



Original article

Nest-site selection, territory quality and breeding performance in a Blue Tit *Cyanistes caeruleus* population

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ABSTRACT

Patterns of territory selection and sources of variation for reproductive performance in a Blue Tit *Cyanistes caeruleus* population breeding in nest-boxes during years 2007 and 2008 in a holm oak forest are analyzed. Territory selection has been assessed as a function of two fixed effect factors: territory location (peripheral vs. interior in the nestbox patch) and nestbox type (entrance hole: 26 mm vs. 32 mm). Breeding density was independent of these factors. Pairs nesting in periphery nest-boxes and in small-holed nestboxes owned territories bigger than those nesting in interior and large-holed nestboxes, respectively. The breeding traits studied were laying date, clutch size, hatching success, fledging success and breeding success. Egg laying was earlier in periphery territories and small-holed nestboxes. Between-year variation was a factor significantly affecting to all breeding traits. Clutch size declines in late clutches. Hatching success was higher in territories with more tree density. Although egg laying started earlier in some territories, the mean breeding success was similar in all of them. However, territories with the greatest contribution of individuals to the population were those with small-holed nestboxes. Breeding success in successful pairs had a tendency to be higher in pairs with late clutches and in those nesting in interior territories with large-holed nestboxes. Both decreased breeding success and total breeding failure were much more important in the second breeding year than in the first one. The high breeding density of Blue Tit, favored by the experimental design of nestbox plot, did not suggest significant variation between territories in terms of breeding success achieved. Implications for nestbox management are discussed.

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1. Introduction

At landscape scale, huge extensions of holm oak forests in the Southern Iberian Peninsula are the result of human management over centuries for various uses (grazing, hunting, timber production, etc.). This management has given rise to a agro-silvo-pastoral system named “dehesa” (González-Bernáldez et al., 1976; Joffre et al., 1988). This system is a secondary forest in which the natural holes are scarce or non-suitable for breeding purposes, affecting the population numbers of secondary hole-nesting birds and, specifically, the Blue Tit *Cyanistes caeruleus*. This species is closely dependent of the occurrence of holes in trees for breeding and roosting (Von Haartman, 1957; Hildén, 1965; East and Perrins, 1988). In this context, the use of nestboxes can compensate the effects of

the habitat alteration on the population dynamics of this species, particularly during the reproductive season (Newton, 1998).

Nevertheless, within any habitat there is a spatial heterogeneity as a result of a set of attributes shaping the selection of a breeding territory carried out by an individual. The choice made by individuals between different potential nesting sites (territories) may have consequences on their reproductive fitness (Cody, 1985; Martin, 1988, 1995; Newton, 1998; Sergio and Newton, 2003; Maícas and Fernández Haeger, 2004; Arriero et al., 2006; Sanz et al., 2010; Maícas et al., 2011). This individual fitness has effects on the overall population recruitment and contributes to its persistence in the habitat. Although it initially was assumed that the choice of habitat made by birds is an ideal free selection (Fretwell and Lucas, 1970), the available evidence seems to prove that the occupancy of an habitat for breeding purposes follows a *continuum* (Kristan, 2003), with the ideal free selection of habitat at one extreme and an ecological trap at the other. Along this *continuum*, different situations may arise which, although not implying a wrong choice of habitat or territory, could constitute

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a non-ideal habitat selection (Bernstein et al., 1991; Arlt and Part, 2007). This model of territory selection is a consequence of the mismatch between the territory choice and its quality, caused in some cases by alterations introduced into the habitat. Such a mismatch produces effects which can reduce one or more components of fitness, affecting the recruitment rate of individuals.

The breeding success in birds depends on a range of factors such as the breeding timing, habitat heterogeneity, choice of different micro-environments, territory size, edge effect, predation rate, parasitism, etc. In hole-nesting birds, a key factor explaining the breeding success could be the hole entrance size, as small entrance size is important in preventing access by large predators, namely the predation risk depends on hole attributes (Nilsson, 1984; Möller, 1989; Christman and Dhondt, 1997; Wesolowski, 2002). Another key factor considered has been the timing of annual breeding as a function of the laying date. According to the available evidence, this trait is a crucial determinant of reproductive success in insectivorous passerine birds (Perrins, 1970; Thomas et al., 2010). The influence of several factors implies that the breeding territories may differ widely in resources and other attributes affecting the each pair's contribution to the overall reproductive output.

Some studies have presented empirical evidence of maladaptive habitat selection in bird species, some of which are open-nesting species (Gates and Gysel, 1978; Donovan and Thompson, 2001; Shochat et al., 2005; Arlt and Part, 2007) and others cavity-nesting species breeding in nestboxes (Semel and Sherman, 2001; Pöysä and Pöysä, 2002; Mand et al., 2005; Magi et al., 2009). This evidence has been found mainly in habitats modified directly or indirectly by human activity and one of these modifications has been the erection of nestboxes as a resource to provide shelter and breeding space for cavity-nesting species.

Due to the heterogeneity existing in the habitats, when nestboxes are available for tits in forests as potential nesting sites some habitat characteristics around them could account for the nestbox occupancy and the reproductive performance of these tit species (laying date, the hatching and breeding success achieved). This has been shown for Blue Tit and Crested Tit (Arriero et al., 2006; Atienzar et al., 2009; Sanz et al., 2010) in forest habitats geographically close to our study area. In this research, given the availability of potential nest-sites (nestboxes) with small and large entrance size, their different spatial location in the plot (periphery vs interior) and the habitat heterogeneity around the nestboxes, we predict that Blue Tits will achieve the highest breeding success in territories with small-holed nestboxes, high tree density and located in the periphery of nestbox patch.

