



HAL
open science

Nest design in a changing world: Great tit *Parus major* nests from a Mediterranean city environment as a case study

Marcel M. Lambrechts, Anne Charmantier, Virginie Demeyrier, Annick Lucas, Samuel Perret, Matthieu Abouladzé, Michel Bonnet, Coline Canonne, Virginie Faucon, Stéphanie Grosset, et al.

► To cite this version:

Marcel M. Lambrechts, Anne Charmantier, Virginie Demeyrier, Annick Lucas, Samuel Perret, et al.. Nest design in a changing world: Great tit *Parus major* nests from a Mediterranean city environment as a case study. *Urban Ecosystems*, 2017, 20 (6), pp.1181-1190. 10.1007/s11252-017-0670-5 . hal-04258482

HAL Id: hal-04258482

<https://hal.science/hal-04258482v1>

Submitted on 31 Jan 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Published in final edited form as:

Urban Ecosyst. 2017 December ; 20(6): 1181–1190. doi:10.1007/s11252-017-0670-5.

Nest design in a changing world: great tit *Parus major* nests from a Mediterranean city environment as a case study

Marcel M. Lambrechts^{1,*}, Anne Charmantier¹, Virginie Demeyrier¹, Annick Lucas¹, Samuel Perret¹, Matthieu Abouladzé³, Michel Bonnet², Coline Canonne¹, Virginie Faucon³, Stéphanie Grosset², Gaëlle le Prado³, Frédéric Lidon³, Thierry Noell⁴, Pascal Pagano², Vincent Perret³, Stéphane Pouplard², Rémy Spitaliéry², Cyril Bernard¹, Philippe Perret¹, Jacques Blondel¹, and Arnaud Grégoire^{1,4}

¹Centre d'Ecologie Fonctionnelle et Evolutive CEFE, UMR 5175, Campus CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, 1919 route de Mende, 34293 Montpellier Cedex 5, France

²Ville de Montpellier, direction paysage et nature, 34000 Montpellier, France

³Parc de Lunaret, zoo de Montpellier, 50 avenue Agropolis, 34090 Montpellier, France

⁴Université de Montpellier, Univerlacity, place Eugène Bataillon 34095 Montpellier cedex 5, France

Abstract

Investigations of urbanization effects on birds have focused mainly on breeding traits expressed after the nest-building stage (e.g. first-egg date, clutch size, breeding success, and offspring characteristics). Urban studies largely ignored how and why the aspects of nest building might be associated with the degree of urbanization. As urban environments are expected to present novel environmental changes relative to rural environments, it is important to evaluate how nest-building behavior is impacted by vegetation modifications associated with urbanization. To examine nest design in a Mediterranean city environment, we allowed urban great tits (*Parus major*) to breed in nest boxes in areas that differed in local vegetation cover. We found that different measures of nest size or mass were not associated with vegetation cover. In particular, nests located adjacent to streets with lower vegetation cover were not smaller or lighter than nests in parks with higher vegetation cover. Nests adjacent to streets contained more pine needles than nests in parks. In addition, in nests adjacent to streets, nests from boxes attached to pine trees contained more pine needles than nests from boxes attached to other trees. We suggest that urban-related alterations in vegetation cover do not directly impose physical limits on nest size in species that are opportunistic in the selection of nesting material. However, nest composition as reflected in the use of pine needles was clearly affected by habitat type and the planted tree species present, which implies that rapid habitat change impacts nest composition. We do not exclude that urbanization might impact other aspects of nest building behaviour not covered in our study (e.g. costs of searching for nest material), and that the strengths of the associations between urbanization and nest structures might differ among study populations or species.

*Corresponding author: marcel.lambrechts@cefe.cnrs.fr.

Keywords

Nest design; nest-box design; urban habitat; *Parus major*; Great Tit

Introduction

Urbanization is currently a fast developing process worldwide involving more than 50% of the human population (Marzluff 2001). Urban expansion induces degradation of the natural environments and will especially favour species that are able to adapt to cities (e.g. Clergeau et al. 2006; Adams and Lindsey 2011). Recent avian studies of life-history consequences of urbanization focused on breeding traits expressed after the nest-building stage (e.g. first-egg date, clutch size, breeding success, and offspring characteristics; Chamberlain et al. 2009; Marzluff 2017). Urban populations generally lay smaller clutches and have lower breeding success than rural populations perhaps because urban populations face higher resource-associated constraints (e.g. Hůrak 1993; Chamberlain et al. 2009; Møller et al. 2014a,b; Bailly et al. 2016; Demeyrier et al. 2016). However, these studies ignored how and why nest building could be influenced by the degree of urbanization within cities (but see Greenwood 1998; Tomialojc 1992 cited in Hansell 2000; Wang et al. 2008; Suárez-Rodríguez et al. 2013; Møller et al. 2014a,b; Gl dalski et al. 2016; Reynolds et al. 2016). Since nest building is aimed at improving the local environmental conditions of breeding (Hansell 2000; Laland and Sterelny 2006; Deeming 2016), it should proximately depend on the characteristics and the dynamics of the external environment that provides the material required (e.g., Hansell 2000; Schaedelin and Taborsky 2009; Mainwaring et al. 2014; Deeming and Mainwaring 2015). If this were true, human-induced changes in local plant communities should also be directly associated with changes in aspects of avian nest design. Nest characteristics not reported in more natural environments are therefore expected to be found in urbanized environments where local vegetation is removed and replaced by human constructions or new plant communities. In addition, the lower breeding success of city populations might perhaps be caused by the fact that urban breeders build nests of lower quality and that nest quality directly influences breeding success or that aspects associated with nest quality (e.g. nest size) reflects physical abilities to breed (e.g. Mainwaring et al. 2014; Lambrechts et al. 2016b).

The great tit (*Parus major*) allows the quantitative study of changes in nest design in response to environmental change because of at least two reasons. First, great tits can use up to 11 different types of nest material, mainly vegetation (Deeming & Mainwaring 2015). Moss and animal-based material (hair, fur) have been reported in nests of all study areas, and therefore considered to be preferred nest components in this species (e.g. Perrins 1979, Alabrudzi ska et al. 2003, Deeming and Mainwaring 2015). However, recent field studies showed that the characteristics of great tit nests differ between habitats that also differ in plant communities (e.g. Álvarez et al. 2013, Deeming and Mainwaring 2015, Gl dalski et al. 2016). Second, great tits build cavity nests inside standardized boxes erected in city areas with low vegetation cover (e.g. Hůrak 1993, Chamberlain et al. 2009, Møller et al. 2014a,b, Demeyrier et al. 2016). If rapid environmental change would impact the characteristics of the nests, and accepting that the availability of the preferred nest material (e.g. bryophytes,

Mainwaring 2015) might be limited or absent in more urbanized areas, we expected to find an association between nest-size measures and the vegetation cover in city environments.

