

Nest size is positively correlated with fledging success in Corsican Blue Tits (*Cyanistes caeruleus*) in an insular oak-dominated habitat mosaic

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Received: 2 May 2016/Revised: 24 June 2016/Accepted: 25 July 2016/Published online: 24 August 2016
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Abstract Avian nests function to provide a safe environment for parents, eggs and nestlings. Positive associations between nest size and other components of breeding performance are expected in two conditions. First, larger nests protect nest occupants better against environmental fluctuations (e.g., weather) than smaller nests. This implies that nest size is a determinant of survival in nest occupants. Second, if reproduction is physically costly, “stronger” parents are expected to be able to build both larger nests and rear more offspring. Here we present the findings of a 17-year correlative nest box study in Corsican Blue Tits (*Cyanistes caeruleus ogliastreae*) that examined the associations between nest size and different aspects of breeding success. We found that females with larger nests produced more fledglings, but did not produce more hatchlings or heavier nestlings than females with smaller nests. The analyses involving nest size controlled for other female characteristics (first-egg date, clutch size, female age) and environmental factors (oak habitat type, weather during the nestling stage) which we assumed could influence aspects of breeding success. Our findings concerning associations between the size of the nest and breeding success differ from those reported in previous studies in other geographic regions, perhaps because the costs that are associated with reproduction or the local environmental conditions that influence breeding performance are population specific.

Our correlative study illustrates that avian studies of niche construction may benefit from long-term multi-factor investigations.

Keywords First clutch · Breeding success · Animal construction · Niche construction

Zusammenfassung

Bei korsischen Blaumeisen (*Cyanistes caeruleus*) in einem eichendominierten Inselhabitatmosaik korreliert die Nestgröße positiv mit dem Ausfliegerfolg

Vogelnester fungieren als sicheres Umfeld für Elternvögel, Eier und Nestlinge. Positive Beziehungen zwischen Nestgröße und anderen Komponenten der Reproduktionsleistung sind unter zwei Voraussetzungen zu erwarten. Erstens bieten größere Nester ihren Bewohnern besseren Schutz vor schwankenden Umweltbedingungen (zum Beispiel dem Wetter) als kleinere Nester. Dies würde bedeuten, dass die Nestgröße für das Überleben der Nestinsassen einen entscheidenden Faktor darstellt. Zweitens wäre, sofern die Fortpflanzung physische Kosten mit sich bringt, zu erwarten, dass „kräftigere“ Elternvögel sowohl größere Nester bauen als auch mehr Junge großziehen können. Hier stellen wir die Ergebnisse einer 17-jährigen korrelativen Nistkastenstudie an korsischen Iberienblaumeisen (*Cyanistes caeruleus ogliastreae*) vor, bei der die Beziehungen zwischen Nestgröße und verschiedenen Aspekten des Bruterfolgs untersucht wurden. Wir stellten fest, dass Weibchen mit größeren Nestern mehr flügge Jungvögel aber nicht mehr Schlüpflinge oder schwerere Nestlinge hervorbrachten als Weibchen mit kleineren Nestern. Für die Auswertungen nach Nestgröße wählten wir andere Weibcheneigenschaften (Erstgelegdatum, Gelegegröße,

Communicated by F. Bairlein.

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Alter des Weibchens) und Umweltfaktoren (Eichenwaldtyp, Wetter während der Nestlingsperiode), von denen wir annehmen, dass sie ebenfalls Einfluss auf Aspekte des Bruterfolges haben könnten, als Kontrollgrößen. Unsere Befunde bezüglich der Beziehungen zwischen Nestgröße und Bruterfolg unterscheiden sich von denen früherer Studien aus anderen geografischen Regionen, möglicherweise da die Kosten im Rahmen der Fortpflanzung oder die lokalen Umweltbedingungen, welche den Bruterfolg beeinflussen, populationspezifisch sind. Unsere korrelative Studie verdeutlicht, dass ornithologische Untersuchungen zur Nischenbildung von langfristigen multifaktoriellen Forschungsarbeiten profitieren können.

Introduction

Many animal offspring develop in constructions, like nests, containers, burrows or holes (Hansell 2000; Schaedelin and Taborsky 2009; Møller et al. 2014b). Animal constructions are among the first examples mentioned in discussions concerning extended phenotypes (Dawkins 1982; Schaedelin and Taborsky 2009; Mainwaring et al. 2014) or processes of “niche construction” (e.g., Laland and Sterelny 2006).

A large nest could be considered the product of niche construction aimed to improve the living conditions and survival probabilities of the nest occupants. Nest size is therefore expected to be positively associated with breeding success. First, larger nests might be able to offer better environments to occupants. For instance, larger nests might have physical properties that favor the thermodynamic conditions inside the nest, therefore improving the energy budgets and survival probabilities of the breeding parents (e.g., incubating females) or the developing offspring (Nice 1957; Skowron and Kern 1980; Slagsvold 1989a, b; Nager and van Noordwijk 1992; Hansell 2000; Lima 2009; Schaedelin and Taborsky 2009; Deeming et al. 2012; Mainwaring et al. 2012, 2014; Møller et al. 2014a, b; Gładalski et al. 2016). Thus, if nests create more optimal microclimates for offspring growth, then larger nests should result in greater breeding success. This would also imply that nest size per se might impact directly on other aspects of breeding performance. Second, the strength of the association between nest size and other aspects of breeding performance might result from physical abilities of the parents. For instance, if different aspects of reproduction are physically costly, individuals of higher phenotypic quality are expected to be able to construct larger nests, incubate more eggs and rear more nestlings (e.g., van Noordwijk and De Jong 1986). Individual quality (e.g., van Noordwijk and De Jong 1986; Doutrelant et al. 2008) might then be the common cause (direct or indirect) of the

existence of positive associations between different aspects of breeding, like nest size and brood size.

