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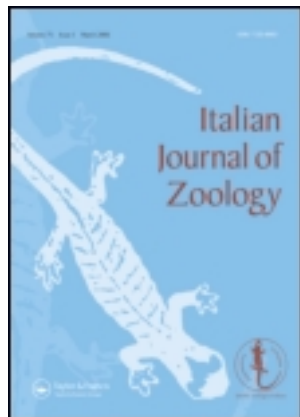
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Adaptive plasticity of blue tits (*Parus caeruleus*) and great tits (*Parus major*) breeding in natural and semi-natural insular habitats

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Adaptive plasticity of blue tits (*Parus caeruleus*) and great tits (*Parus major*) breeding in natural and semi-natural insular habitats

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ABSTRACT

The breeding performance and foraging of blue and great tits, and the abundance of arthropods living on the trees of an oakwood and of a coniferous reforestation were studied in Sicily, in order to: 1) compare breeding parameters in natural and semi-natural habitats within the same area; 2) estimate the degree of overlap in peak resource and peak demand of young tits, and the overlap of nestling diet of the two species in the two habitats. Both species had earlier laying dates, laid more eggs and raised more fledglings in the oakwood than in the reforestation; they achieved the same fledging success within the same habitat type. These differences are probably due to the earlier and higher food peak in oak compared to pine. Food brought to the nestlings differed between habitats and between species: blue tits always brought small prey from a limited number of taxa, while great tits changed both prey taxa and size depending on habitat. The more flexible food of the great tit is in line with the smaller reduction in number of fledglings in pine reforestation compared to oakwood. It is suggested that tits have developed a mechanism to lay eggs at different dates in accordance with the habitat resource where adults catch prey for nestlings. Finally, mean clutch sizes of blue tits between habitats were well correlated, but the process seemed different in the great tit. Significant correlation was indeed detected between the proportion of great tits breeding in oakwood and the difference in the clutch size between the habitats. This suggests that more great tits settled in oakwood in years when conditions were more suitable to produce bigger clutches.

KEY WORDS: *Parus caeruleus* - *Parus major* - Oakwood - Pine reforestation - Breeding - Peak resource - Peak demand - Adaptation.

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INTRODUCTION

Blue and great tits are common and widespread throughout Europe and North Africa; their breeding ecology has been studied extensively in many habitat types in central Europe, as well as in Mediterranean areas (e.g.: Isenmann, 1987; Barba & Gil-Delgado, 1990; Gil-Delgado *et al.*, 1992; Blondel *et al.*, 1991, 1993; Banbura *et al.*, 1994; Dias & Blondel, 1996; Massa & Lo Valvo, 1996; Lambrechts *et al.*, 1997; Massa, 2002). They feed their young mainly on tree-feeding caterpillars; generally, both species lay greater clutches and fledge more young in deciduous woods than in other habitats. Lower fledging success in habitats other than deciduous woods may depend on (i) habitat heterogeneity, which produces a mismatching between peak resource and peak demand (Dias *et al.*, 1996; Blondel *et al.*, 1999), (ii) wood fragmentation, which influences the habitat availability and consequently breeding success (Ridington & Gosler, 1995; Hinsley *et al.*, 1999), and (iii) edge effects and microclimate variability (Perrins & Mc Cleery, 1989; Clamens, 1990). Reduction of fledging success in tits is associated with later breeding (Perrins & Mc Cleery, 1989; Nager & van Noordwijk, 1995), that, in turn, may depend on (i) territory and adult quality (Dhondt, 1989; Perrins & Mc Cleery, 1989; Verhulst *et al.*, 1995), (ii) increasing parental self-maintenance costs (Hinsley *et al.*, 1999), (iii) food supply (Källander, 1973; Banbura *et al.*, 1994; Grieco, 2002), temperature and exposure to severe weather (Nager & van Noordwijk, 1995; Hinsley *et al.*, 1999).

During a long-term research, carried out in a Mediterranean island (Sicily), we investigated the reproductive performance of great and blue tits in two woodplots, which are parts of the same wooded area, a natural oakwood and a pine reforestation. The aims of the present paper were: 1) to compare their breeding traits in the two woodplots; 2) to estimate the degree of overlap between the peak resource and the peak demand of nestling tits in the two types of wood; 3) to study the overlap in nestling diet between the two tit species in the two habitats.

