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Nestbox Orientation: A Species-Specific Influence on Occupation and Breeding Success in Woodland Passerines

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Summary

Capsule Nestbox orientation has species-specific influences on nestbox occupation and breeding success for woodland passerines.

Aims To determine if nestbox orientation had any influence upon nestbox selection or breeding success for three co-occurring woodland passerines: Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*, and Pied Flycatcher *Ficedula hypoleuca*.

Methods We analysed 15 consecutive years of breeding data (1990-2004) from 295 nestboxes in the UK using circular statistical analyses to examine the influence of orientation upon nestbox occupation and breeding success for three study species.

Results The three species used nestboxes of all orientations during the 15-year period. The frequency of nestbox occupation by Great Tits correlated with orientation (the mean number of nests in boxes oriented south-southwest was lower than the mean number of nests in boxes facing other directions). There was no such relationship for Blue Tits or Pied Flycatchers. Nestbox orientation influenced the breeding success of Pied Flycatcher (the mean number of young to fledge from boxes oriented south-southwest was lower than from boxes facing other directions). There was no such relationship for Blue or Great Tits.

Conclusion Nestbox orientation can be an important influence on occupation and breeding success, but this differed between species. Intriguingly, although the directionality reduced nestbox occupation (Great Tit) and breeding success (Pied Flycatcher) was the same (south-southwest), there was a disparity in the influence of orientation for Great Tit (orientation influenced the frequency of occupation but not success) and Pied Flycatcher (orientation did not influence occupation but did affect success). We discuss these disparities, considering the possible influences of mating strategy, breeding phenology, nestbox microclimate, and offspring quality.

<u>Introduction</u>

Reproductive success depends on many interacting factors and consequently most nest-building species expend time and energy selecting their nest site according to their specific requirements. Nest-site selection and subsequent breeding success can be influenced by many disparate environmental and habitat-dependent variables (Stauffer & Best, 1982). For the 13% of bird species that nest in cavities (Newton, 1998), orientation of the cavity entrance is a variable that can influence both nest-site selection and breeding success (Martin *et al.*, 1997).

Several cavity-nesting bird species have a directional preference that influences their choice of nest cavity; for example, the majority of cavities used by White-breasted Nuthatches *Sitta carolinensis* and Pigmy Nuthatches *S. pygmaea* face southeast (McEllin, 1979). Other species exhibit a directional avoidance; for example, European Starlings *Sturnus vulgaris* avoid cavities facing west-northwest (van Balen *et al.*, 1982). These non-uniform patterns of cavity occupation may have evolved to facilitate regulation of nest microclimate (Inouye *et al.*, 1981; Burton, 2006). Orientation can affect cavity temperature; for example, east-facing cavities are warmed by the early-morning sun (Raphael, 1985; Dhondt & Phillips, 2001) while nesting in cavities facing certain (often site-specific) directions can influence exposure to prevailing wind and rain (du Feu, 2003).

Orientation can also influence breeding success, either with or without influencing nest-site selection. However, relatively few studies have explored these complex relationships. For some species such as the Mountain Bluebird *Sialia currucoides* and the Black-capped Chickadee *Poecile atricapillus*, orientation appears to have no influence on either cavity selection or breeding success (Peterson & Gauthier, 1985; Mennill & Ratcliffe, 2004). Other species select their nest cavity independently of orientation, although orientation affects subsequent breeding success. For example, while Eastern Bluebirds *Sialia sialis* do not choose nest cavities according to orientation (Pinkowski, 1976) individuals nesting in northeast-facing cavities fledge a significantly higher number of young than those using cavities oriented west (Dhondt & Phillips, 2001). Conversely, a species may exhibit an orientation preference that is not converted into increased reproductive success. For example, although Tree Swallows *Tachycineta bicolor* exhibit a preference for cavities facing south-southeast, this does not influence the number of young that they fledge (Rendell & Robertson, 1994). Finally, orientation is a potential influence on both cavity selection and breeding success, such that nest-site selection becomes a direct adaptation to increase reproductive success (Misenhelter & Rotenberry, 2000). This has not been well-studied for secondary cavity-nesting birds, but has been observed for species that build domed nests with a side entrance hole: late-breeding Cactus Wrens *Camplylorhynchus brunneicapillus* that build nests with an entrance facing their preferred direction (southwest to northwest) fledge at least one young on 72.1% of occasions compared with 53.7% for individuals using nests facing any other orientation (Austin, 1974). These studies hint at the complex relationships that can exist between orientation, occupation and breeding success. However, this complexity has been established through disparate, often small-scale, studies of different species in diverse habitats and, for cavity-nesting species, almost exclusively for birds using natural cavities.

