J Ornithol (2007) 148 (Suppl 1):S3–S15
DOI 10.1007/s10336-007-0161-1

REVIEW

Coping with habitat heterogeneity: the story of Mediterranean blue tits

Jacques Blondel

Received: 20 December 2006 / Revised: 22 May 2007 / Accepted: 23 May 2007 / Published online: 27 June 2007

Abstract A prerequisite for understanding adaptation is to understand how populations respond to environmental heterogeneity. We chose the blue tit *Cyanistes caeruleus* and Mediterranean habitat mosaics which exhibit a large diversity of habitats for analysing the effects of environmental heterogeneity on phenotypic variation. Three main factors of heterogeneity have been considered: (1) whether dominant tree species are deciduous or evergreen, (2) the geographic configuration of habitats and landscapes, and (3) the degree of infestation by parasites, which considerably varies in space. Several study sites equipped with nestboxes and traps for collecting the droppings of caterpillars falling from the leaves of trees have been monitored over several decades in a series of habitats in mainland and insular (Corsica) landscapes. Depending on the geographic configuration of habitat patches within landscapes, the large phenotypic variation observed in many demographic, morphometric and behavioural traits has been shown to result either from a plastic response to habitat variation or from genetically determined specialisation to local habitats. Blue tits in deciduous habitats started to breed ca. 1 month earlier than in evergreen habitats, but patterns differed between the mainland and Corsica. On the mainland, populations may be locally maladapted because of gene flow across habitat patches, which results in a low supply/demand ratio of food, poor breeding performance and a source–sink population structure. In Corsica, higher phenotypic variation resulted from lower dispersal ranges in islands, a component of the insular syndrome. Genetically-based habitat-specific specialisation to local habitats on this island is a demonstration that adaptive responses of suites of life history traits to habitat-specific selection regimes may operate on a scale which is much smaller than the scale of potential dispersal and gene flow. Adaptive responses of blue tits to two constraints, i.e. high levels of parasitism and low amounts of food, have been studied in detail. The very small amount of measured genetic divergence between populations contrasts with the large inter-population phenotypic variation which is observed in many traits. This is one more example that natural selection can produce rapid and sometimes strongly adaptive morphological divergence in the absence of discernable differentiation at neutral DNA loci, and that weak genetic differentiation does not necessarily mean phenotypic resemblance.

Keywords Gene flow · Local specialisation · Maladaptation · Phenotypic plasticity · Source–sink

Introduction

A major challenge in evolutionary ecology is to understand why and how populations vary as they do, in morphology, ecology, behaviour and physiology. This is a prerequisite for understanding adaptation, explaining the origin of biodiversity, and predicting the evolutionary responses of organisms to several components of global change. Most populations exhibit some kind of phenotypic variation as a response to habitat heterogeneity which is universal whatever the spatial scale and the parameters considered (Bell et al. 1993). Ten years ago, Schluter (1996) noticed that "few studies convincingly demonstrated that population

Communicated by F. Bairlein.

J. Blondel (✉)
CEFE-CNRS, 1919 Route de Mende,
34293 Montpellier cedex 5, France
e-mail: Jacques.blondel@cefe.cnrs.fr

differences in phenotypes are adaptive in the evolutionary sense. The extent to which adaptive population variation relates to variation in local selection pressures and gene flow between populations has rarely been studied in detail". This statement remains largely true despite many studies on this theme. The challenge is to decipher the proximate and ultimate mechanisms that produce and maintain phenotypic and genetic variation. Depending on species-specific dispersal ranges of organisms between their place of birth and growth and their place of first reproduction, the response to spatial heterogeneity depends on the size, structure and geographical configuration of habitat patches within landscapes. This response may be either ontogenetic phenotypic plasticity, which occurs when genetically identical organisms reared in different environments display different phenotypes (Stearns 1989; van Noordwijk 1989), or local specialisation, that is the evolution of traits that have been selected in a given environment and do not change if the organism migrates to another environment. Both phenotypic plasticity and local specialisation are adaptive responses to environmental variation and are subject to selection. Several factors, including the scale, amplitude and variation of environmental heterogeneity, determine which of these two mechanisms is selected for. As Singer and Thomas (1996) put it, long-term comparative and experimental studies are needed to answer these questions on phenotypic variation and to analyse the mechanisms that produce it. One reason why few studies have addressed the problem of spatial phenotypic variation is that many long term field studies, especially on birds, must compromise between number of study sites, plot size, and data collection, generally putting an emphasis on thorough investigations in single-area populations. I will address these questions from a long term study of blue tits *Cyanistes caeruleus* over a series of study sites in the Mediterranean region (e.g. Blondel et al. 2006).

