Effect of habitat type and nest-site characteristics on the breeding performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in a Mediterranean landscape

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Compared to coniferous forests, deciduous woodlands have often been considered a more suitable habitat for Blue and Great Tits. We compared reproductive parameters of both species in oak woodland and pine plantation patches within a Mediterranean landscape. We found no inter-habitat differences in breeding traits of Blue Tits, but clutches of Great Tits were larger and were laid earlier in the oak woodland than in the pine plantations. However, the breeding success of Great Tits was similar in both habitats, indicating that both species are able to adequately adjust their breeding strategies to conditions of recently-colonized habitat, and that these strategies vary between species. At a smaller scale, we found that the clutch size was affected by the dominant tree species surrounding the nests in both species. Laying date in Blue Tits and clutch size in Great Tits was related to the development of the shrub layer, reinforcing the importance of understory over forest avifauna especially in managed monocultures.

1. Introduction

In Spain, a large part of the region is covered by pine forests resulting from deliberate forestry policy carried out over the last century (ICONA 1979). More precisely, 3.8 million ha were reforested during 1945–1986, and 90% of the reforested area was planted with pine (Ortuño 1990). The recent appearance of such forests and their characteristic simple architecture, subjected to management, may negatively affect food avail-ability for insectivorous birds (e.g., Zanette *et al*. 2000). Therefore, the population densities of tits (Paridae) in these novel habitats could be lower than in native pine forests (Maícas & Fernández Haeger 1996). On the other hand, the size distribution of plantations in Spain is strongly skewed towards stands smaller than 2 ha (Díaz *et al*. 1998). Such practices, along with other land-use changes occurring throughout the Mediterranean region (Blondel & Aronson 1999), have contributed greatly to the mosaic patterns of many landscapes

of the Spanish plateau where reforested pine plantations coexist with small fragments of ancient natural woodland, remnants of once extensive forest cover.

On the Iberian Peninsula, as in the rest of the Western Palaearctic, Blue and Great Tits (*Parus caeruleus* and *P. major*) prefer deciduous over evergreen (coniferous or sclerophyllous) forests (Cramp 1998, Tellería *et al*. 1999). Such preferences may have a genetic basis (Partridge 1974) and reflect a lower abundance of food resources in the evergreen habitats, as shown for sclerophyllous forests by Blondel *et al*. (1991) and for coniferous forests by Fidalgo (1990) and Massa and Lo Valvo (1996; but see Mägi *et al*. 2009). Accordingly, tits produce larger clutches in deciduous than in coniferous forests (Sanz 1998), i.e., the inclination for deciduous habitats seems to be adaptive. In coniferous forests, the shortage of natural cavities for nesting also contributes to lower attractiveness as breeding habitat than in deciduous forests (Newton 1994). In coniferous forests, and managed pine plantations in particular, Great Tits breed in lower densities and Blue Tits are rare or absent (e.g., Carrascal & Tellería 1990, Maícas & Fernández Haeger 1999). The lack of cavities precludes the establishment of tit populations in large homogeneous pine forests; if nest boxes are provided, densities of these birds increase sharply (Maícas & Fernández Haeger 1996, Mänd *et al*. 2005, 2009, Pimentel & Nilsson 2007). The lack of cavities may present a problem in breeding habitats with otherwise higher suitability (such as in deciduous forests) if the density of breeding pairs exceeds an optimal level and density-dependent effects become apparent ("density-trap hypothesis"; Mänd *et al.* 2005, 2009).

Differences in feeding conditions between deciduous and coniferous forests have been suggested as the primary culprit for the existence of clear habitat-related variation in basic reproductive parameters in these species (e.g., van Balen 1973). However, in spite of evidence that tits perform better or invest relatively more (breed earlier and produce larger clutches) in deciduous than in coniferous forests at the beginning of the breeding season (e.g., Isenmann 1987, Belda *et al*. 1998, Massa *et al*. 2004), the final breeding outcome (the number of fledged young) is similar or higher in coniferous habitats (Maícas & Fernández Haeger

