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Original article

Influence of fine-scale habitat structure on nest-site occupancy, laying date and clutch size in Blue Tits *Cyanistes caeruleus*

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ABSTRACT

Most birds have specific habitat requirements for breeding. The vegetation structure surrounding nest-sites is an important component of habitat quality, and can have large effects on avian breeding performance. We studied 13 years of Blue Tit *Cyanistes caeruleus* population data to determine whether characteristics of vegetation structure predict site occupancy, laying date and number of eggs laid. Measurements of vegetation structure included the density of English Oak *Quercus robur*, European Beech *Fagus sylvatica*, and other deciduous, coniferous and non-coniferous evergreen trees, within a 20-m radius of nest-boxes used for breeding. Trees were further sub-divided into specific classes of trunk circumferences to determine the densities for different maturity levels. Based on Principal Component Analysis (PCA), we reduced the total number of 17 measured vegetation variables to 7 main categories, which we used for further analyses. We found that the occupancy rate of sites and the number of eggs laid correlated positively with the proportion of deciduous trees and negatively with the density of coniferous trees. Laying of the first egg was advanced with a greater proportion of deciduous trees. Among deciduous trees, the English Oak appeared to be most important, as a higher density of more mature English Oak trees was associated with more frequent nest-box occupancy, a larger number of eggs laid, and an earlier laying start. Furthermore, laying started earlier and more eggs were laid in nest-boxes with higher occupancy rates. Together, these findings highlight the role of deciduous trees, particularly more mature English Oak, as important predictors of high-quality preferred habitat. These results aid in defining habitat quality and will facilitate future studies on the importance of environmental quality for breeding performance.

1. Introduction

In many birds, especially territorial species, one of the main determinants of fitness is the quality of the breeding habitat (e.g. Davenport et al., 2000; Langen and Vehrencamp, 1998; Pärt, 2001; Sergio et al., 2009). In the last few decades, measuring habitat quality–fitness relationships has posed a challenge of major importance for ecologists because of the need to consider biodiversity values for conservation of birds species, and also for landscape managers because of increasing anthropogenic influences and habitat loss (Sih et al., 2000). Ecologists have used different indices to estimate habitat quality for birds (see e.g. Chandler and King, 2011; Janiszewski et al., 2013), and one of these indices is the vegetation structure around nest-sites (e.g. Atiénzar et al., 2009, 2010; Bell et al., 2014; Wilkin et al., 2007, 2009). Both experimental and observational studies have demonstrated that the vegetation structure around nest-sites has an influence on breeding performance (e.g. Pärt, 2001; Arriero et al., 2006). Especially in insectivorous species of birds, the vegetation is one of the main environmental factors affecting food availability in forest habitats

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(van Balen, 1973; Blondel et al., 1991). Higher food availability during brood-rearing increases offspring growth and survival (Kroll and Haufler, 2007; Mägi et al., 2009). Thorough knowledge about these relationships can have implications for effective conservation of biodiversity, harvest management in forestry and also reforestation plans (Arriero et al., 2006).

In this study, we used 13 years of breeding data of a population of Blue Tits *Cyanistes caeruleus*, to evaluate the effect of vegetation structure on nest-site occupancy and two key parameters of breeding performance closely linked to fitness: laying date and clutch size. Blue Tits are small, territorial passerines, typically breeding in pairs. While they breed in heterogeneous environments and in a variety of forest types, which differ in quality (e.g. Lambrechts et al., 2004), they are often considered Oak forest specialists (e.g. Perrins, 1979; Lambrechts et al., 2004; Blondel et al., 2006). Parents feed their chicks with invertebrates, particularly caterpillars, which are the main food item available during the brood-rearing phase (Perrins, 1991; Cholewa and Wesolowski, 2011). Availability of caterpillars and other arthropods depends on the timing of spring growth of leaves, which differs between tree species (Blondel et al., 1993). Tits (*Paridae* family) are sensitive to small differences in vegetation structure (Wilkin et al., 2007; Atiénzar et al., 2010) and also suffer reduced breeding performance in human-modified habitats (Hinsley et al., 2009). Hence, they can serve as a good model species to evaluate habitat quality effects on breeding performance (Blondel et al., 1993), and to guide landscape management.

Due to experiments performed in this population during the incubation and nestling stages, we were not able to incorporate other parameters of breeding performance (e.g. number of fledglings). Laying date and clutch size are often correlated with other parameters of breeding performance, such as number of fledged offspring, and subsequent offspring survival and recruitment (e.g. Perrins, 1965; Norris, 1993; Verboven and Visser, 1998; Both et al., 2000). Observational and experimental studies have also indicated that laying date and clutch size are influenced by food availability (Blondel et al., 1991; Nager et al., 1997; Bourgault et al., 2009; Smith et al., 2013). Site occupancy is one of the most important basic predictors that over the long-term reflects habitat quality (Sergio and Newton, 2003; Janiszewski et al., 2013).