The study has two main goals. Firstly, to analyze the effects of the nestbox plot model on the occupancy patterns of nestboxes by Blue Tit. Secondly, to ascertain whether or not a link between some attributes of territories and reproductive traits of Blue Tit exists. Finally, we will discuss the implications of our results for the nestbox management in young holm oak forests.

2. Material and methods

The study area is located in Sierra Morena, southern Spain, at an average altitude of 550–650 m.a.s.l. The vegetation in this landscape is dominated by a Mediterranean holm oak forest *Quercus ilex* ssp. *ballota*, with tall trees scattered over connected patches of grassland and scrub. The nestbox patch is located into that forest landscape with a surface of over 900 ha being the edges of the patch far away from the boundaries of the forest. More details on habitat characteristics have been published elsewhere (Maicas and Fernández Haeger, 1999).

The nest-box plot contained two types of nestboxes: 50% were large-holed nestboxes (hole-entrance size of 32 mm Ø) and 50%

were small-holed ones (hole-entrance size of 26 mm Ø). Nestboxes had an alternate distribution in every row of the nest-box plot: each type of nestbox had around two nestboxes of other type.

Throughout the whole study period (years 2007 and 2008 pooled), of the 218 nestboxes available, the different nesting species occupied 171 nestboxes, being Blue Tit and Great tit the most abundant species: 128 (58.7%) and 31 (14.2%) breeding pairs, respectively. The available nestboxes for Blue Tit were 100% because it starts to breed in the area earlier than Great Tit and Nuthatch (Julian day 85, 95 and 87, respectively; Julian day 1 = January 1). The other nestboxes were occupied by Nuthatches *Sitta europaea* (8 pairs), Crested Tits *Lophophanes cristatus* (1 pair), Wrens *Troglodytes troglodytes* (1 pair) and Rock Sparrows *Petronia petronia* (1 pair). The number of unoccupied nestboxes was 48 (22%).

2.1. Territories spacing and size

The nest-box plot contained two types of nestboxes: 50% were large-holed nestboxes (hole-entrance size of 32 mm Ø) and 50% were small-holed ones (hole-entrance size of 26 mm Ø). Nestboxes had an alternate distribution in every row of the nest-box plot: each type of nestbox had around two nestboxes of other type. To obtain a more even distribution of the nestboxes, we designed a regular grid over the ground showing equal distances of 50 m apart using GPS technology. The nestboxes were erected to the nearest tree to the (UTM) coordinates of each point and the grid points distribution was consequently not regular, resulting in an uneven nestbox spacing.

Due to this irregular distribution, spatial limits between the nestboxes can be designed using the Dirichlet tessellation, in which straight line segments are placed midway between adjacent neighbours, producing convex polygons (Thiessen areas or Voronoi polygons) (Adams, 2001). This methodology has also been applied to know the effect of several factors on the fitness of Great Tit (*Parus major*) using time series data of this species (Wilkin et al., 2006, 2007).

Using a tessellation technique with GIS software (the ArcGis programme), we formed Thiessen polygons around each nestbox and used their sizes to measure nestbox spacing (Fig. 1a). The edge of the polygons was calculated using as the buffer radius the average distance between the nestboxes set up. This average distance from the tree to which the next box is fixed produces a rounded edge which represents the theoretical geometric limit of the available territory for the breeding pair which occupies these peripheral nestboxes. However, it can be assumed that these pairs can enlarge their territory outwards more easily than those pairs which occupy the interior territories. The same methodology was used for the Blue Tit territories as for the other tit species, Great Tit and crested tit (the three species competing for holes and food) breeding in the nestboxes, both in 2007 and 2008 (Fig. 1b and c). In this case, the distance used to establish the limits of the polygon was the average distance between the nestboxes occupied by these species. The estimation of the size of the peripheral territories is conservative and it should be assumed that the pairs breeding in peripheral nestboxes have territories which could be of bigger extension than considered. There is empirical evidence (Tremblay et al., 2005) that foraging distances of Blue Tit range from on average 25.2 ± 12.3 m to 53.2 ± 22.9 m apart from the nest in two Corsican evergreen habitats covering a mean surface area of 0.196 ha and 0.785 ha, respectively.

As habitat characteristics with relevance to the territory selection by Blue Tit we did choose the entrance hole size of nestbox (hereafter ENTRANCE), territory location (TERR) and tree density in each territory (TD). The spatial distribution of the nestboxes in