1996, Mänd *et al*. 2005). These findings suggest that tits may adopt different breeding strategies using habitat type as a cue for predicting ensuing feeding conditions (Mänd *et al*. 2005). Hence, birds breeding in coniferous forests may opt to invest less in the number of eggs laid since food availability in this habitat may be lower than in deciduous forests (e.g. van Balen 1973). A reduction in clutch size may also occur merely due to seasonal effects (later clutches tend to be smaller), that is, as a result of shifts in laying date. Because food abundance peaks later in the season in coniferous habitats, birds may delay the onset of laying to adapt their breeding time to local environmental conditions (caterpillar phenology). However, tits would also fail in their response when faced with novel environments. Evidence for this comes from studies on Mediterranean Blue Tits, in which breeding in sclerophyllous oakwoods may retain life-history traits adapted to deciduous forests (see Blondel 2007 and references therein). This apparent maladaption of Blue Tits in the evergreen habitat might result from the gene flow between rich deciduous habitats (source), to which the birds seem well-adapted, and poor sclerophyllous habitats (sink).

At a small scale, i.e., within an individual's home range, heterogeneity in vegetation structure around the nesting sites could be responsible for local variation in breeding parameters among individual territories within the same habitat type (Nager 1990, Dhondt *et al*. 1992, Arriero *et al*. 2006, Wilkin *et al*. 2007). Taking into account the importance of temporal and spatial variation of food supplies in shaping an individual's reproductive parameters we can deduce that habitat features, such as dominant tree species, tree height or the successional phase of the shrub layer surrounding the nest site, could be very important from a bird point-of-view. In this sense, caterpillar (main summer-season prey of tits) abundance varies depending on some of the aforementioned variables (e.g., Fischbacher *et al*. 1998, Summerville *et al*. 2003). Hence, apart from between-habitat differences in reproductive traits, environmental variation within habitat types might inform us about the mechanisms (strategic decisions or energy constraints) underlying some patterns, such as larger average clutch size in deciduous forests.

The purpose of this study was two-fold. Firstly,

we address the influence of habitat type on the breeding performance of two tit species through the installation of nest boxes in two adjacent habitats: one to which birds may be well adapted – deciduous forests – and another representing a novel habitat type – pine plantations. These two habitat types presumably differ in their carrying capacity and/or attractiveness for birds within the Mediterranean region. The mosaic pattern of different habitats permits an exploration of the response (mismatching or phenotypic plasticity) of tits when confronted with a recently-colonized habitat. At a finer-grained level, we also determine how nest-site features (vegetation characteristics in the surroundings of nests) within a given habitat type affect the reproductive performance (primary fecundity, breeding success), and how Blue and Great Tits possibly differ in their breeding strategies to cope with the novel plantation environment. Explorations of potential associations between nest-site features and breeding parameters produce knowledge useful for combining the economic aspects of forest management and the promotion of forest avifauna.

2. Material and methods

2.1. Study area

This study was conducted during the breeding season (from April to mid-June) of 2005 in Los Quintos de Mora, Toledo province, central Spain (39º25' N, 4º04' W), a national game preserve managed by the Organismo Autónomo Parques Nacionales (OAPN). This area exhibits considerable habitat heterogeneity and is partitioned into two main landscape units including a huge floodplain ("raña") 800 m above sea level, and a surrounding mountain range (Sierra del Pocito and Sierra de los Torneros) with a maximum elevation of 1235 m a.s.l. In the mountain areas, Pyrenean oak (*Quercus pyrenaica*), zeen oak (*Q. faginea*), strawberry tree (*Arbutus unedo*) and Mediterranean shrubs dominate, but in humid environments ash (*Fraxinus angustifolia*) and heath (*Erica* spp.) are also common. The plain is covered by scattered holm (*Quercus rotundifolia*) and zeen oaks with understory pasture and fragments of pine (maritime pine *Pinus pinaster* and stone pine *P. pinea*)

plantations from the 1940s. These pine patches penetrate the areas of the mountain range where they are mixed with the original vegetation forming a habitat mosaic. For more details about the history of vegetation in this natural reserve, see Tornero (2003).