MATERIALS AND METHODS

The study area is located in a wooded area of 1600 ha (Santo Stefano di Quisquina, ca. 600 m a.s.l., province of Agrigento) and it is divided into a natural wood, dominated by the deciduous downy oak *Quercus pubescens* and by the evergreen holm oak *Q. ilex*, and a reforestation of *Pinus halepensis* ca. 40 years old (for more details see Massa & Lo Valvo, 1996). In 1993, 102 nestboxes were placed, and in 1997 50 more were added, so that nesting tits territories did not overlap between natural and planted woodplots. From April to July 1993 till 2002, all nestboxes were visited weekly and the following information was recorded: 1) date of the first egg, assuming that females laid one egg each day; 2) clutch-size; 3) hatching date; 4) brood size at 10 days; 5) number of fledglings. All chicks were ringed when they were 10 days old. A detailed study was carried out in 1997, 1998, 1999 and 2001 on a total of 18 broods of blue tits and 12 of great tits in the oakwood, and of 13 broods of blue tits and eight of great

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tits in the pine reforestation, when nestlings were 10-13 days old. The activity of nestlings and their parents was recorded for 30-60 min at each nest, in different times of the day, for a total of 67.30 h, using a video camera very sensitive to the light (BoxWatch Colour Cartridge Camera) fixed to nest-boxes and connected with a VHS recorder, both powered by 12-V batteries. Prey items were identified from the videos and their size was measured; prey length was assessed by comparison with the head length of the tits. Sixty-four percent of the prey brought by blue tits to their nestlings were identified in the oakwood and 70% in the reforestation. For great tits the corresponding figures were 70% in the oakwood and 90% in the reforestation.

Additionally, prey abundance was investigated in the same areas and periods. In 1993-99, foliage arthropods (between 1.5 and 4 m from the ground) of tree species characterizing the woodplots were sampled weekly, by extracting them with a Univac portable suction sampler (Arnold *et al.*, 1973) from the branches of 15 trees for 15 min, in order to obtain quantitative estimates of arthropod abundance (not resource availability, for the reasons reported by Holmes, 1990), useful for comparisons between the habitats.

Laying date, clutch size and number of fledged chicks were compared among habitats, years and species using three-way ANOVA (SAS, 1987). Indices of diet breadth and overlap were calculated based on the relative frequency of prey taxa. Diet breadth (B_A) was calculated using Levins' (1968) standardized formula $B_A = B - 1/n - 1$, where $B = 1/\sum p_i^2$ and p_i is the proportion of the diet contributed by the i -th taxon. The value of B_A ranges from 0 to 1, with larger values indicating a broader diet. Diet overlap was measured using Morisita's (1959) similarity index: $C = 2 \sum p_{ij}p_{ik} / \sum p_{ij} [(n_{ij}-1)/(N_j-1)] + \sum p_{ik} [(n_{ik}-1)/(N_k-1)]$, where p_{ij} and p_{ik} are the proportions that taxon i makes up of the diets of species j and k , respectively, n_{ij} and n_{ik} are the number of individuals of taxon i in the diets of species j and k , and N_j and N_k are the total number of individuals in the diets of species j and k . The value of C ranges from 0 to 1, with larger values indicating a greater dietary overlap. To describe the composition and abundance of prey the Detrended Correspondence Analysis (DCA) was used (Benzecri, 1973; Hill, 1973; Gauch, 1982; SAS, 1987); this is a multivariate ordination method applied to a data matrix that includes frequency (%) and size of taxa preyed upon by each tit species in each habitat (Digby & Kempton, 1987; Pielou, 1984). Finally, statistical differences between slopes were measured by testing regression lines for equality of slopes (Sokal & Rohlf, 1989).

RESULTS

Breeding performance

During the ten-year period, reproductive traits of the two tit species differed between the two habitats, with consistently early breeding, larger clutch size and number of fledglings in the oakwood than in the pine reforestation (Table I). The correlation between the number of breeding pairs and that of eggs laid was not significant in the oakwood (blue tit: $r = 0.27$, great tit: $r = 0.48$) and in the reforestation (blue tit: $r = -0.17$, great tit: $r = 0.51$). Significant differences were detected in the laying date, clutch size and number of chicks fledged between the two habitats, and in the laying date and number of fledglings among years (Table II). Species per habitat interactions for clutch size and number of fledglings, and habitat per year for laying date were also significant ($P < 0.001$). Table III reports the Tukey pairwise comparisons. Clutch size in the oakwood was not greater in the years with high abundance of caterpillars (see below), and laying date was not related to the resource peak of the previous year. Tits showed a

synchronous start of laying in the oakwood, but in the pine reforestation always started breeding 14-15 days later than in the oakwood. Laying date was the same for both species in the oakwood (5-30 April) and in the reforestation (25 April-15 May); it did not differ between tit species in the same habitat (Table III). Clutch size was significantly larger in the oakwood than in the reforestation for both species (Table III). In the oakwood blue tit clutch size was significantly larger than the great tit one (Table III). The number of fledglings of both species was significantly higher in the oakwood than in the reforestation (Table III). Laying dates of both species in both habitats were correlated (Fig. 1); differences between slopes of the two tit species were not significant ($t = 0.0153$, $df = 16$, $P = 0.494$). Although correlated with laying dates in the oakwood, those in the reforestation varied much less. This can be noted by the smaller variance of the annual laying dates in the pine reforestation, and by the difference within each year between the habitats, that is more strongly correlated to the laying date in the oakwood than in the pine reforestation. Conversely, mean clutch sizes between habitats were correlated only for blue tits, and not for great tits (Fig. 2); differences between slopes of the two tit species were significant ($t = 2.5809$, $df = 16$, $P = 0.01$). However, whereas, in the blue tit, clutch size was more variable in the pine reforestation, there was no difference in variability between the habitats in the great tit. A significant correlation was detected between the proportion of all great tit pairs breeding in the oakwood and the difference in clutch size between the habitats (Fig. 3; $y = 0.0739x + 0.5653$, $R^2 = 0.04107$, $P < 0.05$).

