The Auk 110(3):511-520, 1993

HABITAT HETEROGENEITY AND LIFE-HISTORY VARIATION OF MEDITERRANEAN BLUE TITS (*PARUS CAERULEUS*)

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ABSTRACT.—The extensive variation in breeding traits of Mediterranean Blue Tits (*Parus caeruleus*) is hypothesized to result from large differences in the timing and abundance of food resources, depending on whether the dominant tree species of the habitat is deciduous (*Quercus pubescens*) or evergreen (*Q. ilex*). Data were collected on tree phenology, food abundance (caterpillars), and breeding traits of tits in one mainland deciduous habitat, two mainland evergreen habitats, and one evergreen habitat on the island of Corsica. In the mainland deciduous habitat, an early breeding time and a large clutch size were associated with an early and abundant food supply. In the evergreen habitats (both on mainland and on Corsica), the leafing process occurred three weeks later and the abundance of caterpillars was much lower. On Corsica, tits started to lay three weeks later than in the deciduous mainland habitat and laid about 30% fewer eggs. As in the deciduous mainland habitat, the breeding process seemed to be adjusted to the patterns of food availability. In the two mainland evergreen habitats, tits started to breed earlier and laid more eggs than expected from the patterns of food availability so that they mismatched the best period to raise their young. The apparent maladaptation of tits in these evergreen mainland habitats is hypothesized to result from an asymmetric gene flow between rich deciduous habitats (source), where well-adapted birds produce many fledglings, and poor evergreen habitats (sink), where the density is maintained through immigration from rich habitats. *Received 4 February 1992, accepted 20 November 1992.*

MANY PARTS of the Mediterranean region are "checkerboard" landscapes with a large variety of habitats due to small-scale heterogeneity in such factors as altitude, geological substrate, isolation, and especially variation in dominant tree species (deciduous broad-leaved, evergreen broad-leaved, coniferous). In addition, land-use practices have contributed greatly to the mosaiclike pattern of many Mediterranean landscapes. Because the Blue Tit (*Parus caeruleus*) occurs in many forest types and has been extensively studied across its range, this species is a good model for evaluating the extent to which life-history traits are adapted to local environments. Large variation occurs in breeding traits of Blue Tits over their range (Fig. 1). On average, birds start to breed earlier and have a lower clutch size (with a larger among-habitat variation of these traits) in the Mediterranean region than in central and northern Europe (Fig. 1). For example, the Mediterranean includes populations that have the earliest (21 March; population 14 on Fig. 1) and among the latest (11 May; population 22) onsets of breeding in Europe. Patterns of variation in laying date and clutch size of the Blue Tit at 12 Mediterranean study sites in the Mediterranean bioclimatic region, ranging from the Canary Islands to the northern limit of the Mediterranean, show some regular trends (Table 1): (1) three populations in deciduous oakwoods have the largest clutch size and start to breed early; (2) populations in evergreen oakwoods have a smaller clutch size and breed later in season; and (3) some populations in evergreen oakwoods breed extremely late and have a very small clutch size, especially those that are isolated on islands (Canary Islands, no. 13; Corsica, no. 22). There is an inverse relationship between laying date and clutch size ($r = -0.729$, $P = 0.003$, $n = 15$).

Because food supply has consistently been shown proximately and ultimately to determine important breeding traits such as laying date and clutch size (Lack 1966, Klomp 1970, Drent and Daan 1980, Ricklefs 1983, Martin 1987, Perrins and McCleery 1989, Zandt et al. 1990), we hypothesize that the large among-habitat variation of breeding traits in the Mediterranean region represents a response to large variation in the food supply.

