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The role of nest-box density and placement on occupation rates and breeding performance: a case study with Eurasian Blue Tits

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The use of nest-boxes to study bird breeding biology, as well their use as a management tool, is widespread. The exact placement of nest-boxes may affect individual preference for these breeding sites; however the influence of determinant factors (e.g., nest-box density) in occupation rates or breeding parameters has not been sufficiently covered. Here, we used the Eurasian Blue Tit as a model species to determine factors influencing nest-box selection in a transformed habitat: a pine plantation. Our study design consisted of 100 nest-boxes arranged at different heights (positioned "high" at 3.0–5.0 m, or positioned "low" at 1.5–2.0 m), and with different degrees of clustering (clustered in groups of 6, or isolated by at least 80 m from the nearest nest-box). We calculated the potential territorial area for each nest-box and the distance to the nearest neighbour. We investigated the influence of nest-box position and breeding pair density on occupation rate and breeding success, controlling for habitat structure. Eurasian Blue Tits preferentially selected nest-boxes located high on the tree and with fewest neighbours. Laying date was earlier in higher nest-boxes and in those with fewer neighbours and at a greater distance from the nearest neighbour. The number of nestlings was positively related to shrub cover and medium tree height. Fledgling mass was higher when distance to the nearest neighbour was greater and fledgling tarsus length was positively related to oak-species abundance. Our results suggest that disentangling the important factors for nest-box placement and spatial dispersion in the landscape is important to adapt to species-specific requirements in each given habitat.

1. Introduction

Many hole-nesting passerines in the Western Palearctic, such as the Eurasian Blue and Great Tits (*Cyanistes caeruleus* and *Parus major*), the European Pied and Collared flycatchers (*Ficedula hypoleuca* and *Ficedula albicollis*) and the Eurasian Nuthatch (*Sitta europaea*), prefer deciduous to evergreen forests (Cramp & Perrins 1993, Newton 1998, Mänd *et al*. 2005). This preference has been explained by the greater abundance of potential nest cavities (Balen *et al*. 1982, Newton 1998), as well as by greater food availability (Balen 1973, Perrins 1991, Riddington & Gosler 1995) in deciduous compared to coniferous forests.

In Spain and elsewhere in Europe, forestry policies enacted over the last century have resulted in large areas covered by pine plantations (Díaz *et al*. 1998, Barrientos 2010). Birds may be forced to select these sub-optimal coniferous forests (Sanz *et al.* 2010), and these new habitats have resulted in lower densities of Tits breeding in them than in native deciduous woodland habitats (Maícas & Fernández-Haeger 1996). Previous studies found that an increase in potential nest-holes by nest-box provisioning increases secondary cavity nester densities, in native preferred oak woodlands (Robles *et al.* 2011, 2012), and monoculture plantations (Pimentel & Nilsson 2007, Mänd *et al.* 2009, Silva *et al.* 2012). Thus, nest-box provisioning has been suggested as an effective conservation tool for these species in habitats like monoculture plantations or young native stands, where natural cavities are scarce (Mänd *et al*. 2009, Robles *et al*. 2011). However, little is known about the influence of nest-box density or placement height on nest-box use (occupation rate) or breeding performance in transformed habitats, as an excess number of next-boxes are often arbitrarily placed (see Lambrechts *et al.* (2010) for an extensive review and references therein).

The size and position (e.g., height, orientation) of the entrance hole appears to determine which individual or species will occupy nest-boxes (e.g., Barba & Gil-Delgado 1990, Dhondt & Adriaensen 1999, Zingg *et al*. 2010). Usually birds select cavities with reduced predation risk or competition (Newton 1994, Sorace & Carere 1996, Robles & Martin 2013), which allows for high levels of brood survival (Wesołowski 2002, Lõhmus & Remm 2005). The density of nest-boxes is therefore a key (see Charmantier & Perret 2004), but often neglected, parameter. Population density, and consequently competition among breeding pairs, have strong effects on the population dynamics and reproduction of territorial birds (see Adams 2001 for a review, see also Wilkin *et al.* 2006). It has been shown that breeding parameters in many bird species, including Tits, are negatively affected by population density, such as clutch size (Kluijver 1951, Lack 1958, Perrins 1965), fledgling mass (Both 1998, Garant *et al*. 2004) and offspring recruitment (Both & Visser 2001). Also, in studies on nest-box provisioning it is important to control for habitat traits around the nesting sites, such as heterogeneity of vegetation structure, tree height or the succession stage of the shrub coverage, as these variables can be responsible for local variation in breeding parameters such as laying date or clutch size (Nager 1990, Arriero *et al*. 2006, Wilkin *et al*. 2007).

