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Across and within-forest effects on breeding success in Mediterranean Great Tits *Parus major*

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Forest type and habitat structure can have profound effects on different aspects of avian life histories. These effects may, however, strongly differ across and within forests that vary in vegetation composition and structure, especially when an ancient forest has been replaced by a new forest. To test for these differences in effect, we studied Great Tit *Parus major* life-history traits (280 first clutches) in two Mediterranean evergreen forests during 2005–07: an ancient Holm Oak *Quercus ilex* and a reforested pine forest. A comparison between forests revealed that females breeding in the Holm Oak forest started laying one week later, and produced larger clutches and broods both at hatching and at fledging. Chicks raised in the Holm Oak forest also fledged in better condition. Within forests, however, the reproductive success was not higher for pairs breeding in nestboxes surrounded by oaks within the pine forest, and also reproductive success was not lower in nestboxes surrounded by pines within oak forest. Instead, vegetation maturity around nestboxes, rather than tree species composition, affected hatching success. Surprisingly, hatching success was higher in nestboxes surrounded by immature vegetation. We suggest that this may be due to a lower nest predation rate in nestboxes surrounded by immature vegetation, compared to nestboxes surrounded by mature vegetation. We suggest that different factors appear to affect variation in breeding success in Mediterranean Great Tits comparing across forests (e.g. food availability) vs. within a forest (e.g. nest predation).

Key words: hatching success, Mediterranean forests, nest predation, *Parus major*, territory vegetation maturity

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Many environmental and anthropogenic factors contribute to habitat heterogeneity in the Mediterranean region, among which are altitude, slope, forest management and land-use practices (Blondel & Aronson 1999). A clear example comes from reforestations of *Pinus* sp. plantations, which represent a new habitat in southeastern Iberian Peninsula (Maícas & Fernández 2004). These plantations have replaced most of the ancient Holm Oak *Quercus ilex* forests (Tremblay *et al.* 2003), and this transformation of the native forest may have evolutionary consequences for forest bird populations (Smith *et al.* 2008). Because tree species composition has been regarded as the main parameter influencing forest bird life-history traits, comparing breeding traits among different types of forests may provide insights into how birds would respond to local conditions (e.g. in remnant Holm Oak patches within the pine forests), and what factors (e.g. differences in food availability) might affect breeding traits (see Blondel *et al.* 1993, Lambrechts *et al.* 2004).

Vegetation structure (e.g. variation in density and age of the trees, presence and development of the shrub layer, etc.), on the other hand, promotes small-scale heterogeneity, which is sometimes enhanced by human activities (e.g. silvicultural practices for preventing forest fires; Baeza *et al.* 2003). Differences in vegetation structure might cause differences in breeding parameters among individuals nesting relatively close to each other (Dhondt *et al.* 1992, Enoksson *et al.* 1995, Arriero *et al.* 2006) or in the efficiency of predators searching for nests (Davis 2005). For example, among forest birds, those breeding in nestboxes surrounded by mature vegetation within a forest usually show higher reproductive output than those nesting in immature vegetation, so breeding territories placed in mature vegetation are considered of higher quality for birds (Riddington & Gosler 1995, Hinsley *et al.* 2002, Arriero *et al.* 2006).

Therefore, the analyses of both tree composition and vegetation structure are important to understand the processes underlying how birds behave in a structured landscape, especially when the vegetation composition is not homogeneous and the ancient forest has been replaced by a different one. Habitat structure takes on greater importance in managed forests, where management practices may accentuate variation among nearby areas with similar natural characteristics, enhancing, for instance, predation risk (Thompson 2007) or reducing food availability (Arriero *et al.* 2006). Hence, knowledge of the influence of tree composition and habitat structure on life-history traits in birds must be considered by managers to design effective conservation, management and reforestation plans (Lusk *et al.* 2003, Quevedo *et al.* 2006).

The Great Tit *Parus major* is a generalist species that readily accepts artificial nestboxes and breeds in many forest types (Cramp & Perrins 1993). Different reproductive traits have been shown to vary among forest types (e.g. van Balen 1973, Riddington & Gosler 1995, Sanz 1998). Moreover, it is also known that, among tits (*Paridae*), small changes in habitat structure can have profound effects on reproduction and condition (Otter *et al.* 2007, Wilkin *et al.* 2007), making this species a good model for evaluating the extent to which reproductive traits are affected by habitat features (e.g. Sánchez *et al.* 2007, Wilkin *et al.* 2007). The effects of forest type on breeding traits are known since a long time for this species. However, most of these studies have compared deciduous (food-rich) and evergreen (poor-food) forests. Additionally, studies that combine forest type and vegetation structure appear to be less common in the literature (but see Tarvin & Garvin 2002, Fort & Otter 2004, Díaz 2006).

We aimed to study the effect of habitat on Great Tit reproductive parameters at two levels, across forests (different forest types) and within a forest (considering habitat structure and tree composition around nestboxes). Thus, we selected two forests representing two different forest types: a Holm Oak forest, an example of the ancient forest of the Mediterranean region, and a pine forest, an example of relatively new reforested areas, both located at the same latitude.