Standardized man-made boxes accessible to researchers allow the routine monitoring of cavity nests and their contents facilitating the investigation of relationships between nest size and other aspects of breeding performance (Newton 1994; Lambrechts et al. 2010; Mainwaring 2015) that are logistically very difficult to study in other species that do not breed inside nest boxes. In the most frequently investigated model species (Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*), descriptive nest box studies reported most often weak positive associations between proxies of nest size on the one hand and timing of breeding, hatchability of the eggs, brood size or fledging success on the other (Alabrudzińska et al. 2003; Tomás et al. 2006; Lambrechts et al. 2012, 2016b; Álvarez et al. 2013; Tomás et al. 2013). Some of these studies found significant relationships between size components of the nest (e.g., cup dimension, fraction or mass of moss or sticks, nest depth) and aspects of breeding performance. For instance, Great Tits produced smaller clutches in nests with more moss (Alabrudzińska et al. 2003; Álvarez et al. 2013). Two field studies at more northern latitudes (Poland and UK) reported significant positive associations between nest components and other aspects of breeding performance, although the strength of these associations differed between Great and Blue Tits that occupied the same box types in the same study plots (Deeming and Pike 2015; Gładalski et al. 2016). However, most nest box studies interested in reproductive consequences of nest size usually lasted a couple of years (see also Lombardo 1994; Rendell and Verbeek 1996; but see Lambrechts et al. 2016b) despite the fact that nesting conditions may vary substantially across years in long-term studies, and were rarely combined with quantitative studies of environmental factors (e.g., weather, dominant vegetation) during the nestling stage (e.g., Mainwaring et al. 2014). Nest characteristics and their associations with other aspects of breeding remain underappreciated research topics compared to other life history traits that are expressed after nest building [e.g., timing of reproduction, clutch size, nestling provisioning (Mainwaring et al. 2014; Møller et al. 2014a, b; Lambrechts et al. 2016a, b)].

In Corsica, individual female Blue Tits differ in the characteristics and size of their cavity nests (e.g., Mennerat et al. 2009; Lambrechts et al. 2015, 2016a). However, the associations between nest size and other aspects of breeding performance have not been explored with long-term studies. Here, we report the results of a 17-year descriptive study of nest size and three measures of breeding success (number of hatchlings, number of fledglings, nestling body mass) in Corsican Blue Tits, whilst also taking into account other life history traits (first-egg date, clutch size, female

age) and environmental factors (ambient temperature and rainfall during the period of nestling growth, dominant oak species). These abiotic and biotic factors are usually considered in long-term avian field investigations of breeding success (e.g., Perrins 1979; Blondel et al. 1990, 2006; Møller et al. 2014a, b; Charmantier et al. 2016; Lambrechts et al. 2016a, b). The main aim of this study was to explore associations between nest size and breeding success that can then be further investigated with field experiments in the future. Based on the literature and the background information available for the Corsican study system, we made the following assumptions to guide our analyses involving nest size:

1. Nest size, laying date, clutch size and/or female age have been considered as proxies of female quality (Przybylo et al. 2001; Doutrelant et al. 2008; Mainwaring et al. 2008; Lambrechts et al. 2014, 2015, 2016a, b). If these aspects of female quality reflect abilities to breed, such as the physical ability to build larger nests or to rear more offspring (e.g., Álvarez and Barba 2008; Moreno 2012; Lambrechts et al. 2016b), we expected to find positive associations between different aspects of breeding success (number of hatchlings and fledglings, nestling body mass) and the four proxies of female quality indicated above. We thus expected to find higher breeding success in females with larger nests, in females breeding earlier in the season, in females with larger clutches and/or in older, perhaps more experienced, females (cf. Lambrechts et al. 2016b). Our analyses of the associations between nest size and different aspects of breeding success therefore also took other aspects of female quality potentially influencing breeding success into account (first-egg date, clutch size, female age).
2. Because the physical condition of the breeders may be better in environments that provide more prey, and where clutches are larger (e.g., Blondel et al. 2001, 1999; Lambrechts et al. 2004; Blondel et al. 2006), we also expected higher breeding success in habitat dominated by broadleaved deciduous oak (*Quercus pubescens*) providing more prey to rear the nestlings than in habitat dominated by evergreen oak (*Quercus ilex*) providing fewer prey for the rearing of nestlings (cf. Tremblay et al. 2003; Lambrechts et al. 2004; Blondel et al. 2006; Charmantier et al. 2016). Oak habitat type was therefore also added in the analyses of the associations between nest size and breeding success.
3. Finally, if colder or wetter environments influence parental abilities (cf. Deeming et al. 2012; Lambrechts et al. 2016a) and reduce breeding performance, we would also expect to find associations between aspects of breeding success and the average weather parameters (ambient temperature, rainfall) expressed during

the stage of nestling growth. The weather expressed during the nestling stage was therefore also taken into account.