To investigate the relationship between the habitat and these parameters of breeding performance (laying date and clutch size) as well as nest-site occupancy, we studied the characteristics of the trees, including their maturity, in the near vicinity of nest-boxes. Although previous studies have investigated the relationship between vegetation and various measures of breeding performance in Blue Tits and Great Tits *Parus major*, most of them have studied this on a coarser scale, for example by comparing parameters of breeding performance between deciduous and coniferous forests (e.g. Blondel et al., 1993; Mägi et al., 2009). Some more detailed and finer-scale studies have also investigated the relationship between parameters of breeding performance and the local densities of a single tree species, like food-rich oak trees (Wilkin et al., 2009; Bell et al., 2014). However, comprehensive fine-scale studies that simultaneously investigate several vegetation characteristics, including both the local densities and maturity levels of trees of different species surrounding the nest-sites, and relate these detailed vegetation characteristics to parameters of breeding performance are scarce (for exceptions see Arriero et al., 2006; Hinsley et al., 2009; Atiénzar et al., 2010). Specifically, the objectives of this paper are to examine the relationship between fine-scale vegetation characteristics, particularly the local densities and maturity of different tree species, and 1) nest-site occupancy, 2) laying date and 3) the number of eggs laid. Based on these analyses, we aim to identify the main vegetation indices as predictors of habitat quality.

2. Material and methods

2.1. Study area and study population

The study was conducted over 13 consecutive breeding seasons (2001–2013) on a nest-box breeding Blue Tit population at 'De Vosbergen' estate near Groningen in the North of The Netherlands (53°N, 06°E). The 54 ha study area consists of mixed deciduous and coniferous forest interspersed with areas of open grassland. The study area contains about 188 wooden nest-boxes (inner dimensions: ca. 9.0 × 12.5 × 25 cm, with a 2.6 cm entrance hole) designed especially for Blue Tits. Nest-boxes have been installed in excess in the study area since 2001 and are dispersed at relatively regular intervals over the whole study area.

2.2. Breeding performance

Every breeding season (April–June), for each nest-box, breeding activities from the nest-building until the fledging phase were monitored. During the nest-building phase from the beginning of April all nest-boxes were checked regularly. For each Blue Tit breeding pair, we recorded the date of laying the first egg (hereafter referred to as 'laying date') and the number of eggs laid.

Various studies and experiments were carried out on this population during the years of monitoring, which may have influenced different parameters of breeding performance (See Korsten et al., 2006; Kingma et al., 2009; Vedder et al., 2010, 2012; de Jong, 2013; Schut et al., 2014). Some experiments were carried out during or before the onset of laying and some of them were carried out after the onset of incubation. Because of this, we did not use breeding performance parameters determined after clutch completion, and only selected data which were not influenced by experiments (See Supplementary material, Table S1). The selected parameters were: nest-box occupancy, laying date, and number of eggs laid. A nest-box was considered occupied in a particular year when it contained a nest with at least one egg. The occupancy rate was calculated for each nest-box on the basis of its availability (on rare occasions nest-boxes were occupied by other species such as Great Tits, and Coal Tits *Parus ater*, or nest-boxes were absent or damaged and could not be used for breeding that year) and number of years occupied during the 13-year period. Laying date was defined as the date of laying the first egg (1 April = day 1). Number of eggs was the total of all eggs laid. As a result of collection of eggs in some years without replacement with dummy eggs (see Supplementary material, Table S1), it was not possible to determine the originally intended clutch size, as females may, or may not, have compensated by laying additional eggs. For these years, the eggs were collected for most of the clutches in the population leaving the within-year comparisons meaningful. In recognition of this potential influence we use the term number of eggs laid instead of clutch size. We excluded second clutches, which occurred only rarely, as well as replacement clutches after failed first breeding attempts, from our analyses.

Experiments had an influence on the observed laying date and the number of eggs laid in 2006–2007 (unpublished results) and also on the number of eggs laid in 2009 (Vedder et al., 2012; for details see Supplementary material, Table S1). As a result, for those years and breeding performance parameters, we only included control-treated nest-boxes in our analyses.

2.3. Measurements of habitat characteristics

The vegetation structure of the habitat was measured by sampling the trees surrounding the nest-boxes. Tree sampling took place during two periods; the vegetation around 100 of the nest-