Setting the scene

The study model, the blue tit is a small 9–13 g passerine which is widespread in most forests of Europe from southern Scandinavia to the Canary Islands, preferring broad-leaved forests at low and mid altitudes (Snow 1954). Vaurie (1957) described two well-distinct groups of subspecies: the *caeruleus* group of temperate central Europe with eight subspecies, and the Mediterranean *teneriffae* group with six subspecies. The *teneriffae* group includes all the populations of North Africa and the Canary Islands, but the four and possibly five subspecies of this oceanic archipelago show considerable variation in both systematics and ecology (Garcia-Del-Rey et al. 2006). The Canary Islands complex differs so much from all other blue tit forms that it has been proposed by Kvist et al. (2005) to constitute a distinct species, *Cyanistes teneriffae*. At the scale of the whole distributional range of the species, phenotypic variation is mostly clinal, with birds becoming smaller with thinner bills and more contrasted colours from the north-east to the south-west of the range of the *caeruleus* complex (Martin 1991). Subspecies of the *teneriffae* complex are smaller with relatively longer bill, longer tarsus, larger sexual size dimorphism and more contrasted coloration. Hypotheses that have been proposed for explaining variation of the species at this scale mostly relate to classical ecogeographic rules, such as Gloger's rule, and typical Mediterranean features such as foraging substrate, the kind of food provided by Mediterranean-type ecosystems, and climate (Martin 1991).

Our aim was to investigate the patterns of variation of the blue tit near the southern edge of its geographical distribution, on the borders of medio-European and Mediterranean regions, where forests are mosaics of temperate, mostly deciduous, and Mediterranean, mostly evergreen sclerophyllous vegetation, two types of vegetation that differ in a number of ways (e.g. Blondel and Aronson 1999). Rather than examining morphological traits that are expected to vary over large areas and for which the mechanisms of variation are difficult to demonstrate, we mostly focussed on traits that are directly related to fitness. We chose traits that are easy to collect in the field from populations breeding in nest-boxes, which can be subject to experiments, and which address the extent of adaptation to local environments, mostly demographic traits that more or less directly depend on food resources. Over the whole distributional range of the blue tit, fitness-related traits such as laying date and clutch size are highly variable. In central and northern Europe, blue tits start to breed on average between mid-April and mid-May and lay around 10–12 eggs. In the Mediterranean region, they start to breed on average 1 week earlier and produce smaller clutches, but the point is that the variation of these traits is much higher with a standard deviation, being 60% higher for laying date and up to three times higher for clutch size (Blondel et al. 1993). The Mediterranean region includes populations exhibiting almost the whole range of laying dates that have been found over the distributional range of the species, from mid-March to the first decade of May. The same is true of clutch size which varies from 5 to 11 eggs.

Mediterranean landscapes are mosaics of habitats with a large diversity of plant species and topographic features, such as mountain ranges which isolate myriads of small catchments and introduce many discontinuities and potential barriers to gene flow. In many landscapes, habitats are dominated either by the deciduous downy oak *Quercus humilis* or by the evergreen sclerophyllous holm oak *Q. ilex*. Habitat patches differ in size, from some tens to