Methods

Nests were monitored in 11 study plots within 10-km flight distance from the village of Muro, Corsica, as described in Lambrechts et al. (2004, 2015, 2016a). In each plot, only one oak species was dominant, either *Quercus humilis* (five plots) or *Quercus ilex* (six plots). Nests were built in wood-concrete Schwegler B1 boxes (Schorndorf, Germany) or concrete boxes all with approximately the same nest-chamber size.

From the end of March to the end of June, boxes were usually visited once a week to check the progress of each breeding attempt reflected in the progress of nest building, the first-egg laying dates (in Julian days), the number of eggs, the number of hatchlings, the number of full-grown nestlings, and the number of fledglings (e.g., Blondel et al. 2001, 2006; Lambrechts et al. 2004; Charmantier et al. 2016). We also measured the vertical distance between the bottom floor of the box and the top of the external nest wall under the entrance hole following measure *a* presented in Hansell (2000) or measure *B* presented in Álvarez and Barba (2008). This widely used measure was termed “nest height” (Álvarez and Barba 2008; Lambrechts et al. 2012, 2014, 2015), “nest depth” (Hansell 2000) or “nest thickness” (Hurtrez-Boussès et al. 1999) in other studies of cavity nests. Nest volume was estimated as a proxy of nest size by multiplying the height of the external nest wall with the inner surface of the standardized box floor (ca. 113 cm²) (cf. Hurtrez-Boussès et al. 1999). The height or the volume of the cavity nest has been used as a proxy of nest size in studies that compared breeders that occupied the same box type (e.g., Hurtrez-Boussès et al. 1999; Lambrechts et al. 2012, 2014, 2015, 2016a, b). Individual nests were measured (1) up to 1 week before the initiation of egg laying, (2) during egg laying, and/or (3) after egg laying before hatching (cf. Lambrechts et al. 2014, 2015). Breeding success was not associated with the reproductive stage during which the nest measures were taken (before versus during versus after the period of egg laying) (all $p > 0.44$, Table 2). The protocols associated with the timing of nest measurements therefore did not seem to impact breeding success.

Because the nests were most often not visited every day at the end of the incubation stage, the hatching date was calculated based on the physical development of the nestlings within a few days after the onset of hatching (see also Descamps et al. 2002). The nestlings usually reach the

body size of the adults from 13 days post-hatching onwards (Gibb 1950; Perrins 1979; Neub 1979). In all the study years, the nestling body mass was measured mostly at 14–16 days post-hatching, rarely for younger (11–13 days post-hatch) or older nestlings (>16 days post-hatch) (cf. Lambrechts et al. 2004). Because on a given date, nestlings from the same brood could differ in age, plumage development was scored and used as a reliable estimate of nestling age following Gibb (1950).

Females were in the vast majority of cases captured within the nest chamber when the nestlings were at least 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 Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris. The age of the female parent was determined either by using wing plumage colors or, for previously ringed birds, from the monitoring records (cf. Blondel et al. 2006; Lambrechts et al. 2004, 2012). Because of time or logistic constraints or difficulties to monitor nests, not all the factors considered in this study were quantified for all the nests measured. For instance, some nests were lost before the nestlings fledged (Table 1) or some female parents could, for unknown reasons, not be trapped during their first breeding attempts.

In some years, nests, eggs or nestlings were removed in the framework of experimental studies. The breeding attempts where nest contents were experimentally changed were not considered in our analyses. In some study years when *Protocalliphora* blowflies were investigated (cf. Mennerat et al. 2008, 2009), a cotton bag was inserted under nests 2–4 days before the expected hatching dates or just after hatching. Because the cotton bags might have

changed the nest environment, nests that were inserted into a cotton bag were excluded from the analyses.

Records of the daily minimum temperature (degrees Celsius), the daily maximum temperature (degrees Celsius), and the daily rainfall (millimeters) were provided by Météo France for the meteorological station of Calvi in Corsica. This weather station is situated at a maximum of 20 km from each of the study plots, and therefore expected to provide reasonably accurate information on the spatiotemporal variation in climatic factors expressed at a wider spatial scale (see also Grosbois et al. 2006; own observations). We averaged the daily minimum and maximum ambient temperature to obtain a measure of the daily average ambient temperature. Subsequently, we calculated for each nest during the 2 weeks following the calculated hatching date the average daily ambient temperature and the cumulative amount of rainfall. This period covers the weather during nestling growth. This implies that for nests with unhatched eggs these weather factors could not be calculated.

We classified the nests into nests with at least one fledging and nests with no fledglings. For the nests with no fledglings, two types of breeding failure were defined following Lambrechts et al. (2016b): predated nests when eggs or nestlings suddenly disappeared and/or when clear signs of predation were noticed, and deserted nests when unhatched clutches or dead broods were found (Tables 1, 2).

