

REPRODUCTIVE CHARACTERISTICS AND DIFFERENTIAL RESPONSE TO SEASONAL TEMPERATURES OF BLUE AND GREAT TITS (*CYANISTES CAERULEUS* & *PARUS MAJOR*) IN THREE NEIGHBOURING MEDITERRANEAN HABITATS

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RÉSUMÉ. — *Caractéristiques de la reproduction et réponse différentielle aux températures saisonnières des Mésanges bleue et charbonnière (Cyanistes caeruleus & Parus major) dans trois habitats méditerranéens voisins.* — L'écologie de la reproduction de la Mésange bleue (*Cyanistes caeruleus*) et de la Mésange charbonnière (*Parus major*) a été étudiée en Sicile durant 18 années dans trois différents habitats voisins, à savoir des chênaies, des plantations de pins et des plantations mixtes pins et feuillus. Les Mésanges tant bleues que charbonnières, ont, en chênaie, pondu jusqu'à deux semaines plus tôt que dans les plantations. Nos résultats indiquent que les deux espèces ont eu un succès reproducteur statistiquement plus grand en chênaie que dans les plantations avec, dans ces dernières, un meilleur succès dans les formations mixtes que dans les pinèdes. Nous avons également confronté les caractéristiques de la reproduction aux températures de l'air locales afin de voir si l'avancement de la date de ponte s'étalait sur une longue période d'années. Bien qu'une variabilité de l'époque de la ponte ait été observée dans les trois habitats, une relation négative a été obtenue, indiquant que le début de la nidification avait progressivement été avancé tout au long des 18 années d'étude. De son côté, la température de l'air a progressivement augmenté durant la même période. Le modèle d'analyse de covariance utilisé a montré que la relation entre la ponte et les températures de l'air en mars restait marquée pour les deux espèces, mais différait statistiquement dans les trois habitats. En chênaie, les poussins se sont envolés un jour plus tôt que dans les plantations et ceux des formations mixtes ont grandi plus vite que ceux des pinèdes. Finalement, dans les trois habitats, la taille des pontes et le nombre de poussins à l'envol n'ont pas varié durant les 18 années d'étude, suggérant que les disponibilités alimentaires n'auraient pas changé. Les chenilles représentaient les principales proies dans les chênaies et les formations mixtes, moins en pinède où les mésanges nourrissaient leurs poussins avec des aliments plus divers. La présente étude souligne l'importance pour les insectivores des forêts de feuillus, naturelles ou régénérées, ainsi que le rôle potentiel en matière de conservation d'une gestion forestière planifiée.

SUMMARY. — The breeding ecology of the Blue Tit (*Cyanistes caeruleus*) and Great Tit (*Parus major*) was studied for 18 years in three different neighbouring habitats in Sicily, comprising oakwoods, reforested pine and a reforested mix of pine and broad-leaved trees. Both Blue and Great Tits laid eggs up to two weeks earlier in oakwoods than in the reforested areas. Our results indicate a statistically greater breeding success for both species in the oakwoods compared to reforested habitats, with the mixed reforested habitat having a greater success than that of reforested pine habitat. We also correlated reproductive characteristics with local air temperature to verify if the laying date of tits advanced over a long period of years. Even though a variable egg-laying trend was recorded in the three habitats, an overall negative trendline was obtained indicating that the onset of nesting advanced through the 18-year study period. On the other hand, the air temperature trend was positive over the same period of time. The model of covariance analysis showed the relationship between egg-laying and March air temperatures remained consistent for both tit species, it was statistically different for each of the three habitats. Nestlings in the oak habitat fledged one day earlier than in reforested habitats and nestlings in the mixed habitat grew faster than nestlings in the pine habitat. Finally, clutch-size and number of fledglings remained consistent over the 18-year period in all three habitats, suggesting that prey availability may not have changed. Caterpillars comprised the primary prey in the oak and mixed habitats, less in the pine, where tits fed chicks with a more diverse food. The findings of this study indicate the importance of broad-leaved forests, whether natural or regenerated, for insectivorous species, and hence the potential conservation role of forestry management planning.

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The Great Tit (*Parus major*) and the Blue Tit (*Cyanistes caeruleus*) are insectivorous birds, generally associated with European oak woodlands. The timing of egg-laying is important during the tit breeding season (*i.e.* spring), with much temporal variation being caused by changes in local air temperature. Furthermore, global climate change has been predicted to have localized effects on the emergence of insects, some of which comprise important food items for tit nestlings. For example, air temperature influences both the time when oak buds open (or bud-burst), and the time when caterpillars (the primary tit prey item) hatch. Tit breeding success requires that the timing of reproduction is precisely timed to overlap with the period of peak caterpillar biomass. In general, there is a five week lag from the time of egg-laying to when nestlings are one week old, when selection pressure for survival is at its greatest (van Noordwijk *et al.*, 1995). Tits provide an ideal opportunity to investigate the interactions between initial predictive information (*i.e.* photoperiod or change in day length) and supplementary information (*i.e.* ambient air temperature) to optimize the timing of seasonal breeding under changing climatic conditions. Long-term studies carried out on tits in Great Britain, France and the Netherlands revealed that the link between oaks, caterpillars and tits is highly sensitive to changes in temperature (e.g.: Lack, 1966; Varley, 1970; van Balen, 1973; Varley *et al.*, 1973; Perrins, 1973, 1979, 1990; van Noordwijk *et al.*, 1980, 1981; Zandt *et al.*, 1990; Blondel *et al.*, 1993; Visser *et al.*, 1998, 2003; Cresswell & McCleery, 2003; Wilkin *et al.*, 2009). At temperate habitats in Europe, Great and Blue Tits' egg-laying dates have been found to be negatively correlated with spring temperature, and significantly correlated with bud-burst in deciduous habitats (e.g. Clamens, 1990). Furthermore, the onset of breeding has been shown to begin earlier with increasing air temperature (e.g. McCleery & Perrins, 1998; Visser *et al.*, 1998; Both *et al.*, 2009). In parallel temperature has been found to have similar effect on the temporal activity of a range of arthropod species (Avery & Krebs, 1984).