Here we present the results of a six-year study of associations between nest-size components and vegetation cover in an urban population of great tits (*Parus major*) from a Mediterranean city area dominated by pine trees (*Pinus* spp.). The birds were allowed to nest in different box types that differed in nest-chamber size. Because the largest box type exceeded the internal size of the box designs most often used in the existing long-term academic studies (Lambrechts et al. 2010), nest-builders were given opportunities to invest extensively more in the construction of the nest than in previous studies. When the availability of green space would impact the availability of nest material and/or the physical abilities of the nest-builders, we expected to find larger or heavier nests in parks with more vegetation cover than in streets with less vegetation cover. In addition, we present the results of a three-year study of nest composition in the same study population. Our study especially focused on pine needles as nest material because of several reasons. Pine needles can be easily separated from the other nest components, they belong to a well-defined taxonomic group (*Pinus*), sources of pine needles (the spatial position of trees) could be easily identified, and they were not indicated as nest material in former published studies of cavity nests (e.g. Table 4.1 in Deeming & Mainwaring 2015). We predicted to find more pine needles in nests adjacent to streets dominated by pine plantations compared to parks providing more green space. In additional analyses, other nest components (e.g. preferred nesting material, wood-based material, herb-based material) were also considered. Finally, our study took into account other biotic (e.g. female characteristics, clutch type) and abiotic factors (e.g. nest-chamber size) that might influence nest design.

Methods

Great tits are among the commonest bird species in European cities and also in the city of Montpellier, southern France (43°36'N 03°52'E) (Caula et al. 2008). To attract breeders from this secondary-cavity nesting bird, we placed nest boxes in 5 study sites in the city of Montpellier. In the different sites, boxes were erected adjacent to streets, i.e. at less than 10 m from a street border, and throughout parks (Demeyrier et al. 2016 for details).

Between 2011 and 2016, we measured great tit nests built in four box types. Three box types were made from layer larch (*Larix decidua*) that differed in the internal bottom area and nest chamber size (Small=6cm x 6cm, 36cm² versus Medium=11cm x 11cm, 121cm² versus Large= 14.5cm x 14.5cm, 210cm², internal depth under the entrance 16 cm) (Demeyrier et al. 2016). The layer larch box types did not differ in the other design characteristics and had average values of the box dimensions that were used to study *Paridae* in Europe (Lambrechts et al. 2010). The fourth box type were wood-concrete Schwegler B1 boxes (bottom area ca. 113cm², internal depth under the entrance ca.13.5 cm), a box type used in long-term studies (Lambrechts et al. 2010; Lambrechts et al. 2016a, b; Bueno-Enciso et al. 2016). The contents of the boxes were monitored with standardized protocols from the second half of March onwards till mid-July. These monitoring protocols have been applied for several decades in Mediterranean southern France (e.g., Blondel et al. 2006; Lambrechts et al. 2010; Demeyrier et al. 2016). The contents of the boxes were noted at least twice during each of

the reproductive stages (nest building, egg laying, incubation, nestlings) and used to identify the breeding species. The date on which the first egg in a clutch was laid and the size of the clutch could be determined from the weekly checks of the nest contents (Perrins and McCleery 1989; Blondel et al 2006; Demeeyrier et al. 2016).

Nest size

During six breeding seasons (2011-2016) we measured the vertical height of the external nest wall with a ruler after removal of the box front door, following measure B presented in Álvarez and Barba (2008), also defined as nest depth in Hansell (2000, measure 'a', p. 43) or nest thickness in Hurtrez-Boussès et al. (1999). The height of the external nest wall can be measured rapidly without removing the nest from the box (Lambrechts et al. 2012). This nest measure was multiplied by the internal surface of the bottom of the nest-chamber to obtain a measure of the volume of the nest used as a proxy of nest size (e.g. Hurtrez-Boussès et al. 1999; Lambrechts et al. 2016a, b). Because the nests become flatter with the progress of the breeding attempt (Slagsvold 1989; own observations), we measured the external height of the nest walls before the eggs hatched. We measured the height of the external nest wall during the week before the onset of egg-laying, during egg-laying and/or after egg-laying stopped prior to incubation (Lambrechts et al. 2012; 2016a, b). We also considered for each breeding attempt one nest measure per reproductive stage per nest-box (e.g. Lambrechts et al. 2014). We measured the nests from first and later breeding attempts. We assumed that the first breeding attempts were initiated no later than 30 days later after the date of the first egg found in that year (Nager and van Noordwijk 1995; Lambrechts et al. 2016a, b).

From 2013 onwards, parents were trapped, ringed, sexed and aged following basic protocols (Blondel et al. 2006). The parents were trapped with box traps inside the nest-chambers during the nestling stage. Ring numbers and plumage colours also allowed to determine the age (yearling versus older) of the female parent. The identity of the female parents was known for ca. 40% of the sample of nest measures available. The same female could be trapped more than once during a single breeding season (e.g. first versus later breeding attempt) or during different breeding seasons.

Nest mass and composition

During three consecutive years (2014-2016), great tit nests were collected after the breeding season, and kept for at least one month at summer room temperature in laboratory conditions for drying. In 2014, dried nests were taken apart and measured by three contributors (AL, SP, MML) and students to determine the mass of the dried nest components as described in Britt and Deeming (2011). For each nest we determined the total mass of the nests after they were fully taken apart. Our measures of nest mass excluded soil, dust, dried invertebrates, bird faeces, abandoned eggs or nestlings, or species-specific plumages from parents or nestlings. However, despite the extensive efforts to separate the different nest components following Britt and Deeming (2011), we noticed that the animal-based material (e.g. hair or fur) was often tightly mixed up with moss, more often when nests produced fledglings. Because moss and animal-based material have been reported in all great tit nests examined in Europe (e.g. Mainwaring et al. 2015, own observations), we defined both nest components