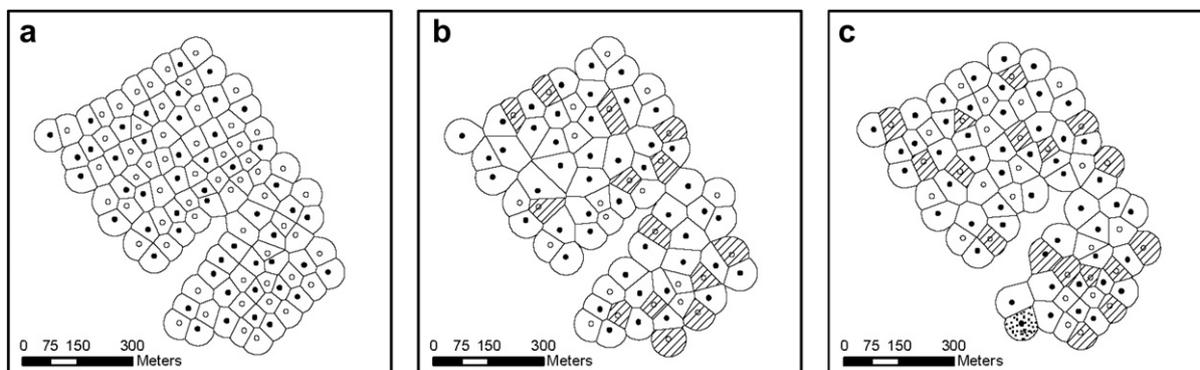


Fig. 1. (a) Tessellated polygons for all nestboxes in the study area providing an estimate of nestbox spacing; (b) Nestboxes occupied by Blue Tit (white polygons) and great tit (streaked polygons) in 2007 and their tessellated polygons which provide a model for territory size; and (c) Nestboxes occupied by Blue Tit, great tit and crested tit (dotted polygons) in 2008 and their tessellated polygons. Open circles: large-holed nestboxes; solid circles: small-holed nestboxes.

a regular pattern allows us to classify them into two groups: interior (territories located in the nestbox patch inner and with no possibilities of expand) and peripheral (territories located in the nestbox patch edge and with possibilities of expansion beyond the geometrical limit). It is assumed that the hypothetical expansion of territories could increase the breeding output of Blue Tit (Maicas and Fernández Haeger, 2004).

The combination of both factors, spatial location and entrance hole size of the nestboxes, generates four categories of potential territories: peripheral and interior territories both with small and large-holed nestboxes. The surface of all territories occupied by Blue Tit in each category of territories was used to calculate its breeding density (Table 1).

For each territory, the number of trees was calculated by superimposing the polygons over the orthophoto of the area (year

2004) in which the tree canopies are easily identifiable. Tree density can be taken as an indicator of the quality of the territories, a high correlation between tree numbers and territory size exists ($r = 0.632$ $p < 0.001$), since food availability for Blue Tits during the breeding period is closely linked to the holm oak canopies (Herrera, 1980; Díaz et al., 1998).

The mean tree density in Blue Tit territories, a predictor for the habitat quality, did not differ from that of available territories both in year 2007 (Student $t_{1140} = -0.176$ $p = 0.86$; 70.8 ± 19.4 trees/ha $n = 62$ and 70.2 ± 18.9 trees/ha, $n = 80$, respectively) and in year 2008 ($t_{1151} = -0.041$ $p = 0.97$; 76.0 ± 19.8 trees/ha $n = 65$ and 75.9 ± 19.3 trees/ha $n = 88$, respectively). The quality of the breeding territories of Blue Tit has been studied by using the relationship between the independent variables and the reproductive traits, thus determining which of these variables are linked to the fitness components analyzed here (Table 2).

Table 1

Several attributes of Blue Tit population nesting in peripheral and interior territories with small and large-holed nestboxes during the reproductive periods of 2007 and 2008. OST = Overall surface of the territories (ha) occupied by Blue Tit in each category of territory. Mean (\pm SD) are provided for some attributes.

	Periphery		Interior	
	Hole 26	Hole 32	Hole 26	Hole 32
Year 2007				
OST	11.36	3.8	13.1	9.95
Available nestboxes	24	21	32	32
Breeding pairs	23	8	25	6
Occupancy rate	96	38	78	19
of nestboxes (%)				
Density (pairs/ha)	2.0	2.1	1.9	0.6
Mean territory size (ha)	0.49 ± 0.11	0.47 ± 0.03	0.52 ± 0.13	0.35 ± 0.12
Mean tree density (trees/ha)	77.3 ± 21.8	76.4 ± 22.9	65.5 ± 16.7	63.8 ± 11.2
Year 2008				
OST	10.27	2.6	9.9	4.5
Available nestboxes	23	22	32	32
Breeding pairs	21	6	27	12
Occupancy rate	91	27	84	38
of nestboxes (%)				
Density (pairs/ha)	2.0	2.3	2.7	2.7
Mean territory size (ha)	0.49 ± 0.1	0.43 ± 0.06	0.37 ± 0.08	0.37 ± 0.03
Mean tree density (trees/ha)	85.2 ± 23.9	87.1 ± 15.7	72.2 ± 18.0	72.9 ± 16.5
Mean density (both years)	2.0	2.2	2.3	1.7
Mean territory size (both years)	0.49 ± 0.1	0.45 ± 0.06	0.44 ± 0.14	0.36 ± 0.08
Mean occupancy rate (both years)	93.5	22.5	81.0	28.5

2.2. Field data and reproductive traits

Nestboxes were type Schwegler (Model 2M; wood-concrete material) and were erected in December 2006. Their entrance hole size is 26 or 32 mm and the internal diameter is 12 cm. The height above the ground of the nestboxes has not been measured but according to a visual estimate ranged between 3 and 5 m. Nestboxes were inspected weekly throughout the breeding season until

Table 2

ANCOVA results predicting the relationships between some sources of variation and breeding performance of Blue Tit. TERR (territory location), ENTRANCE (entrance hole size of nestbox) and YEAR are fixed effect factors; TD (tree density), TS (territory size) and LD (laying date) are the covariates. Only significant terms are included.