In recent decades, the average surface air temperature of the globe has increased significantly (IPCC, 1990; Huang *et al.*, 2000). Because many bird species that inhabit forests are highly susceptible to changes in temperature, an increase in temperature may result in a marked change in bird behavioural ecology, including habitat selection (e.g. Hubálek, 2004). In addition, differences in habitat type may affect tit breeding behaviour. For example, Blue Tits occupying deciduous oakwoods on the France mainland initiate egg-laying one month earlier than those occupying evergreen oakwoods in Corsica, while tits occupying evergreen habitats on the mainland begin laying at an intermediate time (Blondel *et al.*, 1993). In fact, conspecifics occupying adjacent but different habitats may have a 2-3 week difference in the onset of breeding (Massa *et al.*, 2004). Furthermore, the resource availability of these different habitats has been shown to result in a large variation in clutch-size (e.g. Blondel *et al.*, 1993). To delineate the roles of climate change and habitat differences on tit breeding behaviour, long-term studies (*i.e.* across decades) of these birds are required.

Here we investigate the breeding behaviour of Blue and Great Tits across an 18-year period in adjacent habitats, on a Mediterranean island. We set out to determine whether differences in the breeding behaviour of tits are due to constant habitat differences and/or climatic fluctuations. We (i) compare the breeding traits of Blue and Great Tits in three adjacent wood-plots with different vegetation characteristics and (ii) establish the presence of general trends with respect to the date of egg-laying and climate parameters.

METHODS

STUDY AREA

The study area is in a 1600 ha forest, situated at an elevation of 600-800 m a.s.l., at the Mount Cammarata Nature Reserve (Santo Stefano di Quisquina, Agrigento province) on the island of Sicily, Italy (between 37°35'59.17"N-13°33'21.32"E and 37°36'56.95"N-13°31'51.31"E). The forest of the nature reserve comprises three different habitats: (i) a natural wooded area, dominated by the deciduous Downy Oak *Quercus pubescens* and by the evergreen Holm Oak *Quercus ilex* (herein reported as 'oak'), (ii) a reforested evergreen pine area dating 45 years, comprising *Pinus halepensis* and *Cedrus atlantica* (Massa *et al.*, 2004) (herein reported as 'pine'), and (iii) a section of the reforested pine area (*Pinus halepensis* and *Cedrus atlantica* dating 45 years) that was transformed by silvicultural

management in 1996 to include broad-leaved trees (*Quercus*, *Fraxinus*, *Acer* and *Ulmus*) (herein reported as ‘mix’). The third habitat has been included in our study since 1997.

FIELD PROCEDURES

Over 150 nest-boxes were placed in the three habitats; the oak and pine habitats in 1993 and the mix habitat in 1997. Care was taken to ensure that the territories of nesting tits did not overlap between natural and planted wood-plots (Fig. 1). Nest-boxes were built from coniferous wood of 1 cm thick, and were placed at 3–4 m above the ground in the dominant trees of each habitat type. They had the following specifications: entrance hole diameter 3.4 cm, chamber size 15 x 10.5 x 15 cm, distance between lower edge of entrance hole to bottom of nest chamber 7.8 cm. From April to June each year (1993–2010 for oak and pine, 1997–2010 for mix) we visited all nest-boxes once per week. We recorded the following parameters: (i) laying date of first egg, based on the assumption that females lay one egg per day, (ii) clutch-size, (iii) hatching date, (iv) brood size at 10 days, (v) number of fledglings, (vi) % breeding success [*i.e.* (no. fledglings / no. eggs laid) x 100]. All nestlings were ringed when 10 days old. Additionally, during the period between hatching and fledgling in 2006–2010, we also determined the growth trend of nestlings by weighing a sample of nestlings on an electronic balance (± 0.1 g) between 08:00 and 14:00 at three day intervals. Furthermore, a detailed study of nestlings at 8–12 days old was completed in 1997–2010 on a total of 25 Blue Tit broods and 18 Great Tit broods in the oakwood, 12 Blue Tit broods and 10 Great Tit broods in the reforested mix, 24 Blue Tit broods and 16 Great Tit broods in the reforested pine. A light sensitive video camera (BoxWatch Colour Cartridge Camera) was used to record the activity of the nestlings and their parents for a minimum of 120 min at each nest, at different times of the day, resulting in the acquisition of a total of 260 h of footage. The video camera was fixed to the nest-boxes and connected to a VHS recorder, both being powered by 12-V batteries. Prey type items were identified from the video footage, as well as the rate of food intake and the number of nestling faecal sacs that were removed by the parents from the nest-box. Overall, about 60% of the prey brought by adult Blue Tits and 70% brought by adult Great Tits to their nestlings, were identified.

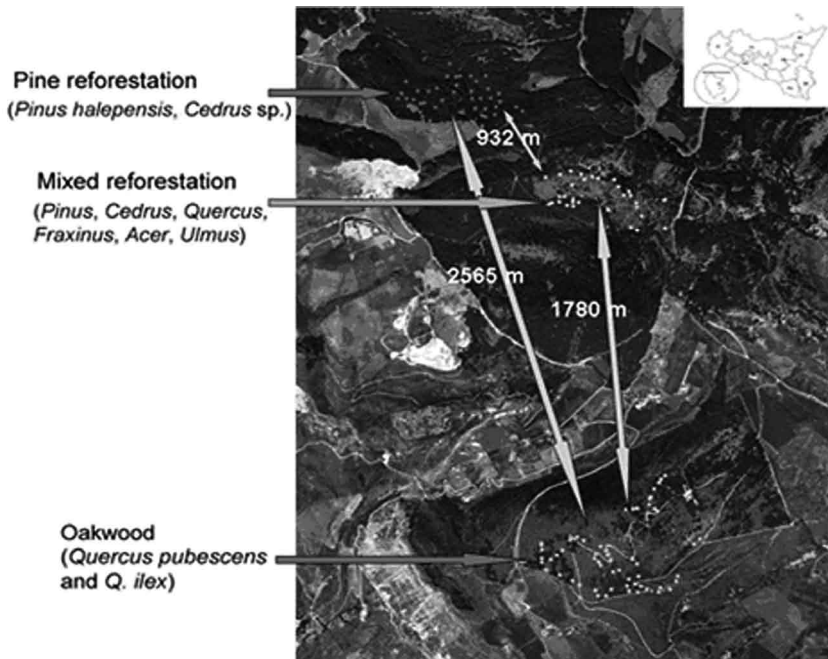


Figure 1. — The Mount Cammarata Nature Reserve of Sicily in Italy, showing the three study habitats (oak woodland, reforested pine and reforested mixed of broad-leaved trees and pine) and the distance in metres separating each habitat area. The dots correspond to nest-boxes.

