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Are nest sites actively chosen?

Testing a common assumption for three non-resource limited birds

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Abstract

Many widely-accepted ecological concepts are simplified assumptions about complex situations, which remain largely untested. One example is the assumption that nest-building species actively choose nest sites when they are not resource limited: an assumption that has seen little direct empirical testing as most studies on nest-site selection start with the assumption that individuals choose nest sites actively, rather than simply by chance. We used 15 years of data from a nestbox scheme in the UK to test the assumption of active nest-site choice in three bird species that differ in breeding and migratory strategy: blue tit (*Cyanistes caeruleus*), great tit (*Parus major*) and pied flycatcher (*Ficedula hypoleuca*). Nest-site selection was non-random (implying active nest-site choice) for blue and great tits, but not for pied flycatchers. We also considered the relative importance of year-specific and site-specific factors in determining occupation of nest sites. Site-specific factors were more important than year-specific factors for the tit species, while the reverse was true for pied flycatchers. Our results show that nest site selection, in birds at least, is not always the result of active choice and thus that active choice should not be assumed automatically in studies of nesting behaviour. We highlight the need to test key ecological assumptions empirically in complex ecosystems, and the importance of doing so across taxa, rather than for single “model” species.

Key words: Nest-site choice, habitat selection, population dynamics, spatial distribution, landscape ecology

Introduction

Many widely-accepted ecological concepts, particularly those concerning temporal and spatial variation in population dynamics, are essentially simplified implicit assumptions about a complex ecological community. For example, it has been assumed that birds ringed as nestlings have an equal chance of being recaptured as adults, such that reliable first-year survival rates can be calculated from recapture data. However, a study specifically testing this assumption found it to be flawed (Freeman and Morgan, 1992). Other examples of key ecological assumptions that have been found to be erroneous when empirically tested include: (1) that disease acts independently of other mortality-causing factors in mammal epidemiological models (tested by Jolles et al., 2006); (2) that a "typical" age structure can be applied to fish populations to accurately assess density-dependent productivity effects (tested by Zabel and Levin, 2002) and (3) that island communities are more susceptible to biological invasion than continental landmasses (tested by Sol, 2000). Importantly, the use, whether implicit or explicit, of such erroneous assumptions reduces the validity of the research results predicated upon them (Thompson, 2002). However, the lack of research that tests widely-accepted ecological assumptions can constrain efforts to move understanding of complex topics forward (Nykänen and Koricheva, 2004).

Reproductive success depends on many interacting factors and consequently most nest-building birds are thought to expend time and energy choosing their nest site (Gaston and Slagsvold, 1985). However, studies on nest-site selection generally start with a fundamental assumption: that individuals choose nest sites actively, rather than simply selecting a particular site by chance (e.g. Hagelin and Miller, 1997; Ramsay et al., 1999; Dornack et al., 2004). To our knowledge, there has been no empirical testing of the assumption of active nest-site choice against the alternative of random selection for secondary cavity-nesting bird species (i.e. those species which use natural or previously-excavated cavities).

It is important to test the assumption of active nest-site choice explicitly rather than simply examining the factors that might cause non-randomness. If nest-site selection is, in fact, random, research into the factors that could hypothetically influence nest-site selection is pointless. More importantly, if a multivariate statistical approach with many environmental variables is used to establish factors influencing nest-site "choice", it is possible, or even likely, that some variables will be considered significant by chance: effectively causing a type I error. This possibility has received little attention despite the plethora of studies using this approach (e.g. Marks, 1986; Bekoff et al., 1987; Blem and Blem, 1991; Pogue and Schnell, 199; Dornack et al., 2004). Conversely, if empirical testing reveals that nest sites are selected non-randomly (i.e. actively chosen) there is impetus to widen the scope of the study to research nest-site selection processes. Widening the study is particular importance where criteria driving nest-site choice are cryptic. In multivariate testing likely candidate factors tested are usually based on *a priori* knowledge, often from studies on other species (Jones, 2001). If such testing is used as the first step in analysing spatial patterns of nesting and all factors are found to be non-significant, it could be wrongly concluded that the species in question was nesting randomly (because of the absence of evidence to the contrary), when in fact the causal factors were simply absent from the model. If the species is already known to be nesting non-randomly, this cannot happen. At worst, the result of a study is confirmation that active choice is occurring, but the mechanism of choice remains unknown.