Evergreen trees renew but a fraction of their foliage (ca. 30%) yearly, since their leaves are photosynthetically active for several years (three years in the Holm oak, *Quercus ilex;* Floret et al. 1989). By comparison with deciduous oaks that renew their whole foliage each year, this pat-

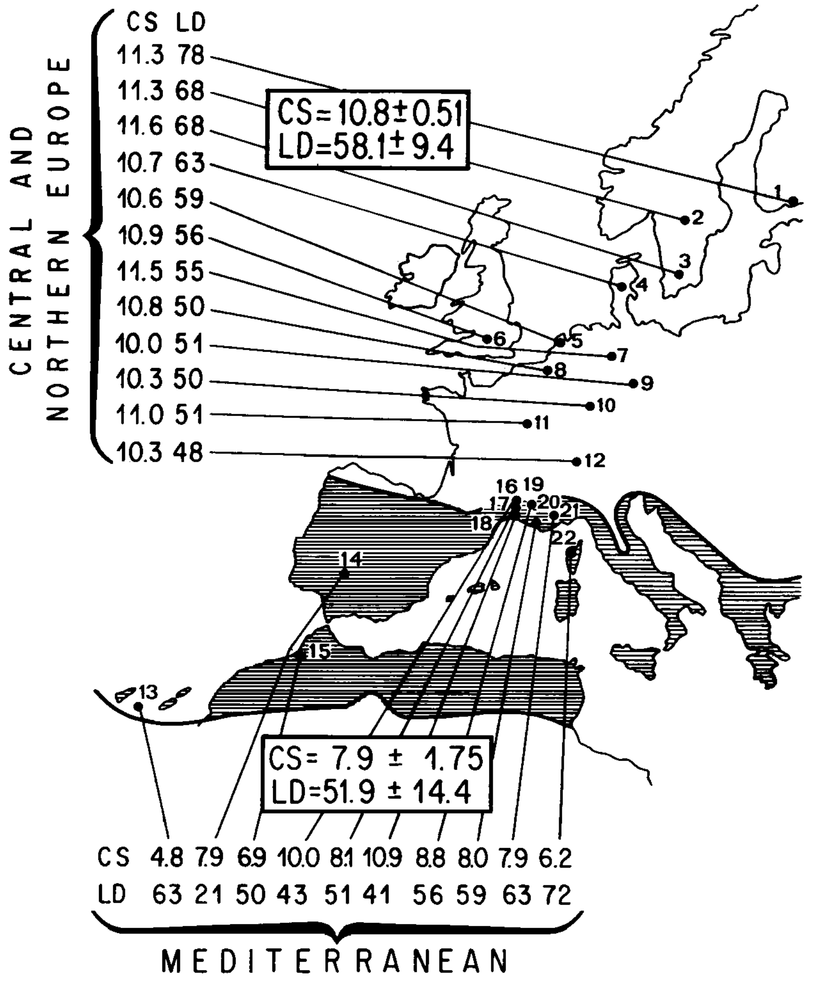

Fig. 1. Mean clutch sizes (CS ± 1 SD) and laying dates (LD ± 1 SD) of Blue Tits (*Parus caeruleus*) in different localities of Western Palaearctic. Dates in March dates (32 = 1 April). Sources: (1) Hildén 1990; (2, 3) Källander 1983; (4) Frederiksen et al. 1972; (5) Lack 1950; (6) Perrins 1965; (7) Berndt et al. 1983; (8) Delmée et al. 1972; (9) Zang 1980; (10) Neub 1977; (11) Leclercq 1977; (12) Glutz von Blotzheim 1962; (13) B. Schottler pers. comm.; (14–18, 20) Isenmann 1987; (19, 22) Blondel 1985; (21) Orsini pers. comm.

tern has two important consequences for phytophagous animals. First, since most (70%) of the photosynthetic system is active year-around, a large part of the energy available in spring is used by this system so that only a fraction is allocated to the production of new leaves. Accordingly, the leafing process should occur later and more slowly in evergreen than in deciduous trees in which a much larger part of the available energy is allocated to the production of new leaves. Second, since most phyllophagous insects, such as caterpillars, cannot eat leaves more than a year old because they are too hard and include tannins and other biochemical repellents (Feeny 1975, Crawley 1983), there should be less production of insects in evergreen than in deciduous trees in which all the leaves produced in spring are available to the insects. Therefore, the spring bloom of deciduous vegetation should be sharper and faster, with a higher peak of production resulting in a sharper, but shorter, pulse of arthropods, than in evergreen vegetation. Such a pattern is generally true in highly seasonal environments when compared with less-seasonal ones (Lack 1950, Rabenold 1978). If these hypotheses are true, the lower amount of food available late in the season in evergreen as compared with de-

TABLE 1. Clutch size and laying date of the Blue Tit in 12 Mediterranean habitats.[a]