DATA ANALYSES

Based on the assumptions that the data distribution was normal, the variance in the three habitats was the same, and the difference between species was not significant, we compared the laying date and clutch-size of each species in the three different habitats using one-way ANOVA. We subsequently tested the significance of multiple comparisons using the post hoc Tukey HSD test (SAS, 1987). Because the breeding success data were not normal, we compared breeding success in the three habitats using the Kruskal-Wallis non parametric test. In this case, we tested the significance using

a series of the Wilcoxon test. We adjusted the False Discovery Rate p-value, as suggested by Verhoeven *et al.* (2005), to not increase the first species error probability. Additionally, because the correlation between the date of egg-laying and mean value temperature for the month of March resulted higher ($r = -0.32$) than the date of egg-laying along the 18 years of study ($r = -0.14$), we used the covariance analysis (ANCOVA) to test whether there were interactions between air temperature, habitat and species. In this study, ‘habitat’ is a ‘three-level’ factor, due to the three habitat types, while ‘species’ is a ‘two-level’ factor, due to the two tit species. Two models were developed to investigate whether species and/or habitat differences influence the timing of reproduction. The first model took into account species differences (laying date \approx March temperature \times habitat \times species), while the second model took into account habitat differences (laying date \approx March temperature \times habitat). We used the mean air temperature records collected at the closest meteorological station (c. 10 kms from Cammarata).

With respect to food intake rates and faecal sacs removal rates obtained from the video footage, the mean rate per hour per nestling per nest was calculated for comparative statistical analysis. In this way, the number of samples for each process corresponded to the total number of nests included in the analysis (*i.e.* $n = 108$ nests). In addition, comparative data was obtained with respect to the frequency that each prey type was delivered to the nestlings by the adults of the two tit species in each of the three habitats. The chi square test was used to analyse these data to indicate the difference in resource availability in each of the three habitats, through testing the hypothesis of association between habitat and prey type. To avoid a high number of empty cells, we included only the seven most frequent prey types in the contingency table. Overall, the total number of observations used in the statistics was 2970 for Blue Tits and 628 for Great Tits.

For all statistical analyses the significance level was set to 0.05.

RESULTS

BREEDING PARAMETERS

In each habitat, both Blue and Great Tits laid their eggs during the same time-frame. In the oak habitat, the average egg-laying date was 19 April, in the mixed habitat it was 29 April, and in the pine habitat it was 4 May (Tab. I; Figs. 2, 3). For Great Tits, the difference in the date of egg-laying across the three habitats was highly significant ($F_{2,437} = 113.04$, $P < 0.0001$). All multiple comparisons were also significant (Tukey test: mix-pine, $P < 0.0001$; oak-pine, $P < 0.0001$; oak-mix, $P < 0.0001$). For Blue Tits, the difference in the date of egg-laying across the three habitats was also highly significant ($F_{2,701} = 180.65$, $P < 0.0001$), as were all multiple comparisons (Tukey test: mix-pine, $P < 0.0001$; oak-pine, $P < 0.0001$; oak-mix, $P < 0.0001$).

We observed a small significant negative correlation between the date of egg-laying and clutch-size in both species in pine, in Great Tits in reforested mix (Tab. II). Conversely we observed a small correlation between the date of egg-laying and the number of fledglings, significant only for Great Tit on pine (Tab. II). Second clutches were not observed in either species in any of the three habitat types and years, confirming our previous results. For both species, the highest average clutch-size and number of fledglings were recorded in the oak, while the lowest values of both parameters were recorded in the pine (Tab. I). We found statistical differences in the clutch-size with respect to habitat type, except for Great Tits in the mix versus pine habitats (Great Tit, $F_{2,434} = 60.99$, $P < 0.0001$; multiple comparisons, mix-pine:

TABLE I

Breeding parameters of the Blue and Great tits in different Sicilian woodland habitats between 1993 and 2010. Oak = natural oak woodland, Pine = reforested pine habitat, Mix = reforested pine and oak mixed habitat. Laying date is expressed in number of days after 1st March. sd = standard deviation, n = number of clutches

		Laying date			Clutch-size			No. fledglings			Breeding success%	
		mean	sd	n	mean	sd	n	mean	sd	n	mean	sd
Blue Tit	oak	49.9	9.7	407	8.57	1.6	405	6.4	1.7	362	74.9	19.5
	mix	60.5	8.3	139	7.2	0.5	131	4.5	1.8	84	63.3	24.3
	pine	65.3	9.2	158	6.3	1.3	151	3.2	1.4	118	50.2	24.9
Great Tit	oak	51.2	9.0	236	8.1	1.4	234	6.2	1.4	215	76.8	17.2
	mix	60.9	10.4	89	6.5	0.4	86	4.6	1.5	67	69.9	24.9
	pine	65.6	9.0	115	6.5	1.4	104	3.3	1.8	70	51.6	28.7

