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Causes and Consequences of Intraspecific Variation in Nesting Behaviors: Insights from Blue Tits and Great Tits

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Nest building is an important and yet under-studied stage of the reproductive cycle in many taxa, including birds, and whilst we have a decent understanding of interspecific variation in avian nesting behaviors, our understanding of intraspecific variation in nesting behaviors is much less developed. This is largely because an insufficient number of studies have been performed on any one species to draw robust conclusions. Fortunately, though, the amount of research on the nesting behaviors of nestbox-breeding blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) has increased dramatically in recent years and their nesting behaviors are now sufficiently well-studied to offer useful insights into intraspecific variation in avian nesting behaviors. Studies show that individuals of both species select nest sites based on the presence and/or absence of conspecifics and heterospecifics and whilst neighbors were assumed to adversely affect focal individuals by competing for resources, they are now considered beneficial as they provide information about habitat quality and contribute to anti-predator defenses. Nest-building females accurately gauge local weather conditions and respond to predictable variation in environmental conditions by building nests with variable amounts of cup lining material to create suitable nest microclimates for nestlings. Meanwhile, both species vary the amount of aromatic plant materials in their nests in relation to the abundance of nest-dwelling parasites and pathogens and as aromatic plant materials also play a role in sexual selection then nest materials can have multiple functions. The height of nests is negatively correlated with the local risk of predation but whilst predator avoidance favors lower nests, sexual selection favors taller nests. In fact, higher quality females build taller nests that contain more green plant material which in turn influences the amount of care provided by males. This suggests there is considerable intraspecific variation in nesting behaviors in blue and great tits, and in birds generally, and highlights that birds are adept at adaptively varying their nesting behaviors in response to multiple factors. There is, however, a paucity of evidence directly linking such variation in nest building behaviors to reproductive success or fitness more broadly and so further studies could usefully examine such links because trade-offs between competing selection pressures may constrain adaptive nesting behaviors.

Keywords: passerines, nest building, reproductive success, social behaviors, environmental adjustment, parasite avoidance, predator avoidance, sexual selection

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INTRODUCTION

All birds and most fish, reptiles, monotremes, amphibians, insects, molluscs, and arachnids exhibit oviparous reproduction and thus, reproduce by laying eggs. Oviparous reproduction consists of little or no embryonic development within mothers and differs from those taxa with viviparous reproduction, such as mammals, in which a considerable amount of embryonic development occurs within mothers who subsequently give birth to live young (Clutton-Brock, 1991; Lessells, 1991; Alonzo and Klug, 2012). As birds and (mammalian) monotremes are endotherms, then the eggs and hatchlings of altricial and semi-precocial species need to be warmed up and in turn, this means that the location and design of nests influence offspring development and are thus under strong selection pressures (Hansell and Deeming, 2002; Mainwaring, 2016). However, the optimal location and design of nests are likely to be the result of evolutionary trade-offs between competing selection pressures because, for example, the benefits accrued through locating nests in conspicuous locations that are exposed to the warm sun must be traded-off against the increased risk of predation at those conspicuous locations (Collias and Collias, 1984; Collias, 1997; Hansell, 2005; Lima, 2009).

INTERSPECIFIC VARIATION IN NEST LOCATION AND DESIGN

There is a huge amount of interspecific variation in the location and design of birds' nests, ranging from raptors building huge stick nests in trees, passerines constructing small cup nests in bushes, oceanic seabirds laying their eggs on bare cliff ledges and waders laying their eggs in scrapes on the ground (Hansell, 2000). The evolutionary causes and ecological consequences of such interspecific variation have been well-studied using comparative techniques (reviewed by Martin, 1993; Mainwaring et al., 2014b). Such variation is determined over evolutionary timescales by the risk of predation and hence, by natural selection (e.g., Martin, 1995; but see Martin and Li, 1992) but also by aspects of sexual selection (Soler et al., 1998). Meanwhile, interspecific variation in nest location and design at least indirectly affect various aspects of parental care and offspring development through associated variation in the daily risk of nest predation (e.g., Remeš and Martin, 2002; reviewed by Martin, 1993). Thus, we have a good understanding of the causes and consequences of interspecific variation in the location and design of birds' nests although our understanding of intraspecific variation is comparatively poor.

INTRASPECIFIC VARIATION IN NEST LOCATION AND DESIGN

Intraspecific variation in the location and design of birds' nests is generally determined by some combination of five main factors: social behaviors over spatial scales, environmental adjustment, parasite avoidance, predator avoidance, and sexual selection (Hansell, 2000; Mainwaring et al., 2014b). Our understanding of intraspecific variation in nest location and design is relatively poor as there are usually an insufficient number of studies performed on any one species to gain a comprehensive understanding of variation in their nest building behaviors. Whilst other reviews have examined, for example, the design and function of the nests across all bird species (Mainwaring et al., 2014b), and also how climate change is likely to affect all bird species (Mainwaring, 2015b) and all taxa globally (Mainwaring et al., 2017), this review examines intraspecific variation in nest location and design in two of the most popular species for inclusion in scientific research. The nest building behaviors of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) are now sufficiently well-studied to be able to offer some useful insights, which is at least partly because they are amongst the most widely used model species in scientific research globally (Lambrechts et al., 2010). Pertinently, the amount of research focusing on the nest building behaviors of both blue tits and great tits has increased rapidly in recent years and here, I synthesize our current understanding of the causes and consequences of intraspecific variation in their nest building behaviors before highlighting those areas where further research may prove fruitful.

BLUE TITS AND GREAT TITS

Both blue tits and great tits are seasonally breeding insectivorous birds that spend the winter months in mixed species flocks with other passerine birds. In late winter, the mixed species flocks begin to break up and both blue tits and great tits begin forming pair bonds and selecting nest sites as early as January (Stokes, 1960). Blue tits (**Figure 1**) breed inside tree cavities or nestboxes and whilst the females build the nest and incubate the clutch of 7–13 eggs alone, both parents contribute to provisioning the nestlings (Gibb, 1950; Perrins, 1970, 1979, 1991). Great tits (**Figure 2**), meanwhile, nest in tree cavities or nestboxes and similarly to blue tits the females build the nest and incubate the clutch of 7–9 eggs alone before both parents contribute to provisioning the nestlings (Betts, 1955; Gosler, 1993). The nestlings of both species are fed with caterpillars, whilst the adults eat insects during the summer months and increasing amounts of both fruit and seeds during the winter months (Cramp and Perrins, 1993; Otter, 2007).

Studies of blue tits and great tits breeding in natural cavities and in the complete absence of nestboxes are rare. However, a notable exception comes from a study of the birds inhabiting remnants of the original primeval forest that used to cover much of Europe that still remain in Białowieża National Park in eastern Poland. That study has examined the ecology of birds within the primeval woodland (e.g., Wesołowski, 1989, 2000, 2002, 2003; Wesołowski and Maziarz, 2001; Wesołowski and Stańska, 2001; Wesołowski et al., 2002; Wesołowski and Tomiałojć, 2005; Hebda and Wesołowski, 2012; Maziarz et al., 2016) including some of the nesting behaviors of blue tits and great tits. Pertinently, blue tits were found to have an abundance of potential nesting cavities and preferentially selected those located in live trees and those with narrow openings as those features minimized the risks from predation and nest soaking (Wesołowski and Rowiński, 2012, 2014). Great tits, meanwhile, also had an abundance of potential

FIGURE 1 | Female blue tit incubating eggs (Photo: Mark C. Mainwaring).

FIGURE 2 | Female great tit incubating eggs (Photo: Ian R. Hartley).

nesting cavities and preferentially selected those with narrow openings and those located at intermediate heights in living tree trunks with intermediate girths at breast height as such features reduced the risks from predation and nest soaking (Maziarz et al., 2015). More broadly, both species selected their nest sites in a non-random manner (Maziarz and Wesołowski, 2013) indicating intraspecific variation and selection on the location of their nests.