Arthropod abundance

Arthropod abundance varied during the years, but was always much greater in the oakwood than in the pine reforestation. The abundance, due to huge numbers of caterpillars of *Tortrix viridana* (Lepidoptera, Tortricidae) in the oakwood, was much higher in 1993, 1997, and 1999 than in the other years, when this moth was less frequent. In the reforestation area, samples of

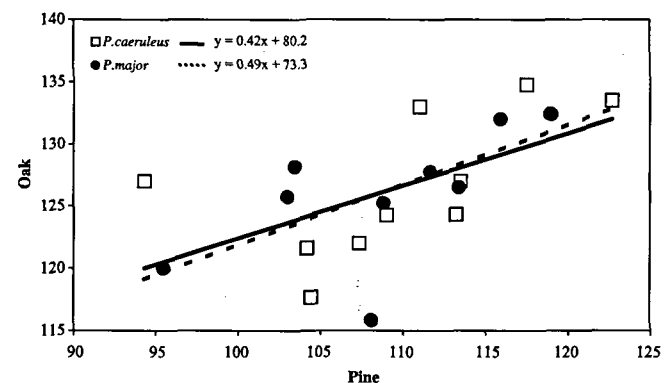


Fig. 1 - Correlation between laying dates of blue and great tits in the oakwood and in the pine reforestation.

TABLE I - Breeding parameters of blue tit and great tit in the oakwood and reforestation of Sicily in the ten years 1993-2002. Laying date is expressed in Julian dates.

	Year	Laying date			Clutch size			No. of fledglings			% fledging success
		Mean	SD	n	Mean	SD	n	Mean	SD	n	
<i>Parus caeruleus</i> <i>Pinus</i>	1993	134.8	7.34	9	6.44	1.33	9	4.44	2.19	9	69.0
	1994	117.7	9.29	3	7.33	0.58	3	1.00	1.73	3	13.6
	1995	124.3	4.84	6	5.50	1.38	6	3.83	3.06	6	69.7
	1996	133.5	11.90	4	5.20	2.00	4	5.00	2.10	4	96.2
	1997	133.0	3.46	3	6.00	1.73	3	0.67	1.15	3	11.1
	1998	127.0	2.00	3	5.33	1.15	3	4.33	1.53	3	81.3
	1999	124.3	3.55	7	7.00	1.00	7	4.14	2.19	7	59.2
	2000	122.0	11.40	4	6.50	0.58	4	4.50	1.73	4	69.2
	2001	127.0	3.56	4	5.00	2.58	4	1.50	3.00	4	30.0
	2002	121.6	6.72	21	5.81	0.87	21	3.52	2.62	21	60.7
Mean 1993-2002		126.5	5.70	64	6.0	0.79	64	3.3	1.61	53	56.0
<i>Parus caeruleus</i> <i>Quercus</i>	1993	117.5	7.71	22	8.95	1.96	22	7.82	2.40	22	87.3
	1994	104.4	8.52	32	8.93	1.49	29	7.10	3.34	29	79.5
	1995	113.2	10.55	26	8.31	1.93	26	7.50	2.28	26	90.3
	1996	122.7	10.20	24	8.50	1.50	24	8.30	1.90	24	97.6
	1997	111.0	5.19	18	9.10	1.92	21	6.52	3.01	21	71.7
	1998	113.5	6.00	17	8.41	1.12	17	7.41	1.33	17	88.1
	1999	109.0	5.87	34	8.94	1.64	35	5.89	3.82	35	65.8
	2000	107.3	4.94	26	9.31	1.38	26	8.88	1.70	26	95.5
	2001	94.3	7.18	27	8.41	1.31	27	7.07	2.43	27	84.1
	2002	104.2	8.86	23	8.52	1.70	23	4.83	4.25	23	56.6
Mean 1993-2002		109.7	7.88	249	8.7	0.35	249	7.1	1.17	228	81.7
<i>Parus major</i> <i>Pinus</i>	1993	132.4	9.30	9	6.43	0.79	7	4.00	2.89	7	62.2
	1994	128.2	6.69	12	7.50	0.93	8	6.38	2.77	8	85.0
	1995	126.5	11.22	6	5.50	1.52	6	4.83	1.72	6	87.9
	1996	132.4	9.30	9	6.40	0.80	7	5.00	1.10	5	78.1
	1997	132.0	0.76	8	6.00	0.76	8	2.75	1.98	8	45.8
	1998	127.8	2.99	4	5.75	1.26	4	5.25	1.50	4	91.3
	1999	125.3	4.95	8	7.00	2.07	8	1.00	1.93	8	14.3
	2000	115.8	2.64	6	6.50	0.84	6	2.00	2.10	6	30.8
	2001	120.0	10.03	4	6.50	0.58	4	3.00	3.46	4	46.2
	2002	125.8	8.66	4	5.50	2.08	4	0.00	0.00	4	0.0
Mean 1993-2002		126.6	5.40	70	6.3	0.64	62	3.4	2.03	44	54.2
<i>Parus major</i> <i>Quercus</i>	1993	118.9	10.99	15	7.00	2.00	14	6.00	2.63	14	85.7
	1994	103.5	3.98	11	8.78	0.97	9	7.56	1.67	9	86.1
	1995	113.4	7.34	19	8.05	1.84	19	7.63	2.06	19	94.8
	1996	119.0	9.20	17	7.70	1.29	17	6.90	2.10	17	89.6
	1997	115.9	5.65	13	7.40	1.30	15	5.93	2.19	15	80.2
	1998	111.7	2.31	21	8.95	1.24	21	8.33	1.83	21	93.1
	1999	108.8	3.99	10	8.00	1.25	10	6.50	2.59	10	81.3
	2000	108.1	7.50	10	7.33	1.83	12	3.75	3.57	12	51.1
	2001	95.5	7.68	15	8.73	1.28	15	6.13	3.50	15	70.2
	2002	103.0	6.23	8	8.00	1.41	8	5.75	3.81	8	71.9
Mean 1993-2002		109.8	7.59	139	8.0	0.66	140	6.4	1.28	131	80.4