Using nestboxes to study the influence of orientation

Directional preference in primary cavity-nesting species (species which excavate their own cavity) can be directly inferred (Zwartjes & Nordell, 1998). However, secondary cavity-nesting species (those which use natural or previously-excavated cavities) are influenced by the availability of existing cavities. In extreme cases, all natural cavities might be oriented in one direction (Stauffer & Best, 1982), disguising any orientation preference or effect on breeding success (Gaedecke & Winkel, 2005). Nesting success of birds using natural cavities can also be difficult to determine reliably. Artificial nestboxes are ideal for studying nest-site selection and breeding success. If nestboxes are erected randomly (or nearly so), they offer considerable directional choice. Any skew in the nestbox resource should be minor and can be compensated for in analysis. Monitoring nesting success is also much easier in nestboxes as it involves limited disturbance.

In addition to the convenience of using nestboxes for evolutionary ecology studies, there is also a practical need for such research. Bird nestboxes have been used for many years as a method of *in situ* conservation. They can increase the number of potential nesting sites and improve the success of each nesting attempt (Minot & Perrins, 1986; Newton, 1994; Purcell *et al.*, 1997; Lõhmus & Remm, 2005). Providing nestboxes in wooded habitats is particularly important given woodland bird decline (Quine & Freer-Smith, 2000; Fuller *et al.*, 2005; Amar *et al.*, 2006). Research into the influence of nestbox orientation on occupation and breeding success could aid conservation efforts by allowing maximally effective placement of nestboxes for the promotion of a given species.

Study aims

In this study, we use data from a long-term woodland nestbox scheme in the UK to analyse the influence of orientation on nestbox occupation and breeding success by three typical co-occurring species: Blue Tit *Cyanistes* (= *Parus*) *caeruleus* (L.), Great Tit *Parus major* L., and Pied Flycatcher *Ficedula hypoleuca* (Pallas). To our knowledge, no quantitative research has been previously undertaken on the influence of orientation on both nest-site selection and breeding success for any of these species. Moreover, we are aware of only one study on directional preferences of Blue and Great Tits using natural cavities (van Balen *et al.*, 1982) and one study of Pied Flycatchers using nestboxes (Gaedecke & Winkel, 2005). Neither of these studies link patterns in nest-site selection to breeding success. Here, we determine: (1) whether these species exhibit any directional preference or avoidance in their choice of nest site; and (2) whether any such variation in nestbox selection might be adaptive to variations in breeding success. Then, using a comparative approach between species (two resident monogamous passerines and one migratory passerine which exhibits polygyny), we explore possible reasons for the disparities in the influence of orientation on nestbox selection and breeding success by considering mating strategy, breeding phenology, nestbox microclimate, and offspring quality.

<u>Methods</u>

Study rationale

Because nest-site selection and breeding success can be influenced by many interacting factors, multivariate techniques are usually considered the best method of analysis. However, multivariate analyses are only suitable for linear variables (measured on ratio, interval, ordinal, or nominal scales), not for circular variables. Circular variables can only be included in multivariate tests using arbitrary categories, a process which involves considerable data loss and substantially increases the risk of type I errors. Accordingly, the best method of establishing orientation patterns is to analyse orientation data univariately on a continuous scale using circular statistics which allow for 0° and 360° being equivalent (Batschelet, 1981) while taking possible confounding linear variables (see below) into account (Møller, 1992).

Study area

This study was undertaken at Nagshead Nature Reserve (Gloucestershire, U.K., 2°34'0"W, 51°47'0"N). The reserve has a nationally important diversity of breeding birds (Proctor & Pollard, 2000) and manages an extensive nestbox scheme which started in 1942 and is now the longest-running nestbox scheme in the U.K. (Campbell, 1968). The nestboxes are located in a pre-1850 broadleaf plantation, dominated by Pedunculate Oak *Quercus robur*. The nestboxes were not erected according to any intentional directional criteria and there are at least 10 nestboxes in each 30° compass sector. As nestboxes are provided in abundance (mean occupation rate 71.74%), birds have choice in the nestbox resource, such that determining selection, preference and avoidance patterns is possible (Petit & Petit, 1996).

Orientation of nestboxes

To determine the orientation of each nestbox, a line-of-sight compass (Silva Voyager 8040) with a resolution of 1° was used to record the bearing of an imaginary line passing perpendicularly through the entrance hole from directly in front of the nestbox. The reading was transformed to give the angle faced by that nestbox in degrees from magnetic north (Rendell & Robertson, 1994). All measurements were taken at least 10m from the nestbox to ensure an accuracy of ± 1° (verified trigonometrically and by pilot experimentation).

Other nestbox variables

Several variables, other than orientation, pertaining to the placement and habitat surrounding each nestbox were measured as part of a larger study. These variables were: (1) height of nestbox above ground; (2) slope angle facing away from the nestbox; (3) number of trees in a circular plot around each nestbox (nestbox plot size = 0.05ha; plot radius = 12.52m: James & Shugart, 1970); (4) percentage shrub cover (primarily Holly *Ilex aquifolium* and Bramble *Rubus fruticosus agg*) in the nestbox plot; (5) percentage field-layer (primarily Bracken *Pteridium aquilinum*) in the nestbox plot; and (6) canopy coverage percentage calculated using canopy photography (A. Goodenough, *in prep*). To mitigate against non-orientation factors

becoming confounding variables, each of these parameters was correlated with orientation to ensure that there was no coincidental correlation after linear data had been log (*ln*+1) or arcsine square root transformed as necessary to normalise them (see results).