thousands of hectares, but each of them is quite homogeneous with more than 95% of the trees belonging to a single oak species. A crucial element of the story is that the spring flush of leaves, measured as leaves develop from the dormant buds to fully developed leaves, starts 1 month earlier in deciduous oaks than in evergreen oaks. Bud burst is a key event because it triggers the hatching of caterpillars, the preferred prey of blue tits, which will start to feed on young leaves. This event activates food chains which cascade from oak leaves through caterpillars to insectivorous blue tits and follow different temporal trajectories in the two types of oak forest. In addition to this large qualitative difference in timing, there is also a large quantitative difference. Caterpillars are much more abundant in downy oaks because the whole foliage is renewed each year in deciduous oaks as compared to only 30% in evergreen oaks, and only young leaves are edible by caterpillars (Blondel et al. 1999). The 1-month difference in bud burst and leaf production between the two oak morphotypes results in an early, high-amplitude peak in caterpillar production in downy oak forest and a late, low-amplitude peak in holm oak forest. This combination of large differences in phenology and abundance of caterpillars is crucial because food supply has repeatedly been shown to proximately and ultimately determine the values of breeding traits such as laying date, clutch size and breeding success in income breeders such as small passerines (Lack 1968; Drent and Daan 1980). The question which arises is: how do blue tits respond to these large differences in timing and abundance of food resources?

Addressing the questions

The selective advantage of breeding time and clutch size can be considered in terms of the ratio between food supply and demand where supply is the amount of food truly available to breeding individuals, and demand is the quantity of food that parent tits must harvest to meet their requirements and those of their nestlings (Tremblay et al. 2003). Assuming that breeding performance in seasonal environments depends on how well birds adjust demand to supply within a temporal window of caterpillar availability which is not longer than 2 weeks or so (Banbura et al. 1994), one can make two main predictions. First, tits breeding in caterpillar-rich habitats will produce more offspring than those breeding in caterpillar-poor habitats because a broad and high-amplitude peak in caterpillar biomass provides more food which is available for a wider temporal window than does the narrower and lower-amplitude peak in poor habitats (Fig. 1). Second, for any given amount of food, breeding performance will be optimal if tits start to breed at such a date that nestling demand

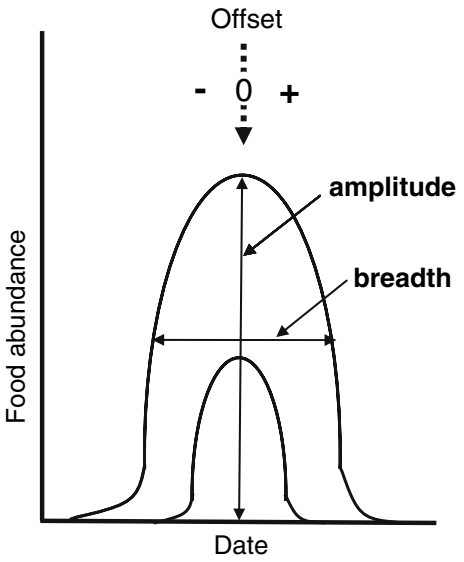

Fig. 1 Model showing how variation in amplitude and breadth of food abundance may affect the width of the temporal window allowing successful breeding. The *vertical arrow* indicates the peak of food abundance. Any offset of breeding time to earlier (–) or later (+) dates between this peak and the peak of food demand by blue tits *Cyanistes caeruleus* will decrease the supply/demand ratio and will result in lower breeding performance (modified from Tremblay et al. 2003)

is highest at the peak of food availability, when chicks are around 11 days old. This occurs when the offset between supply and demand does not deviate from zero (Fig. 1). In that case, the number of offspring is proportional to the magnitude of the caterpillar spring flush. If, for some reasons, populations do not succeed in closely tracking changes in food productivity and availability across habitats, any negative (–) or positive (+) deviation from this optimal timing will decrease breeding performance, and the consequences of this mismatching will be inversely proportional to the magnitude and breadth of the spring flush of caterpillars.

We addressed these questions in relation to three main factors of heterogeneity which characterise most Mediterranean landscapes for birds: first, whether dominant tree species in forests are deciduous or evergreen; second, the geographic configuration and degree of isolation of habitats and landscapes; and third, the degree of infestation by parasites which considerably varies in space (Hurtrez-Boussès et al. 1997). We chose a nested system of study sites including two landscapes with a similar configuration of habitat patches in southern France: a landscape on the mainland near the city of Montpellier, and a landscape on the island of Corsica (Fig. 2). These two landscapes are located at a similar latitude (between 42°N and 43°N) and altitude (ranging from 80 to 370 m) and are isolated from each other with no exchanges of tits