Latitude (°N)	No.	Clutch size		Laying date		
		Deciduous	Evergreen	1 March–14 April	15 April–30 April	1 May–15 May
44°07′[b]	19	—	8.8	—	25 April	—
43°58′	16	10.0	—	13 April	—	—
43°54′	**17**	—	8.1	—	**20 April**	—
43°53′	**18**	10.9	—	**10 April**	—	—
43°51′	**23**	—	**8.6**	—	**21 April**	—
43°40′	24	10.0	—	7 April	—	—
43°22′[b]	20	—	8.0	—	20 April	—
43°15′	21	—	7.9	—	—	2 May
42°34′[c]	**22**	—	**6.2**	—	—	**11 May**
37°50′	14	—	7.9	21 March	—	—
34°02′	15	—	6.9	—	19 April	—
28°20′[c]	13	—	4.8	—	—	3 May

[a] Bold figures indicate habitats considered in this study. Numbers in second column refer to population numbers of Figure 1 (populations 23 and 24 not included in Fig. 1).

[b] More than 800 m above sea level.

[c] Island.

ciduous habitats should result in differences in how well birds are adapted to their local habitat.

The aim of our paper is two-fold. First, we try to identify proximate and ultimate factors that determine the timing of breeding and clutch size of Blue Tits in four Mediterranean habitats that differ in their dominant tree species and degree of isolation. Second, we investigate to what extent local populations living in habitat patches, which differ in the timing and the abundance of their food supply, have evolved locally adapted traits. Answering these questions requires a large body of data on life-history traits, food resources and the phenology of the dominant trees.

STUDY AREAS AND METHODS

Three habitats are located near Montpellier, southern France: a deciduous habitat (hereafter referred as MD; no. 18 on Fig. 1 and Table 1) where downy oak (*Quercus pubescens*) is the dominant tree species; and two evergreen habitats (MES and MEP; no. 17 and no. 23) where Holm oak (*Q. ilex*) is the dominant tree species. The fourth habitat is an evergreen oakwood dominated by Holm oak on the island of Corsica (IE; no. 22). Most of the vegetation on Corsica is evergreen, especially at low altitudes where the Blue Tit is most abundant. The three mainland habitats (MD, MES and MEP) are part of the same landscape (same altitude, substrate and climate so that the only factor in which they differ is dominant tree species). More details about the habitats may be found in Blondel (1985) and Isenmann et al. (1987). Nest boxes (50 to 140 depending on years and sites) have been erected in each habitat at a density of two nest boxes per hectare. Nest boxes were visited at least once a week for routine inspection throughout the breeding season.

Climatic data were obtained (years 1975–1991) from official meteorological stations (Service Technique d'Etudes des Facteurs Climatiques de l'Environnement, INRA) located inside or close to the study areas. Mean ambient temperature and rainfall for the months January to April are 7.3 to 8.0°C and 241 to 250 mm, respectively, in the three mainland habitats, and 9.3°C and 378 mm in the Corsican habitat.

The spring development of oak leaves was checked from 1987 to 1991 using the procedure of Du Merle and Mazet (1983). Random samples were taken from 25 oaks every three to four days at different heights (2 to 20 m) in the tree in five areas within each habitat. In each area, five trees have been sampled and six apical buds per tree have been checked. Bud burst and the development of the leaves were assigned to one of seven categories ranging from stage 1 where the bud is completely closed to stage 7 where the new leaf is fully developed (see Fig. 2). During each visit, the number of buds at each state was multiplied by the number of that stage and then weighted to 100 so that the final figure for each date gives the average stage of the leafing process in the habitat. Data were fitted to a logistic equation (Fig. 2). This procedure gives the timing and the duration of the spring development of the tree.