The aim of the present study was to evaluate the importance of nest-box height and density on the breeding biology of the Eurasian Blue Tit in a Mediterranean pine plantation. We expected that (i) nest-box height will influence nest site preference, as Eurasian Blue Tits prefer higher nest-boxes in order to reduce predation risk (e.g., Nilsson 1984, Newton 1994, Sorace & Carere 1996); (ii) Eurasian Blue Tits will show preference for low intra- and interspecific density sites (Wilkin *et al.* 2006), since nest-box density determines territory size and nest-site defense (Zingg *et al.* 2010); iii) habitat characteristics around occupied nest-boxes will determine reproductive output (e.g., Sanz *et al*. 2010), mediated by food availability.

2. Material and methods

2.1. Study species and area

The Eurasian Blue Tit is a 7–11 g forest passerine, common in mixed and deciduous forests throughout the Western Palearctic (Cramp & Perrins 1993). They also breed in evergreen forests such as pine plantations (Maícas & Fernández Haeger 1999). Eurasian Blue Tits readily accept nest-boxes for breeding.

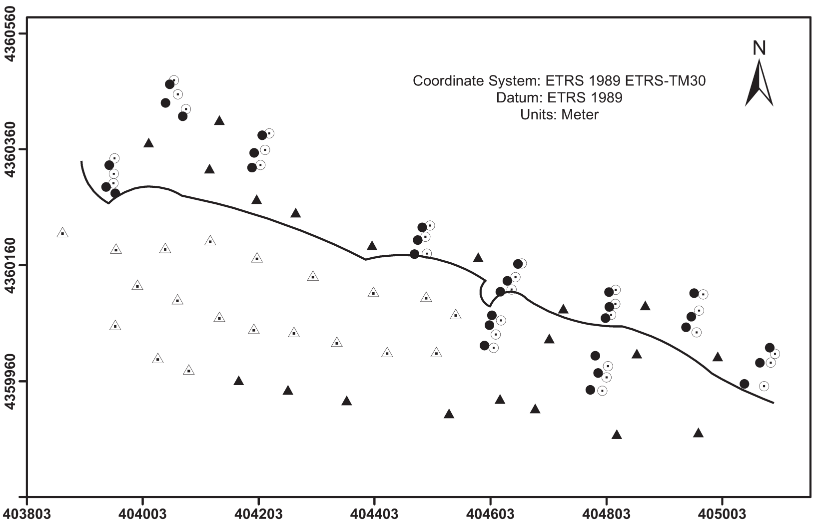

Fig. 1. Distribution of nest-boxes along the Azafranal path (black line) in the spring of 2012. Black circles: high + aggregated nest-boxes. Open circles: low + aggregated nest-boxes. Black triangles: high + isolated nest-boxes. Open triangles: low + isolated nest-boxes.

The study was conducted in the 2012 breeding season in Quintos de Mora (Toledo province, central Spain, 39°24’23” N, 4°4’19” W), a government-owned game reserve. The pine stand is located on a hillside dominated by Maritime Pine (*Pinus pinaster*) with some dispersed Portuguese Oak (*Quercus faginea*), and Holm Oak (*Q. ilex*) stems embedded in the pine matrix.

In the study plot (Fig. 1), 100 wooden nest-boxes (internal dimensions: 12 × 11.5 × 16.5 cm) were distributed in different positions and densities. We placed 60 nest-boxes forming 10 groups of 6 (“clustered”, ≤ 10 meters of separation between consecutive nest-boxes within the group; 160 m separation between groups), with three nest-boxes at a height of 3.0–5.0 meters (“high”), and the other three at 1.5–2.0 meters (“low”). The remaining 40 nest-boxes were spaced at 80 meters intervals (“isolated”) forming lines along the study site, twenty of them high and the other twenty low, following a similar scheme that described above. Nest-boxes were protected from predators (mustelids, woodpeckers) with wire mesh and a polyvinyl chloride (PVC) pipe (length: 70–90 mm, diameter: 40 mm) fixed to the hole-entrance.