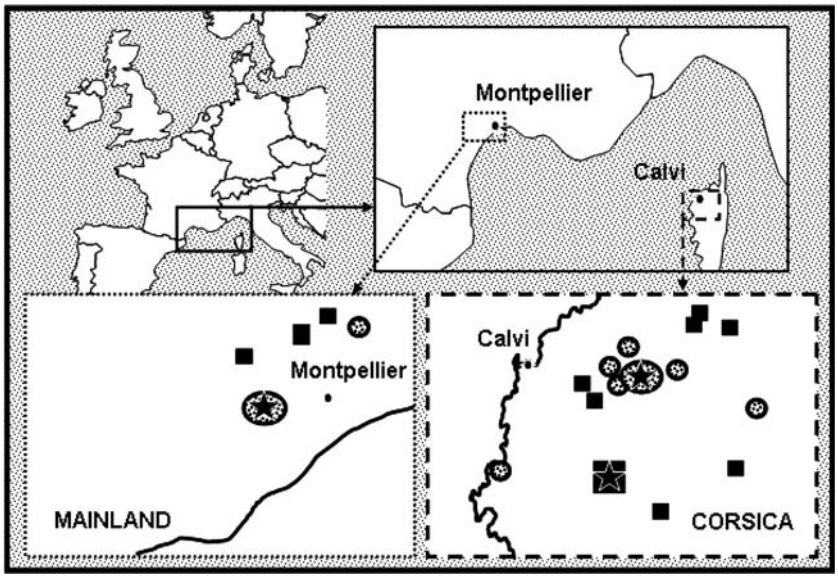

Fig. 2 Locations of the two landscapes and study sites. *Stippled circles* denote sites dominated by deciduous downy oaks *Quercus humilis* and *black squares* denote sites dominated by evergreen holm oaks *Q. ilex*. *Stars* denote the main study sites used for long-term studies

between them. The nominal form *C. caeruleus* occurs on the mainland and the *ogliastrae* subspecies, which is 15% smaller, in Corsica. Each landscape is a mosaic of small oak forests. In each of them, we selected, within a range not exceeding 30 km, at least three patches of evergreen oaks and two patches of deciduous oaks. The size of habitat patches was at least several hundred hectares. One point of importance is that, on a larger geographical scale, deciduous oaks are more common than evergreen oaks on the mainland whereas it is the reverse on the island. In addition, mainland blue tits of the Mediterranean region are connected to other populations further north whereas Corsican populations are geographically isolated. Habitats were equipped with nest-boxes at a density of ca. two nest-boxes per ha. Food abundance has been measured from caterpillar droppings falling from the trees and collected in trays. The proportion of caterpillars in nestlings' diet positively correlated with the amount of frass collected, indicating that frass is a reliable indicator of caterpillar abundance (Banbura et al. 1994). We were able to monitor and quantify the three components of the food chains, namely oak leaves, caterpillars and tits. All these habitats have been monitored over more than 30 years for some of them and provided more than 5,000 breeding attempts (e.g. Blondel et al. 2006). Over the study period, our approaches were observational and experimental, both in the field and in a series of 27-m^3 aviaries located near our laboratory in Montpellier.

Optimising breeding in heterogeneous environments

A first step was to check whether blue tits correctly synchronise their breeding time to food patterns in the most common habitat of each landscape, i.e. deciduous on the mainland and evergreen in Corsica. If they do so, they will start breeding at such a date that their chicks will be around 11 days old at the peak of caterpillar abundance. This was clearly the case as shown by a good synchronism between the development of leaves, caterpillar availability and the period of chick raising which resulted in a good matching between demand and supply (Fig. 3a). The later and lower peak of food in the evergreen habitat of Corsica made populations breeding there start to lay more than 4 weeks later (on average 12 May ± 4 days compared to 7 April ± 8 days) and produce 30–40% smaller clutches (on average 6.4 ± 0.4 eggs compared to 9.8 ± 1.6). Tits equally optimised their food supply/demand ratio and had a similar breeding success, producing on average 5.0 and 7.5 fledglings in the two habitats, respectively. In addition, fledglings in the rich mainland habitat were on average 0.5–1 g heavier, after correction for the size difference between the two subspecies.