A nestbox scheme with a surplus of nestboxes is the ideal situation to test the hypothesis that nest sites are actively chosen as determining preference and avoidance patterns requires a non-resource limited situation (Petit and Petit, 1996). Use of nestbox data also means that the total number of ‘cavities’ is known for species that preferentially use nestboxes over natural cavities. The selection of nest sites can, therefore, be directly inferred (Pogue and Schnell, 1994), without the need to quantify the difference between nest sites and random sites (e.g. Lusk et al., 2003). Using nestbox data also allows the consideration of a much-overlooked issue closely linked to active nest-site choice: the relative importance of year-specific and site-specific factors in determining nest site occupation. Many studies have shown the importance of year-specific factors on avian reproduction (Newton, 1998) and thus it might be predicted that, in a relatively homogenous habitat, year-specific factors will have a greater influence on nestbox occupations than site-specific factors. Although one study has looked at this question for nesting success (Radunzel et al., 1997), to our knowledge no research has been undertaken to determine the relative importance of year-specific and site-specific factors in the occupation of nest sites.

In this study, we use 15 years of nestbox occupation data for blue tit (*Cyanistes caeruleus,* L. 1758), great tit (*Parus major,* L. 1758) and pied flycatcher (*Ficedula hypoleuca,* Pallas 1764) to test the assumption of active nest-site choice. If the common assumption of active nest choice is true, we would expect the hypothesis that nest-site use is non-random to be supported in all three study species. Then, using a comparative approach between species (two resident monogamous passerines and one migratory passerine which exhibits polygynous nesting behaviour), we test whether site-specific or year-specific factors explain more variance, and are thus relatively more important, in determining the occupation of nest sites. We hypothesise that year-specific factors will be more important for all species, as discussed above. Finally, we discuss how the results of this study are of relevance both to ecology in general and to research into resource use and breeding behaviour among birds, mammals and reptiles/amphibians, as well as ovipositing in insects.

Materials and Methods

Study area

The study was undertaken at Nagshead Nature Reserve (Gloucestershire, UK), which covers 308 hectares centered on 2°34’0”W, 51°47’0”N. The reserve is home to the longest-running nestbox scheme in the UK (Campbell, 1968). In this nestbox scheme, boxes are provided in super-abundance (around 28% of all boxes at the study site remain unoccupied each year), such that determining preference and avoidance patterns is possible (Petit and Petit, 1996). Neither intra-specific nor interspecific competition should ever become a limiting factor, even for species nesting late in the breeding season. The nestboxes are located within a pre-1850 broadleaf plantation dominated by Pedunculate oak (*Quercus robur,* L. 1758).

Field data

Data on nestbox occupation during the 15-year 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 visits to each nestbox throughout the 15 breeding seasons. Nestbox occupations for the three species with a sufficient number of records (blue tit, great tit and pied flycatcher) were analysed. Only data from the 295 nestboxes that were appropriate for the study species as regards size and shape (rectangular with a sloping roof; approximate internal measurements: 110mm width, 170mm depth, 210mm mid-point height) and that were available throughout the entire study period, in the same position, were included in the study. This removed physical constraints to nesting thereby ensuring any observed non-random selection is the result of choice, not necessity (Lumsden et al., 1980). It also ensured that when occupations were compared between nestboxes over time, the availability and characteristics of each nestbox was temporally consistent. This gave an analysable dataset of 4,425 ‘nestbox years’ (295 nestboxes * 15 years). Nestboxes were categorised as occupied when a nest had been constructed and at least one egg laid.

Statistical analyses

To determine if there was a significant deviation from randomness in the occupation of different nestboxes, the frequency of occupation of each of the 295 nestboxes over the 15 years was compared to a hypothetical Poisson distribution (Fowler et al., 1998). This was done using separate iterations (one for each species) of a one-sample Kolmogorov-Smirnov test. This approach has previously been used in theoretical computer modelling of female distribution at avian lekking sites (Gibson et al., 1990). To establish the relative importance of year-specific and site-specific factors on whether a nestbox was occupied, a binary occupation variable was constructed for each study species (0 = unoccupied; 1 = occupied). These were analyzed using separate iterations of Cochran’s Q test: a non-parametric test analogous to Freidman’s test that can be used as an equivalent of a two-way ANOVA for binary variables. The analyses were calculated according to the equations given by Siegel (1956). It should be noted that significant between-site variation in a Cochran’s analysis indicated only that occupation of nestboxes were statistically different one from another (i.e. non-uniform), not that this difference was anything other than random variation (McCulloch, 1985). Accordingly, use of the Cochran’s Q test complemented the use of the Kolmogorov-Smirnov test (see above).