By the end of 2004, we chose four 12-ha forest plots (one dominated by oaks, three dominated by different pine species) along a habitat gradient for the installation of 391 wooden ($14 \times 14 \times 20$ cm, entrance hole 30 mm diameter) nest boxes. The nest boxes were arranged 30–40 m apart along transects. Ninety-two nest boxes were set on a river bank (Arroyo de Valdeyerno 890 m a.s.l., hereafter Valdeyerno) that runs through Sierra de los Torneros, where Pyrenean oaks and, to a lesser extent, zeen and holm oaks are the most abundant tree species. Ninety-nine nest boxes were installed in a nearby pine plantation called Bermú (65% planted pine, 35% oak of natural regeneration as a mixture; 840 m a.s.l.). The rest of the nest boxes were placed in two other forest plots dominated by pine species (Camino del Cejo: 105 nest boxes, 80% pine, 20% oak; Camino del Mesto: 95 nest boxes, 85% pine, 15% oak; both plots at 780 m a.s.l.). In these latter two forest plots the shrub layer is scarce due to management operations (thinning, clearing) and is comprised mainly of gum cistus (*Cistus ladanifer*) and rosemary (*Rosmarinus officinalis*).

2.2. Breeding data

In the field we identified occupancy rates, nesting species, the date of the first egg (1 = 1 April), clutch size, hatching success (proportion of eggs hatched), breeding success (proportion of eggs that resulted in fledged young), and possible nest desertion and predation rates. Deserted nests refer to nests with eggs found cold or nestlings found dead. Potential predators included Great Spotted Woodpecker (*Dendrocopos major*) and mustelids (pine marten *Martes martes* and stone marten *M. foina*), which are the most common predators in the study area. Second broods were only recorded for Great Tits.

2.3. Nest-site features

Vegetation composition and cover were estimated

Table 1. Factor loadings of the principal component analysis for the descriptor variables of vegetation structure, measured at 391 sampling sites (circular plots of 40 m in diameter). Significant variables for each principal component are marked with bold.

Factor	Pc1	Pc2	Pc3	Pc4
No. pines	0.156	−0.011	**−0.803**	−0.019
No. holm oaks	−0.150	**−0.901**	0.010	0.007
No. oaks (pedunculate oaks and Pyrenean oaks)	0.073	−0.120	**0.880**	−0.187
No. zeen oaks	0.190	0.069	−0.083	**−0.783**
No. trees	0.132	**−0.904**	0.061	0.046
Shrub cover (%)	**−0.903**	0.039	−0.089	−0.213
Herbaceous cover (%)	**0.960**	0.046	−0.197	−0.114
Bare ground (%)	−0.371	−0.133	0.479	0.514
Average tree height (m)	0.090	0.201	0.460	−0.534
Eigenvalue	2.324	1.728	1.678	1.145
% variance explained	25.83	19.22	18.64	12.72

by eye in a 20-m radius around each nest box. The radius approximately accounts for an area that tits commonly use for feeding (usually within 20–25 m; Smith & Swatman 1974, Grieco 2002). This area is hereafter referred to as 'territory'. For each territory, we estimated (a) the total number of trees, (b) the number of (species specific) different pine species, holm oaks, zeen oaks, Pyrenean oaks and pedunculate oaks (*Quercus robur*), (c) the height of dominant trees, (d) shrub cover (%), (e) herbaceous-plant cover (%) and (f) the cover of bare ground and rock surface (%). As the variables describing vegetation in the territories were correlated, a principal component analysis (PCA) with a Varimax rotation was performed to diminish the redundancy of these variables. PCA successively generates axes of variation that are linear combinations of the original variables. These axes are ordered such that the first accounts for maximum variation in the original data, the second for most of the remaining variation, and so on (Cody 1985). The PCA for nest-site characteristics yielded four factors that collectively accounted for 76.4% of the total variance (Table 1). The first axis (component Pc1) contrasted territories with a well-developed shrub layer (negative loading) to those with a well-developed herbaceous layer (positive loading). The second component (Pc2) was directly related to tree cover and the number of holm oaks. The third component (Pc3) defined a gradient related to the dominant tree species, separating territories dominated by oaks (at the positive end) from

territories dominated by stone and/or maritime pine (negative extreme). Finally, the fourth component (Pc4) accounted for the number of zeen oaks in the territories.

2.4. Statistical analyses

Data on proportions were arcsine square root-transformed prior to analysis to fulfil requirements for parametric testing. Effects of habitat type and nest-site characteristics on laying date, clutch size and breeding success were analysed by means of generalized linear models (GLM) using Statistica 6.0. In the first step, we compared the three forest plot types that were dominated by pine trees. Subsequently, if there were no significant differences between them, data from pine forests were pooled into a single category (pinewood) to compare two coarse, main habitat types, viz. oak woodland and pinewood. We also compared the reproductive parameters of Blue and Great Tits after controlling for the effect of habitat type. Finally, we explored the relationships between nest-site characteristics and tits' reproductive parameters by including habitat type and their interactions as factors into the GLM. The statistics reported are the result of a backward deletion procedure in which all non-significant terms were dropped in a one-by-one manner from the full model. For comparisons of predation and desertion rates, Chi-square test was applied. Data are given as means ± SD.