In the framework of a study on the mechanisms that produce phenotypic variation, an interesting point was to investigate whether this 1-month difference in breeding time between the two populations is a proximate plastic response to environmental variation, or whether it results from genetic differentiation as a response to local selection pressures. We answered this question from experiments in aviaries using chicks from late-breeding Corsican tits and from early-breeding mainland tits which had been hand-raised in a common garden environment in Montpellier. These captive tits successfully bred and were submitted to four light treatments, starting at different times of the year (see Lambrechts et al. 1997a for details). In a first experiment, birds were kept in aviaries under a natural photoperiod. Eleven pairs from Corsica started to breed 1 month

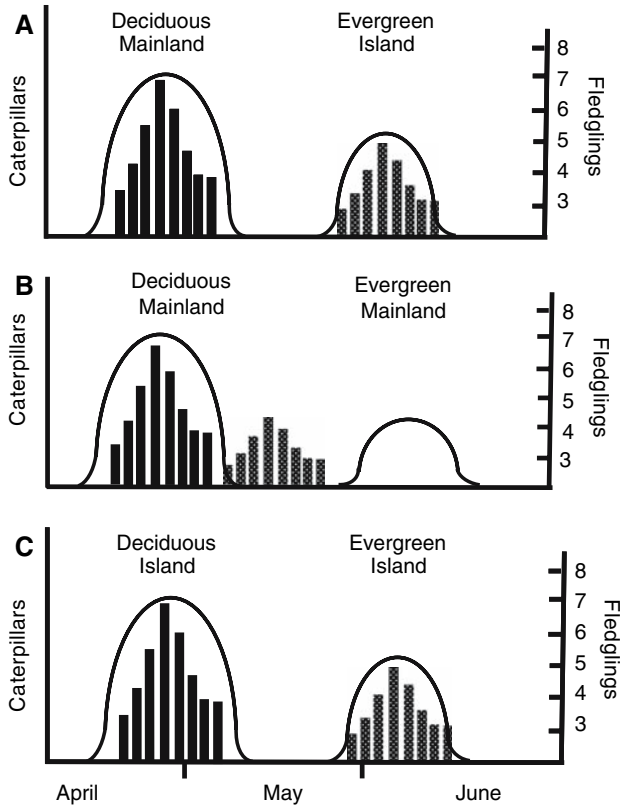

Fig. 3 Caterpillar abundance (*curves*) and number of fledglings (*histograms*) in deciduous and evergreen habitats on the mainland and in Corsica. **a** Between-landscape scale. **b** Within-landscape scale on the mainland. **c** Within-landscape scale on Corsica. See text

later than eight pairs from the mainland, exactly as did free-living birds in their respective populations of origin, suggesting a genetically-based response mechanism. In a second experiment, the two samples of birds (seven pairs from Corsica and four pairs from the mainland) were submitted to an artificially advanced spring through a progressive increment of artificial light by 15 min per week, starting in November before the gonads developed. The two samples advanced their breeding time to adjust to this artificial spring but still kept their 1-month difference in laying date. In a third experiment, birds were exposed at once from mid-December onwards to a sudden increase of photoperiod with an artificial long day length exceeding the day length which triggers laying in the late Corsican population (17 h light–7 h dark). They also advanced their breeding time, but the two samples started to breed on average at the same date, thus erasing the 1-month difference in laying date. Finally, in a fourth experiment, the same treatment performed in summer instead of winter provided the same result. These experiments showed that these mainland and island blue tits can start breeding at any time of the year when submitted to a suitable artificial light treatment. They are a demonstration that the 1-month difference in breeding time does not result from phenotypic plasticity but is a genetically-based local specialisation of populations to the consistent and predictable difference in the local timing of food availability. Response to photoperiod varies depending on populations and is the proximate mechanism which explains the large population differences in the onset of breeding between the two habitats. Because the onset of reproduction must start long before the food demand of nestlings is maximal, adult tits must use proximate mechanisms to anticipate the most favourable period for raising young which will occur more than 1 month later. Photoresponsiveness is the most reliable cue for adjusting reproduction because it opens and closes a window of time within which other proximate factors that vary from year to year, for example, temperature or food, finely adjust the onset of breeding in each particular year.

