
<tr>
<td>1058 nest measures</td>
<td>Q. ilex</td>
<td>2–12</td>
<td>10.2–26.0</td>
<td>0–92.9</td>
</tr>
</tbody>
</table>

Table 2: Average nest height (in cm) used as a proxy of nest size and weather (average ambient temperature in °C, rainfall in mm) during the week preceding a nest measure in first clutches produced by great tits and blue tits from two regions (Mainland southern France vs. Corsica) and two oak-habitat types (Q. pubescens vs. Q. ilex). Also indicated are standard deviations, ranges and the number of measures of nest height. Because nests were built in the same box type, nest height can be used as a proxy of nest size.
to predation. In small standardized chambers, movement or opportunities of escape are extremely limited, and larger species might thus require smaller nests than smaller species to minimize the risk of predation (Kaliński et al. 2014; Lambrechts et al. 2014, 2015). However, we currently do not have data allowing to investigate whether smaller nests reduce the risks of predation (Lambrechts et al. 2016). Field experiments that examine breeding success in response to altered nest size could test associations with brood predation, although the outcome of such experiments will depend on the presence or absence of nest predators during the test period (e.g. Kaliński et al. 2014). Lambrechts et al. (2014, 2015) also proposed that smaller species might be less resistant to cold, therefore perhaps requiring larger, more insulated, nests than larger species. However, the ecological or evolutionary origins of these strong species-specific effects remain poorly understood, opening interesting avenues to explore in more detail the relationships between species size and nest size across a larger number of closely related hole-nesting breeding passerines. Positive interspecific relationships between nest size and species size have already been reported in comparative analyses that considered data from both open-nesting and cavity-nesting species, although the strength of these relationships differs between taxonomic groups (e.g. Deeming 2013).

Nest size showed a considerable amount of variation within each species despite a large overlap in the range of nest sizes between great and blue tits. Other factors, such as individual-specific characteristics, are expected to proximately influence nest size and should explain the wide variation observed within species. Our study focused on three individual-specific phenotypic traits considered to reflect qualities of the individuals. First, we predicted that females that produced more eggs in first clutches should be able to build larger nests (see also Lambrechts et al. 2012, 2016). However, we found that nest size was not associated with clutch size, despite our data set being the largest available for box-breeding passerines. Second, we also found that lay-date was not related to nest size in first clutches, although another experimental field study of blue tits showed that the nests of replacement clutches were smaller than the nests of first clutches (Lambrechts et al. 2012). Finally, as in other studies (e.g. Tomáš et al. 2006; Álvarez & Barba 2008; Lambrechts et al. 2012), female age was not related to nest size in our study populations, also indicating that former experience with nest building or breeding did not influence the size of nests. However, the nest volumes of our Schwegler boxes represent

### Table 3: Results from a mixed model on nest height (Type 3 tests of fixed effects) with species (great tit *P. major* vs. blue tit *C. caeruleus*), region (Mainland southern France vs. Corsica), oak-habitat type (broad-leaved deciduous *Q. pubescens* vs. evergreen *Q. ilex*), reproductive stage (nest measured prior vs. during the period of egg-laying), weather during the week preceding the nest measure (average ambient temperature, rainfall), first-egg date (in Julian dates), clutch size and female age as fixed effects. Box identity, year, study plot and female identity (ring number) were considered as random factors.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num df</th>
<th>Den df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Smaller nests in great tits</td>
<td>1</td>
<td>889</td>
<td>22.56</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Region</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larger nests in Corsica</td>
<td>1</td>
<td>889</td>
<td>8.28</td>
<td>0.0041</td>
</tr>
<tr>
<td>Habitat</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larger nests in evergreen oak patches</td>
<td>1</td>
<td>889</td>
<td>4.29</td>
<td>0.0385</td>
</tr>
<tr>
<td>Stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First-egg date</td>
<td>1</td>
<td>889</td>
<td>0.03</td>
<td>0.863</td>
</tr>
<tr>
<td>Female age</td>
<td></td>
<td></td>
<td>2.42</td>
<td>0.12</td>
</tr>
</tbody>
</table>

**Fig. 1:** Nest height (in cm) against the cumulative rainfall (in mm) during the week preceding a nest measure. Indicated are data points and the estimated slope taking the other variables into account (see Methods and Table 3 for more details).
only circa 30% of the nest volumes that great tits and blue tits are able to construct when larger box types are provided (e.g. H. Löhrl in Glutz von Blotzheim & Bauer 1993; Møller et al. 2014a; data taken by AG and MML). We therefore do not exclude the possibility that in smaller nest-chambers, the costs of nest building might be negligible and disconnected from energy-based constraints. Perhaps the relationships between nest size and other individual phenotypic traits would indeed be revealed more prominently if builders constructed bigger nests in larger nest-chambers which were closer to the extreme of their phenotypic capabilities (Lambrechts et al. 2010, 2016). Studies of tit nests built in natural cavities rather than in nest-boxes would bring an invaluable perspective in this context (e.g. Maziarz et al. 2015).