2.2. Field methods

From early April to late June, we checked nest-boxes daily to record first-egg date (1 = 1 April), clutch size, hatching date and the number of fledglings. Breeding adults were caught using spring traps at the nest while feeding young at 8 days old, and sexed according to the presence (female) or absence (male) of a brood patch. All birds were individually recognised with numbered metal rings, and at capture, we measured tarsus length to the nearest 0.01 mm with a digital caliper, and body mass with an electronic portable balance to the nearest 0.1 g following the protocol described in Perret (2004).

When nestlings were 13 days old they were banded and measured similarly to adults. Post-fledge nests were visited 22 days after hatching to establish the breeding success of each pair (i.e., proportion of eggs that resulted in fledged young).

Density of breeding pairs was 0.98 pairs / ha. This was lower than in oak dominated forests in the same reserve (4.40 pairs / ha, García-Navas & Sanz 2011a), but similar to those in other studies in Mediterranean pinewoods (0.40–0.70 pairs / ha, Pimentel & Nilsson 2007; 0.77 pairs / ha, Maícas *et al*. 2011). We did not find any natural cavity in this habitat which could act as a nest-hole and potentially influence Tit population density, probably due to the scarcity of primary cavity-excavators. Moreover it has been previously stated that the use of nest-box data ensures that the number of “cavities” is nearly known for species that preferentially use nest-boxes over natural cavities (Goodenough *et al*. 2009). However, a small minority of birds may have bred in natural cavities.

2.3. Territory features

We visually estimated vegetation composition and cover, always by the same researcher (ESD), in a 25 m radius around each nest-box. This radius accounts for the area that Tits commonly used for feeding (Smith & Sweatman 1974, Grieco 2002). This area is usually referred to as a “territory”. Following Sanz *et al*. (2010), we estimated for every territory (a) the total number of trees, (b) tree species (among pines and oaks) abundance, (c) the height of dominant trees, (d) shrub cover (%), (e) herbaceous cover (%) and (f) the cover of bare ground and rocky surface (%).

The orientation of the entrance of each nest-box was quantified in the field (in degrees with respect to north) and transformed into a categorical variable as follows: 1–90° as NE; 91–180° as SE; 181–270° as SW; and, 271–360° as NW.

2.4. Territory model

The position of each nest-box was georeferenced, and Arc Map ver.10 was used to generate layers with the nest-boxes occupied by Tits. We used such GIS software to generate quantitative predictions about the spacing of nest-boxes and the potential size and shape of territories based on the relative location of nest-boxes within the perimeter of the woodland. By using a Dirichlet tessellation technique, we formed Thiessen polygons (Rhynsburger 1973, Tanemura & Hasegawa 1980, Chiu *et al*. 2013) around each nest-box, and used their sizes as a measure of nest-box spacing (Fig. 2a, Wilkin *et al*. 2006).

We included Great Tits in our territorial analyses because this species competes with Eurasian Blue Tits for breeding holes and territories (Minot 1981, Minot & Perrins 1986), although these species often share territories as there is some niche separation (Dhondt *et al.* 1984, Dhondt & Adriaensen 1999). We then assessed “tessellated territories” (estimated territory polygons) around nest-boxes occupied by Eurasian Blue and Great Tits (Fig. 2b), and used them as a simple model for territory size (see Wilkin *et al*. 2006). For each tessellated territory, the number of contiguous neighbours was also counted as a measure of crowding pressure. To compensate for excessively large tessellated polygons in areas of low nest-box density, we systematically imposed a range of ceilings upon the size of territory polygons, at a ceiling level of 1 ha. All polygons above this size were replaced with a value of 1 ha while polygons below 1 ha in size remained unaffected, following Wilkin *et al*. (2006).

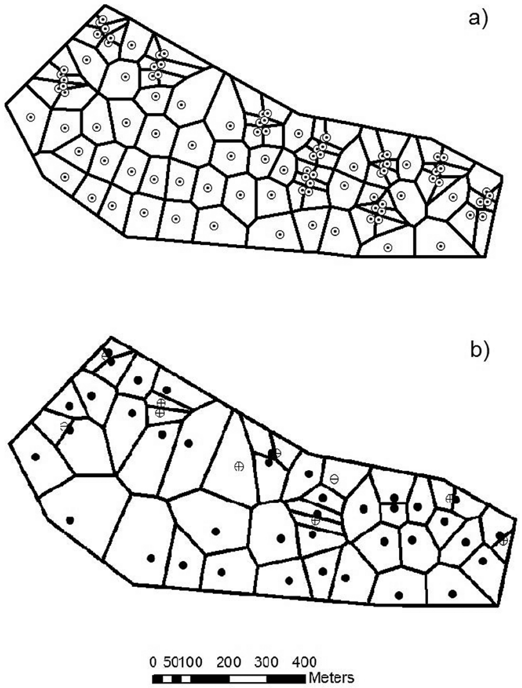

Fig. 2. Definitions of polygons and territories for breeding Eurasian Blue and Great Tit density. An area of pinewood in Quintos de Mora showing (a) all nest-boxes with their tessellated polygons, the areas of which provide an estimate of nest-box spacing, (b) nest-boxes occupied by Eurasian Blue (solid circles) and Great Tits (crossed circles) in 2012 with their tessellated interspecific polygons, which provide a simple model for territory size.