METHODS

Study area

The study was conducted in two natural parks, Sierra Mariola (38°44'N, 0°33'W, 900 m a.s.l.) and Font Roja (38°39'N, 0°32'W, 1090 m a.s.l.) in eastern Spain (Fig. 1). The distance between these areas is about 8 km. Despite the short distance, vegetation composition and climatic conditions are different because of differences in altitude, orography and mountain orientation. For instance, based on available temperatures gathered from a meteorological station located within Font Roja and, from another meteorological station 4 km far from Sierra Mariola, mean maximum temperature during June was 3.5°C lower in Font Roja.

In both forests, human activity has created a vegetation structure mainly characterized by regeneration of stands of even age. From March to July during three breeding seasons (2005 to 2007), a total of 110–121 nestboxes in Sierra Mariola and 118–140 in Font Roja were checked. All nestboxes were located using a geographic positioning system (Garmin 12).

Habitat features

Sierra Mariola (SM hereafter) is a pine forest product of the replacement of the former vegetation (scrub vegetation and Holm Oak forests). This forest and surroundings have been profoundly modified by shepherding and forest fires, being human clearing practises going on to date. Young trees and open areas are quite common. The tree layer around nestboxes was composed almost exclusively of Aleppo (the most abundant species), Umbrella and Maritime Pines (*Pinus halepensis, P. pinea* and *P. pinaster* respectively). Isolated patches of Holm Oaks are also present. Up to 20 different species were identified in the shrub layer (up to 3 m in height) with young Aleppo Pine stands being the most abundant species. Other abundant shrub species were Prickly Junipers *Juniperus oxycedrus* and Kermes Oaks *Quercus coccifera*. Shrubs were included in our study because many birds were observed foraging on them

Figure 1. Study areas located in eastern Spain, Sierra Mariola (SM) and Font Roja (FR). Light grey colour shows the boundary of both natural parks, dark grey colour indicates the area where nestboxes were located.

(pers. obs.) and thus can be considered as a secondary habitat for tits (Díaz *et al.* 1998).

Font Roja (FR hereafter) is an evergreen Holm Oak forest, a remnant of the ancient forest which covered vast extensions in the southeastern Iberian Peninsula. In particular, this forest has been exploited for centuries to extract firewood and charcoal. The Holm Oak is the most abundant species followed by the far less common Aleppo Pine at the altitude where nestboxes were placed. Deciduous trees, the most representative being Flowering Ashes *Fraxinus ornus* and Portuguese Oaks *Quercus faginea*, are also found, though they are quite isolated and thus do not form clear 'deciduous patches'. The understory was dominated by the shrub Laurustinus *Viburnum tinus*.

Vegetation cover and species composition were quantified by performing three 50-m line intercept transects starting from each nestbox. For each transect, we measured the cover of both trees (more than 3 m in height) and shrubs (range 0.5–3 meters) for those that intercepted the line (see Elzinga *et al.* 2001, Hill *et al.* 2005 for further information). Vegetation under 0.5 m was not considered. The direction of transects from the nestbox was chosen at random, though we did require that each transect differ by at least 45º from the adjacent one; angles were measured with a compass. Transects were performed throughout the year (2006–07), but in FR the sampling was done in spring and summer to allow easy identification of deciduous species. We considered that vegetation structure did not differ appreciably during the study period.

Additionally, sampling plots of 25-m radius centred at each nestbox were established to measure the average diameter of the five thickest trunks measured at breast height (d.b.h.; using a 1-m metric tape), and the number of young (5–10 cm d.b.h.) and old trees (> 30 cm d.b.h.; Arriero & Fargallo 2006) classified by eye after previous training. To increase the accuracy of the count of the trees, the 25-m radius circle created around each nestbox was split into four sections.

Vegetation was sampled from all nestboxes in SM but only from 116 (83% of the maximum number present) in FR. The remaining FR boxes were excluded because the slope was too steep to safely sample vegetation. All vegetation measurements were made by the same author (FA).

GIS-procedure and vegetation gradient

We used ARCGIS, version 9.1 spatial analyst for processing vegetation data. Transect data were georeferenced in a Transverse Mercator Complex WG1984, Complex UTM-Zone 30 N coordinate system. From each transect, we calculated the spatial distribution of several tree species and shrubs with Inverse Distance Weighted (IDW) interpolation techniques (Wilkin *et al.* 2007). This method estimates cell values by averaging the values of sample data points in the vicinity of each cell. The closer a point is to the centre of the cell being estimated, the more influence, or weight, it has in the averaging process. Thus, a complete vegetation map of each forest was generated. Finally, after creating three different buffers around each nestbox (25, 50 and 75-m radius), we estimated different vegetation parameters (tree species, tree and shrub cover) for each one with a specially written program that uses an overlapping zonal statistical technique. This method examines environmental variation within search buffers formed with fixed and predetermined radii around each breeding location. A clear advantage of this approach is the ability to examine environmental variation over a range of spatial scales by altering the radius of the search buffers (see Wilkin *et al.* 2007). The maximum distance around each nestbox (75 m) was selected to be biologically meaningful for breeding traits such as laying date (Wilkin *et al.* 2007) and because it is within the range of the foraging area for Great Tit breeding pairs (Naef-Daenzer 2000).