To investigate the factors that influenced our measures of breeding success in nests from first clutches with at least one fledgling, we applied the mixed procedure (type 3 tests of fixed effects; SAS 9.4). We considered the number of hatchlings, the number of fledglings or the average full-grown nestling mass (13–16 days post-hatch) as the

Table 1 The number of first breeding attempts and the number of nest measures per breeding season, also indicating the percentage of predated nests, the percentage of deserted nests, the average (\pm SD) cumulative amount of rain during the 2 weeks following the calculated hatching date, and the average (\pm SD) of the average daily ambient temperature (T) during the 2 weeks following the calculated hatching date

Year	Nests	Deserted (%)	Predated (%)	Nest measures	Rain	Ambient T
1998	6	33.3	0	7	3.8 \pm 2.6	18.2 \pm 1.1
1999	4	0	100	7	7.5 \pm 2.3	18.7 \pm 0.4
2000	28	14.4	7.1	35	8.8 \pm 3.7	17.8 \pm 1.1
2001	69	8.7	8.7	104	14.5 \pm 6.1	15.9 \pm 2.0
2002	56	19.6	10.7	60	22.8 \pm 13.5	16.9 \pm 1.1
2003	86	10.5	5.8	90	0.9 \pm 0.5	18.8 \pm 0.5
2004	106	5.7	1.9	123	30.6 \pm 30.2	15.4 \pm 1.1
2005	29	10.3	3.4	45	10.2 \pm 7.3	17.9 \pm 0.9
2006	32	25	3.1	38	3.9 \pm 2.6	17.0 \pm 1.2
2007	96	12.5	13.5	121	29.5 \pm 12.9	17.1 \pm 0.9
2008	17	29.4	35.2	71	35.1 \pm 42.7	16.9 \pm 1.0
2009	34	2.9	5.9	38	11.4 \pm 24.8	17.7 \pm 1.2
2010	94	8.5	13.8	112	26.8 \pm 7.2	16.1 \pm 0.4
2011	87	2.3	9.2	110	3.9 \pm 6.8	16.7 \pm 0.7
2012	93	17.2	6.4	93	62.2 \pm 22.5	16.8 \pm 0.2
2013	33	6.1	3.0	42	10.3 \pm 8.3	17.5 \pm 0.4
2014	75	9.3	6.7	144	10.4 \pm 6.3	16.8 \pm 0.8

Table 2 The mixed procedure (type 3 tests of fixed effects) using the number of hatchlings, the number of fledglings or the average full-grown nestling mass (13–16-days post-hatch) as dependent variables, and the height of the external nest wall (in cm), the oak habitat (*Quercus humilis* versus *Quercus ilex*), the cumulative amount of rain during the nestling stage (in mm), the average daily ambient temperature during the nestling stage (in °C), the reproductive stage when the thickness of the nest was measured (before versus during versus after egg laying), the date of the first laid egg (*First-egg date*; Julian days), the size of the incubated clutch and the female age (yearling versus older) as fixed effects

	Number of hatchlings	Number of fledglings	Nestling body mass
Height of the external nest wall	$F = 1.41$ $df = 1, 99$ $P = 0.238$	$F = 4.52$ $df = 1, 99$ $P = 0.036$	$F = 0.01$ $df = 1, 94$ $P = 0.908$
Oak habitat	$F = 0.24$ $df = 1, 99$ $P = 0.626$	$F = 2.77$ $df = 1, 99$ $P = 0.099$	$F = 4.96$ $df = 1, 94$ $P = 0.028$
Rain	$F = 0.71$ $df = 1, 99$ $P = 0.40$	$F = 0.40$ $df = 1, 99$ $P = 0.53$	$F = 3.43$ $df = 1, 94$ $P = 0.067$
Ambient T	$F = 0.01$ $df = 1, 99$ $P = 0.944$	$F = 0.39$ $df = 1, 99$ $P = 0.536$	$F = 2.06$ $df = 1, 94$ $P = 0.155$
Stage	$F = 0.00$ $df = 2, 99$ $P = 0.996$	$F = 0.32$ $df = 2, 99$ $P = 0.729$	$F = 0.74$ $df = 2, 94$ $P = 0.481$
First-egg date	$F = 0.00$ $df = 1, 99$ $P = 0.96$	$F = 3.55$ $df = 1, 99$ $P = 0.062$	$F = 46.85$ $df = 1, 94$ $P < 0.0001$
Clutch size	$F = 1478.6$ $df = 1, 99$ $P < 0.0001$	$F = 409.6$ $df = 1, 99$ $P < 0.0001$	$F = 20.48$ $df = 1, 94$ $P < 0.0001$
Female age	$F = 5.83$ $df = 1, 99$ $P = 0.018$	$F = 6.70$ $df = 1, 99$ $P = 0.011$	$F = 0.00$ $df = 1, 94$ $P = 0.969$

Box number (220 different boxes), the year of study (1998–2014, except 1999), the study site (11 plots) and the ring number (488 different identified females) were considered random factors (see “Methods” for details). This analysis excluded data from deserted or predated nests

dependent variables, and the height of the external nest wall (in centimeters), the oak habitat (deciduous versus evergreen), the cumulative amount of rain during the 2 weeks following the hatching date, the average daily ambient temperature during the 2 weeks following the hatching date, the reproductive stage when the nest wall was measured (before versus during versus after egg laying), the first-egg date (in Julian days), the size of the incubated clutch and female age (yearling versus older) as fixed effects. The box number (220 different box numbers), the year of study (1998–2014, except 1999), the study site (11 plots) and the ring number (488 different females) were considered as random factors. These statistical approaches were also used in other studies of nest size (e.g., Lambrechts et al. 2016a, b).