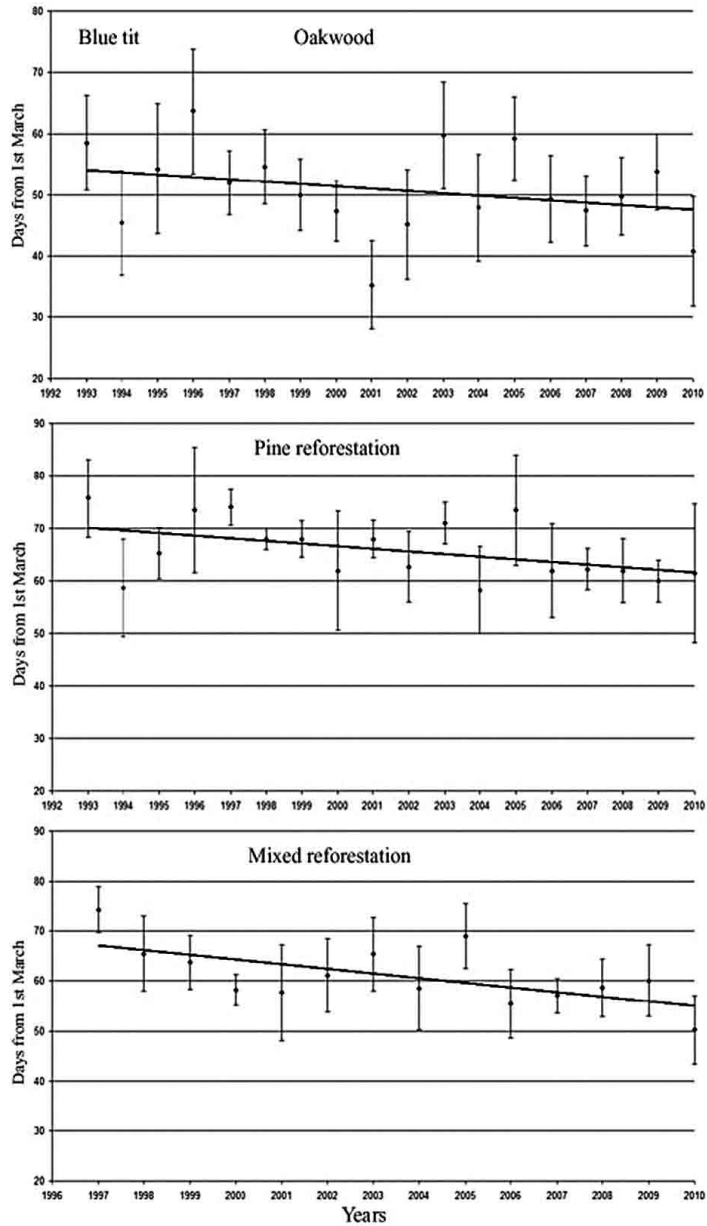


Figure 2. — Blue Tit egg-laying date (dot = mean, bar = standard deviation) in the Sicilian oak woodland, reforested pine habitat and reforested pine and oak mixed habitat from 1993 to 2010.

$P = 0.80$; oak-pine: $P < 0.0001$; oak-mix: $P < 0.0001$; Blue Tit, $F_{2,699} = 100.48$, $P < 0.0001$; multiple comparisons, mix-pine: $P = 0.0026$; oak-pine: $P < 0.0001$; oak-mix: $P < 0.0001$). We also found a significant difference in the breeding success between the three habitat types (Great Tit, $F_2 = 24.56$, $P < 0.0001$; Blue Tit, $F_2 = 54.39$, $P < 0.0001$), with some difference in the multiple comparisons (Great Tit, mix-pine: $P = 0.036$; oak-pine: $P < 0.0001$; oak-mix: $P = 0.014$; Blue Tit, mix-pine: $P = 0.26$; oak-pine: $P < 0.0001$; oak-mix: $P < 0.0001$).

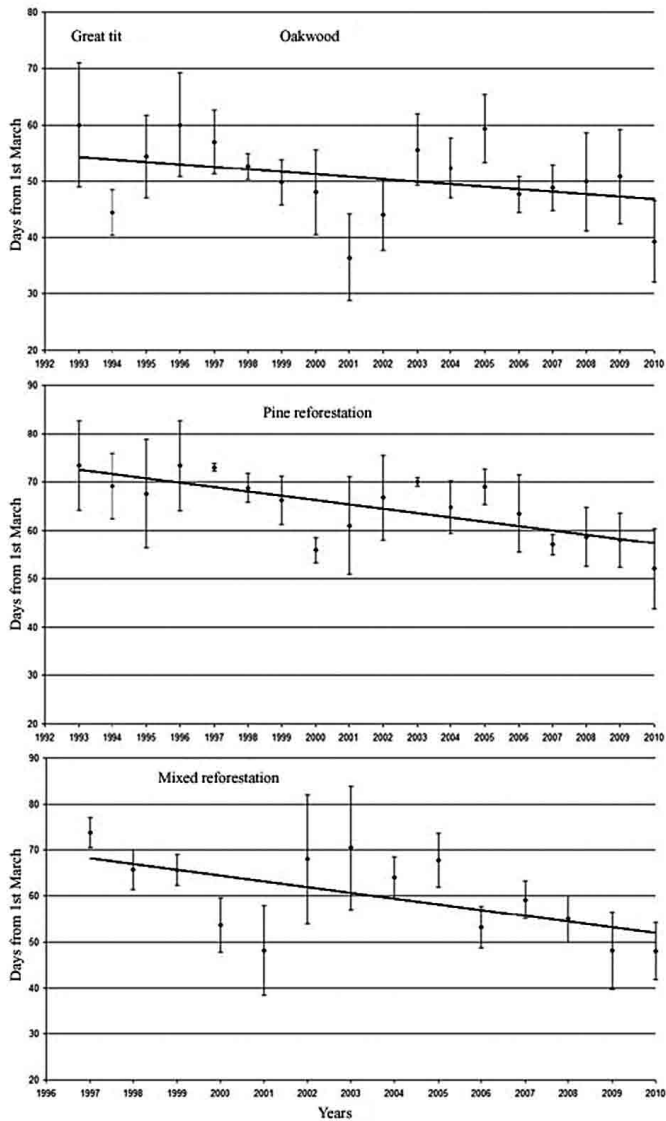


Figure 3. — Great Tit egg-laying date (dot = mean, bar = standard deviation) in the Sicilian oak woodland, reforested pine habitat and reforested pine and oak mixed habitat from 1993 to 2010.

TABLE II

Correlation between egg-laying and clutch-size and between egg-laying and number of fledglings

		egg-laying: clutch-size	egg-laying: number of fledglings
Great Tit	oak	$r = -0.43$; $p = 0.08$	$r = 0.21$; $p = 0.41$
	mix	$r = -0.67$; $p = 0.01$	$r = -0.16$; $p = 0.57$
	pine	$r = -0.47$; $p = 0.05$	$r = 0.47$; $p = 0.05$
Blue Tit	oak	$r = -0.12$; $p = 0.64$	$r = 0.20$; $p = 0.43$
	mix	$r = -0.51$; $p = 0.06$	$r = -0.18$; $p = 0.54$
	pine	$r = -0.48$; $p = 0.04$	$r = 0.10$; $p = 0.69$

PREY DELIVERED TO NESTLINGS

Both Blue and Great Tit nestlings grew faster in the oak habitat than in the reforested habitats. This increase in growth rate allowed the oak habitat nestlings to fledge at least one day earlier than nestlings in the reforested habitats. In addition, the nestlings in the mix grew faster than nestlings in the pine (Figs. 4, 5).