The most important food item for tits is caterpillars (Perrins 1965, Van Balen 1973, Zandt et al. 1990). These are always the preferred prey when available and by far the most important on a biomass basis in all areas including the Mediterranean (Zandt et al. 1990, Blondel et al. 1991a). We estimated the abundance of caterpillars by collecting their droppings falling from the foliage of the trees. Data were collected in two evergreen oakwoods (IE and MEP) in the years 1988–1991 and in the deciduous mainland oakwood (MD) in 1991 using the method of Tinbergen (1960; see

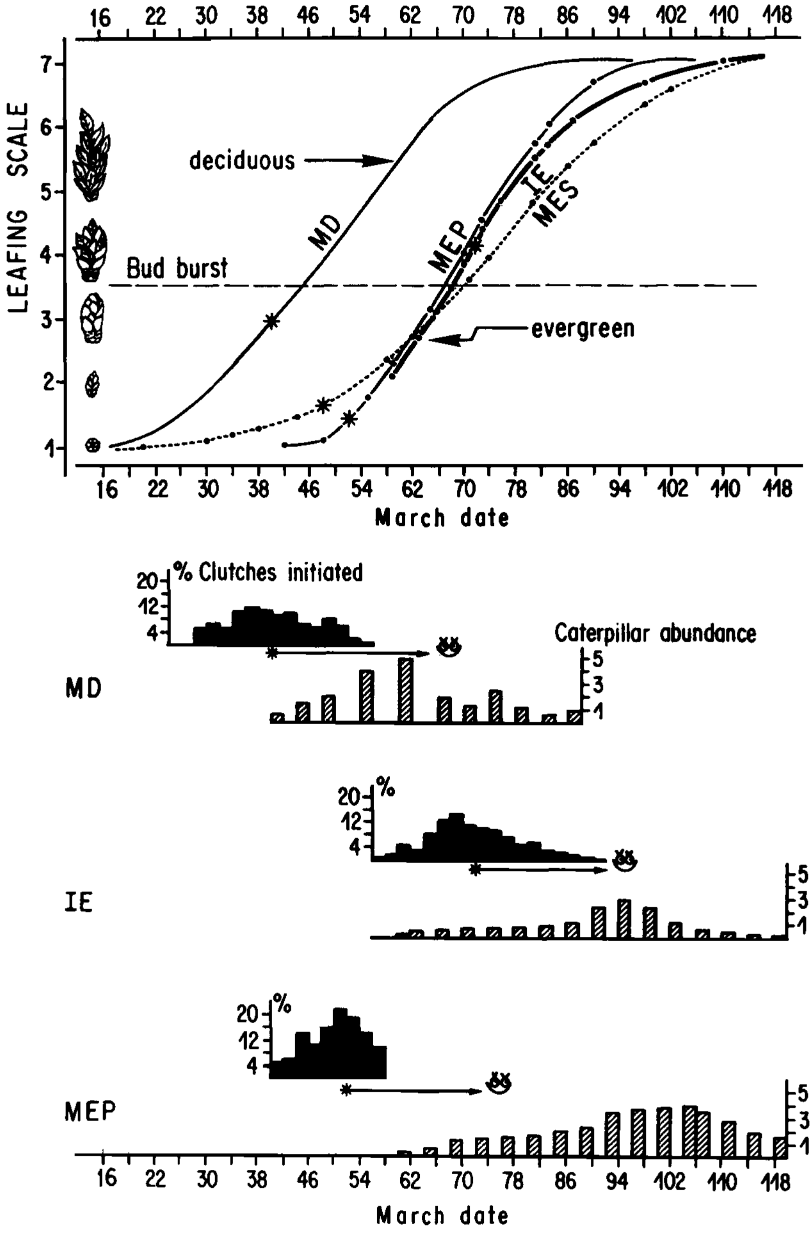

Fig. 2. *Upper:* Leafing phenology of deciduous oaks (habitat MD on mainland) and evergreen oaks (MES, MEP on mainland; IE on Corsica). Vertical axis indicates stages of development of young leaves. Asterisks indicate laying date of Blue Tits. *Lower:* Percent clutches initiated and variation in caterpillar abundance with date. Symbols to right of arrows indicate mean date when nestlings are on average 10 days old. The lengths of arrows differ because of differences in clutch size. Dates presented as March dates (32 = 1 April).

Zandt et al. 1990). Droppings were collected twice a week over the breeding season on 0.25-m^2 trays erected under the canopy of the oaks. We sampled 10 to 25 oaks using one tray per tree. Abundance of caterpillars in the habitat was expressed as an index ranging from 0 to 5 (see Fig. 2).