Results

We took 1240 nest measures from 945 different first breeding attempts monitored between 1998 and 2014 (Table 1). In this sample, heights of the external nest walls

varied between 2 and 12 cm, thus the nest volumes were between ca. 225 and 1350 cm³ when the height of the external nest wall was multiplied by the bottom surface of the internal nest chamber.

The deserted nest, the predated nests, and the nests with at least one fledgling had nearly the same nest size as reflected in the average vertical height of the external nest wall (deserted 6.3 ± 1.9 cm, range 2–12, $n = 91$ versus predated 6.4 ± 1.8 cm, 2.5–12, $n = 113$ versus at least one fledgling 6.4 ± 0.7 cm, 2–12, $n = 847$).

Nest size, as reflected in the height of the external nest wall, was positively associated with the number of fledglings ($p = 0.036$; Table 2). However, the size of the nest was not related to the number of hatchlings or the average body mass of the nestlings in a brood ($p > 20$).

As expected, other biotic or abiotic factors were also associated with aspects of breeding success. For instance, females with larger clutches had more hatchlings ($p < 0.0001$) or more fledglings ($p < 0.0001$) after controlling for nest size or environmental factors. In addition, nestlings were heavier in breeding attempts with smaller clutches or in breeding attempts that

occurred earlier in the season (both $p < 0.0001$). Older females had more hatchlings ($p = 0.018$) and more fledglings ($p = 0.011$) than yearling females. Nestlings were heavier in deciduous oak patches than in evergreen ones ($p = 0.02$; Table 2).

Discussion

In our analyses that controlled for nest predation or nest desertion, we found that the breeding success as reflected in brood size or nestling body mass was more closely associated with female characteristics (nest size, clutch size, first-egg date or female age) and to some extent with environmental factors (oak habitat type, but not weather during the nestling stage). We are not aware of any other long-term field study of the size of cavity nests in relation to breeding success that simultaneously took all these biotic and abiotic factors into account. Sample sizes were also substantially larger than those used in previous studies of cavity nests.

The females with the larger nests had more fledglings after controlling for other aspects of female quality influencing breeding success. In addition, the older, and thus more experienced, females or those with larger clutches had more fledglings. All this suggests that one or more unidentified aspect(s) of female quality, such as aspects of female health (e.g. Tomás et al. 2006; Doutrelant et al. 2012), might have been responsible for these associations. In the other published Blue Tit studies, the heavier or larger nests did not have a higher breeding success than the lighter or smaller nests (Tomás et al. 2006, 2013; Lambrechts et al. 2012). For instance, the experimental change of nest size and nest components (aromatic plants) in Spanish Blue Tits did not significantly impact laying date, clutch size, hatching date, hatching success and brood size on day 6 post-hatching or did not have detectable influences on breeding success (Tomás et al. 2013). In Blue Tits from mainland southern France, the size of the nest was not related to the number of hatchlings, the number of fledglings, hatching success, fledging success or nestling mass, after controlling for factors frequently investigated in box studies and known to influence breeding performance (Lambrechts et al. 2012, 2016b). All this suggests that the associations between the size of the nest and breeding success differ across geographic regions, perhaps because the costs that are associated with reproduction or the local environmental conditions that influence breeding performance are population specific. Perhaps the nest components, rather than total nest size per se, influence aspects of breeding performance, as reported in previous correlative studies (e.g., Alabrudzińska et al. 2003; Álvarez et al. 2013; Deeming and Pike 2015; Gładalski et al. 2016). For

instance, the amount of cup lining incorporated into nests is bound to influence the microclimate experienced by nestlings far more than moss in the bottom of the nest boxes because it is what the nestlings sit on and are in direct contact with. In addition, the links between female-built nest size and breeding success might be mediated by the behaviors of the non-building male parents. For example, one study has shown that when the Blue Tit nests were experimentally enlarged or reduced, male risk-taking behaviors were significantly lower at those nests reduced in size (Tomás et al. 2013). This could mean that a male's behavior may well mediate the link between the female's nest building behavior and the pair's level of reproductive success.

Future studies could focus on individual characteristics of the nest builders that were ignored in this empirical study. For instance, studies in other study areas explored effects of blood parasite infestation levels (e.g., Tomás et al. 2006), plumage parasite loads (e.g., Mainwaring et al. 2008), plumage colors (cf. Doutrelant et al. 2008), immune system responses (cf. Doutrelant et al. 2012) or blood-related metabolic measures (e.g., Moreno et al. 2008). Such studies could explore whether aspects of the female phenotype might be the common cause for positive associations between different aspects of breeding performance, including nest-building efforts and brood size. These studies could also be combined with experiments that alter nest size (e.g., Tomás et al. 2006) or change the cost of nest building, e.g., when females have to build a new or a larger nest (e.g., Doutrelant et al. 2008; Moreno et al. 2010; Lambrechts et al. 2016b). In addition, future studies could also further quantify or experimentally manipulate the microclimate or composition of the nest (e.g., Deeming et al. 2012; Mainwaring et al. 2012; Lambrechts et al. 2016a), for instance to examine if nest characteristics other than nest size might impact aspects of breeding success (e.g., Álvarez et al. 2013; Deeming and Pike 2015; Gładalski et al. 2016). These studies could also be combined with measurements of nest parasite loads given that *Protocalliphora* spp. are determinants of breeding success in our study system (e.g. Hurtrez-Boussès et al. 1999; Mennerat et al. 2008, 2009).