Dependent	Variation source	F	P
Laying date (df = 1, 108)	Year	10.587	0.002
	Terr	4.265	0.041
	Entrance	6.691	0.011
Clutch size (df = 1, 109)	Laying date	23.495	<0.001
	Year	15.226	<0.001
	Year*Terr	6.628	0.012
Hatching success (df = 1, 109)	Year*Terr * Entrance	5.713	0.019
	TD	4.746	0.032
Fledgling success (all pairs) (df = 1, 109)	Year	7.820	0.006
	Year	23.516	<0.001
Breeding success (all pairs) (df = 1, 109)	Year*terr*entrance	7.465	0.007
	Year	4.692	0.033
Breeding success (successful pairs) (df = 1, 87)	Laying Date	3.902	0.052
	Entrance	3.814	0.054
	Terr*Entrance	3.765	0.056

every fledgling had left the nest. The traits recorded were date of laying onset (January 1 = Julian day 1), clutch size, hatching success (ratio of the number of eggs hatched to the clutch size), fledgling success (ratio of the fledglings raised to the number of eggs hatched) and breeding success (ratio of the number of fledglings raised to the clutch size) eggs hatched and fledglings raised. Second clutches ($n = 5$) were excluded from the analysis.

2.3. Data analysis

Given the laying date have a great relevance in the reproductive output of Blue Tit, an ANCOVA model was constructed in which laying date (LD) was entered as dependent variable; territory size (TS) and tree density (TD) as covariates; and YEAR, entrance hole size (ENTRANCE) and territory location (TERR) (all of them as fixed effects factors) as categorical variables. The relationship between territory attributes and reproductive traits of Blue Tit has been analyzed with another ANCOVA model in which clutch size, hatching success, fledgling success and breeding success are the dependent variables; YEAR, entrance hole size and territory location were entered as fixed effect factors; and as covariates the territory size, tree density and laying date. The hatching, fledgling and breeding success have been were ArcSin transformed. Combined data from two years were used in all ANCOVA. Unless otherwise stated, mean and standard deviation are given in the text. The GLM procedure of Statistica software package (StatSoft Inc., version 7) was used. Several books have provided key help about statistical methodology (Zar, 1984; Doncaster and Davey, 2007).

3. Results

3.1. Patterns of nest-site selection

Throughout the whole study period (years 2007 and 2008 pooled), of the 218 nestboxes available, the different nesting species occupied 171 nestboxes, being Blue Tit and Great tit the most abundant species: 128 (58.7%) and 31 (14.2%) breeding pairs, respectively. The available nestboxes for Blue Tit were 100% because it starts to breed in the area earlier than Great Tit and Nuthatch (Julian day 85, 95 and 87, respectively; Julian day 1 = January 1). The other nestboxes were occupied by Nuthatches *S. europaea* (8 pairs), Crested Tits *L. cristatus* (1 pair), Wrens *T. troglodytes* (1 pair) and Rock Sparrows *Petronia petronia* (1 pair). The number of unoccupied nestboxes was 48 (22%).

Although a higher number of pairs nested in peripheral and interior territories with small-holed nestboxes than in the territories with large-holed ones, this difference is not statistically significant on a yearly basis (Yates corrected $\chi^2 = 0.09$ df = 1 $p = 0.76$ for 2007; $\chi^2 = 0.24$ df = 1 $p = 0.63$ for 2008) (Table 1). The same pattern is repeated when the data are analyzed pooling both years (Yates corrected $\chi^2 = 0.00$ df = 1 $p = 1.00$). As a consequence of the variable number of pairs the occupancy percentage of nestboxes is variable as well being greater in peripheral and interior territories with small-holed nestboxes in both years than in territories with large-holed nestboxes. The occupancy percentage in interior territories with large-holed nestboxes during the second breeding year increased as much as twice the occupancy in year 2007 at these same territories (Table 1).

However, the average breeding density of Blue Tit in both years was very similar, 2.2 and 2.4 pairs/ha, respectively. For each year, the breeding density varied little according to the type of nestbox and the territory location (Table 1). There is no significant difference between the breeding density in periphery and interior territories as a function of the nestbox type and on a yearly basis

($\chi^2 = 0.76$ df = 1 $p = 0.38$ for 2007; $\chi^2 = 0.12$ df = 1 $p = 0.73$ for 2008). The same pattern is observed when pooling data of both years ($\chi^2 = 0.06$ df = 1 $p = 0.81$).

The Thiessen polygon map of the breeding area produced 109 theoretical territories (potential breeding sites), which are the territories available for Blue Tits and other small cavity-nesting species in each breeding season (Fig. 1a). The mean area (\pm sd) of these polygons is 0.35 ± 0.08 ha. Of these available territories, Blue Tits nested in 62 during 2007 and in 66 during 2008, creating breeding territories with an average area of 0.46 ± 0.13 ha and 0.42 ± 0.1 ha, respectively, (One-way ANOVA: $F_{1126} = 14.830$ $p < 0.001$ for difference between both years). As a result, the average area of the territories occupied by Blue Tits each year was greater than that of all available territories (tessellated polygons) (Student t test: $t = -8.966$ df = 171 $p < 0.001$ for 2007; $t = -4.811$ df = 173 $p < 0.001$ for 2008).