Breeding parameters

Nestboxes were visited once per week, and active nests were visited with a pattern that allowed us to assess laying date (assuming that one egg was laid per day; 1 = 1 April), clutch size, and hatching date (with visits every day or every other day around the expected hatching date). As many adults as possible were trapped whilst feeding 11–15 day-old nestlings (hatching date = day 0) using door traps and/or mistnets. Adults caught were sexed, aged (classifying them into yearlings - second calendar year - or older birds using plumage characteristics; Svensson 1992), weighed (using an electronic balance; to the nearest 0.1 g), and their tarsus length measured (using a digital calliper; to the nearest 0.01 mm). As a simple estimate of body condition, the ratio of body weight to tarsus length was used, because body mass scaled linearly to tarsus length ($r = 0.18$, $F_{1,156} = 5.7$, $P = 0.019$). Each adult bird was marked with an individually numbered aluminium ring and colour rings. Some adults that could not be trapped in a particular year could be identified at their nests by reading previously fitted colour rings using binoculars.

For nestlings, tarsus length and weight were measured, and body condition estimated, at day 14. To avoid pseudoreplication, measurements of nestlings from the same nest were averaged to obtain a single value per trait per nest (Eddison 2000), so the statistical unit is the brood. Male characteristics were initially considered in the analyses but, as no explored relationship was significant, results concerning them are not presented.

Failed nests were those in which at least one egg was laid but no chicks fledged. Two measures of breeding success were used: hatching success – the ratio of the number of hatchlings over clutch size; and fledging success – the ratio of the number of fledglings over the number of hatchlings. Hatching success was estimated over nests where at least one egg hatched, and fledging success in nests where at least one chick fledged.

Data analysis

A total of 280 first clutches (164 clutches in SM, 116 in FR), for which we measured the surrounding environment, were used for the analyses. As variables describing habitat structure were highly correlated, principal component analyses (PCA) were run to obtain factors that summarized habitat structure (Varimax rotation, see González 2003) for each buffer (25, 50 and 75 m). The first principal component (PC1) defined a gradient of territory vegetation maturity (Table 1). PC1 correlated significantly with all variables (except for the percentage of tree cover in the 25-m radius). Nestboxes surrounded by mature vegetation were characterized by a greater number of large trunks (diameter larger than 30 cm), while those surrounded by immature vegetation were characterized by high number of young trees with a well developed tree and shrub cover. Positive loadings values of PC1 corresponded to more mature habitat for 25 and 50-m radii, while lower loadings values of PC1 corresponded to more mature vegetation within a 75-m radius around nestboxes. Based on a broken stick analysis (Jackson 1993), PC2 should be also considered here. This variable was mainly related with tree and shrub cover (see Table 1). All the analyses performed with PC1 were repeated with PC2, but none of the results for PC2 were significant and are not presented here.

Across-forest analyses were conducted with linear mixed models (LMM). We included year and forest type

Table 1. Results of three principal component analyses summarising the vegetation parameters, separately for the vegetation measured at 25, 50 and 75-m radii around the nestboxes. Presented are the loadings of each parameter on the principal components. Significant correlations between single vegetation parameters and the extracted principal components are shown in bold.

Radius around nestbox	25 m		50 m		75 m	
Vegetation parameter	PC1	PC2	PC1	PC2	PC1	PC2
Number of trunks 5–10 cm	**–0.637**	–0.06	**–0.669**	**0.115**	**0.678**	**0.470**
Number of trunks > 30 cm	**0.838**	**0.241**	**0.827**	**0.175**	**–0.812**	**0.441**
Mean diameter 5 thickest trees	**0.868**	**0.156**	**0.859**	**0.136**	**–0.843**	**0.388**
Shrub cover (%)	**–0.592**	**0.568**	**–0.635**	**0.535**	**0.650**	**0.224**
Tree cover (%)	0.044	**–0.886**	**–0.180**	**–0.860**	**0.375**	**0.588**
Eigenvalues	2.214	1.194	2.304	1.088	2.395	1.033
Variation explained (%)	44.3	23.9	46.1	21.8	47.9	19.2
Kaiser–Maier–Olkin measure	0.578		0.603		0.637	
Bartlett's test of sphericity	<0.001		<0.001		<0.001	

as fixed factors; female identity as a random effect because some females bred in the same nestbox over several years; and laying date, clutch size, and nestling parameters as dependent variables. Separate models were used for the different dependent variables.

We first focused on the effect of tree species composition surrounding nestboxes. Thus, we considered that a certain tree species or group of tree species (e.g. mixed, evergreen) was dominant around a particular nestbox when it amounted to a minimum of 10% of the total cover, being for other species or group of species lower than 10%. In cases when two or more species or group of species amounted to 10% or more, no single species was considered dominant and these data points were excluded from this particular analysis. Secondly, to study the effects of habitat structure, we considered shrub and tree species separately. For both cases (composition and structure within forest), LMM were run using laying date and clutch size as dependent variables. To analyze the effects on hatching and fledging success, we ran LMM with binominal error using R statistical software 2.6.1 (lmer package). For habitat structure analyses, the gradient of territory vegetation maturity (PC1 for 25, 50 and 75 m) and female condition were included as covariates, year, forest type and female age as fixed factors and female identity as random factor. We included forest type to take into account possible differences in habitat structure owing to the dominant tree species around each nestbox. Statistics were calculated for each of the three buffer distances. When the same pattern was reached for more than one distance for any of the breeding traits analyzed, only the plot for the lowest distance is shown.

Multinomial Logistic Regressions were used to assess the probability of a nest being deserted or predated compared to hatched, including year and forest type as fixed factors and vegetation gradient as a covariate. SPSS 15.0 statistical package was used for statistical analyses unless otherwise indicated.