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Breeding data

Breeding data (clutch size, number of young to hatch, and number of young to fledge) from each Nagshead nestbox during the period 1990-2004 were obtained from the Royal Society for the Protection of Birds (RSPB) who manage the study site. These data were collected during weekly nestbox visits throughout the

8 breeding season. Records for the three species that used nestboxes frequently enough to permit statistical analysis – Blue Tit, Great Tit and Pied Flycatcher – were analysed. Only data from the 295 wooden nestboxes which had a standard shape and size (rectangular with a sloping roof; approximate internal

12 measurements: 110mm width, 170mm depth, 210mm mid-point height) and which had been available throughout the entire period in exactly the same position with the same orientation were included in the study. This avoided variability in nestbox-specific attributes other than orientation (size, shape etc.) and ensured that the orientation of individual boxes was temporally consistent for analysis. This gave a total of

16 3,070 breeding attempts, of which 3,060 had a known outcome. Two relative measures of breeding success (the proportion of eggs to hatch per clutch and the proportion of young to fledge per brood) were calculable from the available data. For each species, the annual data were pooled for each nestbox through the 15-year period to provide average species-specific breeding success per nestbox. This was necessary to

20 mitigate against the temporal pseudoreplication that would have resulted from having multiple samples (breeding attempts) per experimental unit (nestbox) (Hurlbert, 1984). Experimental analysis on individual years indicated that there was no significant difference in the influence of orientation between years, such that data pooling was appropriate for this dataset.

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Statistical analyses

Before analysis, count data were log-transformed (*ln*+1) and proportional data were arcsine square root transformed to normalise them (Townend, 2002). The nestbox data followed a von Mises distribution[a] and

28 did not require transformation. All circular statistics were calculated using Oriana Circular Statistics for Windows version 2.0 (Kovach Computing Services, Pentraeth, Wales).

To establish whether the nestbox resource was itself randomly distributed, two different one-sample tests – Rayleigh's test (for unimodal patterns) and Rao's spacing test (for multimodal distributions) (Bergin,

32 1991) – were performed. To compare the circular distributions of boxes that had been occupied at least once in the 15-year period with those that had not, three Mardia-Watson-Wheeler two-sample tests (one for each study species) were performed (Wallraff, 1974)[b]. Ties between the two datasets were broken by the random allocation of different ranks (Batschelet, 1981). A non-significant result from this test was good

36 evidence that the test species was using nestboxes randomly within the original skewed distribution.

However, there remained a slight risk that a small directional preference could be masked if it coincided with the bias in the nestbox resource. Accordingly, the nestboxes were divided into 12 directional categories (30° binwidth) and 10 nestboxes were randomly selected from each (10 were selected as this was the total number of nestboxes in the least-frequented category). This stratified random subset gave a uniform base distribution against which the circular distribution of boxes which had been occupied at least once during the 15-year period could be compared using chi-square analysis (Lehner, 1996). The grouping technique was done in addition to the Mardia-Watson-Wheeler test as a verification of a randomness result. It was not used as the main method of determining patterns in nestbox usage due to the information loss involved (only 120 boxes could be analysed for reasons explained above, whereas the two-sample test allowed records from all 295 boxes to be used). No measure of nestbox availability during the selection of individual nestboxes could be added into analyses (Johnson, 1980) as: (1) this would have necessitated continual monitoring of the occupation status of all nestboxes; and (2) there arises the question of when nestbox actually becomes 'occupied': whether this is when a nestbox is part of an active territory, when nesting material is first introduced, when the nest is completed, or when egg-laying has commenced.

To detect any relationship between orientation and the frequency of nestbox occupations (i.e. the number of occupations during the 15-year period) by each study species, parametric circular-linear correlation (Fisher, 1993) was used. This technique was also used to identify any relationship between nestbox orientation and the five measures of breeding success (see above) for each study species. Because of the possibility of pseudo-significance, Bonferroni probability values were calculated for these analyses (Rice, 1989). Finally, to establish whether any relationship between orientation and breeding success was the result of a difference in the number of young to fledge per breeding attempt or a difference in the nest failure rate, the orientations of failed nests (no young fledged) and successful nests (at least one young fledged) were compared using the Mardia-Watson-Wheeler test.

Nestbox distribution

The circular distribution of the nestbox resource deviated significantly from uniform (Rayleigh's test $Z =$ 28.222, $n = 295$, $P < 0.001$; Rao's spacing test $U = 160.254$, $n = 295$, $P < 0.001$) with a skew in nestbox orientation towards the northwest (mean vector angle = 317.9°; mean vector length = 0.309) (Fig. 1a). This meant that two-sample tests were necessary to investigate relationships between orientation and occupation.