Data on breeding traits are available for the years 1985–1991 in the three mainland habitats and the years 1976–1991 in Corsica. Laying date is the mean of the dates on which each pair laid its first egg. Since Blue Tits usually lay one egg per day, the date on which the first egg was laid has been extrapolated

TABLE 2. Breeding densities (pairs/nest box), laying date ± 1 SD, clutch size ± 1 SD, breeding success, and timing of the main events of breeding cycle of Blue Tits in deciduous mainland oakwood (MD) and evergreen oakwoods (MEP and MES = mainland; IE = island). Sample size in parentheses. Data for MES from Isenmann et al. (1987).

	Breeding site			
	MD	MEP	MES	IE
Breeding density	0.45	0.07	0.10	0.60
Laying date	10 April ± 6.7 (81)	21 April ± 3.9 (49)	19 April ± 4.3 (88)	11 May ± 6.8 (417)
Clutch size	9.8 ± 1.7 (81)	8.5 ± 2.1 (49)	7.8 ± 1.5 (85)	6.6 ± 1.1 (417)
Breeding success (no. fledglings/egg)	0.60 (64)	0.43 (40)	0.54 (85)	0.65 (380)
Bud stage at laying	3.2	1.4	1.4	3.9
Date of bud opening	14 April	6 May	12 May	8 May
No. days between laying date and bud opening	3	−15	−25	−3
Caterpillar peak date	30 April	13 June		3 June
No. days between bud opening and caterpillar peak date	16	38		26

from the weekly visits to the nest boxes. Clutch size is the mean of the completed clutches laid by each female. We have excluded those clutches where the female never got as far as incubating, and clutches of three or fewer eggs because such small clutches are probably incomplete. Only first clutches will be considered in this paper. Because year-to-year variation in the phenology of the trees and breeding traits of the tits was much less at the within-habitat level than at the between-habitat level, data for each habitat were averaged over the years of the study.

RESULTS

Spring development of vegetation and caterpillar abundance.—The leafing process of the oaks differed strongly between deciduous and evergreen trees. Bud burst (stage 3.5 of leafing process; see Fig. 2, Table 2) occurred three weeks earlier in the deciduous habitat (MD, "March-date" 45 = 14 April) than in the evergreen (MEP, 6 May; MES, 12 May; IE, 8 May). The overall pattern in evergreen oaks was similar in the two mainland sites and on Corsica. This is surprising because Corsica enjoys a warmer, moister climate.

The seasonal variation of caterpillar biomass was closely related to the development of oak leaves, which was expected since caterpillars are dependent on young leaves. For example, young caterpillars of *Tortrix viridana*, an important prey species for tits, cannot enter oak buds until they burst, which occurs three weeks later in the Holm oak than in the downy oak (Du Merle 1983). In the deciduous mainland habitat (MD), caterpillars appeared at the beginning of April, quickly increased in abundance and peaked at the end of April (peak date 61 = 30 April; Fig. 2, Table 2). In the two evergreen oakwoods for which data are available, caterpillars began to emerge three to four weeks later (peak date 105 = 13 June in MEP, and 95 = 3 June in IE), but they were available over a longer period of time, presumably a consequence of the longer leafing process of the Holm oak. Peak abundance of caterpillars occurred 16 days after bud burst in the deciduous oakwood (MD), and 38 and 26 days after bud burst in the mainland (MEP) and the island (IE) evergreen oakwoods, respectively (Table 2). As expected, more caterpillars (index of abundance = 5.0) were found in deciduous than in evergreen oaks (3.9 and 2.6 on the mainland and in Corsica, respectively). Here again, the pattern was similar on the mainland and on the island, although the peak date for caterpillars occurred slightly earlier on Corsica than on the mainland. In summary, the combination of earlier and faster development of new leaves in deciduous than in evergreen oaks, coupled with a parallel trend in arthropod production, supports the predictions made in the introduction.