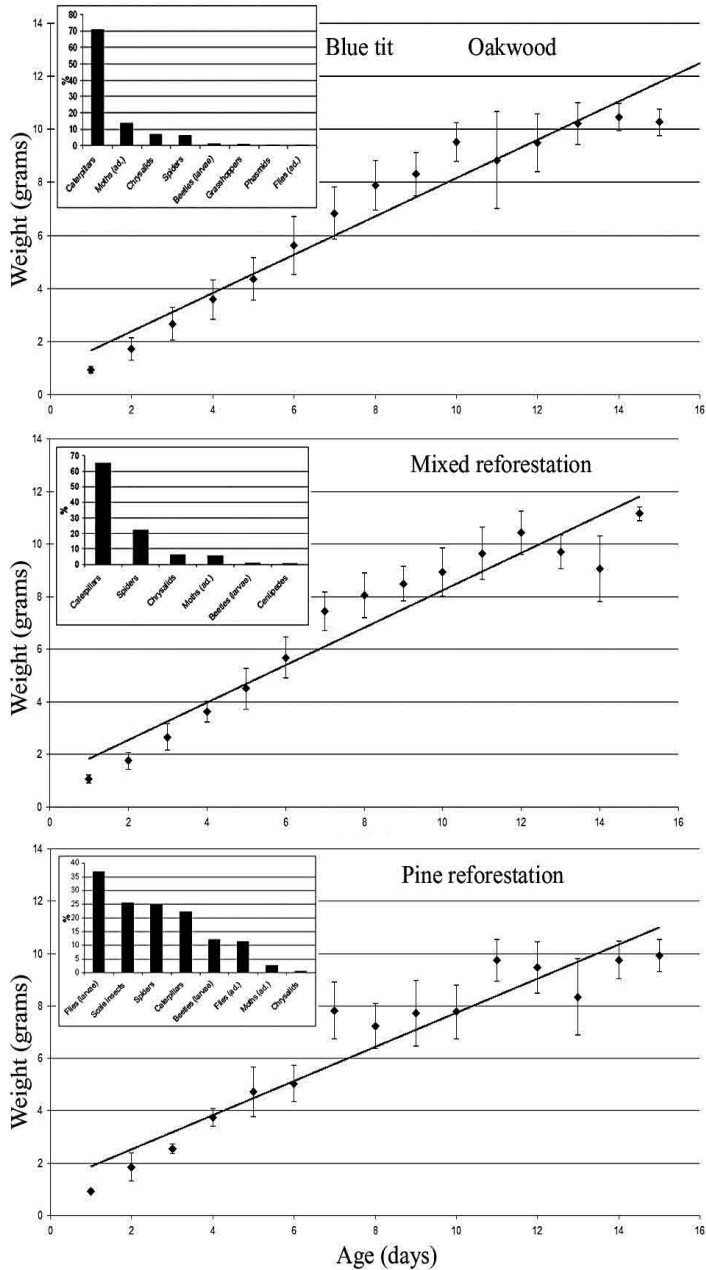


Figure 4. — Growth rate (dot = mean, bar = standard deviation) of Blue Tit nestlings in the Sicilian oak woodland, mixed habitat and reforested pine habitat from 1993 to 2010. In the insets: % of different prey types brought to nestlings.

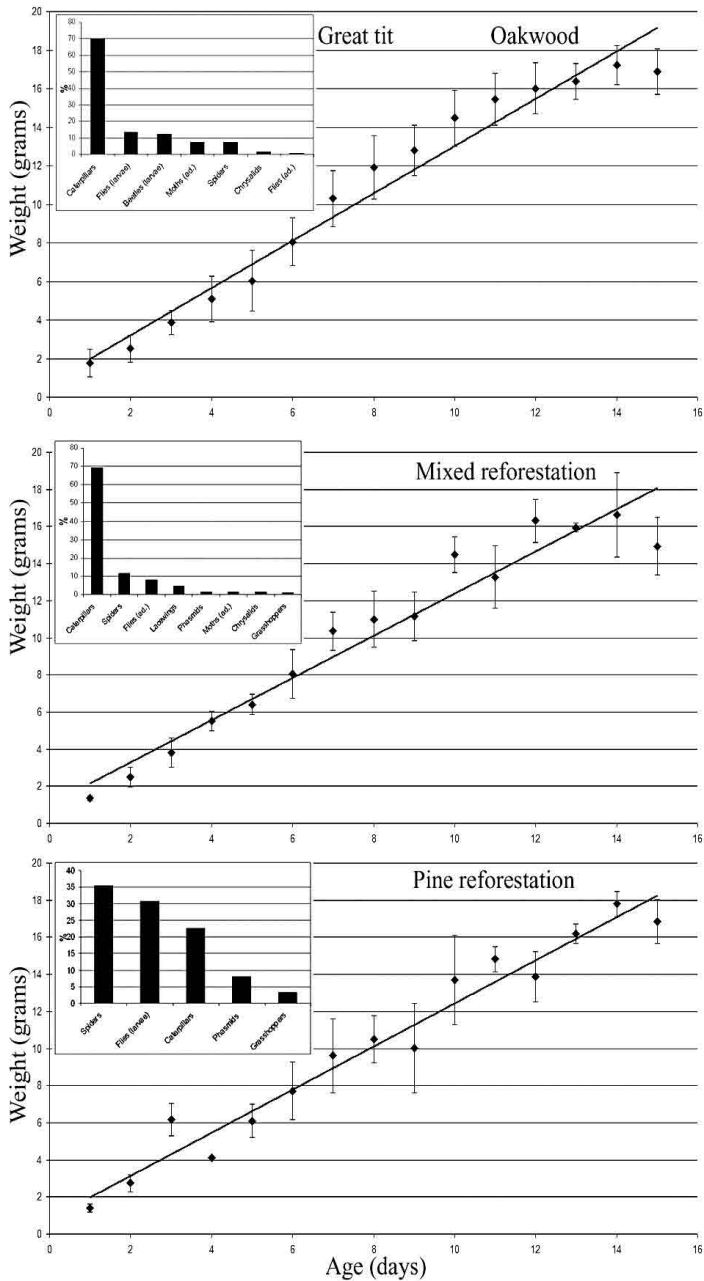


Figure 5. — Growth rate (dot = mean, bar = standard deviation) of Great Tit nestlings in the Sicilian oak woodland, mixed habitat and reforested pine habitat from 1993 to 2010. In the insets: % of different prey types brought to nestlings.

With respect to Blue Tit in the oak habitat, food intake per nestling was $6.19 \pm 2.71 \text{ h}^{-1}$, with nestlings weighing $9.52 \pm 0.73 \text{ g}$ on day 10 after hatching. In the mix, nestling food intake was $5.75 \pm 1.22 \text{ h}^{-1}$, with nestlings weighing $8.94 \pm 0.92 \text{ g}$ on day 10. In the pine, nestling food intake was $7.83 \pm 3.03 \text{ h}^{-1}$, with nestlings weighing $7.77 \pm 1.04 \text{ g}$ on day 10 (Figs. 4, 5). There

was a significant difference in nestling body weight at day 10 after hatching between the three habitats ($F_{2,109} = 24.05$, $P < 0.001$). The number of faecal sacs that were removed by adults was $0.94 \pm 0.37 \text{ h}^{-1}$ in the oak, $0.68 \pm 1.25 \text{ h}^{-1}$ in the mixed and $1.15 \pm 0.65 \text{ h}^{-1}$ in the pine.