Table 2. Reproductive parameters of Blue and Great Tits for four study plots in central Spain. Mean values with standard deviations per nest, and sample sizes (number of occupied nest boxes; in parentheses) are shown. The habitat comparison (*F* and *p* values shown) was done for oak woodland and pinewood so that data from three pine plantations (Bermú, Camino del Mesto and Camino del Cejo) were pooled (see text).

	Oak woodland	Pinewood			Habitat comparison	
	Valdeyerno	Bermú	Camino del Mesto	Camino del Cejo	*F*	*p*
Blue tit						
Density (pairs/ha)	3.5	0.5	1.0	1.3		
Laying date	27.85 ± 11.21 (42)	28.16 ± 12.44 (6)	34.00 ± 8.29 (12)	31.12 ± 9.16 (16)	2.43	0.12
Clutch size	7.47 ± 1.83 (42)	6.83 ± 0.40 (6)	6.81 ± 0.98 (11)	6.43 ± 2.33 (16)	2.06	0.15
Breeding success (%)	85.82 ± 16.61 (37)	87.69 ± 10.90 (6)	77.6 ± 35.17 (10)	90.58 ± 13.05 (11)	0.07	0.79
Desertion rate (%)	7.1	0.0	16.7	25.0		
Predation rate (%)	4.8	0.0	0.0	6.2		
Great tit						
Density (pairs/ha)	1.3	1.2	0.9	0.9		
Laying date	16.94 ± 5.15 (16)	16.67 ± 10.13 (12)	24.60 ± 9.22 (10)	22.82 ± 9.84 (11)	3.51	0.06
Clutch size	9.00 ± 1.31 (16)	6.86 ± 1.35 (11)	6.22 ± 2.63 (9)	5.67 ± 2.91 (9)	13.3	<0.001
Breeding success (%)	85.82 ± 7.56 (12)	87.69 ± 30.3 (7)	77.6 ± 25.7 (9)	90.58 ± 19.5 (8)	0.01	0.98
Desertion rate (%)	18.7	35.7	0.0	18.2		
Predation rate (%)	6.2	14.3	9.0	9.0		
Second broods (%)	17.2	20.0	16.6	11.1		

3. Results

3.1. The effect of territory quality on breeding performance

Great and Blue Tits were the most common species in all plots, making up 41.6% and 40.5% of all occupied nest boxes, respectively. The nest-box occupation rate by Blue Tits was significantly higher in the oak woodland (45.3%) than in the pinewood (11.6%; $\chi^2 = 52.80$, $p < 0.001$). The occupation rates for the Great Tit did not significantly differ between the two types of habitat (17.3% for oak woodland and 12.0% for pinewood; $\chi^2 = 1.75$, $p = 0.18$).

For Blue tits, the three pine-dominated forest plots produced quite similar estimates of laying date ($F_{2,31} = 0.80$, $p = 0.46$), clutch size ($F_{2,29} = 0.50$, $p = 0.61$; in this model, laying date had $F_{1,29} = 11.02$, $p < 0.01$) and breeding success ($F_{2,23} = 0.54$, $p = 0.59$; in this model, clutch size had $F_{1,23} = 0.09$, $p = 0.76$). After this phase the pine plots were lumped into a single category of pinewood to compare with oak woodland, but none of the inter-habitat differences were statistically significant with regard to reproductive parameters (Table 2). Likewise, habitat type did not have a significant effect

on the desertion rate ($\chi^2 = 1.88$, $p = 0.17$) or predation rate ($\chi^2 = 0.93$, $p = 0.76$).