Other nestbox variables

There was no coincidental correlation between orientation and any other measured nest site characteristics (height above ground, slope angle, surrounding vegetation species, vegetation structure and canopy coverage: circular-linear correlation after any necessary transformation to normalise linear data $P > 0.05$).

Nestbox occupation

To ascertain whether species-specific occupation of nestboxes was related to orientation, the circular distribution of boxes that had been occupied at least once in the 15-year period was compared with the circular distribution of those which had never been occupied using Mardia-Watson-Wheeler and chi-square tests (Fig. 1 b-d). The frequency of nestbox occupation was then correlated with orientation using circular-linear correlation (shown for Great Tits in Fig. 2).

Great Tits used nestboxes of any orientation during the 15-year period (Table 1, Fig. 1c). However, the frequency of nestbox occupation by Great Tits (i.e. the number of years that each of the 228 nestboxes occupied at least once by this species during the study period was used: range 1-9 years) correlated with orientation (circular-linear correlation $r = 0.14$, $n = 228$, $P = 0.012$). The mean number of Great Tit occupations of boxes oriented south-southwest (180-209°) was 32% lower than the mean number of occupations of boxes facing all other directions combined (1.7 ± 0.28 SEM occupations in 15 years versus 2.6 ± 0.12 SEM; Fig. 2). This decrease was significant (two-tailed t-test $t = 1.980$, d.f. = 226, $P = 0.049$).

Blue Tits and Pied Flycatchers both used nestboxes randomly within the original skewed distribution (Table 1, Fig. 1 b & d) and there was no relationship between the orientation and the frequency of nestbox occupation for either species (Blue Tit: $r = 0.030$, $n = 283$, $P = 0.766$; Pied Flycatcher: $r = 0.028$, $n = 258$, $P = 0.818$).

Breeding success

Nestbox orientation influenced the number of Pied Flycatcher young to fledge (parametric circular-linear correlation $r = 0.093$, $n = 722$ nests in 241 nestboxes, $P = 0.009$). The proportion of young to fledge also correlated with orientation (Table 2). Conversely, clutch size, the number of young to hatch, and the proportion of eggs to hatch appeared to be independent of orientation (Table 2). Repeating the correlation

analysis on the dataset after removal of two outliers caused by nests with a particularly high number of young to fledge slightly increased the strength of the correlations previously identified and had no influence on the non-significant results. This confirmed that these correlations were not the result of outlying data points. Similarly, repeating the analysis after failed nests (see below) had been removed did not alter the significance of results. To determine the nature of the relationship between orientation and fledging success for Pied Flycatchers, data were grouped into 30° categories (Fig. 3). The highest mean number of young to fledge came from boxes oriented north-northeast (0-29°), the lowest from boxes facing southwest (210-239°) (4.8 ± 0.46 SEM fledged per brood versus 3.8 ± 0.31 SEM). This gave a percentage difference of 24.1% and a difference in real terms of one fledgling per nestbox per brood. Nestboxes with the lowest mean number of young to fledge were grouped in three adjoining directional categories (180-209°, 210-239°, and 240-269°): the south-west compass quarter. This decrease in fledging success was significant: the mean number of young to fledge from boxes oriented in these directions (180-269°) was significantly lower than the mean number of young to fledge from all other directions (3.9 ± 0.14 SEM fledged per brood versus 4.5 ± 0.11 SEM; two-tailed t-test t = -2.560, d.f. = 720, P = 0.010). The percentage difference in productivity between south-southwest facing boxes and nestboxes facing other directions was 15.7% or 0.6 of a fledgling per brood.

There was no difference in circular distribution between Pied Flycatcher nests that failed and nests in which one or more young successfully fledged (Mardia-Watson-Wheeler test W = 4.164, N_1 = 151, N_2 = 572, P = 0.125). This indicated that the lower fledging success in boxes facing south-southwest was caused by a reduction in the actual number of young fledging, not simply by a greater number of failed nests oriented in this direction.

Nestbox orientation did not influence the number of young to fledge for either Blue Tits (circular-linear correlation r = 0.031, n = 1,755 nests in 283 nestboxes, P = 0.178) or Great Tits (r = 0.036, n = 583 nests in 228 nestboxes, P = 0.469), neither was a relationship between orientation and any other breeding parameter identified for these species (Table 2).

<u>Discussion</u>

We examined the influence of orientation on nestbox occupation and breeding success for Blue Tits, Great Tits, and Pied Flycatchers. Results were highly species-specific: for Blue Tits, orientation did not influence occupation or success; for Great Tits, orientation influenced the frequency of occupation but did not affect success; while for Pied Flycatchers orientation did not influence occupation but affected success.