Studies examining blue tits and great tits breeding in natural cavities are rare compared to those studies that have examined both species breeding inside man-made nestboxes (van Balen, 1973; van Balen et al., 1982). The earliest study of nestbox-breeding great tits began near Wageningen in the Netherlands in 1912 and that study was later moved to the nearby Hoge Veluwe in 1944, which was shortly before a parallel study of great tits and blue tits began in Marley Wood in England (Perrins, 1991). The ease with which these studies attracted tits to breed inside the nestboxes did not go unnoticed by other researchers and there are now dozens of studies of both blue tits and great tits across Europe. Their tolerance of routine monitoring activities and of experimental manipulations has led to both blue tits and great tits being amongst the most frequently used model species in ecological, behavioral and evolutionary research globally (e.g., Dhondt, 1977, 1989; Perrins, 1991; Gosler, 1993; Mainwaring, 2011, 2015a; discussed by Møller, 1989, 1992; Lambrechts et al., 2010; Mainwaring et al., 2010; Wesołowski, 2011). Accordingly, both species have been used as model systems in studies examining a range of issues including nest site selection (Slagsvold, 1975), the role of nestbox design in determining reproductive parameters (Karlsson and Nilsson, 1977; Lambrechts et al., 2010; Møller et al., 2014a) and host-parasite interactions (Hebda et al., 2013). Meanwhile, other studies have examined temporal (Visser et al., 1998, 2006) and spatial variation in their reproductive parameters (Visser et al., 2003; Møller et al., 2014b) and as large proportions of birds occupy nestboxes, then other studies have examined their population dynamics (Kluijver, 1951; Sæther et al., 2007).

In this review, I begin by outlining and synthesizing our current understanding of the causes and consequences of intraspecific variation in the nest building behaviors of both blue tits and great tits breeding inside nestboxes, whilst highlighting those instances where nesting materials, such as feathers or aromatic plant material, serve multiple functions. I then go on to highlight those areas where further research is likely to prove fruitful.

SOCIAL BEHAVIOURS OVER SPATIAL SCALES

The selection of a suitable nest site is an important reproductive decision because whilst nest predation events are lethal, even non-lethal effects such as the conditions experienced by the embryos and nestlings within the nest can also have important consequences for individuals throughout their adult life (Metcalfe and Monaghan, 2001; Lloyd and Martin, 2004). In territorially breeding species such as blue tits and great tits, the presence of both conspecific and heterospecific neighbors have traditionally been assumed to have only negative effects on focal individuals. This is because they compete for local resources such as food and nest sites (Minot and Perrins, 1986; Stamps, 1994) whilst also offering opportunities for their reproductive partners to engage in extra-pair copulations (Ramsay et al., 1999; Westneat and Stewart, 2003), meaning that smaller distances between nest sites were expected to be disadvantageous for focal individuals (Taylor, 1976; Stamps and Krishman, 1990). However, more recent evidence suggests that whilst neighboring birds can adversely affect focal individuals in the ways outlined above, neighboring conspecifics and heterospecifics can also provide significant benefits by providing information about breeding habitat quality (Giraldeau et al., 2002; Pärt and Doligez, 2003; Danchin et al., 2004; Dall et al., 2005; Galef and Laland, 2005; Seppänen et al., 2007), opportunities for extra pair copulations with higher quality birds (Kempenaers et al., 1992) and cooperating in anti-predator defense behaviors (Grabowska-Zhang et al., 2012). Consequently, there is evidence that birds select nest sites in close proximity to conspecifics (Boulinier et al., 1996; Valone, 1996; Boulinier and Danchin, 1997; Pärt and Doligez, 2003; Stamps and Krishman, 2005; Pärt et al., 2011; Jaakkonen et al., 2013) and heterospecifics (Parejo et al., 2005; Seppänen and Forsman, 2007) and gain fitness benefits by doing so (Beletsky and Orians, 1989; Betts et al., 2008; reviewed by Valone and Templeton, 2002; Valone, 2007).

In blue and great tits, neighboring conspecifics have usually been assumed to negatively affect focal individuals by competing with them for local resources such as nest sites or food and also by providing opportunities for their reproductive partners to copulate with extra pair birds. Although empirical evidence for conspecific neighbors competing for local resources is limited (Minot and Perrins, 1986), there is evidence that conspecific neighbors do provide opportunities for focal males to be cuckolded as female blue tits actively solicit extra pair copulations with high quality males (Kempenaers et al., 1992). The proportion of extra pair nestlings within blue tit broods is influenced by the number of breeding neighbors within 100 m of focal nestboxes although interestingly, the nearest neighbors accounted for only 39.3 per cent of extra-pair paternities (Charmantier and Perret, 2004). This suggests that females were actively engaging in extra pair copulations with high quality males, rather than the closest males, to increase the genetic fitness of their offspring. Irrespective of the identity of extra pair males, however, male blue tits that suspect that they have been cuckolded reduce their parental investment (García-Navas et al., 2013) meaning that females may have to compensate by increasing their own investment. Thus, the presence of conspecific neighbors can be disadvantageous for blue tits and particularly so for lower quality males who are likely to be cuckolded by higher quality males breeding within the vicinity of their nests.

The presence of neighboring conspecifics can, however, also be advantageous and there is evidence that at the landscape scale, blue tits use social information cues, such as the density of breeding birds and the number of fledglings they produce, to select nest sites (Parejo et al., 2007a,b). Whilst young blue tits breeding for the first time were not equipped with such information and hence, never based their settlement decisions on such cues, older birds did use such information to select nest sites. Interestingly though, their response varied depending on their own reproductive success in the previous year as failed breeders moved to areas with a low density of birds that had high levels of reproductive success whilst successful breeders moved to areas with a high density of birds with low levels of reproductive success (Parejo et al., 2007a). This pattern of social information use was also tested experimentally by transferring nestlings from nests in "decreased" patches to nests in "increased" patches so that nests in "increased" patches contained a higher number of fledglings in poorer condition than nests in "decreased" patches, whilst nests in "control" patches produced an intermediate number of fledglings in an intermediate condition. Adult emigration the following year was higher from "decreased" than from either "control" or "increased" patches, which suggests that resident breeders relied mainly on fledgling quantity to make emigration decisions whilst the emigration patterns of juveniles did not vary in relation to the experimental manipulation of social information cues (Parejo et al., 2007b). At the territory level, meanwhile, great tit pairs with old males preferred to copy the nest site choices of previously settled conspecifics whilst pairs with young males never used such cues. This pattern occurred irrespective of a simultaneous clutch size manipulation experiment whereby clutch sizes were increased or decreased by two eggs (Loukola et al., 2012) and suggests that males were not basing their settlement decisions on the reproductive success of other pairs. Instead, it is likely that older males preferred to nest close to conspecifics because they could acquire extra pair paternities, whilst younger males were wary of being cuckolded. More broadly, it suggests that males may play a greater role in choosing nest sites than has been traditionally thought (Cramp and Perrins, 1993) and this possibility warrants further investigation. More specifically, the study by Loukola et al. (2012) suggests that older males preferred to nest close to conspecifics to obtain extra pair paternities and so studies that experimentally alter the clumping patterns of nestboxes, so that some are solitary whilst others are grouped, and which then examine the age of males and patterns of paternity within those broods are likely to be informative.