2.5. Data analysis

In a first step, nest-site habitat characteristics were synthesised in three vegetation structure factors by means of a Principal Components Analysis with Varimax rotation (PCA, Table 1), in order to minimize multicollinearity among independent variables. The first axis (Pc1) contrasted territories with a well-developed herbaceous cover (negative

Table 1. Factor loadings of the principal component analysis for descriptor variables of vegetation structure measured at 60 sampling sites (circular plots of 25 m in radius). Significant statistics for each principal component are marked in bold (> 0.50).

Factor	Pc1	Pc2	Pc3
Tree height	0.391	**–0.592**	0.204
Shrub cover (%)	0.306	**0.791**	0.078
Herbaceous cover (%)	**–0.929**	0.012	0.184
Soil cover (%)	**0.929**	–0.012	–0.184
No. Pines	**0.673**	0.406	–0.055
No. Portuguese oak	0.180	0.437	**–0.696**
No. Holm oak	–0.138	0.133	**0.905**
Expl. variance (%)	40.119	19.147	15.820
Eigenvalue	2.808	1.340	1.107

loading, Table 1) to those without an herbaceous layer and a greater number of pines (positive loading, Table 1). The second axis (Pc2) defined a gradient related to the shrub cover and medium tree height, separating territories with a meaningful density of shrub and smaller trees (positive) from those having fewer shrubs but taller tress (Table 1). The third axis (Pc3) was directly related to the abundance of non-target tree species (i.e., oaks), where Holm Oak decreases when Portuguese Oak increases, providing a dryness gradient information about the study site (Table 1). We then included these three factors as predictors in our models.

To assess whether the nest-box occupation and variation in breeding parameters of Eurasian Blue Tit could be attributed to the potential explanatory variables, multiple linear regression models were built using the information–theoretic model comparison approach. Alternative models were compared with Akaike's second-order information criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002). Only those more plausible models with AICc ≤ 4 were selected. Standardized regression coefficients (β) were obtained in regression analyses as a measure of the sign and magnitude effects of predictor variables (i.e., analyses were carried out with standardized variables, such that their averages are zero and variances are 1). Parameter estimates (β and *se* β) were averaged using model weights (W_i) derived from all models with AICc ≤ 4. We performed all statistical analyses using R version 3.2.2 (R Core Team 2015).

We determined potential predictors of nest-box occupation by fitting generalised linear models (GLZ) based on all possible combinations of the following variables: group, height, orientation, territory area, number of neighbours and habitat components (Pc1, Pc2, Pc3). This analysis was performed using the glmulti package in R (Calcagno 2011). This package builds all possible unique models involving these variables and is especially recommended to deal with many candidate predictors, often with modest *a priori* information about their potential relevance (Ripley 2004, Calcagno & Mazancourt 2010). We used a binomial distribution (occupied vs. empty) and logit link function. The same procedure was applied to determine whether nest-box position, habitat configuration and density influenced Eurasian Blue Tit breeding parameters and nestling body condition. GLMs were run using laying date, clutch size, brood size (number of 13-day-old nestlings), fledgling mass and fledgling tarsus length as dependent variables. Height, group, orientation, territory area, number of neighbours, distance to the nearest neighbour, Pc1, Pc2, and Pc3 were included as predictors. We controlled for laying date, except in the analysis in which this was the dependent variable. Gaussian distribution and identity function were used in these analyses.

3. Results

Mean potential territory area for Eurasian Blue Tits was 2.17 ± 2.03 ha, (range: 0.38–9.70 ha), mean distance to the nearest neighbour was 55.14 ± 37.55 m (range: 9.54–184.12 m) and the mean number of neighbours was 4.81 ± 1.53 neighbours (range: 2–9 neighbours).