A two-way ANOVA (pooling data of both years) was carried out to analyze the variation of Blue Tit territory size controlling the effects of the variables territory location and entrance hole. The results show that the average size of territories with small-holed nestboxes is greater than that of the territories with large-holed nestboxes (0.47 ± 0.12 $n = 94$ vs 0.41 ± 0.08 $n = 24$, respectively, $F_{1124} = 5.999$ $p = 0.016$) and the average size of the periphery territories is greater than that of the interior ones (0.47 ± 0.09 $n = 55$ vs 0.40 ± 0.13 $n = 63$, respectively, $F_{1124} = 8.988$ $p = 0.003$). However, the interaction of both factors does not produce significant effect on this attribute in the four categories of territories ($F_{1124} = 0.720$ $p = 0.40$).

3.2. Sources of variation for breeding traits

The relationship between laying date of Blue Tit and territory attributes was studied performing an ANCOVA in which the effects of fixed factors such as year, territory location and entrance hole size on the date of laying onset were controlled; the territory size and tree density were used as covariates. According to the results (Table 2), the laying date is significantly linked to the variables year, entrance and territory location. On average, Blue Tit started the egg laying five days earlier in the second breeding year (2008) than in the first one (2007) (Julian days 82 ± 9.7 $n = 58$ and 87 ± 12.1 $n = 58$, respectively), three days earlier in the periphery territories than in the interior ones (82 ± 10.5 $n = 55$ and 85 ± 12.2 $n = 63$, respectively) and seven days earlier in small-holed nestboxes than in large-holed ones (82 ± 10.6 $n = 94$ and 89 ± 13.5 $n = 24$, respectively) (Fig. 2). Timing of egg laying was independent of territory size and tree density.

Clutch size is dependent on year and laying date. The mean clutch size of breeding population was higher in the first year than in the second one (7.4 ± 1.8 $n = 57$ and 6.6 ± 1.64 $n = 53$ eggs, respectively) (Table 3). The laying date is the main within-year source of variation for the clutch size existing an inverse relationship between both traits ($\beta = -0.482$ $t = -4.847$ $p < 0.001$). The interaction of year, territory location and entrance hole size have significant effects on the clutch size of Blue Tit. The post hoc Fisher test showed that this trait was similar in all territories except in those located in the interior zone with large-holed nestboxes during 2008. At these territories the mean clutch size was similar to the majority of territories in the same year but it was lower than in most territories during 2007 (Table 3).

Variability in the hatching success is explained by the variables tree density and year (Table 2). The proportion of eggs hatched tends to increase with tree density ($\beta = 0.212$ $t = 2.178$ $p = 0.03$). On the other hand and unlike the clutch size, the mean hatching success was lower in year 2007 than in year 2008 (Table 3). When all pairs are included in the ANCOVA, the fledgling and breeding

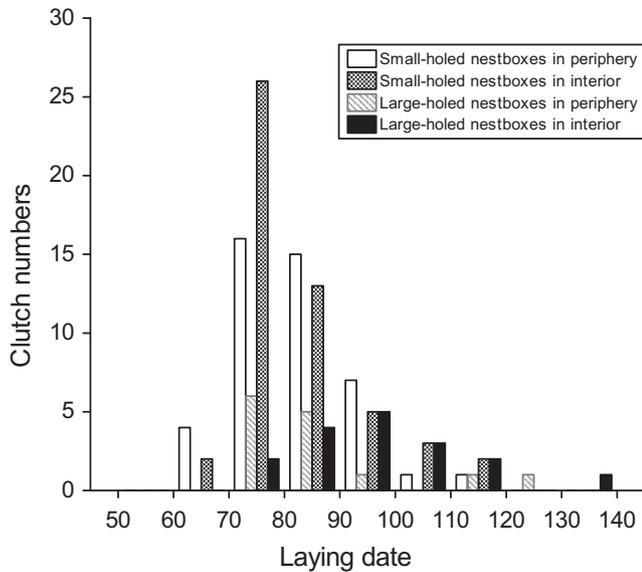


Fig. 2. Laying date as a function of entrance hole size of nestboxes and territory location. Data pooled (years 2007 and 2008).

success were mainly affected by the year. Average fledgling and breeding success was much lower in year 2008 than in year 2007 (Table 3). In the case of fledgling success, a significant effect of the interaction between year, territory location and entrance hole size exists on this trait. The post hoc Fisher tests on the paired comparisons of this interaction showed that year is the most important source of variation for this trait between territories. On a yearly basis, there is not significant difference between territories regarding to the fledgling success.

When only the successful pairs are entered in the ANCOVA, the breeding success is significantly influenced by the main effects of entrance hole size and its interaction with territory location (Table 2). The mean breeding success per clutch is higher in large than in small-holed nestboxes (Table 3). By other hand, the post hoc Fisher testing on the paired comparisons of the significant interaction between both main effects showed that the mean breeding success of Blue Tit was similar in most territories. Only significant differences there were between interior territories with large-holed nestboxes and territories with small-holed nestboxes where the mean breeding success was lower (Fig. 3). The ANCOVA results show also an effect of laying date on the breeding success in successful pairs existing a positive relationship between both traits ($\beta = 0.232$ $t = 1.975$ $p = 0.05$): regardless the category of territory, in the late clutches the breeding success achieved was higher than in early clutches.