Results

Variability in nestbox occupation

Nestbox occupation by each species varied in two ways: the number of occupations per year (Fig. 1a) and the number of years out of a possible 15 that individual nestboxes were occupied (Fig. 1b). In terms of variability between years, blue tits showed the most variability, followed by pied flycatchers, then great tits (occupations varied by 66, 63, and 25 occupations per year, respectively). Blue tits also showed the highest absolute variability in the number of years that individual nestboxes were occupied during the 15 years (0-14 occupations per box), followed by pied flycatchers (0-10 occupations per box) and then great tits (0-9 occupations per box). The variation in nestbox occupation was also calculated using the coefficient of variance which enabled direct comparison between species with appreciably different means. Using this statistic, pied flycatchers showed most variation in nestbox occupations between-years, while great tits showed most variation in occupations between-sites (Table 1).

Do birds actively choose nest sites?

Comparison of the frequency with which each nestbox was occupied to a theoretical Poisson distribution returned a significant result (indicating that the frequency of occupations was significantly different from that expected by random chance) for blue tit (one-sample Kolmogorov-Smirnov test, $Z = 1.388$, $P = 0.042$) and great tit ($Z = 1.529$, $P = 0.019$), but not for pied flycatchers ($Z = 0.721$, $P = 0.676$) ($N = 295$ in all cases).

Relative importance of year-specific and site-specific factors

Comparing nestbox occupations between-year and between-site using Cochran's Q tests (one for each species) showed that significant variation was explained by year-specific and site-specific factors for each species ($P < 0.001$). In terms of the relative importance of these factors, site-specific factors were more important than year-specific factors for the tit species, while the reverse was true for pied flycatcher (Table 2).

Discussion

Do birds actively choose nest sites?

Both blue tits and great tits occupy nestboxes non-randomly. This is presumably attributable to active nest-site selection and contrasts with the apparently random nest-site selection demonstrated by pied flycatchers. That nest sites are actively chosen by the tits agrees with field evidence suggesting that these species actively prospect for nest cavities (e.g. Perrins, 1979). Because blue and great tits form monogamous pairs and select nest sites during peak availability (early in the season), active nest-site choice is possible. This choice has presumably evolved because some nest sites have advantages over others, either: (1) increasing the number of offspring, (2) increasing offspring fitness, or (3) conveying some benefit to the parent birds such as improving post-breeding fitness or reducing the trade-off between current and future breeding success (Misenhelter and Rotenberry, 2000). Candidate variables include surrounding habitat (Mänd et al., 2005), cavity-specific parameters such as orientation (Goodenough et al., 2008a), food resources (Hagelin and Miller, 1997) and between-species interactions (Ramsay et al., 1999), although there may also be trade-offs between multiple nest-site selection cues (Fisher and Wiebe, 2006).

Conversely, pied flycatchers appear to select nestboxes randomly. To reiterate, the most likely explanation, that individuals are constrained by competition, is unlikely as about 28% of all boxes at the study site remain unoccupied each year (Fig. 1b). Moreover, as the flycatchers select boxes after the tit species have actively chosen their boxes, it could almost be expected that analyses on pied flycatcher nesting distribution might indicate that it was non-random even if this was not actually the case, as individuals are automatically selecting from non-random resource (i.e. a false positive result could occur as a facet of the choices made by co-occurring species). That there is still a random distribution of pied flycatcher nests even when this species can only occupy a subset of the total nestbox resource both strengthens this result in its own right, and suggests that competition does not *de facto* constrain nest site selection. There are several other potential explanations for nest-sites being selected randomly. Firstly, it is possible that there is no selection pressure for birds to choose particular boxes as all boxes provide equal opportunities for successful nesting. However, this is not the case for pied flycatchers at the study site, as previous research has demonstrated that breeding success (number of young to fledge) relates to nestbox orientation (Goodenough et al., 2008b). The second possibility to account for the apparent lack of active nest site choice by pied flycatchers is the high search-cost of finding suitable boxes. As the search-cost involved in finding a ‘better’ nestbox increases as the number of available boxes decreases, whether it is beneficial to undertake a prolonged nest-site search is questionable (Alatalo et al., 1988), especially given the risk of losing the current nest site in search of something better. Finally, the flycatcher’s semi-polygynous mating strategy means females select their mate, breeding territory and nest site as one unit which could act to constrain choice (Slagsvold, 1986; Lifjeld and Slagsvold, 1988), especially if females prioritize male quality (Alatalo et al., 1986). Thus mating strategy could act as a limiting factor in nest-site choice. Whether females would exhibit active nest site selection if there were more good-quality males is an intriguing question worthy of further study.