as preferred material and measured the total mass of the preferred material. In the year of 2014, all the nests were verified during one sampling period that lasted on average 1h10 per nest. In the years 2015 and 2016, nest components per nest were determined during four sampling periods. During a first sampling period, pine needles were separated from the other nest material. Pine needles could be easily identified based on shape and length, also using as a reference the pine needles found on the ground or on pine trees within 5 m from the nest boxes. During a second sampling period involving the same nests, wood-based material (e.g. brown-coloured stiff sticks and roots) was selected and separated from the other nest components. During a third sampling period involving the same nests, herb-based material (e.g. sticks from light coloured dried grass or straw) was selected and separated from the other nest components. We therefore also obtained a sample of moss and animal-based material that did not contain the other nest components. During a fourth sampling period, the former samples from each nest were re-verified and classified into the following nest-component classes: pine needles, wood-based material, herb-based material, and preferred material (moss mixed up with animal-based material). Pine needles and wood-based material (e.g. sticks, stems, roots) were structurally considered as stiff and hard whereas moss mixed up with animal-based material (e.g. hair, fur) were structurally considered as soft and flexible. Herb-based material could either be considered as soft and flexible (e.g. grass) or hard and stiff (e.g. straw sticks). Dry mass (accuracy 0.1g) of these nest component classes were taken for each collected nest.

Cavity nests might rapidly decompose in humid natural holes (Hebda and Mitrus 2011). We measured the dry mass of 50 urban nests stored at room temperature twice with an interval of more than one year (23-24 June 2015 *versus* 20 July 2016). The correlation between the two measures was very high ($r=0.994$, $p<0.0001$), which implies that nests stored in dry conditions at ambient temperature did not decompose over a period of at least one year, and that measures of nest mass could be replicated.

Environmental measurements

The four box types used in this study were attached to the trunks of trees at a similar average box-entrance height above the ground (Mean \pm SD: 299 ± 36 cm, Range: 210 - 390cm). The orientations of the entrance holes were determined using a Konustar Compass following Goodenough et al. (2008) and were similar for the different box types (mainly 91-180°). The distance between neighbouring boxes was ca. 100 m to limit intraspecific competition (Remacha and Delgado 2009). The different box types were spatially fully intermingled in the sense that they were erected both in streets and parks in the different study areas in Montpellier (Demeyrier et al. 2016). As described in Demeyrier et al. (2016), we measured the surface covered by vegetation within a 50m radius circle around each box using two dimensional aerial photos taken and provided by the city of Montpellier. For the 50m radius circle around each box, we estimated three vegetation covers: i) the surface of oak canopy cover combining broad-leaved and evergreen oak species (e.g. *Quercus pubescens*, *Q. ilex*), ii) the surface of tree canopy cover and iii) the surface of global vegetation cover (including lawn). Because the aerial photos did not allow identifying tree species, the presence of oak canopy near the nest-boxes had to be verified in the field and indicated on the aerial pictures to estimate their surface area. These variables were taken because great tits use tree holes for

nesting, they are often found in habitat dominated by oak (*Quercus* sp. that host the great tits' preferred insect prey, caterpillars), they are found foraging in tree species other than oak, and they also search for nesting material or food on the ground (e.g. see Perrins 1979; Demeyrier et al. 2016). The surfaces covered by vegetation, tree canopy or oak canopy within the 50m radius around an individual nest box were on average larger in areas that we previously defined as parks (data from 81 different boxes) than in areas that we previously defined as streets (<http://www.merriam-webster.com/dictionary/street>, data from 30 different boxes) (Table 1). A simple two-class classification of habitat type (park versus street) could thus also be used as a simple proxy of availability of green space and trees close to the nesting sites, assumed to reflect environments where nesting material can be found more easily.

The boxes monitored in this study were attached to the trunks of different tree species, mainly Aleppo pine *Pinus halepensis* in parks and stone pine *Pinus pinea* in street habitats. Other tree species to which boxes were attached were *Quercus ilex*, *Platanus hybrida*, *Celtis australis*, *Robinia pseudoacacia*, *Olea europaea* and *Cupressus sempervirens* (see also Caula et al. 2008; 2009 for dominant tree species in Montpellier). Park habitats with boxes were generally characterized by the presence of *P. halepensis* intermingled with *Q. ilex*. Streets with boxes were decorated with plantations of a single tree species, most often *P. pinea*. Park and street environments therefore not only differed in vegetation cover, but also in the presence of the dominant tree species near the boxes that contained a great tit nest.

Statistical analyses

In a first analysis, we considered the whole data set available for the study period 2011-2016 (Table 2). We applied a mixed model procedure (Type 3 tests of fixed effects; SAS 9.4, data not transformed) using nest volume (cm³) or vertical height of the external nest wall (cm) as dependent variables (Normal error). The interactions between box type, clutch type and habitat type, box type (four box designs differing in chamber size), clutch type (first versus later breeding attempts), habitat type (park versus street), reproductive stage (nest measured before egg-laying versus during the period of egg-laying versus after the onset of incubation), the first egg date and the size of the incubated clutch were considered as fixed effects. Study site (five study sites), box identity (134 different boxes), and year (2011-2016) were added as random factors.

In a second analysis, we only took into account the nest measures from the identified females obtained during the study period 2013-2016. We again applied a mixed model procedure using nest volume (cm³) or vertical height of the external nest wall (cm) as dependent variables (Normal error), and the interactions between box type, clutch type and habitat type (cf. first analysis), box type, clutch type, habitat type, reproductive stage, female age (yearling versus older), the first egg date and the size of the incubated clutch as fixed effects. Box identity (112 different boxes), year (2013-2016), and female identity (170 different ring numbers) were added as random factors.

In a third analysis considering the nest mass and the mass of its components (preferred material, needles, wood-based, herb-based, Table 5), we again used mixed models (proc mixed Type 3; SAS 9.4) to investigate the interactions and fixed main effects involving box

type (four box types), clutch type (first clutch versus other clutch), habitat type (park versus street), the first egg date and the size of the incubated clutch. Study site (5 different sites), box identity (75 different boxes), and year (2014-2016) and were considered as random factors. Components of each collected nest were measured only once after the breeding season, so that reproductive stage was not considered in these analyses.

Because the statistical results were similar when the factor habitat type (nests adjacent to streets *versus* nests in parks) was replaced by the factor vegetation cover surrounding the occupied boxes (from a vegetation cover surface of 0.042 representing few vegetation within a 50m radius circle around an occupied box to a vegetation cover surface of 0.999 representing much vegetation within a 50m radius circle around an occupied box), we only present the analyses involving habitat type.