arthropods were very scarce in the breeding seasons considered. In the oakwood the resource peak occurred between the end of April and the first two weeks of May, overlapping well with nestling growth, while in the reforestation we were not able to find any type of peak, since the samples were invariably scarce. Table IV lists the most abundant arthropods captured in 1993-99, subdivided into two main periods, i.e., the mean breeding season of tits in the two habitats from egg laying to fledging (14 April-15 May in the oakwood, 28

April-30 May in the reforestation). Among the different taxa, mainly Lepidoptera, a remarkable interannual variability was observed.

Prey carried to nestlings

Table IV shows that, in the oakwood, chiefly caterpillars were fed to the nestlings, while they were less frequently preyed upon in the reforestation. In the oakwood, blue tits supplied huge numbers of adult moths

TABLE II - Summary of three-way ANOVA analysis of laying date, clutch size and number of fledglings among species, habitats and years. **, $P < 0.001$; *, $P < 0.005$.

Source	df	F		
		Laying date	Clutch size	No. of fledglings
Species	1	0.05	1.65	1.7
Habitat	1	361.32**	118.81**	108.7**
Years	9	20.72**	2.23	3.1*
Species per habitat	1	0.28	6.74**	0.7
Species per year	9	0.92	1.52	2.8*
Habitat per year	9	4.27**	1.44	0.3
Species per habitat per year	9	1.59	0.54	2.2

(mainly *T. viridana*) and to a lesser extent their pupae and spiders, whereas great tits selected a great quantity of caterpillars, beetle larvae and, to a lesser extent, adult *T. viridana*. In the reforestation, differences in nestling diet of the two tit species were more prominent; caterpillars made up much lower proportions (22.8% in the blue tit, 34.5% in the great tit), but the blue tit took beetle larvae, adults tipulids, spiders and coccids, while the great tit took chiefly spiders and fly larvae of Syrphidae Eristalini, whose characteristic respiratory long siphon enables them to live in waters rich in vegetation and organic substances, and larvae of Tipulidae, which live in soil litter. Moreover, in the reforestation, grasshoppers constituted 11.4% of the diet of nestling great tits, particularly tettigoniids (nymphs of *Phaneroptera nana*, adults of the wingless *Odontura arcuata*) and a green phasmid *Bacillus* sp. The diet suggested that blue tits foraged only among tree branches, whereas great tits captured many arthropods on the ground and in the bushes and grass.