Breeding traits of Blue Tit.—Population sizes, expressed as the number of breeding pairs per nest box (excluding repeat and second clutches), varied among habitats. Densities were fairly high in the deciduous mainland habitat (0.45 breeding pair per nest box) and in the evergreen island habitat (0.60), but much lower in

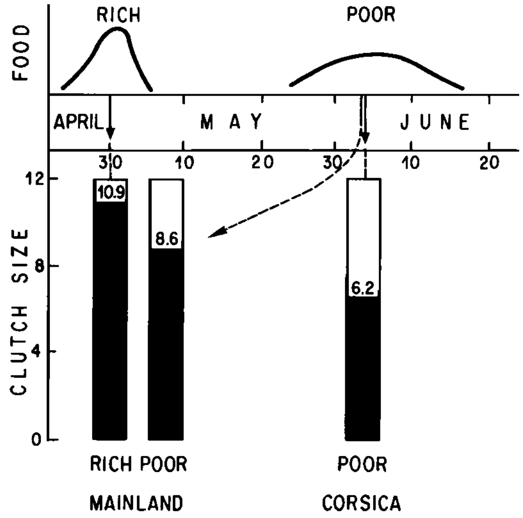

Fig. 3. Adaptedness (to rich mainland habitat and poor Corsican habitat) and maladaptedness (to poor mainland habitat) of clutch size and laying date of Blue Tit. Breeding traits in poor mainland habitat approach those of rich habitat (dashed arrow) because of asymmetric gene flow from latter to former.

the evergreen mainland habitats (0.10 in MES and 0.07 in MEP). A higher occupancy rate of nest boxes in Corsica is consistent with measured higher natural densities of Blue Tits on Corsica than on the mainland (Blondel et al. 1988).

Laying started earliest (mean laying date of all the pairs of the population) in the mainland deciduous oakwood (10 April; Table 2), but one month later in the evergreen oakwood of Corsica (11 May). In the two mainland evergreen habitats, the onset of breeding was intermediate (19 April in MES; 21 April in MEP). Since the three mainland habitats are parts of the same landscape and with the same climate, these differences in the onset of breeding mean that factors other than temperature play an important role in determining laying date. Blue Tits started to lay within a few days of bud burst in the mainland deciduous habitat and in Corsica (Fig. 2), but long before buds opened in the two mainland evergreen oakwoods (MES, MEP). At these two sites, which match the Corsican habitat where tits were expected to show the same general pattern in breeding traits, they started to lay 10 to 11 days later than in the deciduous mainland habitat but three weeks earlier than on Corsica.

DISCUSSION

The main features of life-history variation among these four habitats are the combination of: (1) large clutch size and early laying date in the deciduous oakwood; (2) small clutch size and late laying date in the Corsican evergreen oakwood; and (3) intermediate values for these traits in the two mainland evergreen oakwoods (Fig. 3). Assuming that birds that do best are those that start to breed as early as possible in habitats where food is plentiful (Perrins 1965, 1970, Van Balen 1973), habitats may be separated into richer habitats (i.e. deciduous habitat [MD] on mainland), and poorer habitats (i.e. two mainland evergreen habitats [MEP and MES] and evergreen habitat in Corsica; see Fig. 3). The first three habitats (MD, MES, MEP) are parts of the same landscape over which tits freely disperse. In contrast, the insular evergreen habitat (IE) is isolated from any rich deciduous habitat. As a result, nearly all the habitats within the dispersal range of this Corsican Blue Tit population are of poor quality. Because territory size is to some extent related to the abundance of resources (Lack 1968, Cody and Cody 1972, Nilsson 1976, Brown 1982, Stamps and Tollestrup 1984), densities are much higher in the deciduous habitat than in the evergreen habitats on the mainland. However, Blue Tit densities on Corsica are very high, presumably because of density compensation (or density inflation) in this depauperate insular community (for discussion, see Blondel et al. 1988).

Several studies in temperate Europe have shown that Great Tit (*Parus major*) and Blue Tit laying dates are negatively correlated with spring temperatures (Kluyver 1951, Perrins 1965, Van Balen 1973, Slagsvold 1976, Schmidt 1984, Blondel 1985, Perrins and McCleery 1989). Such a relationship has been found in Mediterranean habitats on the mainland, but not on Corsica (Blondel 1985). Because Corsica is further south and has a much warmer climate than the mainland site (ambient temperatures $\bar{x} = 9.3°C$ for the months January–April vs. 7.3°C on the mainland), the extremely late breeding date of Corsican tits was unexpected.