Results

Nest size and mass

Our statistical analyses considered a total 1087 measurements of nest volume and nest height taken during six breeding seasons, of which 511 measurements were taken from nests from identified females (Table 2). We found that the nests adjacent to streets and the nests in parks did not significantly differ in the average nest volume and the average height of the external nest wall (Table 3, 4). Based on the dry mass of 146 great tit nests sampled during three breeding seasons (Table 5), we also found that the nests adjacent to streets and the nests in parks did not significantly differ in the average nest mass (Table 6). Thus, the birds from the two habitat types built nests of similar size and mass.

The nests were more voluminous in the boxes with the larger floor areas when considering all the breeding attempts or only those from identified females (Table 3, 4). In addition, five identified females had substantially smaller nest volumes when they occupied a layer larch box with a floor area of 121 cm² than when they occupied a layer larch box with a floor area of 210 cm² (Mean±SD 738±138 versus 1365±348 respectively). Two other identified females had substantially smaller nest volumes when they nested in a Schwegler box with a floor area of ca. 110 cm² than when they nested in a layer larch box with a floor area of 210 cm² (621±80 versus 1627±74 respectively). Thus, the strong association between nest volume and box type observed across females was also observed within females. However, the height of the external nest wall was not significantly associated with box type (Table 3, 4). In addition, there was a significant association between nest mass and box type (Table 6). The nests were heavier in the larger box types.

As concerns the female characteristics, nests with earlier first-egg dates had higher external nest walls or were more voluminous than nests with later first-egg dates (Table 3, 4). Nest size was not associated with female age and clutch size (Table 3, 4). The nests were on average more voluminous and the external nest walls on average higher in the first breeding attempts than in later breeding attempts. This was especially the case for the nests that were built in the boxes with the larger floor areas (Significant Box type * Clutch type interactions in Table 3, 4). In addition, the nests from the first breeding attempts were heavier than the nests from the later breeding attempts (Table 6).

Nest composition

The boxes in parks did not contain more preferred material (moss mixed up with animal-based material), wood-based material or herb-based material than the boxes adjacent to streets. However, the boxes adjacent to streets contained more pine needles than in the boxes in parks (Table 6). When we only focused on the boxes adjacent to streets, the pine needle mass was significantly higher in the boxes attached to a pine tree species ($7.7 \pm \text{SD } 10.4$, $0 - 42.3$, $n=31$) than in the boxes attached to another tree species ($0.4 \pm \text{SD } 1.6$, $0 - 8.1$, $n=24$) (Pine: $F_{1,23}=8.02$, $p=0.0094$; Clutch type $F_{1,23}=0.26$, $p=0.62$), including study site (data from two study sites), box identity (data from 29 different boxes) and year (2014-2016) as random factors.

There was a significant association between box type and the mass of most of the nest components considered (Table 6). Thus, the larger box types contained more preferred material, more wood-based material and more herb-based material than the smaller box types. However, nest composition was not or weakly associated with clutch type or the female characteristics (Table 6).

Discussion

Nest size and mass

We expected smaller and lighter nests in the boxes adjacent to streets providing less vegetation-associated resources (e.g. food, nesting material) than in the boxes situated in parks. However, this expectation was not supported by our six-year monitoring of this urban study population because the volume and the mass of the nests were not associated with habitat type. We therefore conclude that the level of urbanization within our study population did not have a noticeable impact on the total size or mass of the nest. This suggests that even in the most urbanized areas nest builders did not face a shortage in the availability of nest material used to fill up the nest-chamber. Our findings are consistent with results from Gładki et al. (2016) reporting that Polish tits from urban park and rural forest did not differ in the average size or mass of their nests. However, we cannot rule out that the searching-associated or foraging-associated costs of nest-building (e.g. Mainwaring and Hartley 2013) might be higher in environments that provide less nest material. For instance, it might be possible that the birds that nested near streets looked for nest material at longer distances from the nest cavity than the birds that nested in parks, therefore possibly increasing the cost of nest building in areas with less vegetation cover. Foraging distances could be investigated in future studies either via radio-tracking techniques or use of unusual nest material (e.g. coloured wool) provided at different distances from the nest cavities (cf. Surgey et al. 2012).

We also found that great tits could double the volume of their nests when they bred in boxes almost twice the average volume of the nest-chambers most often used in long-term academic studies throughout Europe (Lambrechts et al. 2010), whatever the urban environments of nest building. This seems to correspond to a plastic response of females rather than a non-random distribution of females differing in their building capacity, also supported by the fact that individual females that bred during more than one breeding season

adjusted nest volume to box size across different breeding attempts. In addition, we noticed that the nests that were built in the smallest box type could be about 10 times smaller than the nests that were built in the largest box type. Larger box types contained heavier nests and more preferred material. Thus, nest-chamber design clearly imposed physical constraints on nest construction behaviour. Positive associations between aspects of nest size and artificial cavity-size were also reported in rural study populations (Slagsvold and Amundsen 1992; Mazgajski and Rykowska 2008; Kalski et al. 2014; Bueno-Enciso et al. 2016).

Nest mass and composition

Reynolds et al. (2016) reported few statistically significant effects of the urban gradient on nest composition in a one-year study of urban blue tits (*Cyanistes caeruleus*) in the UK. This finding is partly concordant with our results since the nests in the two habitat types did not significantly differ in the mass of the preferred nesting material, the mass of wood-based material and the mass of herb-based material. However, we found that the average mass of pine needles per nest was significantly higher in the boxes adjacent to streets than in the boxes situated in parks. Moreover, for nests adjacent to streets, the average mass of the pine needles was significantly higher when the boxes were attached to a pine tree species than when they were attached to another tree species. Because former published studies never reported pine needles as nesting material in great tits (see Introduction), and because our study area provided year-round large amounts of dried pine needles near the nesting sites (own observations), the simplest explanation is that pine needles will only be used when preferred nesting material (e.g. Deeming & Mainwaring 2015) is in shortage. This would also imply that the presence of pine needles in great tit nests can be considered as a simple and reliable indicator of local habitat change associated with the plantation of human-introduced vegetation. This phenomenon would never have been demonstrated if great tits would not have been opportunistic in the selection of nesting material.