A significant correlation was found between the mean number of arthropod taxa sampled in the oakwood (ob-

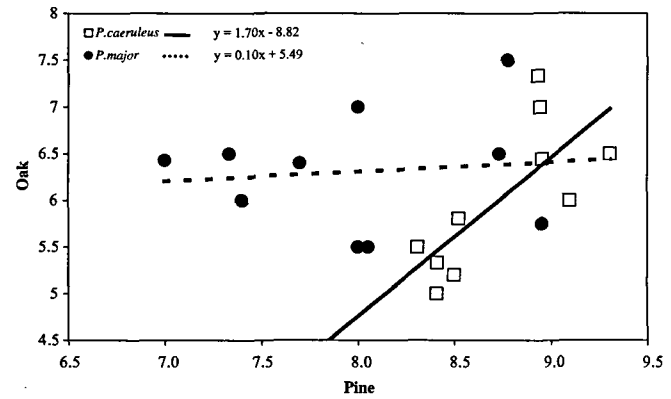


Fig. 2 - Correlation between clutch size of blue and great tits in the oakwood and in the pine reforestation.

tained from column four of Table IV) and their number carried by adults to chicks per hour (columns two and three of Table IV) (great tit: $r = 0.96$, $P < 0.05$; blue tit: $r = 0.97$, $P < 0.05$), and in the pine reforestation (respectively columns seven, five, and six of Table IV) (great tit: $r = 0.44$, $P < 0.05$; blue tit: $r = 0.90$, $P < 0.05$). Therefore, the pattern observed in the nestling diet reflects the mean abundance of prey types recorded in the trees.

Figures 4 and 5 show the multivariate analysis derived from DCA on a factorial plane of frequency of prey and their size. Both factorial axes of Figure 4 discriminate food composition in the oakwood, mainly characterized by Lepidoptera, from that observed in the pine reforestation. Figure 5 highlights three clusters, characterized respectively by small-, medium- and large-size prey. Small size (5-20 mm) characterizes the diet of blue tits in the two habitats, both natural and semi-natural, while prey size does not influence that of the great tit, which better adapts to prey of large-size availability, preying upon arthropods of medium-size (12-32 mm) in oakwood as well as large-size (30-60 mm) in the pine reforestation. Overall, in the oakwood, where food was more abundant, the diets of the two tit species were

TABLE III - Tukey's test applied to breeding parameters of the two tit species. Values in bold are significant

	Laying date			Clutch size			No. of fledglings		
	Blue tit <i>Pinus</i>	Blue tit <i>Quercus</i>	Great tit <i>Pinus</i>	Blue tit <i>Pinus</i>	Blue tit <i>Quercus</i>	Great tit <i>Pinus</i>	Blue tit <i>Pinus</i>	Blue tit <i>Quercus</i>	Great tit <i>Pinus</i>
Blue tit <i>Quercus</i>	P < 0.001			P < 0.001			P < 0.001		
Great tit <i>Pinus</i>	P = 0.998			P = 0.880			P = 0.989		
Great tit <i>Quercus</i>		P = 0.888	P < 0.001		P = 0.001	P < 0.001		P = 0.100	P < 0.001

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more similar than in the pine reforestation, where arthropods were always scarcer than in the oakwood.

Diet breadth

Diet breadth of the two tit species was greater in the pine reforestation than in the oakwood (Table V). Overall, in the oakwood diets were very similar (taxa overlap = 0.95), but the size of taxa was different (0.21) (Table VI). In the reforestation, taxa in the diets diversified (0.60), while their size still showed low overlap (0.32). These differences seem mainly due to the great tit, which exploited different prey items in the two habitats, both as regards the taxa (0.48) and their size (0.40), while the blue tit changed its diet very little in the two habitats (taxa overlap = 0.76; size overlap = 0.96).

DISCUSSION

Breeding traits

One interesting result of this research is the difference, observed during ten years, in the breeding traits of tit species nesting in the oakwood and in the pine reforestation, which are parts of the same wooded area, where gene flow is presumably active. Tits bred earlier, laid more eggs and fledged more young in the oakwood than in the reforestation, probably adjusting their clutch size to the number of young they could best raise, depending on the prevailing conditions of food supply and date (Pettifor *et al.*, 1988; Grieco, 2002). We assume that density dependence of clutch

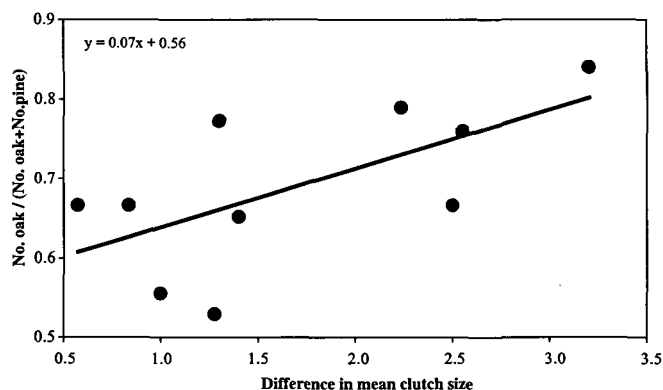


Fig. 3 - Correlation between the proportion of all great tit pairs breeding in the oakwood and the difference in clutch size between the oakwood and the pine reforestation.