Relative importance of year-specific and site-specific factors

Nestbox occupations (a proxy for the size of the breeding population) are affected by breeding success the proceeding year and winter survival. These factors are themselves influenced by other (inter-related) factors such as weather, food supply, competition, and predator density (Newton, 1998). Accordingly, year-specific factors were hypothesised to be important in determining the occupation of nest sites, as indeed was the case. For blue and great tits, however, the greater impact of site-specific factors over year-specific factors on occupations was contrary to expectations. This suggests that the characteristics of the nestbox, its placement and surrounding area, are of greater importance in determining occupation than is frequently assumed in a homogenous habitat. The greater influence of site-specific factors may also relate to the high incidence of nest-site re-use in successive years (Andreu and Barba, 2006). This reconfirms the importance of active nest-site choice by these species discussed above. Conversely, the greater influence of year-specific factors than site-specific factors on nestbox occupations by pied flycatchers was both expected and explicable. This species has undergone a 73% decline at the study site during 1990-2004 and thus year-specific factors were expected to be the main influence on occupations. Random nestbox use by flycatchers (see above) would also reinforce the importance of year-specific factors on nestbox occupations by limiting the impact of site-specific factors and thus allowing year-specific factors to dominate.

Ecological implications of this study

The finding that pied flycatchers apparently select nest sites randomly, contrary to the common assumption of non-random nest-site selection, is important in two ways. Firstly, our results show that nest site selection, in birds at least, is not always the result of active choice and thus that active choice should not be assumed in studies of nesting behaviour. This has implications for future research into breeding (and possibly hibernation) sites of mammals, reptiles and amphibians, and studies on ovipositing behaviour in insects. Secondly, and more generally, our results emphasise the importance of empirically test assumptions. Of particular note is the fact that such testing needs to be undertaken explicitly for each study species: the species-specific nature of the results here suggest using just a single “model” species is inappropriate.

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Figure 1 – Variation in nestbox occupations during the period 1990-2004: (a) between-year; and (b) between-site (in this case between-nestbox). The ‘overall occupation’ figures include occupations for the three study species, together with coal tit (*Periparus ater*), marsh tit (*Poecile montanus*), nuthatch (*Sitta europaea*) and redstart (*Phoenicururus phoenicururus*) that together comprise 3% of occupations. Small circles indicate statistical outliers (more than 1.5 standard deviations from the mean).

Table 1 – Coefficients of variation in nestbox occupations at the study site during the 15-year period of 1990-2004, both between-year and between-site (in this case between-nestbox).

	Coefficient of Variation (%)	
	Between-year	**Between-site**
Blue tit	14.62	47.04
Great tit	22.80	94.45
Pied Flycatcher	41.98	76.60

Table 2 – Difference in nestbox occupations in relation to year-specific and site-specific factors for the three study species (1990-2004).

	Cochran's Q Test Statistics*	
Species	**Between-year (n = 15)**	**Between-site (n = 295)**
Blue tit	$Q = 66.06$ $P = 9.90 \times 10^{-09}$	$Q = 648.76$ $P = 8.42 \times 10^{-29}$
Great tit	$Q = 36.59$ $P = 8.50 \times 10^{-03}$	$Q = 601.26$ $P = 2.80 \times 10^{-23}$
Pied flycatcher	$Q = 143.67$ $P = 1.32 \times 10^{-23}$	$Q = 527.79$ $P = 1.57 \times 10^{-15}$

* The *P* value, not the Q value, should be used to compare the relative importance of year-specific and site-specific factors in determining nestbox occupations within species as sample sizes differ between the variables. Either the Q or *P* value can be used to compare the relative importance of year-specific or site-specific factors between species as the sample size within each variable is consistent.