Pine needles were especially observed in the boxes adjacent to streets with stone pine plantations, and more rarely in the parks dominated by a mixture of evergreen oaks and Aleppo pine. We noticed that some nests adjacent to streets contained large amount of pine needles and few amounts of moss. Mainwaring (2015) mentioned that vascular plants might out-compete moss in areas with enriched soil. This might be the case when street habitats would be found close to fertilized environments or environments where moss is chemically removed (e.g. gardens). In addition, street asphalt might become quite hot during the Mediterranean summers, perhaps also contributing to a decline of bryophytes in highly urbanized Mediterranean environments. However, we currently cannot exclude the possibility that the nest builders were more attracted to the needles of stone pine than those of Aleppo pine given that the needles from the two tree species differ in phenotypic characteristics (e.g. odour, needle shape), that might facilitate or complicate nest building. Choice experiments could test the latter hypothesis, for instance by providing in large quantities dried stone pine needles in park habitats dominated by Aleppo pine.

Finally, urban nests expressed variation in size and composition after controlling for the strong statistical effects of nest-box type or aspects associated with the timing of breeding (clutch type or first-egg date). The simplest explanation for this finding is that the nest-

building efforts might also result from individual-specific decisions associated with aspects of the female phenotype (e.g. Lambrechts et al. 2012; 2016a; Moreno 2012). For instance, females that are able to build larger nests are expected to be able to lay more eggs (Møller et al. 2014a,b; Lambrechts et al. 2016a,b). However, in our urban study population, nest size *per se* was not significantly associated with clutch size, perhaps because urban breeders and southern populations of great tits generally lay small clutches compared to rural breeders and northern populations, whatever the size of the nest chamber (e.g., Hõrak 1993; Chamberlain et al. 2009; Møller et al. 2014a,b; Lambrechts et al. 2016a; Demeyrier et al. 2016). Urban environments therefore might fully disassociate nest size from clutch size. In addition, we found as in former studies that nest size was not associated with female age (e.g. Lambrechts et al. 2016a,b). Thus, non-identified individual-specific factors might be associated with nest size in urban environments of which some have already been explored in non-urbanized environments or in laboratory conditions (e.g. Tomás et al. 2006; Møller et al. 2014a,b; Kalko et al. 2014; Lambrechts et al. 2016a,b; Deeming and Mainwaring 2015). In addition, future urban studies should explore in more detail the possible consequences of nest design for reproductive success (cf. Lambrechts et al. 2016b). Additional suggestions for future research on nests from urban areas have recently been outlined in Reynolds et al. (2016).

Acknowledgements

We would like to thank all the university students (Bachelor, Master) that helped with monitoring of nesting boxes. This work was supported by the French Agence Nationale de la Recherche (ANR-09-JCJC-0050-01, Claire Doutrelant), and the European Research Council (Starting grant ERC-2013-StG-337365-SHE to AC), the city of Montpellier, the University of Montpellier, OSU-OREME, and the Mediterranean Centre for Environment and Biodiversity (LabEx CeMEB).

References

- Adams, CE., Lindsey, KJ. Anthropogenic Ecosystems: The Influence of People on Urban Wildlife Populations. Urban Ecology. Oxford University Press; 2011. p. 116-128.
- Alabrudzi ska J, Kalko A, Słomczy ski R, Wawrzyniak J, Zieli ski P, Ba bura J. Effects of nest characteristics on breeding success of Great Tits *Parus major*. Acta Ornithol. 2003; 38:151–154.
- Álvarez E, Barba E. Nest quality in relation to adult bird condition and its impact on reproduction in great tits. Acta Ornithol. 2008; 43:3–9.
- Álvarez E, Belda EJ, Verdejo J, Barba E. Variation in great tit nest mass and composition and its breeding consequences: a comparative study in four Mediterranean habitats. Avian Biol Res. 2013; 6:39–46.
- Bailly J, Scheifler R, Berthe S, Clément-Demange V-A, Leblond M, Pasteur B, Faivre B. From eggs to fledging: negative impact of urban habitat on reproduction in two tit species. J Ornithol. 2016; 157:377–392.
- Britt J, Deeming DC. First-egg date and air temperature affect nest construction in Blue Tits *Cyanistes caeruleus*, but not in Great Tits *Parus major*. Bird Study. 2011; 58:78–89.
- Blondel J, Thomas DW, Charmantier A, Perret P, Bourgault P, Lambrechts MM. A thirty-year study of phenotypic and genetic variation of Blue Tits in Mediterranean habitat mosaics. BioScience. 2006; 56:661–673.
- Bueno-Enciso J, Ferrer ES, Barrientos R, Sanz JJ. Effect of nestbox type on the breeding performance of two secondary hole-nesting passerines. J Ornithol. 2016; 157:759–772.
- Caula S, Marty P, Martin J-L. Seasonal variation in species composition of an urban bird community in Mediterranean France. Landscape Urban Plan. 2008; 87:1–9.

- Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis*. 2009; 151:1–18.
- Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki M-J, Dinetti M. Avifauna homogenization by urbanization: Analysis at different European latitudes. *Biol Conserv*. 2006; 127:336–344.
- Deeming DC. How does the bird-nest incubation unit work? *Avian Biol Res*. 2016; 9:103–113.
- Deeming, DC., Mainwaring, MC. Functional properties of nests. Nests, eggs, and incubation: new ideas about avian reproduction. Deeming, DC., Reynolds, SJ., editors. Oxford University Press; Oxford: 2015. p. 29–49.
- Demeyrier V, Lambrechts MM, Perret P, Grégoire A. Experimental demonstration of an ecological trap for a wild bird in a man-transformed environment. *Anim Behav*. 2016; 118:181–190.
- Gładalski M, Bałbura M, Kaliński A, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Cyewska I, Bałbura J. Effects of nest characteristics on reproductive performance in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*. *Avian Biol Res*. 2016; 9:37–43.
- Goodenough AE, Hart AG, Elliot SL. Variation in offspring quality with cavity orientation in the great tit. *Ethol Ecol Evol*. 2008; 20:375–389.
- Greenwood JG. Aspects of the breeding biology of great tits *Parus major* L. and blue tits *Parus caeruleus* L. in Belfast. *Ir Nat J*. 1998; 26:99–103.
- Hansell, M. Bird Nests and Construction Behaviour. Cambridge University Press; Cambridge: 2000.
- Hebda G, Mitrus S. Decomposition rate of old nest material in tree holes. *Acta Ornithol*. 2011; 46:101–103.
- Hörak P. Low fledging success of urban great tits. *Ornis Fenn*. 1993; 70:168–172.
- Hurtrez-Boussès S, de Garine-Wichatitsky M, Perret P, Blondel J, Renaud F. Variations in prevalence and intensity of blow fly infestations in an insular Mediterranean population of blue tits. *Can J Zool*. 1999; 77:337–341.
- Kaliński A, Wawrzyniak J, Bałbura M, Skwarska J, Zieliński P, Gładalski M, Bałbura J. Does the threat of European Pine Marten (*Martes martes*) predation influence the height of nests built by Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*)? *Avian Biol Res*. 2014; 7:83–90.
- Laland KN, Sterelny K. Perspective: seven reasons (not) to neglect niche construction. *Evolution*. 2006; 60:1751–1762. [PubMed: 17089961]
- Lambrechts MM, Adriaenssens F, Ardia DR, Artemyev A, Atiénzar F, Bałbura J, Barba E, Bouvier J-C, Camprodon J, Cooper CB, Dawson RD, et al. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. *Acta Ornithol*. 2010; 45:1–26.
- Lambrechts MM, Aimé C, Midamegbe A, Galan M-J, Perret P, Grégoire A, Doutrelant C. Nest size and breeding success in first and replacement clutches: an experimental study in blue tits *Cyanistes caeruleus*. *J Ornithol*. 2012; 153:173–179.
- Lambrechts MM, Blondel J, Bernard C, Caro SP, Charmantier A, Demeyrier V, Doutrelant C, Fargevieille A, Dubuc-Messier G, de Franceschi C, Giovannini P, et al. Exploring biotic and abiotic determinants of nest size in Mediterranean great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). *Ethology*. 2016a; 22:492–501.
- Lambrechts MM, Demeyrier V, Fargevieille A, Giovannini P, Lucas A, Marrot P, Midamegbe A, Perret P, Charmantier A, Doutrelant C, Grégoire A. Great Tits build shallower nests than blue tits. *Avian Biology Research*. 2014; 7:251–254.
- Lambrechts MM, Marrot P, Fargevieille A, Giovannini P, Lucas A, Demeyrier V, Midamegbe A, Perret P, Grégoire A, Charmantier A, Doutrelant C. Nest size is not closely related to breeding success in blue tits: a long-term nest-box study in a Mediterranean oak habitat. *Auk*. 2016b; 133:198–204.
- Mainwaring, MC. Nest construction and incubation in a changing climate. Nests, eggs, and incubation: new ideas about avian reproduction. Deeming, DC., Reynolds, SJ., editors. Oxford University Press; Oxford: 2015. p. 65–74.
- Mainwaring MC, Hartley IR. The energetic costs of nest building in birds. *Avian Biol Res*. 2013; 6:12–17.
- Mainwaring MC, Hartley IR, Bearhop S, Brulez K, du Feu CR, Murphy G, Plummer KE, Webber SL, Reynolds SJ, Deeming DC. Latitudinal variation in Blue tit and Great tit nest characteristics indicates environmental adjustment. *J Biogeogr*. 2012; 39:1669–1677.

- Mainwaring MC, Hartley IR, Lambrechts MM, Deeming DC. The design and function of birds' nests. *Ecol Evol.* 2014; 20:3909–3928.
- Marzluff JM. Worldwide urbanization and its effects on Birds. *Avian Ecology and Conservation in an Urbanizing World.* Kluwer Academic Publishers; 2001. p. 19-47.
- Marzluff JM. A decadal review of urban ornithology and a prospectus for the future. *Ibis.* 2017; 159:1–13.
- Mazgajski TD, Rykowska Z. Dependence of nest mass on nest hole depth in the great tit *Parus major*. *Acta Ornithol.* 2008; 43:49–55.
- Møller AP, Adriaensen F, Artemyev AV, Batura J, Barba E, Biard C, Blondel J, Bouslama Z, Bouvier J-C, Camprodon J, Cecere F, et al. Variation in nest size in relation to clutch size in birds. *Ecol Evol.* 2014a; 4:3583–3595. [PubMed: 25478150]
- Møller AP, Adriaensen F, Artemyev AV, Batura J, Barba E, Biard C, Blondel J, Bouslama Z, Bouvier J-C, Camprodon J, Cecere F, et al. Clutch-size variation in Western Palaearctic secondary hole-nesting passerine birds in relation to nest box design. *Methods Ecol Evol.* 2014b; 5:353–362.
- Moreno J. Avian nests and nest-building as signals. *Avian Biol Res.* 2012; 5:238–251.
- Nager RG, van Noordwijk AJ. Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. *Am Nat.* 1995; 146:454–474.
- Perrins, CM. *British Tits.* Collins; London: 1979.
- Perrins CM, McCleery RH. Laying dates and clutch size in the great tit. *Wilson Bull.* 1989; 101:236–253.
- Remacha C, Delgado JA. Spatial nest-box selection of cavity-nesting bird species in response to proximity to recreational infrastructures. *Landscape and Urban Planning.* 2009; 93:46–53.
- Reynolds SJ, Davies CS, Elwell E, Tasker PJ, Williams A, Sadler JP, Hunt D. Does the urban gradient influence the composition and ectoparasite load of nests of an urban bird species? *Avian Biol Res.* 2016; 9:224–234.
- Schaedelin FC, Taborsky M. Extended phenotypes as signals. *Biol Rev.* 2009; 84:293–313. [PubMed: 19382933]
- Slagsvold T. Experiments on clutch size and nest size in passerine birds. *Oecologia.* 1989; 80:297–302. [PubMed: 28312056]
- Slagsvold T, Amundsen T. Do great tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size? *J Anim Ecol.* 1992; 61:249–258.
- Suárez-Rodríguez M, López-Rull I, Macías García C. Incorporation of cigarette butts into nests reduces nest ectoparasite load in urban birds: new ingredients for an old recipe? *Biol Lett.* 2012; 9:20120931.doi: 10.1098/rsbl.2012.0931 [PubMed: 23221874]
- Surgey J, du Feu CR, Deeming DC. Opportunistic use of a wool-like artificial material as lining of tit (*Paridae*) nests. *Condor.* 2012; 114:385–392.
- Tomás G, Merino S, Moreno J, Sanz JJ, Morales J, García-Fraile S. Nest weight and female health in the Blue Tit (*Cyanistes caeruleus*). *Auk.* 2006; 123:1013–1021.
- Wang Y, Chen S, Jiang P, Ding P. Black-billed Magpies (*Pica pica*) adjust nest characteristics to adapt to urbanization in Hangzhou, China. *Can J Zool.* 2008; 86:676–684.