RESULTS

Breeding traits and tree composition across and within forests

Great Tits started breeding, on average, one week later in FR than in SM (Table 2). Despite this, clutch size, number of hatchlings and number of fledglings were larger in FR. Also, chicks and females were heavier and in better condition in FR, while mean tarsus length was similar in both forests. A year effect was found in most life-history traits ($P < 0.001$, see Table 2), but those effects varied in parallel in both forests and no interaction between forest type and year was significant.

In within-forest comparisons, for SM we first compared breeding traits between nests where the dominant tree species were Aleppo Pines (31% on average vs. < 1% of Umbrella Pine cover) with those where Umbrella Pines were dominant (29%) over Aleppo Pines (< 1%). Laying date and clutch size were similar at all distances considered ($P > 0.05$). Hatching success was higher in nestboxes surrounded by Aleppo Pine (89.93, SE 2.41) than those surrounded by Umbrella Pine (82.78, SE 3.87; $t_{118} = 1.70$, $P = 0.037$) only when considering 50-m radius. Second, when comparing breeding traits between nests placed in pine- (38% vs. 3% of Holm Oak) vs. Holm Oak-dominated patches (26% vs. 5% of all pine species), no differences in any of the breeding traits were found at any of the three distances explored ($P > 0.05$ in all cases).

For FR, two comparisons were also done, firstly between nestboxes dominated by Holm Oaks (43% vs. 2% of Aleppo Pines) and those by Aleppo Pines (21% vs. 3% of Holm Oaks), and second between mixed (56% of deciduous and evergreen vs. 6% evergreen) and evergreen vegetation patches around nestboxes (42% vs. 3% deciduous). Mixed vegetation patches were characterized by an average of 21% of cover of deciduous trees, and an average of 35% of cover of evergreen trees (pines, Holm Oaks). We did not make a comparison with only deciduous trees because they were too scarce to be considered as dominant around nestboxes (cover less than 10%). None of the breeding traits studied differed between any of the vegetation types at any of the three distances considered ($P > 0.05$ in all cases).

Vegetation structure effects on breeding traits within forests

In FR (Holm Oak forest), the percentage of shrub cover around nestboxes was higher (27.59%, SE 13.52, $n = 116$) than in SM (pine forest; 7.40%, SE 7.11, $n = 121$, LMM $F_{1,235} = 36.45$, $P < 0.001$, percentages arcsin transformed). In FR, the average tree diameter around nestboxes was smaller (27.97 cm, SE 5.04, $n = 116$) than in SM (32.37 cm, SE 6.10, $n = 121$, LMM $F_{1,235} = 245.98$, $P < 0.001$) because of both a higher young to old trees ratio (Chi-square test, $\chi^2_1 = 2664.11$; $P < 0.001$) and a higher number of young trees (mean number of young trees: FR: 27.53, SE 16.92, $n = 116$; SM: 13.04, SE 9.12, $n = 121$, LMM $F_{1,235} = 81.49$, $P < 0.001$, frequencies squared-root transformed). In both forests gaps and overlapping in the tree canopy were common.

Table 2. Effects of forest type (*df* = 1, pine SM vs. Holm Oak FR), year (*df* = 2, 2005–2007) and their interaction (*df* = 2) on life-history, chick and female traits in Great Tits using separate linear mixed models. Mean values ± SE are shown for the two forest types.

	LMM			Means per forest type	
Dependent, independent variables	*n*	*F*	*P*	Pine SM	Oak FR
Life-history traits					
Timing of reproduction (1 = 1 April)					
Forest type	255	55.4	<0.001	31.23 ± 2.72	38.58 ± 1.23
Year	262	36.41	<0.001		
Forest type × Year	270	1.09	0.338		
Clutch size					
Forest type	254	29.61	<0.001	6.16 ± 0.36	6.93 ± 0.16
Year	256	10.09	<0.001		
Forest type × Year	257	0.66	0.517		
Number of hatchlings					
Forest type	205	20.98	<0.001	5.82 ± 0.52	6.28 ± 0.23
Year	205	4.41	0.013		
Forest type × Year	206	1.18	0.311		
Number of fledglings					
Forest type	129	19.2	<0.001	5.09 ± 0.73	5.71 ± 0.32
Year	129	1.65	0.195		
Forest type × Year	129	1.37	0.257		
Chick traits					
Tarsus length (mm)					
Forest type	112	0.33	0.570	18.99 ± 0.26	19.24 ± 0.11
Year	112	1.3	0.277		
Forest type × Year	117	2.54	0.083		
Body mass (g)					
Forest type	118	11.52	0.001	15.47 ± 0.55	16.76 ± 0.24
Year	110	0.59	0.556		
Forest type × Year	114	2.33	0.102		
Body condition					
Forest type	122	13.45	<0.001	0.81 ± 0.02	0.87 ± 0.01
Year	117	0.24	0.785		
Forest type × Year	120	1.45	0.239		
Female traits					
Tarsus length (mm)					
Forest type	136	0.56	0.457	19.27 ± 0.30	19.23 ± 0.13
Year	50	4.45	0.017		
Forest type × Year	50	0.64	0.530		
Body mass (g)					
Forest type	130	10.17	0.002	16.54 ± 0.40	17.25 ± 0.18
Year	110	0.52	0.517		
Forest type × Year	110	1.11	0.335		
Body condition					
Forest type	122	8.83	0.004	0.85 ± 0.02	0.89 ± 0.01
Year	83	3.94	0.023		
Forest type × Year	83	0.14	0.867		

Female identity was included as a random effect in each of the models.