In territorially breeding species such as blue and great tits, the presence of heterospecifics can be disadvantageous as they compete for resources such as food and nest sites, with larger and more dominant species gaining preferential access to such resources (Dhondt, 2011). Illustratively, blue tits are smaller and subordinate to great tits and so whilst the breeding density of blue tits was negatively related to the density of great tits, the density of great tits was independent of the density of blue tits (Minot and Perrins, 1986). Resident great tits are also dominant over migratory pied flycatchers and as the tits breed earlier than the flycatchers, then the tits are usually incubating eggs when the flycatchers arrive from their African wintering grounds. When the empty nestboxes that were left unused by the tits were made uninhabitable to the flycatchers prior to their arrival, competition for the nestboxes already inhabited by the great tits increased and although the flycatchers only managed to usurp the tits on two occasions, fights were frequent and at least one male flycatcher died in the struggles (Slagsvold, 1978). Even in the absence of nest site shortages, great tits and pied flycatchers have an antagonistic relationship because great tits with neighboring pied flycatchers have lower clutch sizes than conspecifics without neighboring flycatchers, whilst the flycatchers benefit from neighboring tits by having larger clutch sizes than conspecifics without tit neighbors. This has resulted in an arms race between the two species and in an attempt to hide their eggs from prospecting flycatchers, great tits usually cover them with nesting materials whenever they leave the nest during the egg laying period in order to prevent flycatchers using them as a cue in their nest site selection decisions (Loukola et al., 2014). Nevertheless, there is widespread evidence that several species of migratory passerine birds base their settlement decisions on the settlement decisions of the resident tits (Mönkkönen et al., 1990; Forsman et al., 2002, 2007, 2008, 2009; Forsman and Seppänen, 2011; Loukola et al., 2012, 2013; Jaakkonen et al., 2015). Illustratively, both the average number of species and the total density of migratory birds that chose to breed in habitat patches were positively correlated with the experimentally-varied density of titmice already breeding within those habitat patches, thereby indicating that migrants probably use titmice density as an indicator of breeding habitat quality because they share similar food resources (Forsman et al., 2009). Migrants therefore use the resident tits as a source of information at the landscape level but they also use them as a source of information at the territory level, and particularly so when deciding how many eggs to lay in their clutch. Shortly after their arrival from Africa, pied and collared flycatchers prospect the nests of resident tits about once per day (Forsman and Thomson, 2008) and use the tits' clutch sizes as cues when deciding where to nest, with larger clutch sizes indicating higher quality habitat (Forsman and Seppänen, 2011). Thus, the presence of the resident heterospecific tits was advantageous for the migratory flycatchers as they provided valuable information regarding both where to nest and the level of effort to invest in that particular reproductive event. However, there is evidence that the presence of such heterospecific neighbors may be disadvantageous for great tits by reducing their breeding success (Loukola et al., 2014) meaning that the antagonistic relationship between the resident tits and the migratory flycatchers deserves further research attention.

Heterospecific neighbors can be advantageous for focal species (Seppänen and Forsman, 2007; Dhondt, 2011) but I am not aware of any evidence showing that either blue tits or great tits benefit from the presence of heterospecific neighbors. In summary, this means that patterns of nest site selection in blue and great tits do vary in relation to the presence or absence of both conspecifics and heterospecifics in complex ways that depend on the advantages and disadvantages accrued by individuals and species, respectively. In terms of conspecifics, variation in nest site selection decisions probably reflects variation in the likelihood of gaining or losing paternity and in terms of heterospecifics, dominant great tits can prevent subordinate species from breeding when nest sites are limited although there is good evidence that migratory species such as flycatchers often use the presence of the resident tits to select breeding habitats at the landscape scale and usually reduce the breeding success of the tits by doing so. This has resulted in an arms race between the resident tits and migratory flycatchers whereby the tits attempt to conceal their nest sites from the flycatchers. Meanwhile, a fascinating study examined if patterns of nest site selection were determined by natal experience and showed that great tits naturally occupy larger nestboxes whilst blue tits occupy smaller nestboxes and yet when the nestlings of the two species were swapped between the two nestbox types early in the nestling period, those birds went on to occupy whichever type of nestbox they were raised in during adulthood (Slagsvold et al., 2013). These studies suggest that birds ubiquitously use social information when making decisions regarding where to breed and that those decisions are routinely influenced by social experiences acquired by focal individuals during development and adulthood. Further, such choices have fitness consequences as blue and great tits have lower levels of reproductive success when breeding close to heterospecifics. However, these studies are usually performed on one or two study plots which may mean that the findings are unrepresentative of the species behaviors' which in turn, may limit our ability to draw solid conclusions. Consequently, there is a need for studies that examine birds from multiple study sites.

ENVIRONMENTAL ADJUSTMENT

Nests must provide a suitable microclimate for developing embryos and offspring because suboptimal nest microclimates negatively affect their growth (Drent, 1975; Ar and Sidis, 2002). In passerine birds, optimal embryonic development only occurs within narrow thermal limits, 34–40°C, and extended periods of time spent either below or above these limits result in abnormal embryonic development and mortality, respectively (Webb, 1987; DuRant et al., 2013). The thermal conditions experienced by embryos during incubation also affect their phenotypes after hatching, with both higher and lower than optimal temperatures resulting in nestlings having lower masses and body condition scores at pre-fledging than nestlings that developed in optimal conditions (Dawson et al., 2005; Ardia et al., 2008; Peréz et al., 2008). Birds are therefore under strong selection pressures to select a nest site and construct nests that provide suitable thermal conditions for embryonic development. Parental brooding behaviors can regulate nest microclimates, but such behaviors are energetically costly and parents can mitigate these demands by altering the design of nests in relation to predictable variation in environmental conditions (Mertens, 1977; Møller, 1984; Lombardo, 1994; Hilton et al., 2004; Dawson et al., 2011; Heenan and Seymour, 2012; Ardia, 2013; Heenan, 2013; Windsor et al., 2013; Cruz et al., 2016).

Both blue tits and great tits readily occupy nestboxes and whilst this makes them amongst the most widely used model species in scientific research globally (Lambrechts et al., 2010), the characteristics of the nestboxes may influence nest microclimates. More specifically, birds are able to influence nest microclimates by preferentially occupying nestboxes in relation to the orientation of their entrance hole which influences the exposure to cold winds (e.g., Ardia et al., 2006) and their construction material because woodcrete nestboxes are about 1.5°C higher on average than wooden nestboxes (e.g., García-Navas et al., 2008). Studies show that whilst great tits avoided nestboxes orientated toward south-southwest, there was no such relationship in blue tits, although the orientation of nestboxes did not influence reproductive success in either species (Goodenough et al., 2008). Meanwhile, both blue tits and great tits preferentially occupied woodcrete nestboxes rather than wooden nestboxes, although the breeding success again did not vary between nestbox types (Browne, 2006). Another study also showed that blue tits and great tits preferred to occupy woodcrete rather than wooden nestboxes but this time, nest predation was significantly greater in woodcrete nestboxes (Bueno-Enciso et al., 2016). Pertinently, the height of great tit nests was significantly higher in woodcrete nestboxes than in wooden nestboxes, thus indicating that the construction material influences nest building behaviors. Further, laying dates were earlier in woodcrete nestboxes, and whilst nestbox type did not influence clutch size, the eggs of both species were significantly smaller in woodcrete boxes and pairs occupying woodcrete nestboxes had lower levels of breeding success than conspecifics occupying wooden nestboxes

(Bueno-Enciso et al., 2016). In addition to the characteristics of nestboxes, blue and great tit nest design should vary in relation to environmental conditions as the design of birds' nests vary with increasing temperatures as spring advances in temperate environments (McGowan et al., 2004; Liljesthröm et al., 2009), as altitude decreases (Kern and van Riper, 1984) and as latitude decreases (Crossman et al., 2011; Mainwaring et al., 2014a).

Blue tits and great tits adaptively adjust the design of their nests as ambient spring temperatures increase in temperate environments. The number of days taken to construct nests decreases as the season progresses and whilst there is no seasonal trend in the mass of entire nests nor in the mass of the nests' moss base material, the mass of nests' cup lining material decreases as the season progresses (Mainwaring and Hartley, 2008; Britt and Deeming, 2011; Deeming et al., 2012; Harničárová and Adamík, 2016). This suggests that nest-building females selectively adjust the amount of cup lining material they add to their nests to create nest microclimates for optimal embryonic and offspring development (Glądalski et al., 2016). Meanwhile, the absence of any seasonal changes in the mass of the nests' moss base highlights that nests are multi-functional structures. This is because whilst the cup lining material serves to create optimal environmental conditions for embryonic and offspring development, the moss base material serves to protect the offspring from predators (Mazgajski and Rykowska, 2008; Kaliński et al., 2014) or to play a role in sexual selection (Sanz and García-Navas, 2011; Tomás et al., 2013).