The occupied small-holed nestboxes were the most relevant factor for the addition of new individuals to the population of Blue

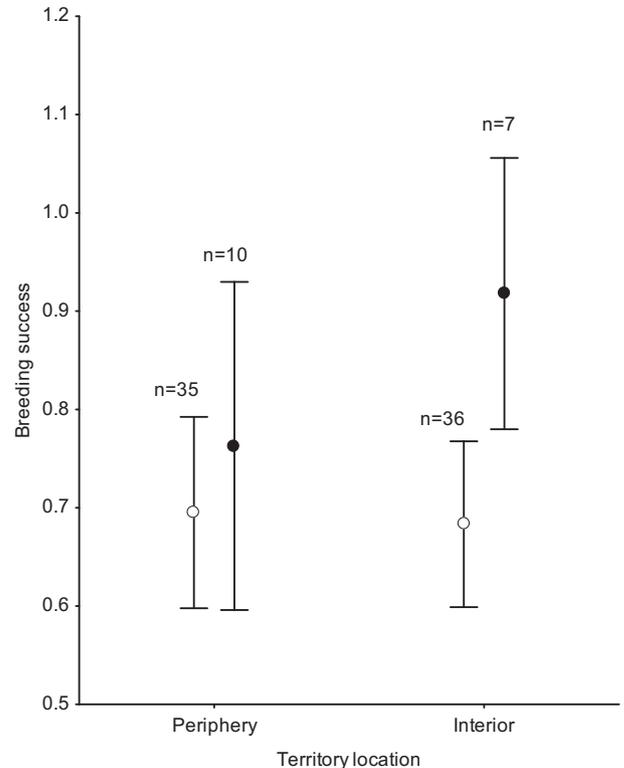


Fig. 3. Breeding success in successful pairs as a function of interaction between the factors entrance hole size and territory location. Vertical bars denote 0,95 confidence intervals. Open circles: small-holed nestboxes; filled circles: large-holed nestboxes. Data pooled (years 2007 and 2008).

Tit. Taking into account the reproductive output achieved by Blue Tit in the different types of territories (both years pooled), the territories with the greatest contribution of individuals to the population of Blue Tit were those with small-holed nestboxes, both peripheral and interior, with 177 (39.2%) and 180 (39.8%) of fledglings, respectively. Territories with large-holed nestboxes made a lower contribution to the population: 56 (12.4%) the peripheral and 39 (8.6%) the interior ones.

3.3. Total breeding failure

A component of interest to the fitness of a population is the total breeding failure experienced by pairs. Reproductive failure was analyzed taking into account the number of nests with total breeding failure where no eggs hatched or no chicks survived in the different categories of territories. The total failure of the clutch or the brood can be related with an effect of direct predation on eggs or the chicks, or an indirect effect due to the desertion or death of

Table 3
Statistics (mean \pm sd) of the breeding traits of Blue Tit depending on the year, territory location and entrance hole size of nestbox. The sample size is in brackets.

	Year 2007				Year 2008			
	Periphery		Interior		Periphery		Interior	
	26	32	26	32	26	32	26	32
Clutch size	7.5 \pm 1.7 (23)	7.3 \pm 1.5 (7)	7.4 \pm 2.08 (22)	8.0 \pm 1.2 (5)	6.7 \pm 1.4 (18)	8.0 \pm 1.2 (5)	6.8 \pm 1.9 (24)	5.7 \pm 1.2 (6)
Hatching success	0.74 \pm 0.28 (23)	0.82 \pm 0.19 (7)	0.76 \pm 0.269 (22)	0.89 \pm 0.15 (5)	0.90 \pm 0.14 (18)	0.89 \pm 0.19 (5)	0.87 \pm 0.12 (24)	1.00 \pm 0.00 (6)
Fledgling success	0.91 \pm 0.26 (23)	1.00 \pm 0.00 (7)	0.98 \pm 0.08 (22)	0.57 \pm 0.52 (5)	0.57 \pm 0.41 (18)	0.42 \pm 0.40 (5)	0.42 \pm 0.42 (24)	0.63 \pm 0.50 (6)
Breeding success (all pairs)	0.66 \pm 0.34 (23)	0.82 \pm 0.19 (7)	0.74 \pm 0.26 (22)	0.53 \pm 0.50 (5)	0.50 \pm 0.38 (18)	0.38 \pm 0.40 (5)	0.34 \pm 0.33 (24)	0.63 \pm 0.50 (6)
Breeding success (successful pairs)	0.70 \pm 0.31 (22)	0.82 \pm 0.19 (7)	0.74 \pm 0.26 (22)	0.88 \pm 0.22 (3)	0.69 \pm 0.24 (13)	0.63 \pm 0.30 (3)	0.59 \pm 0.20 (14)	0.95 \pm 0.10 (4)

parents. Pooling data of both years, total failure affected to 39 clutches (34%). A remarkable result is that only 8 clutches suffered total failure in the first breeding year compared with the 31 clutches in the second one. The reproductive success decreased considerably in year 2008 as a consequence of both an increase in total breeding failure and a decrease of number of fledglings raised per pair.

The total breeding failure is independent of entrance hole and territory location (Yates corrected $\chi^2 = 0.12$ $df = 1$ $p = 0.73$). In territories with large-holed nestboxes, total breeding failure ranges from 12.5 % to 34.4 % of the clutches (both years pooled); in territories with small-holed nestboxes it ranges from 9.4 % to 15.6 %.