Laying date was not significantly related to territory vegetation maturity (Table 3). Since female quality might simultaneously affect laying date and nest site selection, we explored whether female characteristics varied along the vegetation maturity gradient, and their relationships with breeding traits. Laying date was not related to female condition, but old females laid a mean of 2.4 days earlier than young females (Table 3).

Table 3. Results of six linear mixed models on laying date and clutch size within a forest separately, depending on the effects of the vegetation maturity around the nestbox on three different scales (*df* = 1: PC1), year (*df* = 2), forest type (*df* = 1: pine vs. Holm Oak), female age (*df* = 1: second year or older) and female body condition (*df* = 1).

Radius around nestbox	25 m			50 m			75 m		
Dependent, independent variables	*n*	*F*	*P*	*n*	*F*	*P*	*n*	*F*	*P*
Laying date									
Vegetation maturity around box (PC1)	148	0.14	0.710	147	0.05	0.816	149	0.04	0.844
Year	85	56.76	<0.001	85	57.03	<0.001	85	57.06	<0.001
Forest type	138	17.22	<0.001	138	16.03	<0.001	138	15.95	<0.001
Female age	123	7.87	0.006	124	7.91	0.006	124	7.93	0.006
Female body condition	152	0.73	0.394	153	0.72	0.399	152	0.71	0.402
Clutch size									
Vegetation maturity around box (PC1)	152	0.33	0.565	152	0.6	0.441	152	0.97	0.325
Year	152	9.14	<0.001	152	9.16	<0.001	152	9.14	<0.001
Forest type	152	18.61	<0.001	152	16.83	<0.001	152	15.96	<0.001
Female age	152	0.004	0.953	152	0.004	0.952	152	0.003	0.955
Female body condition	152	0.005	0.943	152	0.006	0.940	152	0.005	0.943

Female identity was included as a random effect in each of the six models.

Mean vegetation maturity around nestboxes did not differ between nests of females of different age (three LMMs $F_{1,145} = 0.40$; $F_{1,139} = 0.05$ and $F_{1,144} = 0.22$, $P > 0.05$ for 25, 50 and 75-m buffers, respectively), and female body condition was not affected by the maturity of vegetation (three LMMs $F_{1,156} = 0.33$; $F_{1,155} = 0.19$ and $F_{1,156} = 0.02$, $P > 0.05$ for 25, 50 and 75-m radii, respectively).

Clutch size varied between years and forests, but it was not related to vegetation maturity (LMMs all distances $P > 0.05$) nor to laying date (LMM $F_{1,260} = 2.55$, $P > 0.05$; Table 3). Clutch size was not related to female condition or age (Table 3).

Hatching success was higher in young and dense vegetation patches than in mature and open ones for all the three radii considered (Fig. 2, Table 4), whilst it was not significantly affected by female age or condition (Table 4). However, there was a significant interaction between the maturity of vegetation for all three radii and female condition (Table 4). To explore this interaction further, we split female condition into two groups: poor (values of body condition lower or equal to 0.88) and good condition (values higher than 0.88), classifying approximately half of the females in each category (Fig. 3). For good condition females (mean condition index: 0.92, SE 0.11), hatching success did not vary along the vegetation gradient, while that for poor condition females (0.84, SE 0.01) decreased along the gradient from nestboxes surrounded by immature to these surrounded by mature vegetation for all three radii.

Finally, neither fledging success, nor nestling tarsus length or body mass, were related to vegetation structure at any of the distances around the nests explored ($P > 0.05$ for all three distances).

Causes of lower hatching success in mature areas

We found that hatching success was lower for next boxes surrounded by mature vegetation, at least for fe-

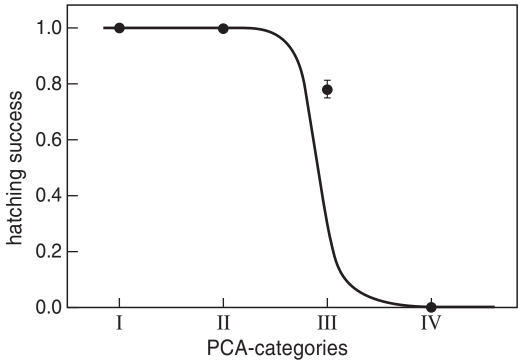

Figure 2. Mean hatching success (±SE: number of hatchlings over number of eggs laid) in relation to the territory vegetation maturity within 25 m around the nestbox. For presentation purposes only (as the analysis was done on the individual data points) mean (±SE) hatching success values are presented for four PCA categories: I (PCA < –1.5), II (–1.5 < PCA ≤ 0), III (0 < PCA ≤ 1.5) and IV (PCA > 1.5). The line is the regression line from a LMM statistical model with binominal errors: hatching success = $1/ (1 + \exp^{-[4.43-5.28 \times PC1\_25m]})$.

Table 4. Results of six linear mixed models on hatching success and fledging success size within a forest separately, depending on the effects of the vegetation maturity around the nestbox on three different scales (*df* = 1: PC1), year (*df* = 2), forest type (*df* = 1: pine vs. Holm Oak), female age (*df* = 1: second year or older) and female body condition (*df* = 1).