size (Both, 1998a, b) may be excluded, because the correlation between breeding pairs and eggs laid was not significant, either in the oakwood or in the reforestation. Moreover, even if the number of nestboxes was the same in each woodlot, both tit species generally occupied more nestboxes in the oakwood than in the reforestation. This suggests a lower density of them in the latter woodlot. The present case is similar to the following ones: 1) that reported by Riddington & Gosler (1995), who compared the breeding performance of great tits in a mature woodland and marginal habitats within 2 km of the woodland; 2) that published by Hinsley *et al.* (1999), who studied 45 woods, between 0.1 and 157 ha wide, within an area of ca. 50 × 30 km,

TABLE IV - Prey of tits in the oakwood and pine reforestation. Columns two-three and five-six: feeding frequency (= number of prey items of a particular type per hour) derived from tape recordings; in brackets, % of identified taxa. Columns four and seven: range of abundance of arthropods carried by adults to chicks, and sampled in the oakwood and pine reforestation.

Arthropods	Oakwood			Pine reforestation		
	Feeding frequency (% of identified prey)		Arthropods sampled during breeding season of tits	Feeding frequency (% of identified prey)		Arthropods sampled during breeding season of tits
	Great tit	Blue tit		Great tit	Blue tit	
			14 April-15 May			28 April-30 May
Araneae	1.5 (8.3)	2.5 (6.9)	3-12	6 (34.3)	7 (16.1)	13-25
Diptera (larvae and adults)	0 (0)	0 (0)	16-34	5.5 (31.4)	8.0 (19.3)	5-45
Caterpillars	10 (55.5)	27 (74.8)	30-494	4 (22.8)	15 (34.5)	3-4
Lepidoptera ad.	3 (16.7)	6 (16.6)	17-133	0 (0)	2 (4.6)	2-4
Coleoptera larvae	3.5 (19.4)	0.6 (1.7)	0	0 (0)	4.5 (10.3)	0
Homoptera	0 (0)	0 (0)	7-27	0 (0)	7.0 (16.1)	2-41
Orthopteroidea	0 (0)	0 (0)	0-4	2 (11.4)	0 (0)	0

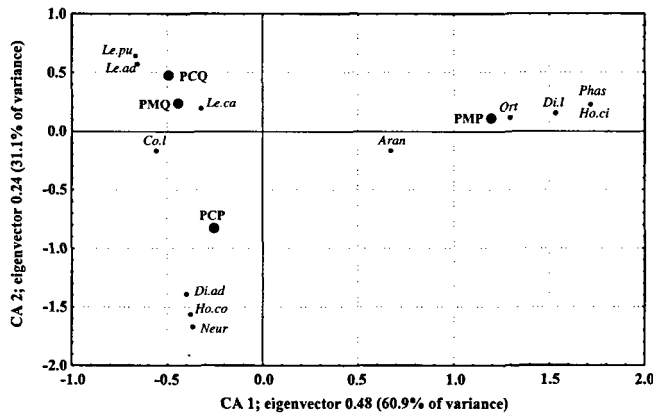


Fig. 4 - Detrended Correspondence Analysis ordination of prey of great and blue tits as function of prey taxa. Abbreviations: PCP, *Parus caeruleus* on *Pinus*; PCQ, *P. caeruleus* on *Quercus*; PMP, *P. major* on *Pinus*; PMQ, *P. major* on *Quercus*; Aran, Araneae; Col.a, Coleoptera larvae; Di.ad, Diptera adults; Di.l.a, Diptera larvae; Ho.ci, Homoptera Cicadidae; Ho.co, Homoptera Coccoidea; Le.ad., Lepidoptera adults; Le.ca, Lepidoptera caterpillars; Le.pu, Lepidoptera pupae; Neur, Neuroptera; Orth, Orthoptera; Phas, Phasmidae.

where blue and great tits showed a reduction of reproductive success, associated with later laying date, when breeding in small woods; 3) that reported by Blondel *et al.* (1999), where, in two sites in Corsica, 25 km apart, characterized respectively by deciduous and evergreen oakwood, blue tits differed markedly in their breeding traits and the differences were genetically based (Lambrechts & Dias, 1993; Lambrechts *et al.*, 1997; Blondel *et al.*, 1999). Generally, between adjacent habitats the absence or small magnitude of differences in breeding traits has been considered the effect of the gene flow among individuals of the two habitats, which should not succeed in evolving optimal laying dates (Blondel *et al.*, 1990; Dias *et al.*, 1996; Thomas *et al.*, 2001). Sometimes the weak temporal synchrony between peak resource and peak demand by birds is considered a possible result of mechanisms selected for synchrony with a specific habitat, which yields lower adaptation in oth-