The only study to have examined altitudinal variation in nest characteristics reported that the design of great tit nests did not vary along an altitudinal temperature gradient in Austria. Despite high altitude locations experiencing cooler ambient temperatures than lower altitude locations, nests built at high altitudes had similar amounts of cup lining materials and similar insulation properties to nests built at lower altitudes (Schöll and Hille, 2015). However, as the birds breeding at higher altitudes laid their eggs later than conspecifics at lower altitudes, then it is likely that during their respective nest building and incubation periods, birds experienced similar ambient temperatures along the altitudinal gradient. This possibility would certainly explain why the amount of cup lining material incorporated into nests and the insulation properties of nests did not vary over the altitudinal gradient, although it is clear that further studies are needed to gain a more complete understanding of how the nest building behaviors of both blue tits and great tits vary with altitude.

Blue tits and great tits are resident across much of the western Palearctic ranging from Norway in the north to Morocco in the south (Perrins, 1979; Gosler, 1993; Sanz, 2002). Given that environmental conditions vary considerably over such broad latitudinal gradients then it is unsurprising that various life history and reproductive parameters of blue and great tits vary with latitude (e.g., Sanz et al., 2000; Møller et al., 2014a,b) although only one study has examined latitudinal variation in their nest characteristics (Mainwaring et al., 2012). As spring temperatures increased with decreasing latitude across seven study sites spread over 5° of latitude in the United Kingdom, the mass of the nests' moss base material did not vary in either species, but the mass of the nests' cup lining material and nest insulation properties decreased in both species. This suggests that nest-building females were able to gauge local environmental conditions and adjust the design of their nests accordingly, although similarly to the situation with altitude, further studies are required before confident assertions can be made. Specifically, studies that experimentally swap nests between locations varying in latitude or altitude provide a powerful way of disentangling the relative contributions of nest site and nest design in creating suitable nest microclimates for embryonic and offspring development.

Blue and great tits appear able to gauge predictable variation in environmental conditions and adjust the amount of cup lining material in their nests to create suitable microclimates for embryonic development. Such flexibility is adaptive as nest temperatures during incubation influence fledging success in blue tits, but not great tits (Deeming and Pike, 2015) and cup lining material mass is positively correlated with hatching success in blue tits and with both hatching and fledging success in great tits (Glądalski et al., 2016). Perhaps worryingly though, environmental conditions are also changing in less predictable ways with anthropogenic climate change. Such climatic changes may affect nest building birds in numerous ways (Møller, 2006; Mainwaring, 2015b) and in blue and great tits, may alter the distribution and abundance of bryophytes (O'Neil, 2000; Jägerbrand et al., 2003) which constitute the main nesting material. Whilst the evidence suggests that both species can adaptively adjust their nest building behaviors to changes in environmental conditions, long-term studies that monitor nest composition (e.g., 18 years: Lambrechts et al., 2016a,b) may be useful.

PARASITE AVOIDANCE

Birds play host to a plethora of parasites including fleas, lice, fungi, mites, leaches, ticks, and bacteria and yet despite their prevalence, the impacts of such parasites on their avian hosts remained poorly understood, apart from commercially valuable game birds, until the 1980's (Loye and Zuk, 1991; Clayton and Moore, 1997). It was then that the seminal paper by Hamilton and Zuk (1982) reported that the elaborate displays of North American birds evolved as a direct consequence of parasite-mediated sexual selection, which highlighted the considerable impacts that parasites have on their avian hosts. Accordingly, empirical studies have since shown that parasites are detrimental to their avian hosts by reducing their survival and reproductive success (e.g., Møller, 1990b, 1993; Burtt et al., 1991; reviewed by Loye and Zuk, 1991; Richner et al., 1993; de Lope et al., 1993; Oppliger et al., 1994; Clayton and Moore, 1997; Tripet and Richner, 1997, 1999; Merino et al., 2000; Proctor, 2003). In great tits, for example, experimental pairs that had hen fleas (*Ceratophyllus gallinae*) added to their nests fledged fewer and poorer quality nestlings than control pairs that had hen fleas eliminated from their nests (Richner et al., 1993). Given that it is now clear that parasites usually have negative consequences for the fitness of their avian hosts, then it is unsurprising that the hosts have evolved a wide variety of defenses to mitigate both the abundance and virulence of the parasites. In birds, such defenses vary from the employment of feather toxins, plumage maintenance behaviors such as the molting of worn feathers, various preening and dusting behaviors and a range of nest building behaviors (Loye and Zuk, 1991; Toft, 1991; Proctor, 2003).

Breeding birds can limit the adverse effects of parasites by choosing nest sites with few parasites and by incorporating plants into their nests that repel parasites. To this end, several species of hole-nesting passerines such as European starlings (*Sturnus vulgaris*), tree swallows (*Tachycineta bicolor*) and both blue tits and great tits incorporate aromatic plant materials into their nests. Their inclusion is noteworthy because they constitute only a small fraction of the plants available as nesting materials within the wider environment, and yet they are highly sought after because they contain a high abundance of volatile secondary metabolites that reduce the abundance of a range of nest-dwelling parasites (Belandrin et al., 1985; Dubiec et al., 2013). Accordingly, there is evidence that birds mitigate the effects of parasites by choosing nest sites containing few parasites (Mappes et al., 1994; Rendell and Verbeek, 1996; Mazgajski, 2007; Suárez-Rodríguez et al., 2013) and by incorporating aromatic plant materials into their nests to reduce either the abundance or virulence of parasites (Wimberger, 1984; Clark and Mason, 1985, 1987, 1988; Clark, 1991; Shutler and Campbell, 2007). Both blue tits and great tits incorporate aromatic plants into their nests (Cowie and Hinsley, 1988; Bańbura et al., 1995) and detailed studies of Corsican blue tits have shown that nest-building females incorporate between one and five aromatic herb species into their nests (Lambrechts and dos Santos, 2000; Lafuma et al., 2001; Petit et al., 2002; Lambrechts et al., 2008; Mennerat et al., 2008). The evidence suggests that aromatic plants are purposely sought out by nest-building females because they are a widely used nesting material despite constituting only a small fraction of the plants available within territories (Dubiec et al., 2013). Further, female blue tits respond to the experimental removal of aromatic plants from their nests by immediately replenishing their nests with more aromatic plant material (Lambrechts and dos Santos, 2000). The inclusion of aromatic plant materials into the nests of blue tits and great tits is determined by the presence of nest-dwelling parasites and their inclusion has important consequences for the behavior and fitness of both the parents and nestlings (Heeb et al., 2000; Bańbura et al., 2001; Słomczyński et al., 2006; Mennerat, 2008). There is variation in the amount of aromatic plant material incorporated into the nests of blue tits, however, and that variation is determined not by the availability of aromatic plant material within territories or by the breeding experience of nest-building females but by female identity as individual females showed preferences for aromatic plant materials that were repeatable both within and across years (Mennerat et al., 2009a). Meanwhile, the inclusion of aromatic plants within nests significantly affects the structure of bacterial communities as the experimental addition of aromatic plant materials reduced the level of bacterial richness on nestling but not adult blue tits (Mennerat et al., 2009c). This appears to benefit the nestlings as the experimental addition of aromatic plants to blue tit nests resulted in faster growth of nestlings in experimental nests than in control broods where mosses, which are a benign plant species, were added to nests (Mennerat et al., 2009b). Although the size of the nestlings did not vary at the pre-fledging stage immediately before they left the nestboxes, these studies suggest that aromatic plant materials do mitigate the negative effects of parasites on their blue and great tit hosts.

The selection of a nest site containing few parasites is an obvious way in which birds can limit the adverse effects of parasites, yet to the best of my knowledge no studies have examined patterns of nest site selection by blue tits or great tits in relation to the variation in the abundance of parasites in potential nesting sites. However, one study highlighted the importance of choosing a nest site containing few parasites by allowing blue tits to breed either in nestboxes with an old nest which contained the most ectoparasites, empty nestboxes which contained an intermediate number of ectoparasites or nestboxes with an old nest fumigated with insecticide which contained the fewest ectoparasites. Pairs breeding inside nestboxes that contained old nests from the previous season, and thus had a high abundance of parasites, had lower levels of reproductive success and the female parents had lower body masses at the end of the breeding season than conspecifics breeding in nests in the other two treatments that contained fewer ectoparasites (Tomás et al., 2007). Thus, the abundance of nest-dwelling parasites has important consequences for their hosts and so studies examining how both species choose their nest sites in relation to the abundance and virulence of parasites would be useful.