3.1. Occupation rates

The Akaike multimodel inference supported a prominent role for nest-box selection of the number of neighbours and nest-box height, which were statistically significant (i.e., 95% credible intervals did not cross zero; Table 2). The AICc fig-

Table 2. Multimodel inference for Blue Tit nestbox selection and breeding parameters in a pinewood in central Spain during 2012 spring. The estimate of the coefficient, unconditional standard error, and sum of weights (estimated following Buckland *et al.* 1997) for each of the parameters in the best models ordered by the value of the AICc criterion (with small sample correction). Only those models with an increase in the AICc statistic $\leq$ 4 were selected for model averaging. Bold numbers indicate significant predictor variables (i.e., variables for which unconditional 95% confidence interval (CI) did not cross zero). *Beta* (β): weighted averages of standardized regression coefficients; *se* β: unconditional standard error of standardized regression coefficients; ΣW_i: sum of weights of the models in which the variable appears; Tarea: territory area per breeding pair; Height: nestbox position related to height (high/low); Group: nestbox position related to group (clustered/isolated); Orient: cardinal orientation of each nestbox; LDate: laying date per breeding pair; Neighb: number of neighbours per breeding pair; Dist: distance to the nearest neighbour pair; Interc: intercept of the model; Pc1, Pc2 and Pc3: habitat structure components (see Table 1).

Occupation	Orient	Pc1	Group	Pc2	Pc3	Tarea	Interc	Height	Neighb		
β	0.025	–0.060	–0.408	–0.265	0.403	0.826	**0.157**	**1.943**	**–1.199**		
ΣW_i	0.182	0.238	0.454	0.560	0.711	0.720	**1.000**	**1.000**	**1.000**		
se β	0.082	0.134	0.572	0.319	0.363	0.688	**0.303**	**0.389**	**0.365**		
Laying date	Pc3	Pc2	Pc1	Tarea	Orient	Group	Interc	Height	Neighb	Dist	
β	0.002	–0.003	–0.005	0.016	0.024	–0.206	**0.000**	**–0.460**	**0.395**	**–0.722**	
ΣW_i	0.092	0.095	0.098	0.132	0.176	0.582	**1.000**	**1.000**	**1.000**	**1.000**	
se β	0.013	0.015	0.017	0.038	0.049	0.228	**0.118**	**0.129**	**0.133**	**0.211**	
Clutch size	Pc3	TArea	Height	Dist	Pc2	Pc1	Group	Neighb	Orient	Interc	LDate
β	0.003	–0.002	0.005	–0.020	0.028	–0.049	–0.087	–0.088	0.126	**0.000**	**–0.561**
ΣW_i	0.056	0.064	0.078	0.123	0.189	0.278	0.357	0.397	0.525	**1.000**	**1.000**
se β	0.011	0.012	0.017	0.052	0.057	0.088	0.138	0.134	0.154	**0.134**	**0.154**
Brood size	Neighb	Orient	Pc1	Group	Height	Dist	TArea	Pc3	LDate	Pc2	Interc
β	–0.004	0.009	0.009	–0.057	0.058	–0.121	–0.084	0.077	–0.105	**0.402**	**–0.004**
ΣW_i	0.082	0.096	0.103	0.195	0.256	0.311	0.352	0.360	0.379	**0.985**	**1.000**
se β	0.018	0.026	0.026	0.116	0.103	0.197	0.135	0.124	0.160	**0.164**	**0.153**
Fledg. mass	Neighb	TArea	Pc1	Group	LDate	Pc3	Pc2	Orient	Height	Dist	Interc
β	0.005	0.007	–0.016	0.026	–0.052	0.048	0.054	–0.139	–0.173	**0.185**	**0.030**
ΣW_i	0.062	0.069	0.107	0.144	0.198	0.203	0.241	0.456	0.487	**0.520**	**1.000**
se β	0.019	0.022	0.039	0.071	0.100	0.095	0.100	0.190	0.223	**0.225**	**0.177**
Fledg. tarsus	Pc2	LDate	TArea	Height	Pc1	Dist	Neighb	Group	Orient	Pc3	Interc
β	0.002	0.000	0.016	–0.025	0.018	0.029	–0.027	0.130	–0.128	**0.247**	**–0.012**
ΣW_i	0.063	0.079	0.107	0.125	0.130	0.137	0.140	0.410	0.446	**0.667**	**1.000**
se β	0.014	0.018	0.039	0.057	0.045	0.071	0.059	0.191	0.179	**0.236**	**0.180**

ure for the null model (i.e., not including any effect) was 140.67, while the AICc for the “worst” model selected was 91.74. High nest-boxes were more likely to be occupied (78.38%) than low nest-boxes (21.62%), the same as those with fewer neighbours (Table 2). The remaining predictor variables – territory area, habitat principal components, group and orientation – had a low strength of evidence and magnitude effects (sum of Akaike weights < 0.80 absolute values of weighted standardized β regression coefficients < 0.10; Table 2).