For Great Tits, the timing of breeding did not significantly differ among the three pine plots ($F_{2,32} = 0.97$, $p = 0.39$), nor were there significant differences among these plots in the number of eggs laid ($F_{2,31} = 2.28$, $p = 0.12$). However, clutch sizes were significantly smaller in Camino del Cejo than in Bermú (LSD test: $p = 0.04$). The proportion of fledged young (i.e., breeding success) did not significantly differ among the three pine-dominated plots ($F_{2,21} = 0.33$, $p = 0.72$). After grouping the three pine plots into a single category (pinewood), laying date did not significantly differ between pinewood and oak woodland (Table 2). The lack of difference is apparently due to the Bermú pine plot that deviated from the rest by exhibiting a mean laying date similar to that of the oak woodland (Table 2). Overall, Great Tits tended to breed slightly earlier in the oak woodland than in the pinewood. Clutch size was significantly affected by habitat type: in the oak woodland, Great Tits laid larger clutches than in the pinewood (Table 2). Breeding success did not vary in relation to habitat type (Table 2). The occurrence of multiple breeding attempts ($\chi^2 = 0.07$, $p = 0.79$), desertion rate ($\chi^2 = 1.20$, $p = 0.29$) and predation rate (χ^2
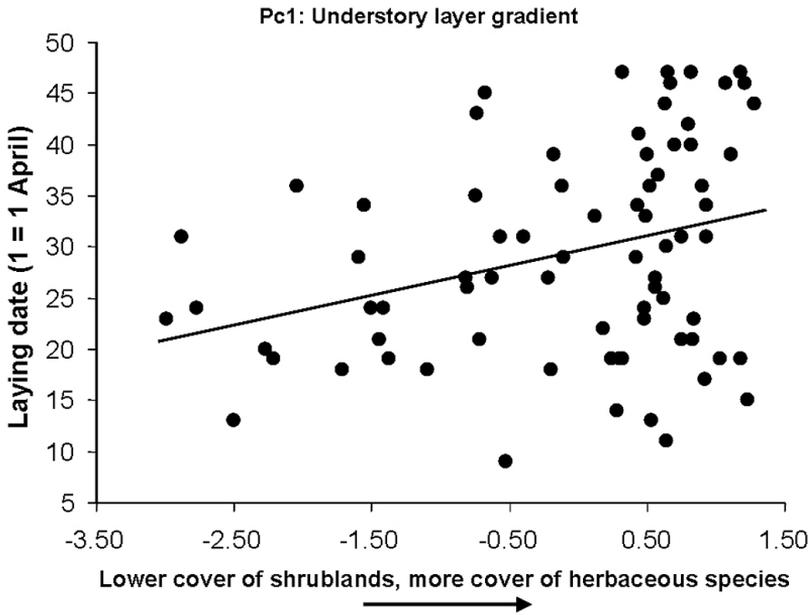
Fig. 1. Relationship between laying date (1 = 1 April) of Blue Tits and herbaceous [–] and shrub [+] plant cover (Pc1).
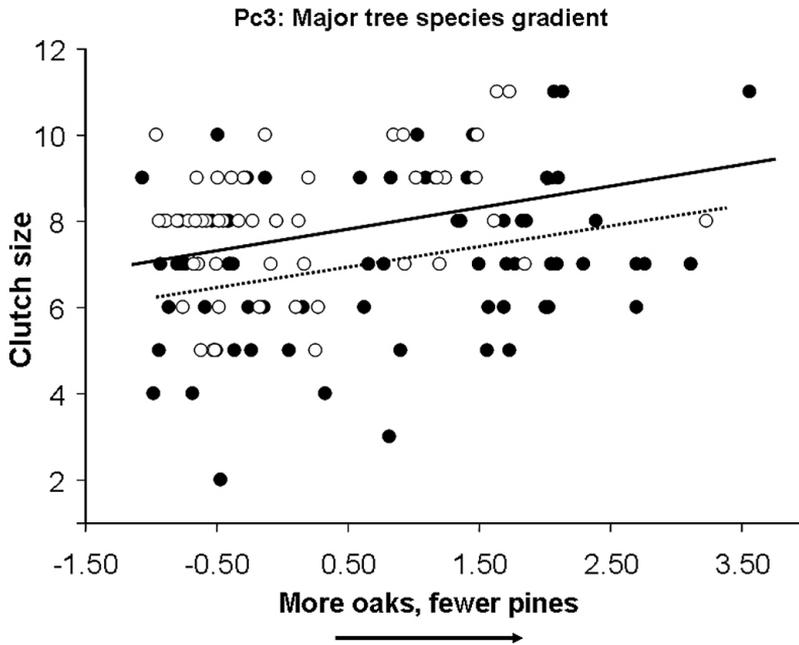
Fig. 2. Relationship between clutch size of Blue (filled dots, continuous line) and Great Tits (open dots, dotted line) and the dominant tree species in the surroundings of the nest site (Pc3).