Mismatching the peak of food

A second step was to check whether the same kind of habitat-specific local adaptation occurs not only between landscapes but also within landscapes. If birds in the patches of the other oak type (evergreen on the mainland, deciduous on Corsica) equally optimise the supply/demand ratio of food, they would start to lay approximately 1 month later in evergreen habitats than in the main deciduous habitat discussed above on the mainland, and 1 month earlier in the deciduous than in the main evergreen habitat discussed above on the island. This was not the case, however (Fig. 3b). Populations in evergreen oaks on the mainland started to breed too early and missed the peak of food, producing few offspring of poor quality with low prospects of being recruited in the population. The most likely explanation for mismatching the peak of local resources is gene flow across habitat patches with genotypes which evolved in the more common habitat emigrating to the less common habitat, thus carrying genes for breeding early in deciduous oaks and much later in evergreen oaks (Dias and Blondel 1996). It is difficult to demonstrate exchanges of individuals between habitats but two lines of evidence suggest asymmetrical gene flow across habitats, potentially resulting in a source-sink population structuring within landscapes. First, using fingerprinting of minisatellite loci for estimating the degree of genetic differentiation of individuals within and between populations on a scale of 50 km or so in the mainland landscape, Dias et al. (1996) showed that birds were genetically more differentiated among caterpillar-rich habitats than between them and caterpillar-poor habitats. This suggests that tits from caterpillar-rich and poor habitats belong to the same populations with caterpillar-rich habitats functioning as sources,

and caterpillar-poor habitats functioning as sinks, with birds breeding in the sinks immigrating from sources where they evolved habitat-specific breeding traits. One more indication for such a pattern is that the effective number of migrants per generation, estimated from Wright's statistics, was much higher between poor putative evergreen sink habitats and rich putative deciduous source habitats than between either evergreen or deciduous habitats (Dias et al. 1996). The second indication comes from quantitative genetics (Charmantier et al. 2004a). There was no significant response to selection despite significant heritability of this trait and significant selection differentials when all birds in the populations were pooled together, but a positive response to selection became significant when only philopatric, that is locally born tits, were considered. This is a strong indication that gene flow from other habitats prevents response to local selection.

This finding on local maladaptation is not new. Other examples of gene flow counteracting local responses to selection and resulting in local maladaptation or phenotypic variation at small spatial scales have already been provided in great tits *Parus major* in the Netherlands by van Balen (1973) and in Belgium by Dhondt et al. (1990). In the Netherlands, great tits started breeding too early in pine woods because they carried genes for earlier breeding in deciduous oak forest. More recently, Postma and van Noordwijk (2005) demonstrated that a consistent difference in clutch size between subpopulations of great tits at a small spatial scale on the island of Vlieland, The Netherlands, was not driven by divergent selection but by gene flow from the nearby mainland. In Mediterranean landscapes, a similar pattern of maladaptation was found in several populations breeding in the less common habitats of the two landscapes. Blue tits in evergreen habitats on the mainland started breeding too early and had a negative offset between breeding time and the caterpillar peak whereas tits in deciduous habitats on Corsica started breeding too late and had a positive offset with interesting exceptions which will be discussed below (Dias and Blondel 1996).

It is noteworthy, however, that whatever the extent of the offset between food demand and food supply in the maladapted populations, there was some habitat tuning in the less common habitat patches of each landscape. Birds started to breed slightly later in the evergreen mainland sites and slightly earlier in the deciduous island study site than in the corresponding commoner habitats of each region (see Fig. 3b for the mainland patterns). The same was true for clutch size which was always higher in deciduous than in evergreen habitats with intermediate values in the less common habitats of each landscape. These shifts in breeding traits are an expression of phenotypic plasticity within a window which allows to compensate to some extent the large offset between food supply and demand.