Nestbox occupation

The three study species use nestboxes of any orientation (Fig. 1 b-d). This finding is consistent with studies on other passerines, including Eastern Bluebirds (Pinkowski, 1976) and Prothonotary Warblers *Protonotaria citrea* (Blem & Blem, 1991). However, although Great Tits did occupy nestboxes of any orientation, boxes facing south-southwest were occupied 32% less frequently than those facing other directions (Fig. 2), a relationship not found for Blue Tits or Pied Flycatchers. For Blue Tits, these results agree with those of van Balen *et al.* (1982) who found no relationship between orientation and selection of natural cavities. Thus, with respect to orientation, the breeding strategy of this species appears identical whether natural or artificial sites are used. However, for Great Tits the findings differ: the non-random pattern in the frequency of occupation identified here was not found by van Balen *et al.* (1982). This may be because the nesting records analysed here were from nestboxes rather than natural cavities or because van Balen's study could only consider data from three years whereas here we used data from 15 years. The lack of nestbox choice in relation to orientation for Pied Flycatchers at Nagshead is contrary to the findings of Gaedecke & Winkel (2005) in Germany. This might indicate site-specific variation in the influence of orientation, or demonstrate that inter-specific competition for nestboxes at Nagshead (higher than in Germany) is forcing occupation of nestboxes facing directions other than that which is preferred (see below).

Nestbox breeding success

Nestbox orientation is an important influence on the number of young to fledge per brood for Pied Flycatchers (Fig. 3). Clutch size and hatching success remain independent of orientation, indicating that orientation is important during the nestling stage alone. This accords with a similar finding for Eastern Bluebirds in the USA (Dhondt & Phillips, 2001). However, the 24.1% difference in fledging success for Pied Flycatchers between the most and least successful orientations found at Nagshead is greater than the 13.7% difference for Eastern Bluebirds found by Dhondt & Phillips (2001). As the number of nests to fail completely does not differ with orientation, it seems that predation (responsible for 57% of failures) and desertion (responsible for 27% of failures) of entire broods is not responsible for the lower fledging success in boxes facing south-southwest.

The non-uniform patterns in occupation (Great Tit) and fledging success (Pied Flycatcher)

Although internal temperatures of nestboxes are known to correlate with orientation in open habitats (Ardia *et al.*, 2006), it has been assumed that shading from the tree canopy in woodland habitats mediates any

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microclimatic effect arising from nestbox orientation (Hickin, 1971; du Feu, 2003). However, preliminary measurements using temperature data loggers (A. Goodenough, unpubl. data) indicate microclimatic variations in nestbox temperature with orientation, even in a wooded habitat: between 12.00-17.00 (GMT) when temperatures peak, nestboxes facing south-southwest have higher internal temperatures than boxes facing other directions by about 1°C. These variations could account for the reduced occupation of nestboxes facing south-southwest by Great Tits and possible thermal stress in Pied Flycatcher nestlings (van Balen & Cavé, 1970; Dawson & Whittow, 2000) which may account for the reduced fledging levels in boxes oriented in this direction. Alternatively, the reduced occupation of nestboxes by Great Tits and the decreased fledging success of Pied Flycatchers facing south-southwest could be due to increased exposure to prevailing wind and rain (Conner, 1975; Austin, 1976; Balgooyen, 1976; Facemire *et al.*, 1990) or a higher level of humidity. The intrusion of rain into the nesting chamber has previously been found to cause nestling death in natural cavities (Nilsson, 1975), while wind direction influences the breeding success of the Cactus Wren (Austin, 1974). Further study to test these possible reasons for the non-uniformity in occupation and breeding success would be interesting, particularly at other sites to establish if there is any spatial heterogeneity in the influence of orientation on avian reproduction.

The lack of any negative effect on breeding success in boxes avoided by Great Tits

Whatever factors are responsible for the non-random pattern in the frequency of nestbox occupation by Great Tits, their breeding success remains unaffected by orientation. This is similar to Tree Swallows in Ontario which also exhibit non-random nest cavity selection that does not influence subsequent breeding success (Rendell & Robertson, 1994). It is intriguing that Great Tits appear to avoid using nestboxes facing south-southwest when breeding success is no lower in these boxes than in those facing any other direction. It is possible that such an effect is masked by other factors, or that offspring quality might be influenced by orientation, such that offspring from boxes facing south-southwest are less fit. As offspring quality is an important determinant of survival and fecundity, any factors that decrease offspring quality would be likely to become strong nest-site selection pressures. Empirical testing of this hypothesis is an important area for further study.