Radius around nestbox	25 m			50 m			75 m		
Dependent, independent variables	*n*	*F*	*P*	*n*	*F*	*P*	*n*	*F*	*P*
Laying date									
Vegetation maturity around box (PC1)	–2.98	151	<0.001	–2.98	151	<0.001	2.8	151	<0.001
Forest type	0.3	151	0.657	0.12	151	0.646	0.12	151	0.512
Female age	–0.5	151	0.614	–0.49	151	0.625	–0.51	151	0.612
Female body condition	–0.54	151	0.588	–0.53	151	0.597	–0.54	151	0.588
Female body condition x PC1	2.88	151	<0.001	2.67	151	<0.001	–2.68	151	<0.001
Fledging success									
Vegetation maturity around box (PC1)	–0.39	120	0.695	–0.32	120	0.746	0.22	120	0.826
Forest type	1.22	120	0.73	1.22	120	0.719	1.29	120	0.714
Female age	–0.21	120	0.834	–0.22	120	0.823	–0.23	120	0.817
Female body condition	–0.14	120	0.893	–0.15	120	0.798	–0.16	120	0.877
Female identity was included as a random effect in each of the six models.									

Female identity was included as a random effect in each of the six models.

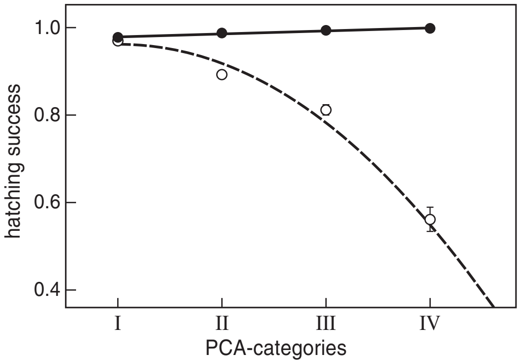

Figure 3. Effects of female condition on hatching success in interaction with the territory vegetation maturity in a 25-m radius around the nestbox. As a measure of female condition we used the ratio of body mass to tarsus length. For presentation purposes only, we classified females whose values for condition were equal to or less than 0.88 as poor condition (dashed line) and females with values higher than 0.88 (solid line) as good condition; and we present mean (±SE) hatching success values for four PCA categories: I (PCA < –1.5), II (–1.5 < PVA ≤ 0), III (0 < PCA ≤ 1.5) and IV (PCA > 1.5). The lines are the LMM regression lines; note that only for low quality females the relationship was significant.

males in poor condition. Therefore, we explored some of the potential causes that might underlie this pattern. Death of embryos might occur if incubation pattern is not adequate, and this could happen if females have to spend more time foraging away from nests to satisfy energy demands or to avoid predation. We therefore explored how vegetation structure was related to the proportion of nests containing unhatched eggs, deserted, or affected by predation. The likelihood of a nest containing unhatched eggs was not related to the surrounding environment at any of the three distances considered (Multinomial logistic regressions $P > 0.05$ for all three distances). However, the probability of nest predation increased with vegetation maturity when considering a 50-m and 75-m radius during incubation (Table 5, Fig. 4), compared to hatched nests. Additionally, during such phase, desertion increased with vegetation maturity for a 75-m radius. On the other hand, nest desertion was not related to vegetation maturity during the nestling phase Instead, nest predation increased with increasing the maturity of the vegetation within 75-m radius around nestboxes. Data for 25 m were all non significant, and therefore, they were not shown. Finally, there were no differences in predation pressure among forest types (64% of nests lost to predators in FR, 54% in SM, Chi-square test $\chi^2_1 = 1.836$, $P = 0.175$). Therefore, most results pointed out that both nest desertion and predation increase with the degree of maturity of the vegetation in these two forests.

Despite the risk of predation, occupation rate of the available nestboxes by Great Tits was not affected by the maturity of vegetation (Multinomial logistic regressions $P > 0.1$ for all three distances), although it tended to be slightly higher in environments with lower nest predation.

Table 5. Probability of nest desertion and nest predation during the egg (n = 280 nests) and nestling phase (n = 223 nests) compared to hatched, depending on the effects of the vegetation maturity around the nestbox (PC1, df = 1) on two different scales. Shown are the results of four Multinomial logistic regressions.

Radius around nestbox	50 m			75 m		
Phase, dependent response*	Wald's χ^2	*B*	*P*	Wald's χ^2	*B*	*P*
Egg phase						
Deserted	1.64	-4.15	0.200	4.56	-4.68	0.033
Predated	4.29	6.67	0.038	3.94	-3.85	0.047
Nestling phase						
Deserted	2.72	6.55	0.099	0.77	-2.28	0.382
Predated	3.39	4.50	0.066	4.78	-3.52	0.029

*Hatched is the reference category.