Food intake per Great Tit nestling in the oak was $2.78 \pm 0.98 \text{ h}^{-1}$, with nestlings weighing $14.46 \pm 1.5 \text{ g}$ on day 10 after hatching. In the mix, nestling food intake was $1.83 \pm 0.47 \text{ h}^{-1}$, with nestlings weighing $14.48 \pm 0.95 \text{ g}$ on day 10. In the pine, food intake was $3.16 \pm 1.16 \text{ h}^{-1}$, with nestlings weighing $13.7 \pm 2.42 \text{ g}$ on day 10. There was a significant difference in nestling body weight at day 10 after hatching between the three habitats ($F_{2,108} = 0.85$; $P = 0.43$). The number of faecal sacs removed by adults was $0.70 \pm 0.27 \text{ h}^{-1}$ in the oak habitat, $0.51 \pm 0.05 \text{ h}^{-1}$, in the mix and $0.66 \pm 0.77 \text{ h}^{-1}$ in the pine (Tab. III).

TABLE III

Food intake and faecal sacs removal per nestling per hour of Blue and Great Tits in the three habitats, obtained from videotapes; n refers to the sample size of nestboxes

		Food intake per nestling h^{-1}		Faecal sacs removal per nestling h^{-1}		
		mean	sd	mean	sd	n
Blue Tit	oak	6.3	2.90	0.6	0.19	25
	mix	5.7	1.22	0.7	1.25	12
	pine	6.3	1.65	0.7	1.10	24
Great Tit	oak	2.9	0.98	0.6	0.04	18
	mix	1.8	0.47	0.6	0.05	10
	pine	3.2	1.16	0.5	0.05	16

Caterpillars comprised the primary prey resource that was fed to Blue and Great Tit nestlings in the oak and mix, with a lower frequency in the pine (Tab. IV). However, prey items delivered to the nestlings were more diverse in the pine habitat, with Blue Tit delivering flies (mainly tipulids), spiders, scale insects, beetle larvae, moths, centipedes, fly larvae and chrysalids. Great Tit delivered primarily spiders and fly larvae, in addition to phasmids, lacewings and grasshoppers.

TABLE IV

Food brought (%) to nestlings by Blue and Great Tits in the three habitats, obtained from footages

	Blue Tit			Great Tit		
	oak	mix	pine	oak	mix	pine
Caterpillars	73.88	62.45	47.53	54.55	58.14	20.88
Moths (ad.)	11.46	8.57	3.13	11.19	2.33	0.00
Chrysalids	5.43	4.90	1.24	0.70	2.33	0.00
Beetles (larvae)	2.71	0.82	6.59	22.84	0.00	0.00
Flies (larvae)	0.18	0.00	2.22	1.86	13.95	30.77
Flies (ad.)	0.18	0.00	18.37	1.86	6.98	0.00
Spiders	5.73	22.86	9.47	6.99	7.75	37.36
Scale insects	0.00	0.00	8.73	0.00	0.00	0.00
Grasshoppers	0.18	0.00	0.25	0.00	2.33	2.20
Phasmids	0.06	0.00	0.00	0.00	2.33	5.49
Lacewings	0.18	0.00	0.00	0.00	0.00	3.30
Centipedes	0.00	0.41	2.47	0.00	3.88	0.00
TOTAL	100.00	100.00	100.00	100.00	100.00	100.00

In the oak, additional prey items delivered to nestlings by Blue Tit included moths, spiders and chrysalids, with a further 0.3 - 2.7% of items comprising beetle larvae, grasshoppers, phasmids, lacewings and flies. In the mix, additional prey items delivered to nestlings by Blue Tit included spiders, moths and chrysalids, with < 1% comprising centipedes and beetle larvae.

In the oak, additional prey items delivered to nestlings by Great Tit included beetle larvae, moths and spiders, with < 2% comprising chrysalids and flies. In the mix, additional prey items delivered to nestlings by Great Tit included fly larvae (mainly tipulids), spiders, chrysalids, moths, phasmids, grasshoppers and centipedes.

Prey type in each of the three habitats was found to be significantly different, with the chi square test being highly significant for both species (Great Tit, $\chi^2_{12} = 260.10, P < 0.0001$; Blue Tit, $\chi^2_{12} = 656.14, P < 0.001$; Figs. 4, 5).

AIR TEMPERATURE AND ONSET OF REPRODUCTION

With respect to the two models taking into account species and habitat variability, no statistical difference was found between them ($F_{1138,1132} = 0.99, P = 0.42$; Tab. V). Hence the 'species' variable was removed from the model (Tab. V). There was no statistical difference between the regression lines of the two reforested habitat types, whereas the regression line of the oak was significantly different to both reforested habitat types.

TABLE V

Analysis of variance and relative statistics of the linear model "laying date \approx March temperature \times habitat"

Model	Linear model		F	DF	p-value
	RSS				
Model 1: data ~ temp * hab * species	81860		0.99	1132	0.42
Model 1: data ~ temp * hab	81432			1138	
Variable	Analysis of variance		F	p-value	
	DF	Mean Sq			
Temperature	1	15807.9	219.78	<0.0001	
Habitat	1	25633.6	356.35	<0.0001	
temperature:habitat	2	583.9	8.12	<0.0004	
Residuals	1138	71.9			
	Statistics		t	p-value	
	estimate	S.E.			
Intercept	77.63	3.85	20.02	<0.0001	
Temperature	-1.22	0.37	-3.26	0.0011	
habitat (CVR)	4.01	5.44	0.74	0.4612	
habitat (QUE)	1.76	4.4	0.4	0.6897	
temperature:habitat (CVR)	0.8	0.52	-1.53	0.1259	
temperature:habitat (QUE)	1.65	0.43	-3.82	0.0012	

The trend in the date of egg-laying was subject to much variation in all three habitats, the oakwood in particular (Figs. 2, 3). Despite this, there was a negative trendline, which indicated that there had been an advance in the onset of nesting across the 18-year study period.