The lack of modified nestbox selection by Pied Flycatchers

Importantly, regardless of the reasons for the non-uniform pattern in fledging success for Pied Flycatchers, there appears to be no modification of nesting behaviour so that boxes with lower fledging success rates are avoided. This seems surprising given the magnitude of the difference in fledging numbers. Several possible reasons may explain this, all of which are opportunities for future study. Firstly, the expectation that Pied Flycatchers should modify their nestbox selection presupposes that such a modification would be possible or effective. At Nagshead, an average 28.26% of nestboxes (83 individual boxes) remain

unoccupied each year so there is always, theoretically, some choice. It is for this reason that terms such as "selection", "choice" and "avoidance" have been used throughout this study (Johnson, 1980). Indeed, in every year there were at least as many unoccupied nestboxes facing directions other than south-southwest as there were Pied Flycatchers nesting in boxes facing south-southwest. Moreover, experimental analysis on individual years indicted that there was no between-year variation in the relationship between occupation and orientation according to the nestbox occupation level, as might be expected if Pied Flycatchers were being prevented from modifying their nest-boxes selection by a lack of choice. However, the surplus of nestboxes discussed above is at reserve-level; not necessarily at individual territory-level. Moreover, mating strategy may further restrict choice opportunities as male Pied Flycatchers often only defend a territory with a single cavity (Lundberg & Alatalo, 1992). Secondly, although a south-southwest orientation appears to adversely influence the young, this negative affect may be offset for the parents by other factors. If the cost of finding a nestbox with an orientation other than south-southwest is high for the parents it may not be outweighed by the benefits (Alatalo *et al.*, 1988). This is particularly true given that Pied Flycatchers undertake a comparatively brief search for mates and nest sites (Dale *et al.*, 1992) when many boxes are already occupied by resident species. When the search-cost of finding nestboxes with different orientations was experimentally decreased by placing eight nestboxes around individual trees in Germany (Gaedecke & Winkel, 2005) Pied Flycatchers did exhibit non-uniform occupation with boxes facing east being preferentially selected. Thus it is possible that absence of modified nestbox selection (but not the orientation-success relationship) found at Nagshead is a result of interactions between the study species. Thirdly, the relationship between orientation and nesting success has taken no account of offspring quality. As the fitness of parent birds increases not with the number of offspring to fledge, but with the number of offspring who survive, enter the breeding population and successfully raise their own offspring, it might be better to fledge fewer, but fitter, young. In this case, adapting nestbox selection to increase the number of young which fledge could cause supra-optimal breeding resulting in an ecological trap (Mänd *et al.*, 2005). Finally, the orientation-success relationship may be a localised and/or a relatively recent phenomenon. This might account for the apparent absence of adaptive nestbox selection, and also demonstrates how important local research is in achieving successful avian conservation.

Conservation management implications

All of the study species will use nestboxes of any orientation. However, modifying nestbox orientation away from the south-southwest may increase the frequency of nestbox occupations for Great Tits.

Orientation influences nesting success for Pied Flycatchers, a species that is declining throughout Britain (Amar *et al.*, 2006) and undergoing severe decline at the edge of the breeding range (Lander, 2003). Individuals that occupy boxes facing south-southwest on average fledge fewer young per breeding attempt than individuals using boxes of any other orientation. If all 53 south-southwest facing nestboxes that we analysed at the study site in the period 1990-2004 had been oriented in other directions (and the same

number of breeding attempts had taken place), nearly 100 extra birds would have fledged: a productivity increase of 3.3%. It is recognised that the number of young to fledge is not always the primary influence on total population size: for example, the declining population of the Spotted Flycatcher *Muscicapa striata* in

4   Britain is the result of decreased first-year survival rates (Freeman & Crick, 2003). However, for Pied Flycatchers, the number of young to fledge is a major factor governing population dynamics (Lundberg & Alatalo, 1992). This suggests that increasing the number of young to fledge at breeding sites (certainly where nestbox availability is limited) by ensuring that nestboxes for Pied Flycatchers are sited in an arc

8   from west through north to south will have a beneficial influence on the total population, regardless of whatever factors may be causing the apparent decline of this species. However, research would need to be undertaken to establish if increased fledging success is translated into increased recruitment into the breeding population, rather than simply increasing post-fledging mortality.

12   With woodland birds in general decline (Fuller *et al.*, 2005; Amar *et al.*, 2006) better understanding of the complexity of interaction between environment, nest-site selection and breeding success, as demonstrated here, is essential to developing a maximally effective conservation strategy.

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Endnotes

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[a] A von Mises distribution is the circular equivalent of a linear normal distribution (Batschelet, 1981). Data following a von Mises distribution do not require transformation before parametric circular statistics are used.

[b] Use of one-sample tests to compare occupation data against a hypothetical uniform distribution were not appropriate as the Nagshead nestbox resource was not uniformly distributed as regards orientation.

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Table 1 - The relationship between orientation and occupation for Blue Tit, Great Tit and Pied Flycatcher nesting in Nagshead nestboxes between 1990-2004.

	Mardia-Watson-Wheeler test					Chi-square test		
	W	n_1	n_2	P		χ^2	d.f	P
Blue Tit	0.442	12	283	0.802		0.304	7	1.000
Great Tit	2.861	67	228	0.239		2.613	7	0.995
Pied Flycatcher	0.931	37	258	0.628		1.923	7	0.964

The Mardia-Watson-Wheeler test was undertaken on the complete dataset ($n = 295$), while the chi-square test was undertaken on a uniformly-oriented nestbox subset of 120 boxes (10 in each 30° category). A non-significant result is evidence of nestboxes of all directions being occupied in the 15-year study period.