Table 1

Differences in vegetation cover, tree canopy cover and oak canopy cover between street habitat (30 different boxes) and park habitat (81 different boxes) in the city of Montpellier (see methods for details).

Factor	Street n=30	Park n=81	
% vegetation cover	0.32 ± SD 0.21 0.04 – 0.75	0.79 ± SD 0.15 0.41 – 0.999	$F=168.1$ $p<0.0001$
% tree cover	0.17 ± SD 0.11 0.02 – 0.42	0.64 ± SD 0.22 0.14 – 0.95	$F=130.2$ $p<0.0001$
% oak cover	0.03 ± SD 0.12 0.0 – 0.60	0.31 ± SD 0.29 0.0 – 0.75	$F=25.9$ $p<0.0001$

Table 2

Average values (\pm SD) and range of the calculated nest volume (in cm^3), nest height (in cm) and the dry mass (in g) of nests in great tits from first and later breeding attempts. Nesters occupied different different habitat types (park versus street) and different box types. n equals the number of nest measurements.

Factor	Nest volume (cm^3) 2011-2016	Nest height (cm) 2011-2016	Nest mass (g) 2014-2016
Habitat type Park	1086 \pm SD 468 108 – 3360 n=800	6.7 \pm SD 1.7 2 – 16 n=800	21.2 \pm SD 9.9 3.3 – 49.9 n=91
Habitat type Street	1069 \pm SD 416 242 – 2520 n=330	6.4 \pm SD 1.5 2 – 12 n=330	26.6 \pm SD 11.9 7 – 63.6 n=55
Box type Layer larch Floor 36 cm^2	174 \pm SD 48 108 – 252 n=6	4.8 \pm SD 1.3 3 – 7 n=6	3.3 – n=1
Box type Schwegler Floor 113 cm^2	622 \pm SD 135 226 – 904 n=149	5.5 \pm SD 1.2 2 – 8 n=149	12.4 \pm SD 3.0 8 – 17.2 n=30
Box type Layer larch Floor 121 cm^2	816 \pm SD 199 242 – 1995 n=451	6.7 \pm SD 1.5 2 – 11 n=451	19.9 \pm SD 6.2 5.7 – 35.5 n=54
Box type Layer larch Floor 210 cm^2	1450 \pm SD 371 420 – 3360 n=524	6.9 \pm SD 1.8 2 – 16 n=524	31.9 \pm SD 10.1 11.7 – 63.6 n=61
Clutch type First	1126 \pm SD 458 108 – 3360 n=944	6.9 \pm SD 1.5 2 – 16 n=944	23.6 \pm SD 11.1 3.3 – 63.6 n=114
Clutch type Later	855 \pm SD 350 180 – 1785 n=186	5.2 \pm SD 1.5 2 – 9 n=186	22.0 \pm SD 10.5 7 – 46.1 n=32

Table 3

The mixed procedure (Type 3 tests of fixed effects) using nest volume (cm³) or the vertical height of the external nest wall (cm) as the dependent variables, and the interactions between habitat type, box type and clutch type, habitat type (park versus street), box type (four box designs differing in chamber size), clutch type (first versus later breeding attempts), reproductive stage (nest measured before egg-laying versus during the period of egg-laying versus after the onset of incubation), the first egg date and clutch size as the fixed effects. Site (5 sites), box identity (134 different boxes) and year (2011-2016) were added as random factors. Sample sizes are indicated in Table 1.

	Nest volume	Height of external nest wall
Habitat type*Box type*Clutch type	$F_{2,934}=0.17$ $p=0.85$	$F_{2,934}=0.51$ $p=0.60$
Habitat type*Box type	$F_{2,934}=0.02$ $p=0.98$	$F_{2,934}=0.19$ $p=0.83$
Habitat type*Clutch type	$F_{1,934}=5.46$ $p=0.0197$	$F_{1,934}=6.25$ $p=0.0126$
Box type*Clutch type	$F_{3,934}=22.44$ $p<0.0001$	$F_{3,934}=9.61$ $p<0.0001$
Habitat type	$F_{1,934}=0.21$ $p=0.65$	$F_{1,934}=0.03$ $p=0.86$
Box type	$F_{3,934}=119.8$ $p<0.0001$	$F_{3,934}=1.34$ $p=0.26$
Clutch type	$F_{1,934}=0.16$ $p=0.68$	$F_{1,934}=0.00$ $p=0.97$
Stage	$F_{2,934}=0.61$ $p=0.54$	$F_{2,934}=0.45$ $p=0.63$
First-egg date	$F_{1,934}=4.77$ $p=0.0293$	$F_{1,934}=9.26$ $p=0.0024$
Clutch size	$F_{1,934}=0.80$ $p=0.37$	$F_{1,934}=0.17$ $p=0.68$

Table 4

The mixed procedure (Type 3 tests of fixed effects) using nest volume (cm³) or the height of the external nest wall (cm) as the dependent variables, and the interactions between habitat type, box type and clutch type, habitat type (park versus street), box type (four box designs differing in chamber size), clutch type (first versus later breeding attempts), reproductive stage (nest measured before egg-laying versus during the period of egg-laying versus after the onset of incubation), female age (yearling versus older), the first egg date and clutch size as fixed effects. Study site (5 sites), box identity (112 different boxes), year (2011-2016) and female identity (170 ring numbers) were added as random factors.