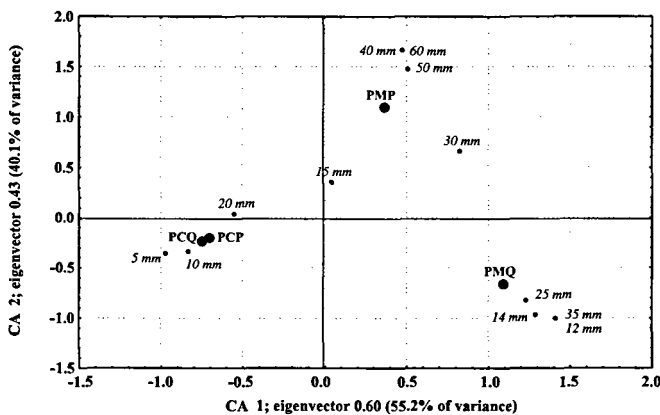


Fig. 5 - Detrended correspondence analysis ordination of prey of great and blue tits as function of prey size.

TABLE V - Diet breadth of nestlings, for prey type (B_A) and size (B_{AS}) in the oakwood and pine reafforestation.

	<i>Parus major</i>		<i>Parus caeruleus</i>	
	<i>Quercus</i>	<i>Pinus</i>	<i>Quercus</i>	<i>Pinus</i>
B_A t	0.142	0.246	0.097	0.319
B_{AS}	0.196	0.255	0.078	0.131

er habitats (Riddington & Gosler, 1995; Thomas *et al.*, 2001). The evolution of a later egg laying date in sub-optimal habitats is prevented by the flow of genes coming from optimal habitats, where eggs are laid synchronously with the peak resource of this habitat (Dias *et al.*, 1996; Blondel *et al.*, 1999). The shifts in laying date in our reafforestation may be viewed as a mechanism by which tits adapt their breeding time to the local environmental conditions (Grieco *et al.*, 2002); considering temporal and spatial distribution of tits breeding in Sicilian natural and semi-natural habitats, we assume that they might have developed a mechanism in order to lay eggs at different dates in accordance with the habitat resource where adults catch prey for nestlings. The nestling period in Sicilian oakwood generally matches well the availability of food, and this applies to caterpillars as well as to other prey items; matching the period of maximum availability of caterpillars is crucial for maximizing the energy flow to the nest, which has in turn important consequences for the breeding success of tits (van Noordwijk *et al.*, 1995). According to Zandt *et al.* (1990), Blondel *et al.* (1990) and Banbura *et al.* (1994), the proportion of caterpillars in the food of nestlings in Corsican populations is usually lower than in the mainland, but Naef-Daenzer *et al.* (2000) reported that spiders may outnumber caterpillars in the diet of the great tit in the early breeding season. Both in continental and Corsican populations, the timing of breeding is synchronized with the peak in caterpillar abundance, so that Banbura *et al.* (1994) considered caterpillars to be the major factor influencing life-history traits of Corsican blue tits. Nevertheless, variable nestling diets with low proportions of caterpillars (with only in some cases fewer fledglings produced) have been reported from coniferous forests (van Balen, 1973, for great tit), suburban gardens (Cowie & Hinsley, 1988, for blue and great tits), orange groves (Barba & Gil-Delgado, 1990, for great tit), Mediterranean sclerophyllous forests (Gil-Delgado *et al.*, 1992, Blondel *et al.*, 1991, Banbura *et al.*, 1994, for blue tit) and deciduous Swiss woods (Naef-Daenzer *et al.*, 2000, for great tit). In our pine reafforestation, characterized by a remarkable scarcity of insects (as also reported in Spain by Illera & Atienza, 1995), tit diets are broader, diet overlap of the two tit species decreases and they (particularly the great tit)

TABLE VI - Diet overlap (prey type in the triangular upper matrix, and prey size overlap in the triangular lower matrix) in the oakwood and pine reafforestation.

	<i>Parus major</i>		<i>Parus caeruleus</i>	
	<i>Quercus</i>	<i>Pinus</i>	<i>Quercus</i>	<i>Pinus</i>
<i>Parus major</i> <i>Quercus</i>	—	0.48	0.95	0.83
<i>Parus major</i> <i>Pinus</i>	0.40	—	0.45	0.60
<i>Parus caeruleus</i> <i>Quercus</i>	0.21	0.30	—	0.76
<i>Parus caeruleus</i> <i>Pinus</i>	0.23	0.32	0.96	—

time breeding to alternative prey (spiders, flies, etc.). While in the oakwood tits bred in such way that the peak resource and peak demand were overlapping, in the reafforestation, where we did not notice a peak resource, they delayed breeding, obtaining a generally lower productivity. It is known that a reduction in reproductive success in tits is associated with later breeding (e.g.: Perrins & Mc Cleery, 1989; Nager & van Noordwijk, 1995).