For both species, clutch-size and number of fledglings were both correlated with March temperature; however this correlation was not significant (Tab. VI). We found a small significant negative correlation between breeding success and March temperatures only in pine for Great Tit (Tab. VI).

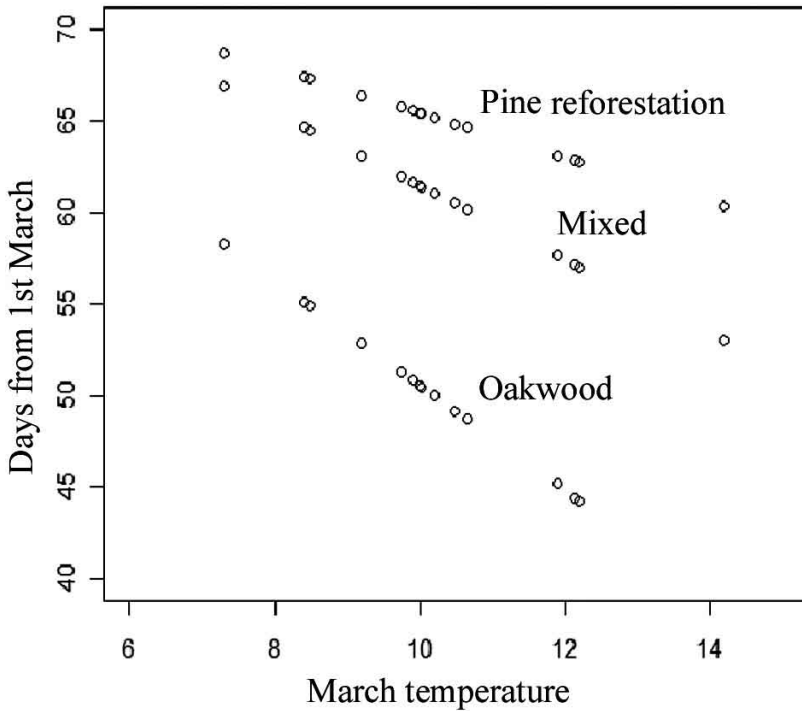


Figure 6. — Model (laying date \approx March temperature*habitat) for both tit species. There was no statistical difference between the regression lines of the two reforested habitats, while the regression line of the oak was significantly different to both reforested habitats.

TABLE VI

Correlations between March temperature and respectively clutch-size, number of fledglings and breeding success

		Clutch-size: March temperature	No. of fledglings: March temperature	Breeding success: March temperature
Great tit	oak	$r=0.17$; $p=0.49$	$r=-0.38$; $p=0.12$	$r=-0.46$; $p=0.05$
	mix	$r=-0.46$; $p=0.1$	$r=0.45$; $p=0.1$	$r=0.36$; $p=0.21$
	pine	$r=0.29$; $p=0.24$	$r=-0.23$; $p=0.37$	$r=-0.34$; $p=0.17$
Blue tit	oak	$r=0.17$; $p=0.48$	$r=-0.03$; $p=0.92$	$r=-0.08$; $p=0.74$
	mix	$r=0.23$; $p=0.43$	$r=0.39$; $p=0.16$	$r=0.36$; $p=0.2$
	pine	$r=0.03$; $p=0.91$	$r=-0.29$; $p=0.24$	$r=-0.34$; $p=0.16$

DISCUSSION

BREEDING TRAITS IN THE THREE HABITAT TYPES

We have previously established differences in the breeding traits of tit species nesting in adjacent oakwood and reforested pine habitats (Massa *et al.*, 2004). Our current study develops these findings, indicating that further differences exist for species utilizing a reforested habitat of mixed pine and broadleaves. These results are of interest, because the mixed reforested

habitat is a transformed part of the reforested pine habitat that has been subject to silviculture. Overall, our results indicate that tits utilizing the oakwood habitat had a greater breeding success than in the reforested areas. However, the more recently established reforested area of mixed tree types was more successful than the reforested areas comprising pure stands of pine. This indicated an ability for the two tit populations to adapt to the habitat as it evolved. These differences should be considered for reforestation management schemes, whereby the planting of broad-leaved trees, within proposed or existing reforested areas comprising pure stands of pine, improves the resource quality of insectivorous birds in Mediterranean woodlands, possibly facilitating long-term conservation effort.

Birds of adjacent habitats often express negligible differences in their breeding traits, due to constant gene flow between these habitats (Blondel *et al.*, 1990; Dias *et al.*, 1996; Thomas *et al.*, 2001). While differences in tit breeding traits were observed between the three habitat types, a proportion of tits, originally ringed as nestlings, were recovered in adjacent habitats as nesting adults in our study. Thus, we must assume that there is a high gene flow between the three habitats. This suggests that the observed differences in breeding traits are not genetic, and are more likely to have resulted from ecological differences, such as resource availability and/or phenotypic plasticity. This contrasts with Husby *et al.* (2010) who report that the correlation between clutch-size and laying-date may differ on the genetic level between populations. In the oak habitat, both tit species bred earlier, laid larger clutches, and fledged more offsprings than in either reforested habitat. Interestingly, the date of egg-laying within each respective habitat was the same for both tit species. This suggests a delicate relationship between these insectivorous birds, their prey and factors influencing prey availability.

Differences in clutch-size between the three habitats might reflect an optimized number of young based on prevailing conditions of food supply and laying date (Pettifor *et al.*, 1988; Grieco, 2002; Massa *et al.*, 2004). For example, the scarcity of resource availability in the pine habitat may result in delayed breeding, in turn decreasing overall productivity (e.g. Perrins & McCleery, 1989; Nager & van Noordwijk, 1995). This agrees with the generally observed trend in Europe, whereby earlier clutches are larger while later clutches are smaller (e.g. Cresswell & McCleery, 2003).

Overall, the two species of tits showed a similar response to each habitat, with respect to date of egg-laying, clutch-size, and breeding success. However, the breeding behaviour of both species was more consistent in the oak than in the two reforested habitats. Different egg-laying dates may reflect the variable availability of prey resources in each habitat that are required by adults to feed their nestlings. The difference in egg-laying dates between Blue and Great Tits in the reforested areas might reflect the different resource exploitation strategies of the two species. For example, Blue Tits are more dependent on caterpillars than Great Tits, which have alternative food sources such as spiders and flies. Furthermore, unlike Blue, Great Tits often catch prey within the wood litter (Naef-Daenzer *et al.*, 2000; Massa *et al.*, 2004). While Blue Tit breeding success was not statistically different between the two reforested habitats, Great Tit breeding success was significantly higher in the mixed than in the pine habitat. This difference might be explained by there being a higher availability of arthropods in the broad-leaved trees of the mixed habitat. Interestingly, Stauss *et al.* (2005) observed that Blue Tits nesting in deciduous woodland match their feeding rate to the size of the brood better than those nesting in mixed woodland, resulting in a higher fledging success from large broods. The shift in laying-date between mixed and pine habitat may be a mechanism by which tits adapt to local environmental conditions (Grieco *et al.*, 2002).