Temperature acts mainly through the spring development of the leaves and the associated arthropod fauna the birds feed upon (Lack 1966, Van Balen 1973, Perrins and McCleery 1989, Zandt et al. 1990). Laying date has been found to be significantly correlated with bud burst in deciduous habitats for Blue Tits by Clamens (1988, 1990) in the Mediterranean region and by Jones (1972) at Oxford for Great Tits. Bud burst is an important event for tits because it is the time when first-instar caterpillars invade the buds and begin to eat the young leaves (Varley and Gradwell 1968, Perrins 1973). Young tits must be in the nest as early as possible in the period of caterpillar abundance, because the most successful young are those that are about 10 days old when caterpillar numbers peak (Perrins 1965, 1990). In order to have 10-day-old young in the nest at the peak of caterpillar numbers, egg development must begin 35 days before for a clutch of eight eggs (4 days to form an egg, 7 days to complete the clutch, 14 days incubating plus a nestling period of 10 days). To do this, birds must anticipate the most favorable period and have to make use of appropriate proximate clues. Tits begin laying as soon as they are able to store enough reserves to produce eggs (Perrins 1970, Martin 1987). Therefore, the onset of breeding varies with food availability because tits cannot store more than a tiny proportion of the reserves needed for the whole clutch. This has been shown by correlations between laying date and food availability at both the among- (Greenwood and Hubbard 1979, Dhondt et al. 1984) and within-habitat level over several years (Perrins and McCleery 1989, Zandt et al. 1990), as well as food supplementation experiments where supplemented pairs bred earlier than unfed control pairs (Källander 1974, Von Brömssen and Jansson 1980, Smith et al. 1980, Ewald and Rohwer 1982, Clamens and Isenmann 1989).

The relationship between laying date and caterpillar abundance indicates that Blue Tits in the mainland deciduous habitat (MD) and in the evergreen habitat of Corsica (IE, Fig. 2) time their laying so that their young are in the nest around the peak of food abundance. Blue Tits lay four weeks later in Corsica than in MD because of the three- to four-week time lag in the leafing patterns and the development of caterpillars in this habitat.

In summary, in the mainland deciduous habitat, the egg laying by Blue Tits, bud opening of oaks, and emergence of caterpillars were all closely correlated with spring temperature as in other deciduous habitats in Europe (Slagsvold 1976, Schmidt 1984). On Corsica, where evergreen trees begin development at temperatures much higher than those that activate the development of the deciduous vegetation on the mainland, laying date is also determined by factors related to the food supply, since it nicely coincides with the period of caterpillar abundance (Figs. 2 and 3). Results of our study support the prediction that selection would favor earlier breeding and larger clutches in rich deciduous mainland habitats, and smaller clutches and later laying dates in poor evergreen island habitats (Fig. 3). Similar effects of current food supply on clutch size have been reported by Van Balen (1973), Klomp (1970), Arcese and Smith (1988), Perrins and McCleery (1989) and Perrins (1990), who found a correlation between clutch size and annual caterpillar density. Combining the data of the two Mediterranean habitats (MD and IE), where there is good correspondence between laying date and food availability, with five other data sets in the Netherlands and Great Britain (see Zandt et al. 1990), laying date is significantly correlated ($r = 0.863$, $P < 0.05$) with the peak date of caterpillar abundance.

Laying date and clutch size in the two mainland evergreen oakwoods were expected to be similar to those on Corsica since the process of leaf development and the variation of food abundance are similar. However, tits in these habitats bred too early so that they missed the peak of caterpillar abundance, and laid too many eggs in relation to the number of young they could successfully raise (Table 2, Fig. 3). Therefore, breeding success (no. fledglings per egg) was lower in these habitats than in either the mainland deciduous oakwood or in the Corsican evergreen oakwood (Table 2; Dias et al. 1994). Their timing would have been correct and the tits would have produced the right number of eggs had they been breeding in the neighboring deciduous oakwoods. Moreover, laying date was not correlated with the bud burst of evergreen oaks in their habitat, but was significantly correlated with the bud burst of deciduous oaks in surrounding habitats ($r = 0.85$, $P < 0.01$; Clamens 1988, 1990). It appears that the leafing process of deciduous oaks predicts laying date in both evergreen and deciduous oaks within the same neighborhood.