= 0.65, $p = 0.42$) did not significantly differ between pinewood and oak woodland.

Great Tits began egg laying earlier than Blue Tits after controlling for the effect of habitat type ($F_{1,124} = 31.67$, $p < 0.001$; the effect of habitat had $F_{1,124} = 5.48$, $p = 0.02$). The interaction between laying date and habitat type was not significant ($F_{1,123} = 0.097$, $p = 0.75$). Neither clutch size nor breeding success differed significantly between the two species. Similarly, there was no significant difference in the desertion rate between the species ($\chi^2 = 0.38$, $p = 0.54$). However, predation rate tended to be slightly higher for Great than for Blue Tits ($\chi^2 = 3.56$, $p = 0.059$).

3.2. Breeding parameters in relation to nest-site characteristics

The laying date of Blue Tits was positively related to Pc1, indicating that earlier clutches were found in territories with greater shrub cover and lower abundance of herbaceous plants (Fig. 1, Pc1: $F_{1,74}$ = 7.24, $p < 0.01$; habitat: $F_{1,73}$ = 0.50, $p = 0.48$). There was a positive relationship between clutch size of Blue Tits and dominant tree species (Pc3) even after controlling for laying date ($F_{1,71}$ = 53.79, $p < 0.001$) and habitat type ($F_{1,71}$ = 4.43, $p = 0.04$). Clutch size increased as the density of oaks increased or that of pines decreased (Fig. 1, $F_{1,71}$ = 10.08, $p < 0.01$). The effect of dominant tree species on the number of eggs did not differ between the two coarse habitat types, as the interaction term between Pc3 and habitat was not significant ($F_{1,70}$ = 0.01, $p = 0.92$). Breeding success of Blue Tits was not significantly related to any of the nest-site characteristics.

Great Tits laid larger clutches as shrub cover (Pc1) and oak density (Pc3) in their territories increased ([Pc1] Pc1: $F_{1,46}$ = 5.95, $p = 0.02$, laying date: $F_{1,46}$ = 4.27, $p = 0.04$, habitat: $F_{1,46}$ = 10.46, $p < 0.01$; [Pc3] $F_{1,47}$ = 3.45, $p = 0.05$; habitat: $F_{1,47}$ = 13.10, $p < 0.001$; Fig. 2). No significant interaction effects on clutch size were found between the principal components Pc1 and Pc3 and habitat type. Moreover, the associations between nest-site characteristics and the timing of egg laying or breeding success were non-significant for the Great Tit.

The only between-tit-species difference in breeding parameters occurred on the dominant tree species (Pc3; Great Tit: 0.09 ± 0.91 SE, Blue Tit: 0.66 ± 1.25 SE; $t = 2.80$, $p < 0.01$).

4. Discussion

4.1. Breeding parameters in different habitat types

We explored the consequences of habitat choice on some reproductive parameters in a human-altered landscape mosaic of optimal (deciduous) and suboptimal (coniferous) habitats. Contrary to expectations, inter-habitat differences in reproductive parameters were not significant for the Blue Tit; however, the results of this one-year study

should be interpreted with caution. We nevertheless observed that the density of breeding Blue Tit pairs was higher in oak woodland than in pinewood. Blue Tits avoid conifers (Cramp 1998), although pine plantations cannot be considered pure coniferous monocultures as they host remnant patches of original vegetation (undergrowth and scattered trees). The recent appearance of these new habitats within the landscape and the resulting decrease of oak woodlands, along with the characteristics of pine plantations (frequently intermingled with fragments of deciduous or sclerophyllous vegetation), could force Blue Tit individuals to select these sub-optimal coniferous forests for breeding (Maícas & Fernández Haeger 1996).