The nest building behaviors of blue tits were also directly influenced by the abundance of fleas inside their nestboxes because the density of fleas affected the nest sanitation behaviors of the female parents, with females occupying experimental nestboxes where fleas had been added performing more nest sanitation behaviors than females occupying control nestboxes without fleas (Tripet et al., 2002). In great tits, meanwhile, both the number of adult fleas and the number of larvae within nestboxes were positively correlated with the fresh mass of the nests (Heeb et al., 1996). Further, the experimental infestation of nestboxes with hen fleas resulted in females at those experimental nestboxes building heavier nests than control females breeding in nestboxes in which hen fleas were experimentally eliminated (Heeb et al., 1996). It is unclear why an increase in the abundance of fleas should cause females to build heavier nests as the bulk of the additional material would presumably have been mosses which have no effect on the abundance or virulence of ectoparasites. In addition to nest building behaviors, parental provisioning behaviors can mask the negative effect of ectoparasites on blue tit nestlings because parents at experimentally infested nests increased their food provisioning rate by 29 per cent meaning that the parents bore the costs of parasitism rather than the nestlings (Tripet and Richner, 1997). Further, the plant material composition of nests varies greatly between species occupying the same habitat. Given that nest-dwelling parasites are much more abundant in the nests of pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*Ficedula albicollis*) than in the nests of blue tits and great tits, then it has been posited that such differences occur because of the species-specific nest material composition because whilst the tit nests consist largely of mosses, the flycatcher nests consist largely of grass and leaves. However, when the nests of pied flycatchers and blue tits (Moreno et al., 2009) and great tits and collared flycatchers (Remeš and Krist, 2005) were experimentally swapped, the abundance of parasites within focal nestboxes remained unaltered, thereby indicating that nest material composition does not influence the abundance of nest-dwelling ectoparasites on co-existing bird species.

In summary, there is good evidence that both blue tits and great tits actively incorporate aromatic plant materials into their nests specifically to limit the adverse effects of a range of nest-dwelling parasites and pathogens. In particular, studies of Corsican blue tits have demonstrated that their inclusion within nests does effectively reduce the abundance and virulence of ectoparasites and bacteria and thus, has positive effects on the fitness of both the nestlings and attending parents (e.g., Lambrechts and dos Santos, 2000; Lafuma et al., 2001; Petit et al., 2002; Lambrechts et al., 2008; Mennerat et al., 2008). However, it is prudent to acknowledge that nest materials can have multiple functions and that aromatic plant materials play an important role in the process of sexual selection in European starlings and other species (Fauth et al., 1991; Gwinner, 1997; Gwinner et al., 2000; Brouwer and Komdeur, 2004). Meanwhile, feathers, which are thought by some to be incorporated into nests to provide a physical barrier between nestlings and ectoparasites instead appear to create a suitable microclimate for offspring development as reported primarily in tree swallows and less commonly in other species (Winkler, 1993; Lombardo et al., 1995; Dawson, 2004; Liljesthröm et al., 2009; Stephenson et al., 2009; Dawson et al., 2011). This suggests that nesting materials do indeed simultaneously serve multiple functions when used by blue and great tits (reviewed by Toft, 1991; Dubiec et al., 2013; Mainwaring et al., 2014b) and that in addition to repelling parasites and pathogens, and acting as sexual signals during courtship, nesting materials may also serve to create optimal environmental conditions for offspring growth and development.

PREDATOR AVOIDANCE

The risk of predation is ubiquitous for breeding birds and natural selection favors those individuals that successfully reproduce without having their nests predated (Caro, 2005). Therefore, the risk of predation exerts strong selection pressures not only on the location and design of birds' nests but also on the behaviors of the parent birds when they visit the nest site (reviewed by Martin, 1993; Lima, 2009; Mainwaring et al., 2014b, 2015; Ibáñez-Álamo et al., 2015). Accordingly, the risk of predation influences aspects of nest site selection (Marzluff, 1988; Forstmeier and Weiss, 2004; Eggers et al., 2006) and nest design (Biancucci and Martin, 2010; Lovell et al., 2013) in a wide range of birds. For example, the open cup nests of common blackbirds (*Turdus merula*) that were experimentally increased in size were predated more often than either control nests that remained unchanged in size or nests that were experimentally decreased in size (Møller, 1990a). Meanwhile, parental nest visitation rates are often negatively correlated with the risk of nest predation (Martin et al., 2000; Fontaine and Martin, 2006) although some studies report that nest predation rates are independent of parental behaviors (Cresswell, 1997). Nevertheless, there is overwhelming evidence that the risk of predation is ubiquitous for breeding birds and empirical studies report that natural selection exerts selective pressures on both the location and design of birds' nests (Lima, 2009; Mainwaring et al., 2014b, 2015; Ibáñez-Álamo et al., 2015).

Both blue tits and great tits are hole nesting species and at the interspecific level, those species breeding in holes usually suffer lower predation rates than both open cup nesting species and ground nesting species (Nilsson, 1986; Martin, 1993). However, it is prudent to consider that such differences may be less pronounced for hole nesting birds breeding inside natural holes rather than in nestboxes because predation rates are generally higher in the former cavity type (e.g., Nilsson, 1984; reviewed by Lambrechts et al., 2010). To the best of my knowledge, though, no studies have examined intraspecific variation in the predation rates of either blue tit or great tit nests, or provisioning parents, in relation to the location of the nestboxes in which they are breeding.

The risk of predation does influence the design of both blue tit and great tit nests though. The overwhelming majority of nest predators are too large to squeeze through the entrance holes of nestboxes and so it is the height of nests within cavities that determines the risk of predation with higher nests within those cavities being more vulnerable to predation than lower nests because the eggs, nestlings, and attending parents are physically closer to the entrance holes of the nestboxes. Mazgajski and Rykowska (2008) provided great tits with both deep and shallow nestboxes that had depths of 21 and 16 cm, respectively, and found that great tits built significantly higher nests within the deep nestboxes than in the shallow nestboxes. As the deep nestboxes had a greater depth than the shallow nestboxes, then the distance between the nest entrance and the nest rim was kept constant in the two nestbox types. Kaliński et al. (2014), meanwhile, added plastic tubes that protruded from the entrance holes of nestboxes so that the distances from the exterior entrance holes to the nest contents were experimentally increased at nestboxes of two different sizes. Both blue tits and great tits built taller nests within nestboxes with anti-predator devices added to them regardless of nestbox size. This had important fitness consequences as nests in smaller nestboxes were predated more frequently by pine martens (*Martes martes*) than nests in bigger nestboxes (Kaliński et al., 2014). The height of great tit nests was inversely related to the risk of predation which means that when the risk of predation was high the height of nests was low, so that in turn, the distance between the entrance hole of the nestbox and the nest contents was greater when the risk of predation was high. Natural selection should therefore favor birds that build shallower and lower nests and so it is not presently clear why both observational (Tomás et al., 2006; Mainwaring et al., 2008; Broggi and Senar, 2009) and experimental (Mainwaring and Hartley, 2009) studies show that both blue tits and great tits preferentially build taller and higher nests whenever they are able to do so. It is likely that higher nests either confer thermoregulatory benefits for the birds by being bulkier (Ar and Sidis, 2002) or possibly that they act as a signal of the female builders' phenotypic quality which influences the non-building males' investment in reproduction (Tomás et al., 2013).