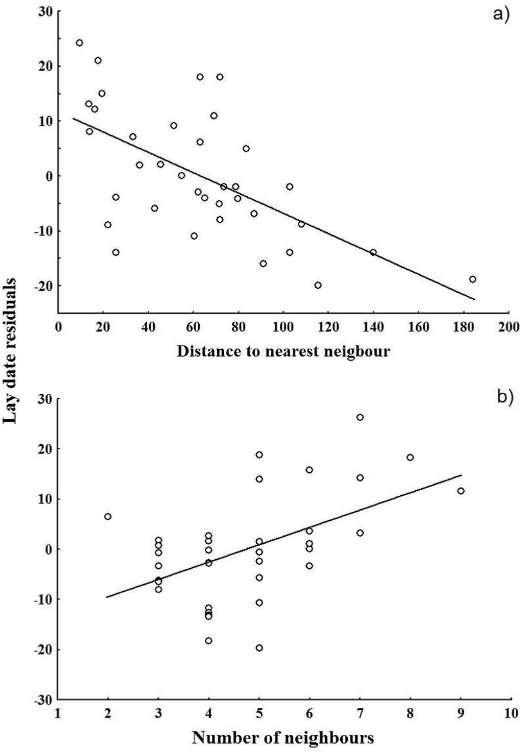

Fig. 3. Partial residual plots illustrating the influence of distance to the nearest neighbour (a) and number of neighbours (b) on mean laying date for Eurasian Blue Tits breeding in a Central Spain pinewood during 2012 spring. Partial residuals are obtained after controlling for the remaining variables considered in the analysis of Table 2.

3.2. Breeding performance

Variation in laying date was explained by an average model including height, number of neighbours, and distance to the nearest neighbour as explanatory variables ($\Sigma W_i > 0.8$ and highest magnitude effects; Table 2). The AICc figure for the null model was 105.51, while the AICc for the “worst” model selected was 89.27. Early laying females selected nest-boxes placed above three meters (high) and breed in sites with fewer neighbours and where distance to the nearest neighbour was larger (Table 2, Fig. 3).

The only variable affecting Eurasian Blue Tit clutch size was laying date, so that clutch sizes decreased as laying dates advanced (Table 2). The AICc figure for the null model was 105.51, while the AICc for the “worst” model selected was 96.13. The average model for brood size included Pc2 as positive significant predictor ($\Sigma W_i > 0.8$; Table 2), thus brood size increased when shrub cover was higher and tree height lower (Table 2, Fig. 4). The AICc figure for the null model was 105.51, while the AICc for the “worst” model selected was 102.45.

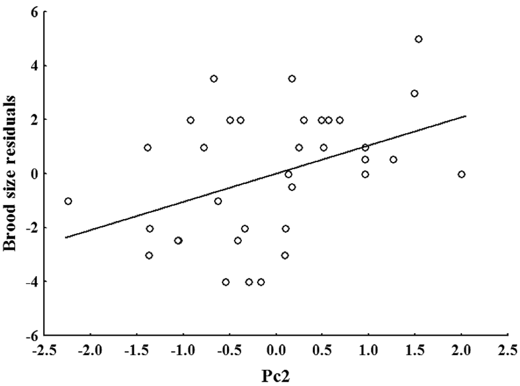

Fig. 4. Partial residual plots illustrating the influence of second PCA component (Pc2) on mean brood size at 13th day for Eurasian Blue Tits breeding in a Central Spain pinewood during 2012 spring. Partial residuals are obtained after controlling for the remaining variables considered in the analysis of Table 2.

Nestling mass was marginally higher when distance to the nearest neighbour was larger ($\Sigma W_i < 0.8$ but the highest magnitude effect; Table 2). Also, the presence of oak species (Pc3) had a marginal role in determining nestling tarsus length ($\Sigma W_i < 0.8$ but the highest magnitude effect; Table 2). The AICc figures for the null models were both 85.74, while the AICc for the “worst” model selected was 83.56 for nestling mass and 85.03 for tarsus length.