The Great Tit is more eclectic in its habitat selection than Blue Tit (Snow 1954). In accordance with this, we found that differences in the nest-box occupation rates between habitat types were not as marked as in Blue Tits. Unlike Blue Tits, the primary fecundity traits of great tits differed between pinewood and oak woodland. Clutch size was higher in the latter, which is consistent with previous studies (e.g. van Balen 1973, Belda *et al.* 1998, Sanz 1998). We also found that clutches were initiated earlier in the oak woodland than in pinewood (only when Bermú data were excluded), which suggests that the former habitat may be actively chosen by earlier breeders (presumably higher-quality parents), or that birds settled in the oak woodland may reach breeding condition quicker due to a greater availability of essential resources in the oak woodland. Interestingly, in Bermú Great Tits started egg laying earlier than in the other pinewood patches; this earlier timing was similar to that recorded in the oak woodland. This fact could be due to the short distance to the nearest oak woodland plot (<2 km). The high density of breeding pairs reported in the oak woodland may have compelled part of the population to disperse in search of vacant territories in nearby forests patches. That being so, the Great Tits of Bermú may be maladapted to this area because they immigrate from a source-habitat patch, i.e., the oak woodland, to which they may be primarily adapted (Blondel 2007). This is in agreement with a previous study carried out in pine stands in Portugal, which found that Great Tits adjusted their timing of breeding and clutch size as if they were in deciduous forests (Fidalgo 1990). Although the mean

laying date of Great Tits in Bermú was almost a week earlier than that of the pairs breeding in the other pine-dominated patches, the proportion of pairs to initiate second clutches did not significantly differ among the three pine plots. This supports Verboven *et al*. (2001) who showed that the frequency of second broods in tits increased as the first breeding attempts begun earlier relative to the food peak, irrespective of absolute laying date. Moreover, we found no evidence for the prediction that second clutches would be favored in coniferous habitats (pine plots) where the peak of food availability occurs later in the season and for a longer period of time (e.g., van Balen 1973, Orell & Ojanen 1986). In terms of the three pine-dominated plots, Great Tits breeding in Camino del Cejo and Camino del Mesto seemed to better adjust their allocation of resources at the beginning of the breeding season with respect to the prevailing local conditions in comparison to pairs in Bermú.

We found no significant effect of habitat type on the breeding success of either Great or Blue Tits. An adaptation to pine plantations may have afforded Great Tits a similar breeding outcome to that attained in the oak woodland, but Blue Tits may have been able to achieve a similar breeding output in oak woodland and pinewood without varying their initial investment in egg production. This difference is striking, since it has been suggested that double-brooded Great Tits would cope better than single-brooded Blue Tits in heterogeneous Mediterranean habitat mosaics due to the former being more opportunistic in their foraging habits (Massa *et al*. 2004, Lambrechts *et al*. 2008). Concerning predation rates, we found no inter-habitat differences in spite of the fact that predators are often concentrated in the more attractive habitats, in our case deciduous forests (Schlaepfer *et al*. 2002). However, predation rates differed between the two tit species; Great Tits were more affected by predator pressure than were Blue Tits, which could be due to the differences in the anti-predator strategy. Female Great Tits usually respond to potential predators by staying in the nest and hissing (Cramp 1998), whereas such behaviour is less frequent in Blue Tits with incubating or brooding females usually leaving the nest in the presence of potential predators (authors' pers. obs.).

4.2. The influence of habitat characteristics on breeding parameters

Vegetation structure and forest maturity can tell us much about habitat quality for insectivorous birds, since these variables are often associated with insect abundance (Cody 1985, Martin 1987, Tye 1992). Habitat quality as a measure of prey availability in the prelaying period is a key factor determining the condition of female Blue Tits and thereby controls their timing of breeding in Mediterranean oak forests (Arriero *et al*. 2006, Blondel 2007). In the present study, the laying date of Blue Tits was strongly correlated with the development of the shrub layer in both deciduous and coniferous plots. Blue Tits with territories with abundant shrubs bred earlier than those inhabiting areas with scarce understory. Similarly, Arriero and colleagues (2006) found that Blue Tits breeding in mature forests laid eggs earlier than those breeding in open and regenerating forests. A dense shrub layer may improve feeding conditions for tits before the caterpillar peak, or it may increase the availability of natural calcium sources (woodlice and millipedes; García-Navas *et al.*, unpubl. data), thereby enhancing the body condition of breeding females with respect to those occupying territories in more open habitats, in turn allowing an earlier onset to egg-laying (e.g., Lambrechts *et al*. 2004). Also, nest boxes in sub-optimal territories may become occupied later in the season or by females in poorer condition, and/or by pairs unable to acquire a high-quality territory (Riddington & Gosler 1995). Moreover, for Great Tits we found no significant effect of shrub cover on laying date, but shrub cover affected the species' clutch size. It remains unclear why shrub cover had an effect on laying date of Blue Tits and on clutch size of Great Tits, and not vice versa. In this sense, it is noteworthy that, in response to presumably better conditions (territories of higher quality), both species differ in their breeding strategy, laying earlier or laying larger clutches. Whatever the strategy adopted, our results suggest the importance of understory as an alternative feeding station for tits (that are mainly canopy gleaners) when the abundance of prey in tree canopies is low, regardless of habitat type; for oak woodland, see Royama (1970), and for pinewood, see Tinbergen (1960).