SEXUAL SELECTION

The design of both blue tit and great tit nests are influenced by natural selection, yet the design of their nests may also act as extended phenotypic signals of the female builders' quality and hence, also be influenced by sexual selection. Intraspecific signaling between conspecifics usually consists of behavioral or physical signals such as elaborate songs, extravagant ornaments such as crests or long tails, or brightly colored plumages (Andersson, 1982). However, some species build structures that signal their phenotypic quality and whilst species such as bowerbirds build structures whose sole purpose is to attract a mate (Schaedelin and Taborsky, 2009), nests also contain eggs and/or offspring which suggests a direct trade-off between the conflicting requirements of natural and sexual selection (Sergio et al., 2011). For nest building behaviors to be extended phenotypic signals of the building individuals' quality, they must reliably indicate the quality of the builder by being associated with energetic costs (Nager and van Noordwijk, 1992; Maynard Smith and Harper, 2003; Moreno, 2012). There is now evidence that constructing a nest is energetically expensive for birds and that whilst those costs are less substantial than provisioning nestlings or incubating eggs, they are nevertheless far more substantial than they were generally considered to be just a couple of decades ago (e.g., Withers, 1977; Hansell and Ruxton, 2002; Soler et al., 2007; Moreno et al., 2008, 2010; reviewed by Mainwaring and Hartley, 2013). Thus, nest building behaviors and the design of completed nests may act as sexual signals and there is widespread evidence that they play a role in sexual selection in species where nests are built by males alone (Lens et al., 1994; Evans and Burn, 1996; Gwinner, 1997; Evans, 1997a,b; Soler et al., 2001; de Neve and Soler, 2002; Brouwer and Komdeur, 2004; Polo et al., 2004, 2010; Veiga and Polo, 2005; Polo and Veiga, 2006; Veiga et al., 2006), by females alone (Moreno et al., 2008, 2010) and by both parents (Soler et al., 1998; Sergio et al., 2011).

For blue tit and great tit nest building behaviors to be extended phenotypic signals of the building females' quality, they must be associated with costs (Moreno, 2012). Evidence of nest building being energetically expensive comes indirectly from studies showing that both species often travel considerable distances to collect nesting materials (Hansell, 1995; Surgey et al., 2012) whilst more direct evidence comes from studies specifically examining the energetic costs of nest building. Two studies have provided blue tits and great tits with food during the nest building period and the first one found that experimental blue tit females constructed heavier nests, with greater amounts of moss base materials but similar amounts of cup lining materials, than unfed control females, despite there being no differences in the nest building period (Mainwaring and Hartley, 2009, 2016). The second study, meanwhile, found that whilst female blue tits at experimentally fed nests built significantly shallower nests in a shorter time period than unfed control females, neither the length of the nest building period nor the depth of nests differed between treatments in great tits (Smith et al., 2012). The contrasting findings of these two studies suggest that the availability of food influences nest building females in complex ways that vary over temporal and spatial scales and further studies in which blue tits or great tits are provided with supplementary food during the nest building period would be informative. Nevertheless, when the nests and eggs of experimental blue tit pairs were removed after 5 days of incubation so that they were forced to build their nests again, they built smaller nests and laid smaller replacement clutches (Lambrechts et al., 2012). Thus, there is evidence that nest building is an energetically expensive activity that is limited by the availability of food (Martin, 1987) in birds generally and also in blue tits, and probably therefore also in great tits, meaning that their nest building behaviors are extended phenotypic signals of the females' quality and may play a role in sexual selection.

Studies examining sexual selection in blue tits and great tits have traditionally concentrated on the role of the ultra violet plumage coloration of breeding adults (Andersson et al., 1998; Hunt et al., 1998; Sheldon et al., 1999; Doutrelant et al., 2008) although it is prudent to consider that most of those studies are based on correlational data rather than experimental approaches, and a meta-analysis showed that there was no overall effect of ultra violet plumage coloration in adults on brood sex ratios (Ewen et al., 2004). There is, however, now observational and experimental evidence that nest building behaviors also play a role in sexual selection. In blue tits, larger females (Mainwaring et al., 2008) and healthier females that were less infected with *Trypanosoma avium* (Tomás et al., 2006) built heavier nests than smaller females and females with higher infection rates of *Trypanosoma avium*, respectively. Meanwhile, other studies report no effect of the phenotypic quality of female great tits on the size of their nests but report that nest size was positively correlated with reproductive success (Álvarez and Barba, 2008). These patterns may be explained by the findings of another study in which female great tits with higher chromatic breast plumage built bigger nests than conspecifics with lower chromatic breast plumage, and especially so when they were paired to males which also had higher chromatic breast plumage (Broggi and Senar, 2009). However, none of these studies provide evidence that males are responding to the cues provided by the nesting behaviors of their female partners. Consequently, as it could be plausibly argued that females of higher phenotypic quality build better i.e., higher nests because it provides their eggs, nestlings or themselves with benefits when they are incubating or brooding, then studies that search for male responses from female cues are required.

In addition to the observational evidence above, there is also experimental evidence that nest building behaviors are a sexually selected trait in blue tits. When the size of blue tit nests were experimentally increased in size, experimentally decreased in size or kept the same size as a control treatment during the nest building period, male provisioning rates did not differ between treatments but their risk taking behaviors during nestling provisioning did vary in relation to nest size (Tomás et al., 2013). Their risk taking behavior was quantified in terms of their trappability at the nestbox and was found to be significantly lower for males at experimentally smaller nests than in males at unchanged control nests or experimentally larger nests. Meanwhile, in a separate part of the same study, male risk taking behaviors were significantly higher at experimental blue tit nests that had aromatic plants added to them than at control nests that had control plants, that were not aromatic, added to them. Such variation in risk taking behaviors between males was important and also adaptive as they were a key determinant of the reproductive success of breeding pairs and thereby also on female fitness because the males' willingness to defend the nest from predators directly benefited the female. However, the manipulation had no effect on brood sizes or any other reproductive parameters that were quantified (Tomás et al., 2013). More broadly, this study highlights that aromatic plants serve multiple functions as whilst they play a role in sexual selection, they also help to repel ectoparasites. Both blue tits and great tits incorporate aromatic plants into their nests (Lambrechts and dos Santos, 2000; Lambrechts et al., 2008; Mennerat et al., 2008, 2009a,b,c).

Whilst female blue tits build the nest on their own, some males carry feathers into the nest after nest building has finished and place them on top of the completed nest. Those males that delivered feathers to their nests had longer tarsi and had higher provisioning rates than those males that did not deliver feathers to nests, and perhaps surprisingly, the females at those nests responded to the delivery of feathers by males by reducing their own nestling provisioning rates. However, not only did the females save energy by provisioning their nestlings less frequently, they also obtained direct fitness benefits as their nestlings fledged in better condition than nestlings raised in nests where males did not carry any feathers into the nest (Sanz and García-Navas, 2011). However, when feathers were added to experimental blue tit nests in order to mimic the nest building behaviors of extra-pair males in two studies, the social males responded by promptly removing the feathers (Mainwaring et al., 2016) and by reducing the amount of care they provided for the nestlings, both in terms of their provisioning rates and their nest defense behaviors, when compared to males at control nests (García-Navas et al., 2013). It is likely that the social males removed the feathers or reduced the amount of care they provided because they assumed that another male had brought in the feather and thus, they were suspicious of having been cuckolded.