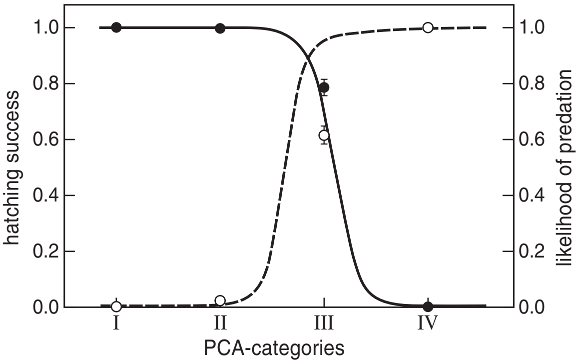

Figure 4. Relationship between mean hatching success (proportion of eggs hatched, solid line) and mean predation level (proportion of nests predated, dashed line) during the incubation period through the territory vegetation maturity gradient in a 50-m radius around the nestbox. For presentation purposes only (as the analysis was done on the individual data points) mean (±SE) hatching success and predation level values are presented for four PCA categories: I (PCA < –1.5), II (–1.5 < PCA ≤ 0), III (0 < PCA ≤ 1.5) and IV (PCA > 1.5). The lines are the regression lines from LMM statistical models with binominal errors.

DISCUSSION

Laying date

Several studies have pointed out that mean laying date differs among forest types (van Balen 1973, Dhondt *et al.* 1984, Blondel *et al.* 1987, Maícas & Fernández 1996, Belda *et al.* 1998). However, Sanz (1998) showed that the effect of the forest type on laying dates disappeared after controlling for differences in altitude and latitude (see also Chabi & Isenmann 1997). Ambient temperature affects the timing of breeding (low temperatures delay the timing) through its effects on vegetation phenology and on the development rate of insects (van Balen 1973, Blondel *et al.* 1991, Belda *et al.* 1998, Sanz 1998), and ambient temperature decreases as altitude increases, so laying date would be expected to be delayed at high altitudes (Fargallo & Johnston 1997, present study). Therefore, differences in mean laying date among habitats may arise because of differences in altitude. Examples directly addressing the effect of altitude over laying dates come from Chabi & Isenmann (1997) and Belda *et al.* (1998). These authors compared laying dates of Blue *Cyanistes caeruleus* and Great Tits respectively at different altitudes within the same forest type and latitude. Based on the results of these two studies, and having into account that FR is placed 200 m higher than SM, we would expect a delay of 4–5 days in the mean laying date in FR. Also, Hopkins (1938 in Wilkin *et al.* 2007) concluded that spring is often delayed by 1 day for every 30 m increase in altitude, which might imply a delay of 6.7 days in FR. Therefore, we may then conclude that most of the difference of one week in laying dates between the two studied forests was likely caused by differences in altitude.

To date, detailed studies relating Great Tit breeding traits to tree composition within a forest are scarce. For example, Wilkin *et al.* (2007) found that laying date was earlier as the number of oaks around Great Tit nests increased, arguing that food availability was the underlaying factor. Also, to the best of our knowledge, the only study relating breeding traits to habitat structure in Great Tits was published by Sánchez *et al.* (2007), who found that nestlings raised in nestboxes surrounded by mature vegetation tended to be in better condition. Van Noordwijk *et al.* (1981) concluded that neither differences in microhabitat nor in temperature among nestboxes explained laying date variability among individuals within a population. Because most nestboxes within each forest were placed at similar altitude (at different altitude between forests), a possible effect of temperature on vegetation phenology and therefore on food availability would be negligible. In the present study, neither the degree of vegetation maturity nor differences in tree composition among nestboxes within any of the forests were cues for the starting of reproduction in the Great Tit populations studied.

Clutch size

Clutch size in Great Tits is typically larger in forests containing more food (Kluijver 1951, van Balen 1973), and it has been shown to decrease with increasing altitude in Great Tits and other species (Klomp 1970, Järvinen 1989, Sanz 1998). Belda *et al.* (1998) found that clutch size of Great Tits was larger in a Holm Oak than in a pine forest placed at the same altitude and latitude. Caterpillars are more abundant in Holm Oaks than in pine trees (Illera & Atienza 1995, Tremblay *et al.* 2003), and this may explain the differences in mean clutch size found between these two forest types. The Holm Oak forest of FR was located at higher altitude than the pine forest of SM, while differences in clutch size were opposite to what would be expected by differences in altitude. This suggests a clear effect of forest type (i.e. food availability), which overrides the effect of altitude.

Within forests, clutch size would be expected to decrease along a food gradient from richer mixed forests (deciduous plus evergreen trees, Tremblay *et al.* 2003), to Holm Oak, to pine-dominated areas (Illera & Atienza 1995, Tremblay *et al.* 2003), and to be larger in young and dense vegetation, which probably holds more food (Cody 1981, Martin 1993) than in mature and sparse vegetation areas (Arriero *et al.* 2006). However, neither tree composition nor territory vegetation maturity around nestboxes affected clutch size. A possible explanation is that neither monospecific tree patches, nor pure 'young' or 'mature' patches are present. Rather, the whole area was a mixture of tree species, without clear dominant species around the nestboxes in many cases, and the index of maturity did not differ much across nestboxes. It seems that differences in these two factors were not enough to generate differences in clutch size.

Therefore, our results suggest that differences in clutch size between forests are mainly related to the forest type, probably through differences in food availability between forests. However, within the forests studied, the vegetation features around nestboxes seem to have low importance in clutch size determination. Some other microhabitat features might be more relevant in affecting reproductive parameters than the ones we actually measured.

Hatching success

Hatching success decreased with vegetation maturity for females in poor condition, while it was independent of vegetation maturity for females in good condition. This suggests that females in poor condition have more problems during the incubation process in mature areas, where probably food is scarcer, and they have to allocate more time to foraging (Hinsley *et al.* 2008). Arriero *et al.* (2006) found higher hatching success in mature areas in a deciduous forest for Blue Tits. Perhaps the relationship between food availability and forest maturity is dependent on the type of forest, and mature areas hold more food in deciduous forests. Given that nestling diet is similar for Blue and Great Tits (Perrins 1979), it seems unlikely that the divergence in the results was caused by the bird species considered.