4. Discussion

4.1. Occupancy patterns and territory quality

The high percentage of nestbox occupancy in holm oak forest indicates that cavities are a scarce resource and, therefore, acts as a limiting factor on the reproduction of Blue Tits in this habitat. In the study area there is an approximate density of 1.4 natural tree-cavities/Ha, that is, 21% of the trees (46 cavities in 220 trees) have some kind of cavities (unpublished data). During the period of reproduction, we have watched some Blue Tits going into and going out from these cavities. However, most cavities are not suitable to be used as nesting sites (depth, orientation, possibility of flooding, vulnerability to predators, etc.). We frequently found that these potential cavities are flooded as a result of the winter and spring rains and are thus unsuitable for nesting during most of the breeding cycle of Blue Tit. Therefore, the density of suitable cavities in trees might be in most years lower than that our estimates and the nesting densities also lower than density in patches with nestboxes.

The erection of 50% of small-holed nestboxes was aimed for encouraging occupancy by Blue Tits rather than other species. Over both years, the same pattern of a high nestbox occupation rate by Blue Tits was repeated, in spite of the intraspecific competition for this resource (Minot and Perrins, 1986; Dhondt, 1989). Nesting in small-holed nestboxes was almost exclusively monopolized by Blue Tit and did lead to an outstanding increase in the occupancy rate, both in interior and peripheral nestboxes as compared to large-holed ones. That result agrees with that observed by Dhondt and Adriaensen (1999), whose experiments showed that the population of Blue Tit increased when the species had small-holed nestboxes available. On the other hand, Maicas and Fernandez Haeger (1999) on the same area of holm oak forest, with a similar density of exclusively large-holed nestboxes, found that the mean breeding density of Blue Tit (1.8 pairs/ha) was very similar to that estimated in this study (2.2 pairs/ha for 2007 and 2.4 pairs/ha for 2008). So, in this case, the effect of small-holed nestboxes on the Blue Tit density has not been as important as it could be expected.

The high density of Blue Tits is linked to the high availability of small-holed nestboxes. The preferent selection of small-holed nestboxes by Blue Tit over large-holed ones is a behavior pattern reducing the risk of predation. In some hole-nesting birds, broods in natural holes with smaller entrances are the most successful. Thus, this attribute of the cavities improve the fitness of individuals nesting in them (Nilsson, 1984; Albano, 1992; Christman and Dhondt, 1997; Wesolowski, 2002; Wesolowski and Rowinski, 2004).

The accumulation of heterogeneous evidence in the case of birds has produced a controversy over whether or not density is an indicator of habitat quality and whether or not it can be used as a surrogate for this quality (Sergio and Newton, 2003; Bock and Jones, 2004; Arlt and Part, 2007). Our results show that small-holed nestboxes were occupied by a high number of breeding pairs but they did not achieve a mean breeding success higher than

those nesting in large-holed nestboxes. This pattern could be a density-dependent effect. However, in terms of addition of new individuals to the Blue Tit population, pairs nesting in small-holed nestboxes made a contribution more important than pairs nesting in large-holed nestboxes. This quantitative pattern of nestbox occupancy suggests that it could be used as an indicator nest-site quality for Blue Tit. It has been shown that site-specific factors were more important than year-specific factors for nestbox occupancy by tit species (great and Blue Tits) (Goodenough et al., 2009a).

Total offspring loss, due mainly to predation, seems to be a very important component of habitat quality and there is empirical evidence in natural conditions that proves the anti-predation function of small-holed cavities (Wesolowski, 2002). However, our results show that total breeding failure is not dependent of the territory location or entrance hole size. Predation cannot be probably predicted by breeding pairs and final result is that breeding failure is equivalent in all territory categories.

4.2. Territory selection and breeding performance

According to the theory of habitat selection, individuals of a breeding population which settled in favorite territories (good territories) would achieve higher fitness than individuals settling in less good territories (poor territories) (Fretwell and Lucas, 1970; Bernstein et al., 1991). Blue Tit is a territorial species in which there is dominance of some individuals over others. This behavioral trait results in an ideal despotic settlement pattern, under which the dominant individuals carry out a pre-emptive selection of good territories over less good ones. In the nestbox plot the good territories for Blue Tit would be those where the first clutches were laid, namely territories with small-holed nestboxes and located in the periphery. This selection pattern contrasts with that displayed by a Blue Tit population in a nearby stone pine plantation where the factors significantly related to the laying date were the territory size and the holm oak numbers. In this conifer forest, most pairs nested in small-holed nestboxes and the territory location did not influence on the laying date (Maicas et al., 2011).

The variability of clutch size throughout the breeding season follows a common pattern for different avian populations: it decreases in pairs starting to breed later in the season (Haywood, 1993; Maicas and Fernández Haeger, 1996; Moreno et al., 1996; Belda et al., 1998; Maicas and Fernández Haeger, 1999; Blondel et al., 2006; García-Del-Rey et al., 2006; Marciniak et al., 2007; Goodenough et al., 2009b; Maicas et al., 2011). The variability of this trait, as a function of the interaction between year, territory location and entrance hole size (the three sources of variation for laying date), shows mainly the effect of year on this trait (the clutch is greater in the first breeding year than in the second one). In each year, Blue Tit laid a similar mean number of eggs in most territories. These results suggest that the temporal component is more important than the spatial component for variation of clutch size in Blue Tit. The relevance of the temporal component is appeared in that between-year differences are a significant source of variation for all breeding traits except for the breeding success in pairs which at least have raised a fledgling.