Further evidence supporting that the oak habitat has the highest resource availability comes from the faster growth rates and larger number of nestlings within a clutch there than in reforested habitats. Within these latter, the mixed habitat supported faster growth rates and larger number of nestlings per clutch than the pine habitat. This supports the hypothesis that broad-leaved trees are very important for the breeding success of tits in the Mediterranean woodlands. Differences in food intake rates ultimately depend on prey quality. For Blue Tits, we found that while there was no significant difference in food intake rates across the three habitats, the fastest nestling growth rate was in the oak habitat, followed by the mixed habitat,

with the pine habitat supporting the slowest growth rate. Hence we suggest that food quality, rather than food quantity, may influence growth rate and hence breeding success. For example, in the pine habitat the food brought to nestlings may be considered of low quality, resulting in a slower growth rate, as well as a lower breeding success in comparison to the other two habitats. Indeed, food delivered to the nestlings in oak and mixed habitats primarily constituted caterpillars, whereas in the pine habitat the proportion of flies was higher in the nestling diet.

With respect to the Great Tit, the difference in food intake rates was much more pronounced in the three habitats. Statistically significant differences were obtained for nestling growth rates and for breeding success. However, as with the Blue, Great Tit appears to have adjusted its behavioural ecology to breed in pine habitats, requiring the selection of alternative food resources, which, as we have already suggested, may be considered of lower quality. Indeed, Great Tits delivered three significantly different food types to their hatchlings based on habitat type. For example, the highest quality prey type was found in the oak habitat (*i.e.* high numbers of caterpillars and beetle larvae), intermediate quality prey type in the mixed habitat (*i.e.* high numbers of caterpillars and fly larvae), and the lowest quality food type in the pine habitat (*i.e.* low numbers of caterpillars, huge numbers of spiders and fly larvae).

DIFFERENTIAL RESPONSE TO TEMPERATURE

The onset of breeding of Blue and Great Tits in Sicily is earlier than that recorded in central Europe. In Sicily, some pairs start to breed as early as March, in contrast to April in central Europe (e.g. Sanz, 2002). This is clearly due to latitudinal differences, resulting in the Mediterranean habitats having higher local ambient air temperatures than central Europe (cf. also Sarà *et al.*, 2005). Moreover, we found that for Sicilian tits the onset of reproduction further advanced as the air temperature increased.

Overall, the correlation between the date of egg-laying for both tit species and March temperature may provide evidence that tits interact with the changing habitats to optimize the timing of seasonal breeding. Prey density on pines is considerably lower than on broad-leaved trees (van Balen, 1973). The overall scarcity of caterpillars in reforested habitats indicates that smaller clutch-sizes and lower number of fledglings may be attributed to other factors that are also dependent on the temperature.

While not all tit populations respond the same way to changes in ambient air temperature, the sensitivity of Mediterranean birds to ambient temperature has already been documented (Silverin *et al.*, 2008). For example, in the Palearctic region, Great Tit laying-date changes faster in southern and western areas, while Blue Tit laying-date changes faster in the northern and western areas, with respect to the winter North Atlantic Oscillation index (Sanz, 2002). Consequently, following warmer and moister winters in the western Palearctic, both Blue and Great Tits lay eggs earlier in the season. These trends matched our observations, whereby increased spring temperatures resulted in earlier egg-laying dates for both species. Nevertheless, the reason why an increase in spring temperature affects only some bird species or populations remains unclear (McCleery & Perrins, 1998; Visser *et al.*, 1998). An increase in spring temperature may negatively affect the synchronization of oak bud-burst and caterpillar emergence, resulting in a shorter developmental period of caterpillars. In turn, climate warming may further impact the synchronization between the tit breeding period and food availability. This would result in the production of smaller clutches, fewer fledglings and lower breeding success in warmer years (Buse *et al.*, 1999). On the other hand, Cresswell & McCleery (2003) reported an increase in the number of fledglings per successful nest with increasing temperature. This may depend on greater habitat heterogeneity and hence greater variety of prey availability in the latter.

In recent decades, an advance in the date of breeding has been recorded in only some Great Tit populations (e.g. Perrins & McCleery, 1989; van Noordwijk *et al.*, 1995; Cresswell & McCleery, 2003; Silverin *et al.*, 2008; Both *et al.*, 2009). This shift may be in response to caterpillars hatching two weeks earlier, in turn in response to an earlier bud-burst of oaks. These respective shifts cause a mismatch between hatching date and food availability for nestlings (Visser *et al.*, 1998, 2003; Visser & Holleman, 2001; Both & Visser, 2005; van Asch *et al.*,

2007; but also see Cresswell & McCleery, 2003). Additionally, it is not the absolute advancement that is important, but the advancement relative to the food peak (Visser *et al.*, 2008). To compensate for this mismatch, insectivorous birds generally produce smaller clutches, which shortens the time between egg-laying and hatching dates, allowing the available food to be concentrated on fewer offsprings (Sanz, 2002). According to van Noordwijk *et al.* (1995), a mismatch and selection for earlier laying occurs only when air temperature warms rapidly. However, a long-term study by Visser *et al.* (1998) between 1973 and 1995 in the Netherlands did not find any advancement in laying date, despite an increase in spring temperatures and an increase in peak food abundance by nine days. More recently, laying dates in the Dutch populations have now advanced significantly (Husby *et al.*, 2010), but still not enough to match with the advancement in caterpillar peak. Conversely, Cresswell & McCleery (2003) demonstrated in the UK, that Great Tits responded to temperature change, resulting in the optimal synchronization of hatching date with the peak of food abundance. Our results, for both Great and Blue Tits, are most similar to those reported for the UK Great Tits by Cresswell & McCleery (2003). Both tit species in our study areas (oakwood and reforested habitats) appeared to retain both nestling number and breeding success despite increasing spring temperatures. The reason for this may be due to a nearly precise overlap in peak food availability and peak demand by nestlings, due to the availability of a range of habitats supporting different insect prey species.

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