The relevant question raised by our study is not so much why Corsican tits breed so late, but why tits in mainland evergreen habitats breed so early and do not shift their breeding traits in order to match the local variation in food resources. One explanation for the poor timing of Blue Tits laying in evergreen mainland habitats is the gene-flow hypothesis (Blondel et al. 1991b). Birds breeding in rich deciduous habitats produce more fledglings of good quality than those breeding in poor ones (Table 2; Dias et al. 1994). Thus, a large proportion of the birds settling in the poor-quality habitats are immigrants from the good-quality habitats and time their breeding in the poor habitats as if they were in rich ones. Hence, their timing is incorrect presumably because asymmetric gene flow from deciduous oakwoods prevents them becoming adapted to evergreen woodland. On Corsica, where nearly all the vegetation is evergreen in the landscape under study, gene flow must be small. Therefore, the population (which belongs to the subspecies *P. c. ogliastrae* Hartert) has been able to evolve life-history traits fairly well adjusted to the local environment. The gene-flow hypothesis is supported by the demonstration of a genetic component of laying date (Blondel et al. 1990, Lambrechts and Dias 1993), which confirms previous studies on the heritability of this trait in the Great Tit (Van Noordwijk et al. 1980). The slightly delayed laying date (10 days) and smaller clutch size (2.3 eggs smaller) in mainland evergreen as compared with deciduous oakwoods suggest that some tuning is proximately achieved through a phenotypic adjustment of both laying date and clutch size to food availability. Similar cases of poorly timed breeding by tits in habitats of differing quality have been reported by Van Balen (1973), Perrins and Moss (1975) and Lemel (1989) for Great Tits, and by Dhondt et al. (1990) for Blue Tits. In a similar context, Emlen (1978) gave evidence of the swamping effect on incipient local adaptation of several bird species in the southern part of the Florida peninsula by gene-flow from populations of the central part. Corresponding populations in similar environments on the island of Grand Bahama evolved appropriate adaptations because gene flow is prevented by the sea barrier.

Our study raises three points that should be clarified by studies in progress. First, we do not know which factors proximately determine laying date in mainland evergreen oaks. Cues must be different on the mainland and in Corsica since the birds begin laying at very different stages in the spring development of the trees. Second, gene flow and asymmetric dispersal among habitat patches on the mainland still has to be demonstrated. However, the poor timing shown by some populations that fledge only a few low-quality young (Dias et al. 1994) predicts that such processes should occur (Pulliam 1988). For a species living in landscapes where habitats are not equally productive and in which there are density-dependent components in reproduction, habitats with an overproduction of individuals may act as "sources" from which individuals will emigrate to habitats with productivity lower than that necessary to maintain the population size. Such "sink" populations will persist because of immigration from the source (Blondel et al. 1991b). Third, what makes an individual decide to leave the habitat where it was born or to stay is unknown. Morphometric data indicate that individuals that settle in the poor mainland evergreen habitats are smaller (shorter wing and tarsus) and have lower breeding success than those that breed in the rich deciduous habitat (Dias et al. 1994). Similar differences found by Van Balen (1973) for breeding success and by Lemel (1989) and Ulfstrand et al. (1981) for body size in the Great Tit support the despotic-distribution model of Fretwell and Lucas (1970), whereby dominant individuals breed in the habitats richest in resources. However, since body size is not necessarily related to an individual's ability to outcompete an opponent (Lemel 1989, Lambrechts and Dhondt 1986), additional studies are required to assess the body condition, history, social status and genetic constitution of individuals according to their decision to stay or to move.

ACKNOWLEDGMENTS

Logistical support was provided by the Association pour l'Etude Ecologique du Maquis (APEEM). We owe special thanks to D. and G. Viale. Financial support was provided by the CNRS, the Ministery of Environment (SRETIE), and the JNICT (Programa Ciência). The CRBPO provided us with rings. We thank P. Isenmann, A. Clamens, B. Schottler, H. Zandt and many students for help with several aspects of this study. Olavi Hildén, Marcel Lambrechts, Christopher Perrins, Michel Raymond, Gary D. Schnell, and John Wiens made useful comments on earlier versions of the manuscript and improved the English.

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