Acknowledgments We thank all the people that helped with the long-term maintenance of the study sites and in particular Philippe Perret and Anne Charmantier. Samuel Caro provided constructive comments on a previous version of the manuscript. This long-term study was financially supported by the Centre National de la Recherche Scientifique and the Observatoire de Recherche Méditerranéen de l'Environnement, and several national or international organizations in the past (European Commission, European META-BIRD project, French Agence Nationale de la Recherche). Communities and land owners in Corsica kindly gave permission for us to visit the different woodland areas for the study of Blue Tits.

References

- Alabrudzińska J, Kaliński A, Słomczyński R, Wawrzyniak J, Zieliński P, Bańbura J (2003) Effects of nest characteristics on breeding success of Great Tits *Parus major*. *Acta Ornithol* 38:151–154
- Álvarez E, Barba E (2008) Nest quality in relation to adult bird condition and its impact on reproduction in Great Tits *Parus major*. *Acta Ornithol* 43:3–9
- Álvarez E, Belda E, Verdejo J, Barba E (2013) Variation in Great Tit nest mass and composition and its breeding consequences: a comparative study in four Mediterranean habitats. *Avian Biol Res* 6:39–46
- Blondel J, Gosler A, Lebreton J-D, McCleery R (1990). Population biology of passerine birds. An integrated approach. NATO ASI series G. Ecological Sciences 24. Springer, Berlin
- Blondel J, Dias PC, Perret P, Maistre M, Lambrechts MM (1999) Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. *Science* 285:1399–1402
- Blondel J, Perret P, Dias PC, Lambrechts MM (2001) Is phenotypic variation of Blue Tits (*Parus caeruleus* L.) in Mediterranean mainland and insular landscapes adaptive? *Genet Sel Evol* 33:S121–S139
- Blondel J, Thomas DW, Charmantier A, Perret P, Bourgault P, Lambrechts MM (2006) A thirty-year study of phenotypic and genetic variation of Blue Tits in Mediterranean habitat mosaics. *Bioscience* 56:661–673
- Charmantier A, Doutrelant C, Dubuc-Messier G, Fargevielle A, Szulkin M (2016) Mediterranean Blue Tits as a case study of local adaptation. *Evol Appl* 9:135–152
- Dawkins R (1982) The extended phenotype. The gene as the unit of selection. Oxford University Press, Oxford
- Deeming DC, Pike TW (2015) Nest surface temperature predicts fledging success of Blue Tits *Cyanistes caeruleus* but not Great Tits *Parus major*. *Acta Ornithol* 50:247–251
- Deeming DC, Mainwaring MC, Hartley IR, Reynolds SJ (2012) Local temperature and not latitude determines the design of Blue Tit and Great Tit nests. *Avian Biol Res* 5:203–208
- Descamps S, Blondel J, Lambrechts MM, Hurtrez-Boussès S, Thomas F (2002) Asynchronous hatching in a Blue Tit population: a test of some predictions related to ectoparasites. *Can J Zool* 80:1480–1484
- Doutrelant C, Gregoire A, Grnac N, Gomez D, Lambrechts MM, Perret P (2008) Female colouration indicates female reproductive capacity in Blue Tits. *J Evol Biol* 21:226–233
- Doutrelant C, Gregoire A, Midamegbe A, Lambrechts M, Perret P (2012) Female plumage coloration is sensitive to the cost of reproduction. An experiment in Blue Tits. *J Anim Ecol* 81:87–96
- Gibb J (1950) The breeding biology of the Great and Blue Titmice. *Ibis* 92:507–539
- Gładalski M, Bańbura M, Kalińskic A, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Cyżewska I, Bańbura J (2016) Effects of nest characteristics on reproductive performance in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*. *Avian Biol Res* 9:37–43
- Grosbois V, Henry P-Y, Blondel J, Perret P, Lebreton J-D, Thomas DW, Lambrechts MM (2006) Climate impacts on Mediterranean Blue Tit survival: an investigation across seasons and spatial scales. *Glob Chang Biol* 12:2235–2249