The hatching success (successful and unsuccessful pairs pooled) varies with tree density, increasing as tree density increases. Given the high and significant positive correlation between this trait and the final breeding success in the successful pairs (Pearson correlation coefficient: $r = 0.748$, $n = 88$, $p < 0.01$), the Blue Tits nesting in territories with higher tree density would have better reproductive output than those nesting in territories with lower tree density. The proximate link between hatching success and tree density could be explained by the availability of food resources: high-quality territories (more tree density) would provide more

food for incubating individuals than low-quality territories (less tree density). Time or energy available are constraints determining the relationships between environmental attributes, parental care (food provision, offspring defence) and offspring traits. Pairs in high-quality territories have more time to invest in different activities producing both larger broods and heavier offspring (Noordwijk and De Jong, 1986; Martin, 1992; Hakkarainen et al., 1998). Reduced hatching success in Blue Tit has been found to be linked to territories with immature and degraded vegetation (Arriero et al., 2006)

Contrasting with the hatching success, the variation of both fledging and breeding success of all pairs was similar across the different categories of territories. Although the egg laying begins sooner in some breeding territories (peripheral and with small-holed nestbox), a hint of territory preference (Rodenhouse et al., 1997; Robertson and Hutto, 2006; Arlt and Part, 2007), it seems not to be differences in their quality in terms of the breeding success achieved.

These results show that habitat variability operates mainly on the hatching success. However, yearly variation is a main factor causing differences on the breeding success of Blue Tit. The influence of yearly variation disappears in successful pairs. In this case, most territories had a similar quality in terms of the breeding success achieved except in a few interior territories with large-holed nestboxes where the mean breeding success was higher. These territories are selected late in the season so that the pairs laying eggs later are more successful. This is a surprising result because, according to the frequently reported relationship between timing of breeding and reproductive output, the breeding success of early Blue Tits should be higher than late ones (Perrins, 1970; Nilsson and Svensson, 1993; Dias and Blondel, 1996; Maicas and Fernández Haeger, 1999; Naef-Daenzer and Keller, 1999; Tremblay et al., 2003; Arriero et al., 2006). Some individuals can take advantage from laying late and a smaller clutch size: their breeding success would be favored by a smaller brood size in a context of less severe intraspecific competition as an effect of decreased density.

There is high abundance of caterpillars (the main food for nestlings) in the canopy of the holm oaks during the nestling growth (Díaz and Pulido, 1993; Blondel et al., 2006; Blondel, 2007) and food availability is therefore directly linked to holm oak density in the territories. A greater density of holm oaks within a territory during the nestling growth would entail more opportunities for foraging with a lower energy cost for the parents. Our results suggest that food availability would not be a limiting factor in the territories. Nevertheless, other authors have shown the relative importance of territory quality to the reproductive performance of Blue Tits (Przybylo et al., 2001; Tremblay et al., 2003, 2005; Lambrechts et al., 2004; Stauss et al., 2005; Arriero et al., 2006; Sanz et al., 2010).

It can be concluded that, although our model of nestbox plot favors a high breeding density of Blue Tits, there seems to be no noticeable mismatch between nestbox choice and territory quality because the average breeding success achieved by pairs (successful and unsuccessful) was similar across the habitat. Therefore, the quality of territories seems to avoid a significant reduction of the density-dependent breeding success. However, the noticeable increasing of total breeding failure in the second breeding year suggests that such as offspring loss is an effect of the density-dependent predation due to the high breeding density.

5. Implications for nestbox management

We have analyzed the influence of several factors which are involved in the reproductive performance of Blue Tits by manipulating a limiting resource for the species, namely cavities for

breeding. Active stand management (Quine et al., 2007; Luck and Korodaj, 2008) using nestboxes to facilitate the reproduction of Blue Tits, can be a useful tool to encourage the colonization and persistence of this species in forest habitats, especially if the trees are young with scarcity of natural holes as it occurs in the young holm oak forests in southern Spain.

Small-holed nestboxes favored Blue Tits more than other species breeding at the same time in the nestbox plot (Great Tit, Nuthatch, Crested Tit). Although it is known that natural cavities with small entrance holes increase the survival value for nestlings and parents in some species (Nilsson, 1984; Albano, 1992; Christman and Dhondt, 1997; Wesolowski, 2002; Wesolowski and Rowinski, 2004), the individuals nesting in small-holed nestboxes did not have a breeding success higher than other individuals. On the other hand, the spatial distribution of the territories (periphery vs interior) was no relevant for the breeding success.

In order to optimize the reproductive performance of Blue Tit in young holm oak forests, it should be considered the importance of the positive relationship between the tree density in the territories and the hatching success because this component of habitat heterogeneity influences the number of nestlings reared by each pair of Blue Tit. A drawback of the model of nestbox plot used is that breeding density of Blue Tit raises at high levels. The short mean distance between available nestboxes (50 m) in the grid is a key factor conditioning this pattern of increased density. The remarkable increase of total breeding failure in the second year (2008), probably is related to an effect of density-dependent predation by local predators (e.g. Goshawk *Accipiter gentilis*, Azure-winged Magpie *Cyanopica cyanus*, Jay *Garrulus glandarius*, Great spotted Woodpecker *Dendrocopos major*, etc.). The predation risk increases in older nestboxes and in areas where density has been increased with nestboxes (Sasvari and Hegyi, 1998; Sorace et al., 2004).

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