Food resources

The mean laying date of blue tits in Sicilian oakwood is typical for Mediterranean continental woods (20 April: Isenmann, 1987; Blondel *et al.*, 1993), and Corsican deciduous oakwood (15-30 April: Dias & Blondel, 1996; Lambrechts *et al.*, 1997), whereas the laying date in pine reafforestation is among the latest in the Mediterranean region (12-15 May in evergreen oakwood of Corsica: Blondel *et al.*, 1993; Dias & Blondel, 1996; Lambrechts *et al.*, 1997; continental Iberian populations: Gil-Delgado *et al.*, 1992). The mean clutch size of blue tits in Sicilian oakwoods is similar to that recorded in Mediterranean continental areas (Blondel *et al.*, 1993; Isenmann, 1987), while in pine reafforestation it is more similar to those reported for evergreen oakwoods in Corsica, mixed woods of North Africa and pinewoods of small islands, such as the Canary and Pantelleria Islands (Blondel *et al.*, 1993; Isenmann, 1987; Lo Valvo & Massa, 1995; Massa, 2002). This may be explained by differences in the resources available in oakwood and pine reafforestation, and environmental quality may be considered one of the main constraints influencing the differences in timing of breeding and in the number of fledglings we recorded.

The change in food resources before laying, during laying, and during chick growth might be the reason of earlier laying we observed in some years, mainly in the oakwood (cf. Martin & Bellot, 1990); the earlier laying

date cannot be related only to the absence of caterpillars, but also to other factors, such as microclimate, which, in turn, may influence the anticipation of the overall abundance of insects, the resource peak and the fledging success (Haywood, 1993; Dhondt *et al.*, 1984). Temperature and precipitation in spring should influence the development of leaves and the associated arthropod fauna that tits prey upon (Perrins & Mc Cleery, 1989; Clamens, 1990; Massa & Lo Valvo, 1996). Lower mean temperatures could delay vegetation development and influence the timing of caterpillar availability (Hinsley *et al.*, 1999). A rainy winter and an earlier summer may influence the demography of insect populations and could account for the breeding performance of tits; an increase in temperature may be the reason of a decrease in clutch size (Haywood, 1993) and, according to Ashmole's hypothesis (Ricklefs, 1980), there is a correlation between clutch size and fluctuation degree of resources, this fluctuation being higher in the north and lower in the south and bringing about a whole resource reduction in the south of tit distribution. Nevertheless, even if lower, resource availability and tit mortality in the south should be more regular throughout the year.

Adaptive plasticity

The change in food of the two species of tits in different habitats was a very interesting result of this research. Clutch size in the reafforestation was lower for both species, suggesting that food supplies were a limiting factor, even if that habitat great tits exhibited more different feeding habits with respect to the oakwood than did blue tits. The great tit showed a higher adaptive ability to prey types compared to blue tit and its more flexible food was in line with the smaller reduction in number of fledglings in pine reafforestation compared to oakwood (great tit reduction: 2.24, blue tit: 3.48). It appears to be a reaction norm of reproductive traits to habitat characteristics; changes in size or type of food brought to the nest may reflect changes in selectivity (Grieco, 2002). Because blue tit nestlings are smaller than those of great tits, prey category and prey size should have more critical fitness consequences for blue tits than for great tits (Banbura *et al.*, 1999); blue tits can have an advantage over great tits when feeding their young because they take smaller caterpillars and hence remove prey before it is suitable for great tits (Minot, 1981). Therefore, great tit breeding performance in the oakwood would be expected to be influenced to some extent by blue tits, whereas in the pine reafforestation, where prey size favoured great tits, such interference should be considerably reduced. Notwithstanding, great tits rearing their young were as successful as blue tits, relative to the reduction in clutch size between oak and pine; in fact, the number of fledglings/number of eggs $\times 100$ for great tit was 54.2% and for blue tit 56% in pine, while in oak both species were more successful (great tit: 80.4%; blue tit: 81.7%). The

performance of both species was also much less variable in oak than in pine; the variation measured was greater in reforestation (blue tit: 11.1 to 96.2%; great tit: 0 to 91.3%) than in oakwood (blue tit: 56.6 to 97.6%; great tit: 51.1 to 94.8%); this may indicate the poorer quality and more variable environment of the reforestation (Riddington & Golser, 1995). Size range of available prey and greater diet breadth of great tits (Naef-Daenzer *et al.*, 2000) should make this species more adapted than blue tit to habitats of lower quality (Barba & Gil-Delgado, 1990).

The fact that the greater the difference in clutch size between habitats, the greater was the proportion of all great tit pairs breeding in the oakwood suggests that more great tits settled in the oakwood in years when conditions were more suitable for producing bigger clutches, in turn suggesting that variation in condition among years was greater than the variation related to population density. It is interesting to note that whereas the blue tit followed the normal pattern of numbers being more variable in the more marginal habitat, the great tit did not conform to this pattern. Thus, both species were more plastic for laying date in the earlier (and better) habitat; for clutch size, the blue tit was more plastic in the reforestation and the great tit reacted by settling more in the oakwood when differences in clutch size were greater.

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