4. Discussion

4.1. Nest site selection

Eurasian Blue Tits in our study site occupied preferentially nest-boxes placed at a height of 3.0–5.0 meters above the ground (lower nest-boxes were placed at 1.5–2.0 meters). According to Nilsson (1984), selection for higher nest-boxes is explained by lower predation risk for nests at greater heights. Data on nest predation rates in natural holes suggest that the preference for higher holes is highly adaptive for secondary cavity nester species, such as the Eurasian Nuthatch and the European Starling (*Sturnus vulgaris*; Nilsson 1984), the European Roller (*Coracias garrulus*; Parejo & Avilés 2011) or the Mountain Bluebird (*Sialia currucoides*; Robles & Martin 2013). High nest placement could be advantageous for birds as it minimizes nest detection and access to ground-dwelling predators (Wesołowski 2002), and preferences may arise as an evolutionary adaptation. In contrast, Wesołowski & Rowiński (2012) found that higher holes were more at risk of being depredated by Forest Dormouse (*Dryomys nitedula*). Therefore, habitat specific features may determine the variation and adaptability of Eurasian Blue Tits in selecting breeding site.

Territories with fewer neighbours were also preferred for breeding by Eurasian Blue Tits. Intensity of intra- and inter-specific competition has been previously described in a related species, the Great Tit, to be strongly affected by individual differences in state, such as age (Drent 1983), body condition (Gosler & Carruthers 1999) and prior residency (Krebs 1982, Sandell & Smith 1991). Our results support the idea that birds selected areas where competitive interactions were reduced (fewer neighbours).

4.2. Nest-site characteristics and breeding performance

Laying date was earlier in high nest-boxes, with fewer territory neighbours and located further from the closest neighbour. This suggests that those pairs settled first in the area after winter dispersal, selected better locations, since the best territories for Eurasian Blue Tits are those in which the earliest clutches are laid (Maícas *et al.* 2011). This pattern is related to the avoidance of predators, in the high positioned nest-boxes, and the active avoidance by other breeders to settle in the same area or the active defence of larger territories by these early pairs.

We found no significant effect of nest-box position on clutch size. Clutch size was only affected by laying date, as it declined throughout the season, as has been extensively described in Eurasian Blue Tits and other single-brooded species (Lack 1954, Perrins 1965, Klomp 1970, Crick *et al.* 1993). Contrary to expected, our data did not show any negative effect of high population density on clutch size, as previously reported by Wilkin *et al.* (2006). This study suggested that this relationship results from adaptive adjustment by females or by food limitation in over-occupied areas. Despite population density in our study site is greater (0.98 pairs / ha) compared to that described in Wilkin *et al.* (2006), we cannot considered it as over-occupied since higher densities have been previously reported at the same area (pinewood: 1.0 and 1.3 pairs / ha; oakwood: 3.5 and 4.40 pairs / ha; Sanz *et al.* 2010, García-Navas & Sanz 2011a). Hence, in our pine plantation, the population density/resource availability ratio may already be highly constrained by habitat type to prevent us of finding a strong influence of competition on clutch size.

Eurasian Blue Tit brood size was larger in those territories where shrub cover was well developed. Similar positive correlations were found in previous studies (Sanz *et al.* 2010, García-Navas & Sanz 2011b), as well as on other species e.g., Eurasian roller (Avilés *et al.* 2000). Also, lower tree height (included in Pc2) would suggest that smaller trees permit higher light incidence, which may be particularly important for understory growth. This seems to be related to the importance of the understory as an alternative feeding substrate for Tits, which are mainly canopy foragers. The continuous transformation of this pine plantation may have changed the pattern of food availability, and as indicated by Harrison & Fahrig (1995), created an heterogeneous environment with mosaics of optimal (high shrub cover and lower trees) and sub-optimal habitats.

Nestling body mass showed a tendency to be higher when distance to the nearest neighbour was greater, suggesting a causal role for population density in reproductive output. It has been previously shown that competition for food is exacerbated in low quality habitats (Dhondt 2010), which may explain why Eurasian Blue Tits preferred to breed far away from competitors in our study area. Similar results have been described for Great Tits (Wilkin *et al.* 2006). These authors explained the density-dependent pattern in fledgling mass as the possible reduction of nestling provisioning (either in quality and/or quantity) in high-density areas, particularly if parents also suffered from increased interference from other pairs. Similar findings have been obtained in the same Great Tit study population (Wilkin *et al.* 2009).