In contrast with our initial expectation that nests might be larger in richer environments where clutches are also larger, we found smaller nests on the mainland where birds lay more eggs than in Corsica where birds lay fewer eggs. In addition, we found smaller nests in the habitat type providing more food (broad-leaved deciduous oak) than in the habitat type providing less food (evergreen oak). The impact of food availability on nest building remains unclear, however, because the availability of natural food has never been measured around the time of nest building, and has previously been quantified at a later stage of the reproductive cycle. In addition, the effect of artificial feeding on nest size differs across experimental field studies (see Introduction), which indicates that the relationship between nest building behaviour and food availability is complex and requires further empirical studies. Factors other than habitat richness are therefore likely to be associated with intraspecific variation in nest size.

We predicted a negative association between nest size and ambient temperature at the time of nest building, which was not supported by our long-term study. We also predicted that nests would be larger earlier in the season, and also larger on the mainland and in deciduous oak habitats. Contrary with our prediction, nests were not larger in the region or the oak habitat where the first clutches were produced earlier in the season, and they were larger in Corsica where ambient temperatures are higher than on the mainland (analyses not shown, but see also Table 2 and Blondel 1985). However, our Mediterranean study populations were exposed to warmer weather than the more northern study populations where significant associations between nest building and ambient temperature have been reported (e.g. Nager & van Noordwijk 1992; Deeming et al. 2012; Mainwaring et al. 2012). Perhaps nest size becomes more strongly causally linked to ambient temperature at more northern, i.e. colder, latitudes (but see Schöll & Hille 2014). However, we do not know to what extent the larger nests might protect the nestlings against changes in ambient temperature in hot environments as observed in Corsica. We also currently do not know if the weather conditions or weather fluctuations over longer time windows (e.g. more than 1 wk before the onset of nest building) might influence nest building. Causal relationships between nest size and ambient temperature could be experimentally investigated in common garden experiments where birds are exposed to different temperature regimes (e.g. Lambrechts et al. 1997b).

We predicted to find larger nests during periods with more rain or in regions where the probability of rain is higher. According to Wesołowski et al. (2002), bigger nests might reduce the risks of nest soaking and might help to maintain eggs, nestlings or incubating or brooding females away from water that might enter the nest-chamber and accumulate at the bottom of the cavity. It was also found that eggs cool faster in wetter nest environments (Hilton et al. 2004). However, we observed a highly significant negative association between nest size and rainfall at the time of nest building. One possible explanation might be that smaller nests are favoured in wetter environments because they dry faster than bigger nests therefore improving the thermodynamic conditions to which the nest occupants are exposed (e.g. see Heenan et al. 2015). In addition, in dry environments, larger nests with more moss might help to regulate nest humidity (cf. Heeb et al. 2000), e.g. to prevent that nest environments become too dry. Finally, heavy rain might complicate nest building when it would impact foraging opportunities and therefore energy budgets or females might avoid roosting in nests with wet material, perhaps penalizing nest building during periods with more rain. The relationship between precipitation and avian nest characteristics remains unclear and deserves to be considered more thoroughly in future studies.

Finally, we do not exclude that hitherto unconsidered factors might influence nest sizes in our study system, such as previously unconsidered factors expressed around the time of nest building (e.g. luminosity, Wesołowski & Maziarz 2012; Kaliński et al. 2014; sub-species effects, Blondel 1985; Blondel et al. 2006). Nest size might also be defined as an adaptive proactive strategy (Lima 2009) to reduce risks of contact with other species entering the nest-chamber, including nest parasites (e.g. Hurtrez-Boussès et al. 2006).


Britt, J. & Deeming, D. C. 2011: First-egg date and air temperature affect nest construction in blue tits Cyanistes caeruleus, but not in great tits Parus major. Bird Study 58, 78—89.


Nest size in Mediterranean Tits


Nest size in Mediterranean Tits