There is good evidence that the nest building behaviors of female blue tits and the occasional feather carrying behaviors of males are both associated with sexual selection and whilst there is less evidence in great tits, this probably results from the scarcity of studies involving that species rather than their nest building behaviors not being influenced by sexual selection. The possibility that females signal their phenotypic quality to males through their nest building behaviors has only recently been considered, having previously been overlooked as it was thought that the expression of a certain amount of ornamentation in females could be explained as a genetically correlated result of sexual selection acting on males (Maynard Smith and Harper, 2003). Thus, empirical studies of female displays are relatively rare (Schaedelin and Taborsky, 2009) and this means that studies of female nest building behaviors in both blue and great tits (Broggi and Senar, 2009; Tomás et al., 2013) and other species (e.g., spotless starlings (*Sturnus unicolor*): Veiga and Polo, 2005; Polo and Veiga, 2006) have significantly advanced our understanding of female displays more broadly. Pertinently, empirical studies have now convincingly demonstrated that the size and composition of female-built blue tit nests directly influences the parental care provided by their male partners and that such care determines both the number and quality of offspring raised (García-Navas et al., 2013; Tomás et al., 2013). Meanwhile, there is also some evidence that females differentially allocate (Sheldon, 2000) their investment in nest building in accordance with the attractiveness of their social partner (Broggi and Senar, 2009; but see Mainwaring et al., 2008) although given the mixed findings to date, then this is an area where further studies are required before robust conclusions can be drawn. Nevertheless, there is good evidence that the nest building behaviors of blue tits and great tits are associated with sexual selection and this may explain why levels of hatching and fledging success are higher in taller nests than in lower nests (Alabrudzińska et al., 2003; Mazgajski and Rykowska, 2008). This suggests that the height of blue tit and great tits nests reflects the outcome of contradictory pressures associated with the need for nests to be low enough to reduce the risk of predation and yet high enough to confer thermoregulatory benefits and/or act as a sexual signal that influences paternal provisioning rates (Alabrudzińska et al., 2003). Further empirical and modeling studies that examine the resolution of this trade-off would be useful as the optimal height of nests is likely to vary both temporally and spatially and in this regard, empirical studies examining how the height of nests vary in relation to the occurrence of nest predators at the landscape scale may be particularly informative.

More broadly, there are three areas in which further research could prove enlightening. First, there is now evidence that the size of blue tit nests act as a sexual signal that informs their partners of their phenotypic quality, yet we still know remarkably little about the relative importance of such signals when compared to other signals such as plumage brightness or song complexity, in influencing their partners' provisioning rates and reproductive investment. In this regard, studies that experimentally disentangle the relative contributions of potential signals by, for example, swapping nests between nestboxes which decouples nest design and plumage brightness in a controlled manner, and then quantifies male provisioning rates are likely to be informative. Second, there is evidence that the height of blue tit and great tit nests act as a sexual signal that informs their partners of their phenotypic quality which means that sexual selection favors birds that build high nests. However, natural selection favors those birds that build low nests as the height of nests is negatively related to the risk of predation. Thus, it seems that natural and sexual selection exert contradictory pressures on the height of nests and given that the risk of predation is greater in higher nests, then it is unclear why the birds build higher nests whenever possible although they may confer thermoregulatory benefits or act as sexual signals that prompt greater male investment in reproduction. Thus, further studies could usefully quantify the thermal properties and moisture retention of nests of varying heights and more broadly, examine how blue and great tits resolve the trade-off between natural and sexual selection over the optimal height of their nests. Third, there is a growing interest in nest building behaviors as a cognitive trait (Guillette and Healy, 2015; Breen et al., 2016) and also on the links between cognition and fitness in the wild (Cole et al., 2012; Cauchard et al., 2013) and so studies that examine the cognitive basis of nest building in blue tits and great tits are likely to prove enlightening.

CONCLUSIONS AND SUGGESTIONS FOR FUTURE WORK

To conclude, blue tits and great tits exhibit a considerable amount of intraspecific variation in the location and design of their nests and our understanding of the causes and consequences of such variation is set to increase further as more studies of birds breeding inside nestboxes are published. There is good evidence that both species select nest sites based on the presence and/or absence of both conspecifics and heterospecifics and whilst neighboring birds were traditionally assumed to adversely affect focal individuals by competing for local resources, they are now considered to sometimes benefit focal individuals by providing information about habitat quality and by contributing to anti-predator defenses. Nest-building females are also able to accurately gauge ambient weather conditions and respond to predictable variation in environmental conditions by building nests with variable amounts of cup lining material to create suitable nest microclimates for nestling growth and development. Meanwhile, both species limit the adverse effects of nest-dwelling parasites and pathogens by incorporating aromatic plant materials that contain a high abundance of volatile secondary metabolites into their nests and reduce the abundance of parasites and thereby increase the fitness of the nestlings and attending parents. The height of their nests is negatively correlated with the risk of predation and so whilst natural selection favors lower nests, it is presently unclear why they build higher nests whenever possible, although it is likely that higher nests confer thermoregulatory benefits or act as sexual signals that prompt greater male investment in reproduction. Indeed, the nest building behaviors of females and the occasional feather carrying behaviors of males are both associated with sexual selection and the size and composition of the female-built nests directly influences male care that subsequently determines both the number and quality of nestlings raised. This suggests that the nest building behaviors of blue tits and great tits vary adaptively in relation to various influences and that nest materials such as feathers and aromatic plants can simultaneously serve multiple functions (Deeming and Mainwaring, 2015) as both play a role in repelling parasites and sexual selection.

The increasing number of studies examining the causes and consequences of intraspecific variation in nest building behaviors in blue tits and great tits, and other species more broadly, reveal a dynamic field of research. There is, nevertheless, plenty of scope for future studies to provide important new insights into their nest building behaviors and whilst I have highlighted specific areas in the sections above, I now highlight some general areas that are also likely to prove fruitful, as further highlighted in **Table 1**. First, there is a need for better designed studies because many studies of blue tits and great tits have just one study plot with one treatment and another plot with another treatment which leaves a single contrast with one degree of freedom (as highlighted by Charmantier and Perret, 2004) thereby limiting the ability to draw solid conclusions. This particularly applies to experimental studies that really need more one study plot with one treatment and another plot with more than one of another treatment. Second, the majority of studies involving nestbox-breeding blue and great tits have been performed in high quality deciduous woodland habitats where the caterpillars on which they feed their nestlings are abundant. However, this is not representative of the full range of habitats in which both species live and means that our understanding of their nesting behaviors may be biased. Thus, further studies could usefully examine the nesting behaviors of great and blue tits living in habitats other than pristine deciduous woodlands, such as urban habitats, which are becoming increasingly prevalent globally (Vaugoyeau et al., 2016). A recent study showed that whilst anthropogenic materials were incorporated into 73 per cent of blue tit nests along an urban-rural gradient in the city of Birmingham, UK, the inclusion of such materials in nests was unrelated to the position along that gradient (Reynolds et al., 2016). However, as the authors of that study suggest, further research is required to assess whether the inclusion of such materials influences the birds' reproductive success. Third, there is evidence that blue and great tit nest building behaviors vary adaptively in relation to, for example, predation risk and environmental conditions and yet direct evidence that nest building behaviors directly influence breeding success remain scarce (but see Álvarez and Barba, 2011; Glądalski et al., 2016; Lambrechts et al., 2016b). This is surprising because higher-quality females building larger nests are expected to enjoy higher levels of reproductive success, whilst larger nests are also expected to provide more protection for the nestlings, in the absence of predation, than smaller nests. However, an 18 year study showed that nest size was unrelated to reproductive success in blue tits (Lambrechts et al., 2016c) and so studies examining how nest size influences breeding success are required. It has been suggested that the absence of a discernible relationship may have arisen because unlike natural holes in trees, nestboxes have a relatively uniform size, even between study sites (Møller et al., 2014a), and as the size of the largest nestboxes are much smaller than the largest natural holes, then this may constrain the ability of higher-quality females that have higher levels of breeding success to build significantly larger nests than lower quality females (Lambrechts et al., 2016c). Alternatively, smaller nests may be beneficial in some instances because, for example, they keep the eggs and nestlings safer from predators and so perhaps we should not expect a relationship between nest size and reproductive success. Either way, studies are required to explicitly examine the link between nest building behaviors and reproductive success as the relationship may well

TABLE 1 | Gaps in the research examining the location and design of blue tit and great tit nests and some suggestions for further research.

Scientific rigor of studies

Research gap

There is a need for better designed studies because much of the research examining the nesting behaviors of blue tits and great tits have one study plot with one treatment and another plot with another treatment which leaves a single contrast with one degree of freedom (e.g., as highlighted and acknowledged by Charmantier and Perret, 2004) thereby limiting the ability to draw robust conclusions.

Suggestion for further research

Studies performed at multiple study sites and across various spatial scales would increase the strength of the conclusions that could be drawn from such studies. This particularly applies to experimental studies that need more than one study plot with one treatment and another plot with more than one of another treatment.