Eurasian Blue Tit chicks raised in more humid areas, with more Portuguese Oaks, fewer Holm Oaks (Pc3), and therefore, with higher caterpillar abundance, had larger tarsi. This predictor, which we called "dryness gradient", suggests an indirect effect of soil dryness in chick's development. The spring of 2012 was especially dry and warm in our study area, with a very low breeding success compared to previous years (see e.g., García-Navas & Sanz 2011b). This, in addition to the "low quality" habitat type (pinewood) of this study, may explain the better chick development in more humid areas with assumed higher caterpillar abundance.

Finally, we found that nest-box clustering design (isolated or clustered) did not influence occupation rate or breeding success. Occupation rates in coniferous habitats have been reported to be lower than in other forest types, such as oakwood or native pinewoods (Maícas & Fernández-Haeger 1996). Approximately, half of the nest-boxes remained unoccupied (51 out of 100). Thus, breeding pairs would likely settle away from potential competitors resulting in a widespread distribution. Low occupation rates and reproductive success suggest that this habitat may be used by those pairs that did not find an available territory in the preferred oakwood habitat.

In conclusion, our findings suggest that the placement of nest-boxes should be carefully planned to adapt to species-specific requirements in each habitat type, to ensure their occupation and favour the breeding performance of secondary cavity nesters. For Eurasian Blue Tits breeding in Maritime Pine plantations, nest-boxes should be placed high above the ground (height ≥ 3 m), and should be separated by at least 60 meters, as this is the average home range for several forest passerines (e.g., 0.40–3.00 ha for Great Tit, Both & Visser 2001; 0.53–2.24 ha for Nuthatch, Enoksson & Nilsson 1983; 0.07 to 1.57 ha for Eurasian Blue Tit in this study). We recommend considering nest-box height and cavity-nester density when providing nest-boxes in pine plantations, and to favour shrub and native tree species recovery (see also Barrientos 2010) in order to improve the habitat quality and thus, benefit forest bird populations. Further, we emphasize the suitability of nest-boxes for behavioural and evolutionary studies, as several forest-dwelling secondary cavity-nesters readily accept them to breed.

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Pesäpönttöjen esiintymistiheyden ja asennuskorkeuden vaikutukset sinitiaisen asutusasteeseen ja pesinnän onnistumiseen

Pesäpönttöjä käytetään yleisesti lintujen pesimäbiologian tutkimiseen ja pesäpaikkojen puutteesta kärsivien lajien auttamiseen. Pesäpöntön asennuspaikka voi vaikuttaa pesäpaikan valintaan, mutta pesäpönttöjen asuttamiseen vaikuttavia tekijöitä ei vielä tunneta riittävän hyvin. Me käytimme sinitiaista mallilajina tutkiessamme pesäpöntön valintaan vaikuttavia tekijöitä ihmisen muokkaamassa ympäristössä Espanjan mäntyplantaaseilla. Asetimme 100 pesäpönttöä eri korkeuksille: matalalle 1.5–2.0 metrin korkeuteen, tai korkealle 3.0–5.0 metrin korkeuteen. Pesäpönttöjä asennettiin tiheään (kuuden pöntön ryhmiin joissa pesäpöntöt ≤ 10 metrin välein) ja harvaan (pesäpönttöjen väli vähintään 80 metriä). Laskimme potentiaalisen reviirikoon jokaiselle pesäpöntölle ja etäisyyden lähimpään naapuriin. Tutkiessamme pesäpöntön asennuskorkeuden ja pesimistiheyden vaikutusta niiden asutusasteeseen ja pesinnän onnistumiseen, huomioimme tilastollisesti ympäristön rakenteen (esim. kasvillisuus) vaikutuksia.

Sinitiaiset suosivat pesäpönttöjä jotka oli asennettu korkealle ja matalaan tiheyteen. Pesinnän ajoitus oli aikaisin korkealle asennetuissa pesäpöntöissä sekä matalaan tiheyteen asennetuissa pesäpöntöissä. Pensaiden peittävyys ja puiden korkeuden mediaani lisäsivät kuoriutuneiden poikasten määrää. Lentoon lähteneiden poikasten massa puolestaan lisääntyi kun etäisyys lähimpään naapuriin kasvoi, ja nilkan pituus kasvoi tammilajien lisääntyessä. Pesäpönttöjen asentamistavan ja pönttöjen tilallisen jakauman vaikutusten erottaminen on tärkeää, jotta voimme paremmin ymmärtää lajispesifisiä elinympäristövaatimuksia erilaisissa ympäristöissä.

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