At the same time, we found that nest predation was significantly lower in nestboxes surrounded by young and dense vegetation, so reduced hatching success in mature vegetation patches may be also mediated by a higher nest predation (see Powell & Steidl 2000, Huhta *et al.* 2003). In our study, predators which could mediate in the hatching decline in nestboxes surrounded by mature vegetation were mostly Montpellier Snakes *Malpolon monspessulanus* (in SM) and Beech Martens *Martes foina* (in FR). In these predators with diurnal activity (Posillico *et al.* 1995, Blázquez & Pleguezuelos 2002), vision plays an important role in prey detection (see Barbadillo *et al.* 1999 for the Montpellier Snake), both snakes and martens locating nests by responding to specific search images (movements) of provisioning birds (Mullin & Cooper 1998). Thus, in nestboxes surrounded by immature vegetation with dense canopy and shrub layer, nests were likely more difficult to locate (high nest concealment), reducing the searching efficiency of visual predators (Davis 2005). Reducing the time allocated to nest defense would allow females to invest more in incubation, therefore increasing hatching success (Martin 1987, Nilsson & Smith 1988, Devereux *et al.* 2006).

Female and nestling traits

Females were in better condition, and produced more and heavier fledglings in the Holm Oak forest. The probable higher food abundance in the Holm Oak forest may have had positive effects on breeding performance both directly, more food for parents and nestlings, and indirectly, stimulating greater reproductive investment in parents (Riddington & Gosler 1995, Huhta *et al.* 1998), which may in turn accentuate the forest type effect on chick quality. Nest predation rate was similar in both forest types, so differences in breeding performance could not be generated by parents investing more in territories with lower predation risk (see Fontaine & Martin 2006).

Within forest, our results showed that nestlings raised in nestboxes located in patches with immature vegetation differed little in size and weight from those raised in patches with mature vegetation, confirming results of Arriero *et al.* (2006) in Blue Tits, and of Sánchez *et al.* (2007) in Great Tits. Therefore, it seems that possible differences in food availability among mature and immature vegetation patches (Arriero *et al.* 2006) were not a limiting factor for raising nestlings in these forests.

Conclusion

Summing up, different factors seem to be operating explaining the variation in breeding success in Mediterranean Great Tits. Firstly, differences in food availability across forests. Secondly, nest predation is playing an important role in determining nest success through the territory vegetation maturity within forests. Considering both habitat attributes (forest type and habitat structure), as well as conditions that might constrain the habitat use (e.g. nest predation, Johnson 2007), we could conclude that immature vegetation territories located in the Holm Oak forest are the ones providing the better conditions for the reproduction of Great Tits among the range of forest conditions considered here. We are aware that only one sample of each type of forest was considered, and that site-specific characteristics (e.g. predator species, vegetation structure, etc.) might vary between forests. It is therefore necessary to repeat this approach in other Mediterranean forests to a better understanding of the factors affecting breeding success in these habitats, and at which spatial scales they operate.

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SAMENVATTING

Het wel en wee van bosvogels is afhankelijk van de boomsoorten in het bos en de structuur van het habitat. Het onderhavige onderzoek richtte zich op de vraag in welke mate de vegetatiesamenstelling en de structuur van bossen effect hebben op het broedsucces bij het eerste legsel van de Koolmees *Parus major*. Hierbij ging de aandacht zowel uit naar een vergelijking van het succes tussen bossen als naar de variatie ervan binnen een bos. Het onderzoek vond plaats gedurende de jaren 2005–2007 in een oud bos met Steeneiken *Quercus ilex* en in een aangeplant bos met naaldbomen in het Middellandse Zeegebied. De eileg begon in het eikenbos een week later dan in het naaldbos. De legselgrootte en de broedselgrootte bij het uitkomen van de eieren en bij het uitvliegen waren in het eikenbos groter dan in het naaldbos. Bovendien was de lichaamsconditie van de jongen (de verhouding van lichaamsgewicht op tarsuslengte) in het eikenbos op het moment van uitvliegen beter dan in het naaldbos. Binnen het naaldbos was het voortplantingssucces voor paren die in nestkasten broedden die door eiken waren omringd, niet groter dan elders in het naaldbos. Evenmin was het succes in het eikenbos in kasten met naaldbomen er omheen lager dan elders in het eikenbos. In plaats van de boomsamenstelling bleek het ontwikkelingsstadium van de vegetatie rond de nestkasten een effect op het uitkomstsucces te hebben: dat lag hoger in nestkasten die omringd waren door een jonge vegetatie. Dit zou een gevolg kunnen zijn van een lagere predatie in kasten die omringd zijn door een zich nog ontwikkelende vegetatie. Er wordt geopperd dat in het Middellandse Zeegebied de variatie in broedsucces van Koolmezen tussen bossen door andere factoren veroorzaakt wordt dan dat binnen een bos. Zo zouden bijvoorbeeld verschillen in voedselaanbod een rol kunnen spelen bij verschillen in broedsucces tussen bossen en verschillen in nestpredatie bij de variatie in succes binnen een bos. (DH)

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