The consequences of variation in nest building behaviors for adult and nestling birds

Research gap

Although we have a reasonable understanding of the causes of intraspecific variation in the design of blue tit and great tit nests, our understanding of the consequences of such variation for both the adults and nestlings remains far from well-understood, although some progress has recently been made (e.g., Tomás et al., 2013).

Suggestion for further research

Studies that experimentally alter the characteristics e.g., height of female-built nests and then examine how male provisioning efforts change in direct response to those nests characteristics, rather than the female, would be useful. It would also be interesting to examine how such changes in parental effort subsequently influence offspring phenotypes both before and after fledging.

The relative influence of nest design as a sexual signal

Research gap

There is evidence that the size of female-built blue tit nests act as a sexual signal that informs their partners of their phenotypic quality, yet we still know remarkably little about the relative importance of nests as signals when compared to other sexual signals, such as the brightness of their plumage or the complexity of the songs, in influencing their males partners' provisioning rates and investment in reproduction.

Suggestion for further research

Studies that experimentally disentangle the relative contributions of such multiple signals by, for example, swapping nests between nestboxes to decouple nest design and plumage brightness in a controlled manner, and then quantify the males' provisioning efforts, would be extremely informative.

The relative influence of natural and sexual selection in determining nest location and design

Research gap

There is evidence that the height of blue tit and great tit nests act as a sexual signal that informs their partners of their phenotypic quality, which means that sexual selection favors birds that build high nests. However, natural selection favors those birds that build low nests as the height of nests, or more specifically the distance between the nestbox entrance and the nest rim, is negatively related to the risk of predation. Thus, it seems that natural and sexual selection exert contradictory pressures on the height of nests within cavities and given that the risk of predation is greater in higher nests, then it is unclear why the birds build higher nests whenever possible.

Suggestion for further research

Further studies could usefully quantify the thermal properties and moisture retention properties of nests of varying heights within cavities and more broadly, examine how blue and great tits resolve the trade-off between natural and sexual selection over the optimal height of their nests.

Nest location and design in a changing climate

Research gap

Studies suggest that both blue tits and great tits are adept at varying the design of their nests to adaptively respond to predictable changes in environmental conditions with increasing latitude, altitude, and increasing spring temperatures in temperate environments, but we currently have little understanding of how nest building behaviors may vary in response to unpredictable changes in environmental conditions associated with anthropogenic climate change. For example, both blue tits and great tits incorporate substantial amounts of mosses into the base layers of their nests and yet climate change is predicted to reduce the cover and growth of most bryophytes in temperate environments (Jägerbrand et al., 2003).

Suggestion for further research

Whilst it appears that both species are presently able to find sufficient amounts of moss to construct their nests, further changes in environmental conditions may mean that bryophytes become a limited resource in the future and so studies that experimentally manipulate the availability of mosses and then quantify the effects on the birds reproductive success could well be informative.

Incorporating empirical data into theoretical models

Research gap

There is a lack of studies incorporating data from empirical studies into theoretical models to examine how intraspecific variation in nest characteristics influence patterns of parental investment and offspring fitness.

Suggestion for further research

Theoretical models that incorporate data from empirical studies to examine how intraspecific variation in nest characteristics are expected to influence parental investment and offspring fitness would be extremely useful to determine the importance of nests as sexually-selected signals of the builders' phenotypic quality. Then, the findings can be used to guide further empirical studies that examine how the females' investment in nest building influences her own and her male partners' investment in subsequent stages of reproduction.

(Continued)

TABLE 1 | Continued

Is nest size directly related to reproductive success?

Research gap

There is widespread evidence that blue tit and great tit nest building behaviors vary adaptively in relation to, for example, predation risk and environmental conditions and yet direct evidence linking nesting behaviors and breeding success remain scarce (but see Glądalski et al., 2016; Lambrechts et al., 2016b). This is surprising because higher-quality females building larger nests should have higher levels of breeding success, whilst larger nests are also expected to provide more protection for the nestlings, in the absence of predation, than smaller nests. However, an 18 year study showed nest size was unrelated to breeding success in blue tits (Lambrechts et al., 2016c) and so studies examining how nest size influences breeding success are required.

Suggestion for further research

Studies are required to explicitly examine the link between nest building behaviors and reproductive success as the relationship may well be a complex one that varies over both spatial and temporal scales. In this regard, studies that experimentally alter nest size are likely to be informative.

Do females chose the nest site alone?

Research gap

It has generally been thought that the females of both species chose the nest site (Cramp and Perrins, 1993) but a recent experiment suggests that males may play a greater role than previously thought. In that experiment, older male great tits actively chose to copy the choices of previously settled conspecifics, independently of females (Loukola et al., 2012), which suggests that older males were basing their settlement decisions on the proximity to conspecifics possibly in order to obtain extra pair paternities. Therefore, studies that examine the relative influence of males and females in choosing the nest site are required.

Suggestion for further research

Studies that experimentally alter the clumping patterns of nestboxes so that some are solitary whilst others are grouped and which then examine the age of males and patterns of paternity within broods may be informative in this regard.

More studies are needed in various habitat types

Research gap

The overwhelming majority of studies involving nestbox-breeding blue and great tits have been performed in high quality deciduous woodland habitats where the caterpillars on which they provision their nestlings are abundant. However, this is not representative of the full range of habitats in which both species live and means that our understanding of their nesting behaviors may be biased. Pertinently, when nestboxes with various cavity sizes are erected in high quality deciduous woodlands, great tits usually occupy nestboxes with the largest cavities (e.g., Karlsson and Nilsson, 1977) and with an abundance of caterpillar prey available, they lay larger clutches and fledge more offspring. However, when nestboxes with three different cavity sizes were provided in the city of Montpellier, France, great tits preferentially chose nestboxes with the largest cavities but whilst birds in those nestboxes laid larger clutches than conspecifics in nestboxes with smaller cavities, they subsequently fledged fewer nestlings (Demeyrier et al., 2016). This suggests that nestboxes with larger cavities were acting as ecological traps in urban areas because whilst the birds actively chose to occupy them, the occupants fledged fewer offspring (Schlaepfer et al., 2002). As there were no differences in hatching success between cavity sizes, then the effect occurred during the nestling provisioning stage and it was thought that it may have been difficult for parents to find a sufficient amount of caterpillars in the insect-poor exotic vegetation within the city to feed the nestlings (Demeyrier et al., 2016).

Suggestion for further research

Further studies should examine the nesting behaviors of great tits and blue tits living in habitats other than pristine deciduous woodlands because it is important to quantify such behaviors in other habitats, such as urban habitats which are becoming increasingly prevalent globally (Vaugoyeau et al., 2016). A recent study showed that whilst anthropogenic materials were incorporated into 73 per cent of blue tit nests along an urban-rural gradient in the city of Birmingham, UK, the inclusion of such materials in nests was unrelated to the position along that gradient (Reynolds et al., 2016). However, as the authors of that study suggest, further research is required to assess whether the inclusion of anthropogenic materials influences breeding success.

The cognitive basis of nest building behaviors

Research gap

It is becoming increasingly apparent that avian nest building requires a considerable amount of cognitive skill and whilst studies of captive birds have been very informative, we have little idea of the cognitive basis of nest building behaviors in either blue tits or great tits.

Suggestion for further research

Studies that examine the cognitive basis of nest building behaviors in blue and great tits are to be welcomed and given that both species readily breed in nestboxes, such studies should be relatively easy to accomplish.

Putting studies of blue tits and great tits into a wider ecological context

Research gap

Whilst the number of studies examining blue and great tit nests is commendable, more studies of dissimilar species are required to increase our understanding of intraspecific variation in nesting behavior.

Suggestion for further research

As both blue tits and great tits are hole nesting birds in which the female alone builds the nest, then studies of open cup nesting species and species in which males alone or both parents build the nest would be particularly useful as they are likely to choose nest sites and build their nests under very different selection pressures to the more widely studied blue and great tits. For logistical reasons, these study species may well be passerines and so studies that examine the nests of raptors, herons or water birds would be very useful.

be a complex one that varies over both spatial and temporal scales.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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