	Nest volume	Height of external nest wall
Habitat type*Box type*Clutch type	$F_{2,306}=0.51$ $p=0.60$	$F_{2,306}=0.21$ $p=0.81$
Habitat type*Box type	$F_{2,306}=0.99$ $p=0.37$	$F_{2,306}=0.85$ $p=0.43$
Habitat type* Clutch type	$F_{1,306}=5.38$ $p=0.021$	$F_{1,306}=5.80$ $p=0.0166$
Box type* Clutch type	$F_{2,306}=5.82$ $p=0.0007$	$F_{2,306}=2.83$ $p=0.0388$
Habitat type	$F_{1,306}=0.59$ $p=0.44$	$F_{1,306}=0.20$ $p=0.65$
Box type	$F_{3,306}=62.2$ $p<0.0001$	$F_{3,306}=0.80$ $p=0.49$
Clutch type	$F_{1,306}=0.48$ $p=0.49$	$F_{1,306}=0.28$ $p=0.59$
Stage	$F_{2,306}=0.24$ $p=0.78$	$F_{2,306}=0.34$ $p=0.71$
Female age	$F_{1,306}=1.64$ $p=0.20$	$F_{1,306}=1.17$ $p=0.28$
First-egg date	$F_{1,306}=1.43$ $p=0.23$	$F_{1,306}=5.59$ $p<0.0186$
Clutch size	$F_{1,306}=0.52$ $p=0.47$	$F_{1,306}=0.21$ $p=0.65$

Table 5

Average values (\pm SD) and range of the dry mass (in g) of nest components in urban great tits from first and later breeding attempts. Nesters occupied different habitat types (park versus street) and different box types. n equals the number of nest measurements.

Factor	Preferred material (g) 2014-2016	Needles (g) 2014-2016	Wood-based (g) 2014-2016	Herb-based (g) 2014-2016
Habitat type Park	17.9 \pm SD 8.5 3.1 – 42.8 n=91	0.5 \pm SD 3.1 0 – 28.7 n=91	1.2 \pm SD 2.6 0 – 22.5 n=91	0.9 \pm SD 1.9 0 – 11 n=91
Habitat type Street	14.7 \pm SD 7.0 4 – 33.9 n=55	4.5 \pm SD 8.6 0 – 42.3 n=55	4.6 \pm SD 5.8 0 – 24.4 n=55	2.3 \pm SD 3.1 0 – 12.4 n=55
Box type Layer larch Floor 36 cm ²	3.1 n=1	0 - n=1	0.2 - n=1	0 - n=1
Box type Schwegler Floor 113 cm ²	11.3 \pm SD 2.8 6 – 16.7 n=30	0.05 \pm SD 0.2 0 – 0.9 n=30	0.4 \pm SD 0.7 0 – 2.3 n=30	0.2 \pm SD 0.7 0 – 3.9 n=30
Box type Layer larch Floor 121 cm ²	15.2 \pm SD 6.4 3.4 – 30.9 n=54	1.9 \pm SD 5.3 0 – 28.7 n=54	1.6 \pm SD 2.2 0 – 10.1 n=54	0.8 \pm SD 1.1 0 – 3.9 n=54
Box type Layer larch Floor 210 cm ²	20.9 \pm SD 8.9 5.9 – 42.8 n=61	3.1 \pm SD 7.9 0 – 42.3 n=61	4.3 \pm SD 6.1 0 – 24.4 n=61	2.6 \pm SD 3.3 0 – 12.4 n=61
Clutch type First	17.9 \pm SD 8.1 3.1 – 42.8 n=114	1.7 \pm SD 6.0 0 – 42.3 n=114	2.1 \pm SD 3.9 0 – 22.5 n=114	1.2 \pm SD 2.3 0 – 11 n=114
Clutch type Later	12.4 \pm SD 6.3 4 – 32.4 n=32	3.1 \pm SD 6.5 0 – 23.4 n=32	3.8 \pm SD 5.9 0 – 24.4 n=32	2.1 \pm SD 3.2 0 – 12.4 n=32

Table 6

The mixed procedure (Type 3 tests of fixed effects) using from collected nests the dry-mass of nests or nest components (Nest mass, Preferred material, Needles, Wood-based, Herb-based) measured after the breeding season as the dependent variables, and habitat type (park versus street), box type (four box types) and clutch type (first versus later breeding attempts) as fixed effects. Site (5 sites), box identity (75 different boxes) and year (2014-2016) were considered as random factors.

Factor	Nest mass	Preferred material	Needles	Wood-based	Herb-based
Habitat type*Box type*Clutch type	$F_{2,57}=0.40$ $p=0.67$	$F_{2,57}=1.18$ $p=0.31$	$F_{2,57}=0.61$ $p=0.55$	$F_{2,57}=0.25$ $p=0.78$	$F_{2,57}=0.56$ $p=0.57$
Habitat type*Box type	$F_{2,57}=1.29$ $p=0.28$	$F_{2,57}=2.10$ $p=0.13$	$F_{2,57}=1.11$ $p=0.34$	$F_{2,57}=5.01$ $p=0.0099$	$F_{2,57}=3.75$ $p=0.0294$
Habitat type*Clutch type	$F_{1,57}=0.91$ $p=0.34$	$F_{1,57}=1.91$ $p=0.17$	$F_{1,57}=0.01$ $p=0.93$	$F_{1,57}=0.00$ $p=0.97$	$F_{1,57}=0.16$ $p=0.69$
Box type*Clutch type	$F_{2,57}=0.67$ $p=0.51$	$F_{2,57}=0.59$ $p=0.55$	$F_{2,57}=1.17$ $p=0.32$	$F_{2,57}=0.28$ $p=0.76$	$F_{2,57}=0.25$ $p=0.78$
Habitat type	$F_{1,62}=2.05$ $p=0.16$	$F_{1,57}=0.54$ $p=0.46$	$F_{1,57}=5.20$ $p=0.0264$	$F_{1,57}=3.08$ $p=0.0848$	$F_{1,57}=0.02$ $p=0.89$
Box type	$F_{3,57}=23.56$ $p<0.0001$	$F_{3,57}=9.31$ $p<0.0001$	$F_{3,57}=0.85$ $p=0.47$	$F_{3,57}=3.80$ $p=0.0148$	$F_{3,57}=4.43$ $p=0.0072$
Clutch type	$F_{1,57}=0.18$ $p=0.67$	$F_{1,57}=4.26$ $p=0.043$	$F_{1,57}=0.20$ $p=0.65$	$F_{1,57}=0.12$ $p=0.73$	$F_{1,57}=0.79$ $p=0.38$
First-egg date	$F_{1,57}=2.81$ $p<0.099$	$F_{1,57}=4.26$ $p<0.043$	$F_{1,57}=0.37$ $p=0.54$	$F_{1,57}=0.36$ $p=0.55$	$F_{1,57}=0.99$ $p=0.32$
Clutch size	$F_{1,57}=3.33$ $p=0.073$	$F_{1,57}=0.01$ $p=0.93$	$F_{1,57}=4.26$ $p=0.0437$	$F_{1,57}=0.01$ $p=0.90$	$F_{1,57}=0.22$ $p=0.64$