- Hansell M (2000) Bird nests and construction behaviour. Cambridge University Press, Cambridge
- Hurtrez-Boussès S, de Garine-Wichatitsky M, Perret P, Blondel J, Renaud F (1999) Variations in prevalence and intensity of blow fly infestations in an insular Mediterranean population of Blue Tits. *Can J Zool* 77:337–341
- Laland KN, Sterelny K (2006) Perspective: seven reasons (not) to neglect niche construction. *Evolution* 60:1751–1762
- Lambrechts MM, Caro S, Charmantier A, Gross N, Galan M-J, Perret P, Cartan-Son M, Dias PC, Blondel J, Thomas DW (2004) Habitat quality as a predictor of spatial variation in Blue Tit reproductive performance: a multi-plot analysis in a heterogeneous landscape. *Oecologia* 141:555–561
- Lambrechts MM, Adriaensen F, Ardia DR, Artemyev AV, Atiénzar F, Bańbura J, Barba E, Bouvier J-C, Camprodon J, Cooper CB, Dawson RD, Eens M, Eeva T, Faivre B, Garamszegi LZ, Goodenough AE, Goslar AG, Grégoire A, Griffith SC, Gustafsson L, Scott Johnson L, Kania W, Keišs O, Llambias PE, Mainwaring MC, Mänd R, Massa B, Mazgajski TD, Møller AP, Moreno J, Naef-Daenzer B, Nilsson J-A, Norte AC, Orell M, Otter KA, Park CR, Perrins CM, Pinowski J, Porkert J, Potti J, Remeš V, Richner H, Rytönen S, Shiao M-T, Silverin B, Slagsvold T, Smith HG, Sorace A, Stenning MJ, Stewart I, Thompson CF, Török J, Tryjanowski P, van Noordwijk AJ, Winkler DW, Ziane N (2010) The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. *Acta Ornithol* 45:1–26
- Lambrechts MM, Aimé C, Midamegbe A, Galan M-J, Perret P, Grégoire A, Doutrelant C (2012) Nest size and breeding success in first and replacement clutches: an experimental study in Blue Tits *Cyanistes caeruleus*. *J Ornithol* 153:173–179
- Lambrechts MM, Demeyrier V, Fargevielle A, Giovannini P, Lucas A, Marrot P, Midamegbe A, Perret P, Charmantier A, Doutrelant C, Grégoire A (2014) Great Tits build shallower nests than Blue Tits. *Avian Biol Res* 7:251–254
- Lambrechts MM, Blondel J, Dubuc-Messier G, Marrot P, de Franceschi C, Perret P, Doutrelant C, Grégoire A, Charmantier A (2015) Great Tits build shallower nests than Blue Tits in an insular oak-dominated habitat mosaic. *Avian Biol Res* 8:117–121
- Lambrechts MM, Blondel J, Bernard C, Caro SP, Charmantier A, Demeyrier V, Doutrelant C, Dubuc-Messier G, Fargevielle A, de Franceschi C, Giovannini P, Grégoire A, Hurtrez-Boussès S, Lucas A, Mainwaring MC, Marrot P, Mennerat A, Perret S, Perret P (2016a) Exploring biotic and abiotic determinants of nest size in Mediterranean Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*). *Ethology* 22:492–501
- Lambrechts MM, Marrot P, Fargevielle A, Giovannini P, Lucas A, Demeyrier V, Midamegbe A, Perret P, Grégoire A, Charmantier A, Doutrelant C (2016b) Nest size is not closely related to breeding success in Blue Tits: a long-term nest-box study in a Mediterranean oak habitat. *Auk* 133:198–204
- Lima SL (2009) Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. *Biol Rev* 84:485–513
- Lombardo MP (1994) Nest architecture and reproductive performance in Tree Swallows (*Tachycineta bicolor*). *Auk* 111:814–824
- Mainwaring MC (2015) The use of man-made structures as nesting sites by birds: a review of the costs and benefits. *J Nat Conserv* 25:17–22
- Mainwaring MC, Benskin C, McW H, Hartley IR (2008) The weight of female-built nests correlates with female but not male quality in the Blue Tit *Cyanistes caeruleus*. *Acta Ornithol* 43:43–48
- Mainwaring MC, Hartley IR, Bearhop S, Brulez K, du Feu CR, Murphy G, Plummer KE, Webber SL, Reynolds SJ, Deeming DC (2012) Latitudinal variation in Blue Tit and Great Tit nest characteristics indicates environmental adjustment. *J Biogeogr* 39:1669–1677
- Mainwaring MC, Hartley IR, Lambrechts MM, Deeming DC (2014) The design and function of birds' nests. *Ecol Evol* 20:3909–3928