Table 2 - The relationship between orientation and breeding success for Blue Tit, Great Tit and Pied Flycatcher nesting in Nagshead nestboxes between 1990-2004.

Species Measure of breeding success	n (Nests)	(Nestboxes)	r	P	Adj. P
Cyanistes caeruleus					
Clutch size	1,745	283	0.021	0.475	1.000
Number of young to hatch	1,723	283	0.029	0.238	1.000
Number of young to fledge	1,765	283	0.031	0.178	0.890
Proportion of eggs to hatch	1,697	283	0.032	0.179	0.895
Proportion of young to fledge	1,539	283	0.025	0.383	1.000
Parus major					
Clutch size	564	228	0.040	0.404	1.000
Number of young to hatch	571	228	0.025	0.694	1.000
Number of young to fledge	583	228	0.036	0.469	1.000
Proportion of eggs to hatch	552	228	0.009	0.953	1.000
Proportion of young to fledge	502	228	0.041	0.435	1.000
Ficedula hypoleuca					
Clutch size	732	251	0.032	0.982	1.000
Number of young to hatch	725	244	0.025	0.970	1.000
Number of young to fledge	722	241	0.093	0.009	0.045
Proportion of eggs to hatch	725	244	0.022	0.803	1.000
Proportion of young to fledge	722	241	0.097	0.007	0.035

Data were analysed using parametric circular-linear correlation (n = number of nests over the 15-year period and the number of nestboxes concerned). Annual data were pooled for each nestbox to provide average species-specific breeding success per nestbox to avoid temporal pseudoreplication. The adjusted *P* value was calculated using the Bonferroni method as per (Rice, 1989) to allow for the multiple calculations for each study species. These are reported in addition to the standard *P* value: note that the use of Bonferroni adjusted *P* values did not change the significance of any test. The sample sizes vary between analyses for the same species because the outcome of all individual stages of a single nest was not always known with certainty, for example clutch size was not always known for early nests, while the number of young to hatch/fledge was unclear for nests that failed late on in the breeding process. For *F. hypoleuca*, it should be noted that seven nests were occupied but predated during egg laying, such that the clutch size was unknown. These were excluded from analyses of breeding success here but included in analyses of occupation to give 739 nests in 258 nestboxes.

Figure 1 – Circular histograms of the Nagshead nestboxes showing: (a) the circular distribution (i.e. the number of nestboxes) facing each direction ($n = 295$); (b-d) the number of boxes in a 120 uniformly-oriented nestbox subset (10 nestboxes in each 30° category) that have been occupied at least once in the 15-year period by Blue Tit, Great Tit and Pied Flycatcher, respectively. The species distributions (b-d) did not deviate significantly from uniform. It was not possible to compare the distribution of occupied versus unoccupied boxes regardless of species as each box was occupied at least four times.

Figure 2 – Mean number of years nestboxes were occupied by Great Tits according to orientation ($n = 583$ nests in 228 nestboxes).