Productivity of Blue and Great Tits was corre-

lated with the dominant tree species in the nest surroundings. Birds having a large number of oaks in their territories laid larger clutches than those settled in territories where pines dominated. This supports the finding by Fischbacher *et al*. (1998), who found a positive correlation between the number of oaks within 20 m from the nest and both clutch size and fledgling weight in a Swiss population of Great Tits. Similarly, Hinsley *et al*. (2008) showed in a study dealing with the effects of habitat structure on parental energy expenditure, that Great Tits with territories with fewer oaks worked harder to raise their chicks. Likewise, at Wytham Woods, UK, nest boxes in oak-rich areas were associated with earlier mean breeding time and higher fledgling mass than nest boxes in oak-poor areas (Wilkin *et al*. 2007, 2009). Results reported here and in the aforementioned studies support the idea that since caterpillars are likely to be patchily distributed and are associated with certain vegetation types (e.g., Summerville *et al*. 2003), the employment of a fine-grained approximation (at the micro-habitat level) seems a more appropriate method for describing variation at biologically meaningful scales than are habitat classifications employed in most studies (Wilkin *et al*. 2009).

We did not find significant associations between local habitat characteristics and breeding success of tits. This may suggest that territory quality (as a surrogate measure of food availability) limits females at the beginning of the reproduction period (i.e., the initial breeding stages egg-laying and incubation) rather than later on when nestlings are being reared (Tremblay *et al*. 2003, Arriero *et al*. 2006).

To sum up, two main findings emerged from this study. Firstly, even though in one of the two species the clutch size was significantly larger in the deciduous forest than in the pine plantations, neither species showed a between-habitat difference in breeding success. This indicates that these birds are able to adjust their breeding strategies to conditions of a novel habitat (here, the potentially more monotonic plantations). On the other hand, our results emphasize the importance of understory as a supplementary food source for canopy gleaners especially early in the season, when Lepidopteran larvae are scarce. This is in agreement with several studies done especially in immature forests and mono-specific plantations, in rela-

tion to bird diversity and richness (e.g. Carrascal & Tellería 1990, Álvarez & Santos 1992 López & Moro 1997, Díaz *et al*. 1998, Díaz 2006). Such substrates are frequently missing from managed forests due to forestry or overgrazing pressure by herbivores. We thus recommend forest management to favor shrub recovery in order to improve the habitat quality and resultant status of forest bird populations.

Tali- ja sinitiaisen pesimämenestyksen suhde ympäristötyyppiin ja -tekijöihin Välimerellä

Lehtimetsiä pidetään usein parempana elinympäristönä tiaisille kuin havumetsiä. Vertailimme tali- ja sinitiaisen (*Parus major* ja *P. caeruleus*) pesimämuuttujia tammimetsässä ja istutusmänniköissä Espanjassa. Sinitiaisen pesimämuuttujat eivät eronneet tammi- ja mäntymetsien välillä, mutta talitiaiset munivat aiemmin ja saivat suurempia poikueita tammi- kuin mäntymetsissä. Pesimämenestys oli samanlainen vertailluissa ympäristöissä molemmilla lajeilla; lajit ilmeisesti kykenevät sovittamaan pesintään liittyvän strategiansa asuttaessaan uuden elinympäristölaikun, mutta strategioissa lienee lajien välisiä eroja.

Pienemmässä mittakaavassa havaitsimme, että molempien lajien munamäärään vaikutti pesän välittömän läheisyyden vallitseva puulaji. Sinitiaisen muninnan ajoittuminen ja talitiaisen pesyekoko riippuivat pensaskerroksen laadusta, mikä viittaa alikasvoksen suureen merkitykseen etenkin talousmetsissä.

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