- Mennerat A, Perret P, Caro SP, Heeb P, Lambrechts MM (2008) Aromatic plants in Blue Tit *Cyanistes caeruleus* nests. No negative effect on blood-sucking *Protocalliphora* blow fly larvae. *J Avian Biol* 39:127–132
- Mennerat A, Mirleau P, Blondel J, Perret P, Lambrechts MM, Heeb P (2009) Aromatic plants in nests of the Blue Tit *Cyanistes caeruleus* protect chicks from bacteria. *Oecologia* 161:849–855
- Møller AP, Adriaansen F, Artemyev AV, Bañbura J, Barba E, Biard C, Blondel J, Bouslama Z, Bouvier J-C, Camprodon J, Cecere F, Chaine A, Charmantier A, Charter M, Chicoñ M, Cusimano C, Czeszczewik D, da Silva LP, Doligez B, Doutrelant C, Dubiec A, Eens M, Eeva T, Faivre B, Ferns PN, Forsman JT, García-del-Rey E, Goldshtein A, Goodenough AE, Goslar AG, Gózdź I, Grégoire A, Gustafsson L, Hartley IR, Heeb P, Hinsley SA, Isenmann P, Jacob S, Järvinen A, Juškaitis R, Korpimäki E, Krams I, Laaksonen T, Leclercq B, Lehikoinen E, Loukola O, Lundberg A, Mainwaring MC, Mänd R, Massa B, Mazgajski TD, Merino S, Mitrus C, Mönkkönen M, Morales Fernaz J, Moreno J, Morin X, Nager RG, Nilsson J-A, Nilsson SG, Norte AC, Ojanen M, Orell M, Perret P, Perrins CM, Pimentel CS, Pinxten R, Priedniece I, Quidoz M-C, Remeš V, Richner H, Robles Díez H, Russell A, Rytönen S, Senar JC, Seppänen JT, Slagsvold T, Solonen T, Sorace A, Stenning MJ, Török J, Tryjanowski P, van Noordwijk AJ, von Numers M, Walankiewicz W, Lambrechts MM (2014a) Clutch-size variation in Western Palearctic secondary hole-nesting passerine birds in relation to nest box design. *Methods Ecol Evol* 5:353–362
- Møller AP, Adriaansen F, Artemyev AV, Bañbura J, Barba E, Biard C, Blondel J, Bouslama Z, Bouvier J-C, Camprodon J, Cecere F, Chaine A, Charmantier A, Charter M, Chicoñ M, Cusimano C, Czeszczewik D, da Silva LP, Demeyrier V, Doligez B, Doutrelant C, Dubiec A, Eens M, Eeva T, Faivre B, Ferns PN, Forsman JT, García-del-Rey E, Goldshtein A, Goodenough AE, Goslar AG, Gózdź I, Grégoire A, Gustafsson L, Hartley IR, Heeb P, Hinsley SA, Isenmann P, Jacob S, Järvinen A, Juškaitis R, Korpimäki E, Krams I, Laaksonen T, Leclercq B, Lehikoinen E, Loukola O, Lundberg A, Mainwaring MC, Mänd R, Massa B, Mazgajski TD, Merino S, Mitrus C, Mönkkönen M, Morales Fernaz J, Morin X, Nager RG, Nilsson J-A, Nilsson SG, Norte AC, Ojanen M, Orell M, Perret P, Perrins CM, Pimentel CS, Pinxten R, Priedniece I, Quidoz M-C, Remeš V, Richner H, Robles Díez H, Russell A, Rytönen S, Senar JC, Seppänen JT, Slagsvold T, Solonen T, Sorace A, Stenning MJ, Török J, Tryjanowski P, van Noordwijk AJ, von Numers M, Walankiewicz W, Lambrechts MM (2014b) Variation in nest size in relation to clutch size in birds. *Ecol Evol* 4:3583–3595
- Moreno J (2012) Avian nests and nest-building as signals. *Avian Biol Res* 5:238–251
- Moreno J, Martínez J, Corral C, Lobato E, Merino S, Morales J, Martínez-de la Puente J, Tomás G (2008) Nest construction rate and stress in female pied flycatchers *Ficedula hypoleuca*. *Acta Ornithol* 43:57–64
- Moreno J, Lobato E, Gonzáles-Braojos S, Ruiz-de Castañeda R (2010) Nest construction costs affect nestling growth: a field experiment in a cavity-nesting passerine. *Acta Ornithol* 45:139–145
- Nager RG, van Noordwijk AJ (1992) Energetic limitation in the egg laying period of Great Tits. *Proc R Soc Lond B* 249:259–263
- Neub M (1979) Brutbiologische Konsequenzen des asynchronen Schlüpfens bei Kohlmeise (*Parus major*) und Blaumeise (*Parus caeruleus*). *J Orn* 120:196–214
- Newton I (1994) The role of nest-sites in limiting the numbers of hole-nesting birds: a review. *Biol Cons* 70:265–276
- Nice MM (1957) Nesting success in altricial birds. *Auk* 74:305–321
- Perrins CM (1979) *British Tits*. Collins, London
- Przybylo R, Wiggins DA, Merilä J (2001) Breeding success in Blue Tits: good territories or good parents? *J Avian Biol* 32:214–218
- Rendell WB, Verbeek NAM (1996) Old nest material in nest boxes of tree swallows: effects on nest-site choice and nest building. *Auk* 113:319–328
- Schaedelin FC, Taborsky M (2009) Extended phenotypes as signals. *Biol Rev* 84:293–313
- Skowron C, Kern M (1980) The insulation in nests of selected North American songbirds. *Auk* 97:816–824
- Slagsvold T (1989a) Experiments on clutch size and nest size in passerine birds. *Oecologia* 80:297–302
- Slagsvold T (1989b) On the evolution of clutch size and nest size in passerine birds. *Oecologia* 79:300–305
- Tomás G, Merino S, Moreno J, Sanz JJ, Morales J, García-Fraile S (2006) Nest weight and female health in the Blue Tit (*Cyanistes caeruleus*). *Auk* 123:1013–1021
- Tomás G, Merino S, Martínez-de la Puente J, Moreno J, Morales J, Rivero-de Aguilar J (2013) Nest size and aromatic plants in the nest as sexually selected female traits in Blue Tits. *Behav Ecol* 24:926–934
- Tremblay I, Thomas DW, Lambrechts MM, Blondel J, Perret P (2003) Variation in Blue Tit breeding performance across gradients in habitat richness. *Ecology* 84:3033–3043
- van Noordwijk AJ, De Jong G (1986) Acquisition and allocation of resources—their influence on variation in life-history tactics. *Am Nat* 128:137–142