Figure 3 – Mean numbers of Pied Flycatcher young to fledge per brood in the 15-year period 1990-2004 according to the orientation of nestbox ($n = 722$ nests in 241 nestboxes).
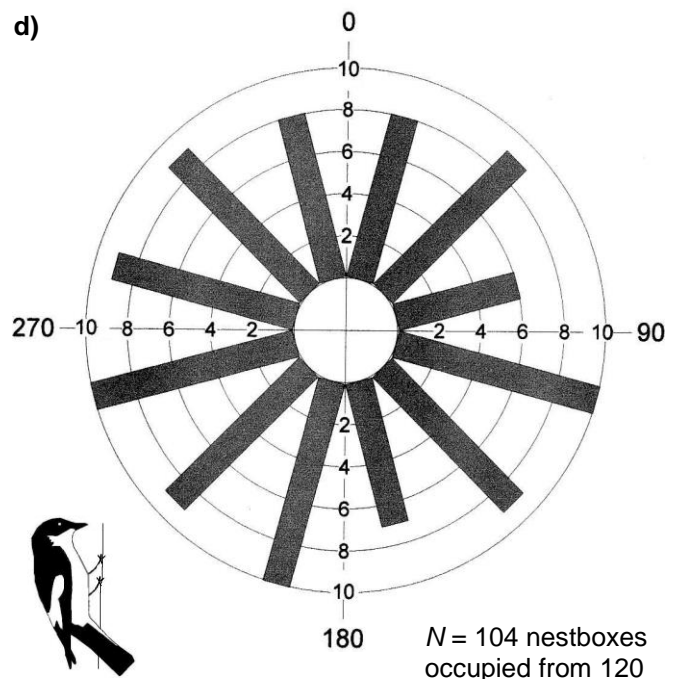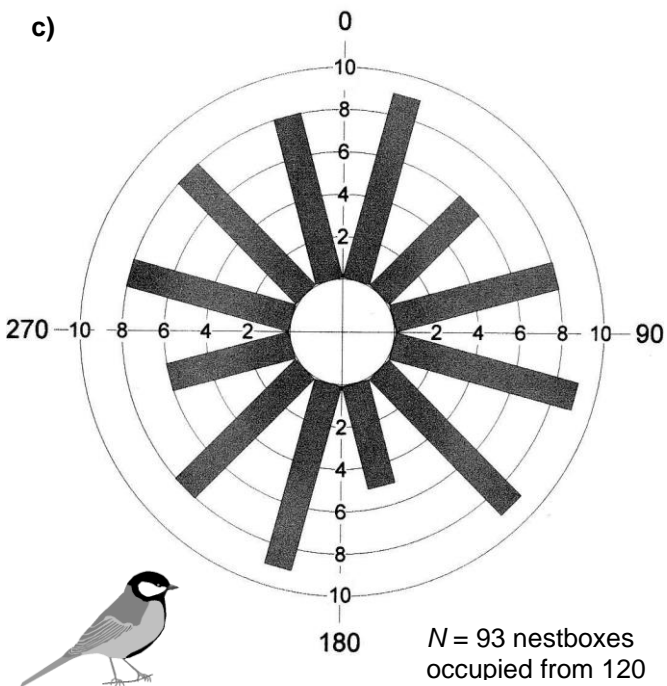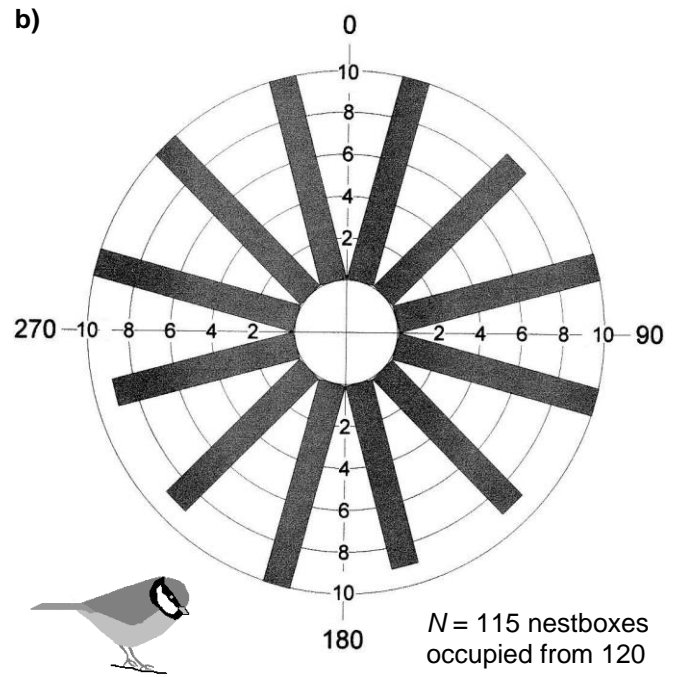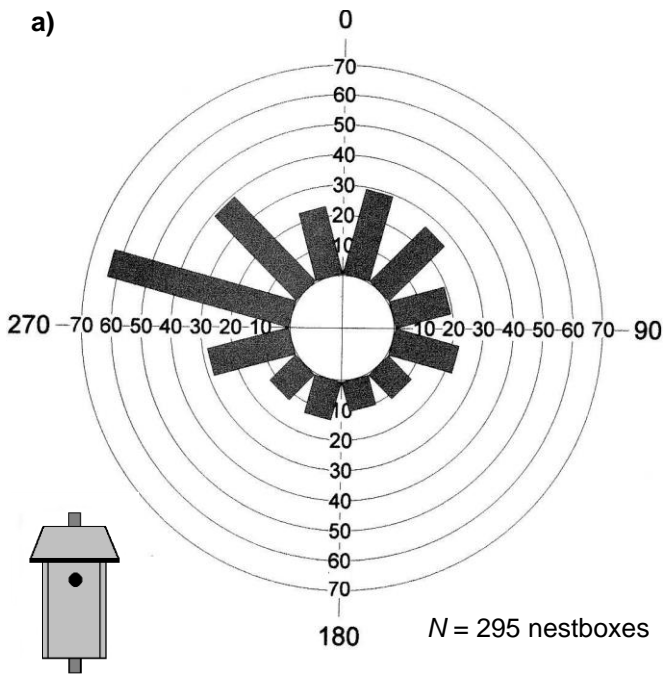
Figure 1

a)

N = 295 nestboxes

b)

N = 115 nestboxes occupied from 120

c)

N = 93 nestboxes occupied from 120

d)

N = 104 nestboxes occupied from 120

Figure 2

Figure 3