The cost of maladaptation

The pattern in which early-breeding phenotypes overflow from deciduous oak patches into evergreen oak patches where birds miss the best time to breed provides a unique, quasi-experimental, opportunity for exploring the energetic and fitness costs of supply-demand offset. Assuming strong selection pressures for breeding when food is plentiful, any offset in the supply/demand ratio should incur a cost for both parent birds and their offspring and should be counter selected, especially in evergreen habitats where food is never abundant. The cost of mismatching the peak of food has been measured by comparing energy expenditure of parent blue tits in two caterpillar-poor habitats where the abundance of caterpillars has been monitored during 10 years. Tits were nicely synchronised with the peak of food in one habitat but there was a negative offset of more than 2 weeks in the second habitat. Comparing the workload and energy expenditure of parent tits from doubly-labelled water experiments, using joules as a currency of energy, Thomas et al. (2001) showed that the cost for rearing chicks increased from around 1.5 kJ per day and per gram of chick in well-matched broods, to up to more than 3.0 kJ in mismatched broods. This cost decreased as the offset between laying date and caterpillar peak decreased. Measures of the daily metabolic effort of adults from the ratio of field metabolic rate over basal metabolic rate (FMR/BMR) showed an increase of this ratio from about three times to more than six times the BMR in mistimed birds. Again, this cost decreased as the offset decreased to reach a value of 3–4 BMR which corresponds to a workload that is typical for breeding birds when provisioning their young (Nagy 1987). The large increase in metabolic effort of mismatched birds which had to work far beyond their sustainable limit was associated with a much shorter persistence time of birds on their breeding sites (1.35 years for males and females compared to 2.16 and 2.23 years in mismatched and matched pairs, respectively (Thomas et al. 2001). Low persistence time, which is a proxy for low prospects of survival, is associated with a much reduced percentage of birds more than 1 year old in the mistimed population; hence, a shorter generation time with many yearlings in this population (Blondel et al. 2006).

Following our predictions on the relationships between breeding performance and the amount of food, the energetic cost of mismatching the peak of food is expected to be a function of the amplitude and breadth of the spring flush of caterpillars. In caterpillar-poor evergreen habitats, mismatching the caterpillar peak has marked effects on breeding performance, for example, brood size and fledging success, because in addition to low food abundance, the window of food availability is much shorter. In contrast,

missing the peak of food should have very little or no effect at all in caterpillar-rich habitats because the amplitude and breadth of food supply allow birds to easily compensate for any variation of food abundance. We do not have data in our study populations on the effects on energy expenditure of mismatching the peak of food in caterpillar-rich habitats. But in a great tit population in the Netherlands, where food abundance was of a same order of magnitude as that in our caterpillar-rich deciduous habitats, Verhulst and Tinbergen (2001) have shown that an offset of up to 20 days before or after the caterpillar peak did not result in any significant change in daily energy expenditure.

Why is phenotypic variation higher on the island of Corsica?

One conclusion of these results is that phenotypic variation of blue tits in Mediterranean landscapes is a response to a combination of spatial heterogeneity in the tempo and mode of food resources and components of landscape genetics. But this is only part of the story. What makes the Mediterranean region truly apart in the north–south succession of life zones in the western Palaearctic is the combination of a highly diversified design of landscapes, because of the millennial impact of humans, and a very complicated geomorphology with habitat islands, true islands and mountain ranges that dissect landscapes and isolate populations, potentially producing local habitat-specific evolutionary responses (Blondel and Aronson 1999).

Our studies of blue tits on the island of Corsica provide one example of the consequences on phenotypic variation of geographic isolation within the Mediterranean. At first sight, the similar geographic configuration of habitat patches in the mainland and insular landscapes was expected to produce similar patterns of mismatching between laying date and the optimal breeding time on the island of Corsica as that on the mainland, but the other way around because evergreen oaks, not deciduous ones as on the mainland, dominate the landscape. However, although our mainland and Corsican landscapes fairly well match each other, more populations were correctly synchronised to the peak of food in Corsica than on the mainland, which makes phenotypic variation of laying date much larger on this island (Fig. 4). In the five habitats of Corsica, tits started egg laying within a range of 29 days as compared to only 9 days on the mainland. In a deciduous oakwood located only 25 km apart from the main evergreen habitat, tits were surprisingly as correctly timed to the caterpillar peak as those in the evergreen habitat, a pattern which strongly differs from that on the mainland where birds breeding in the other oak habitat mismatched the caterpillar peak

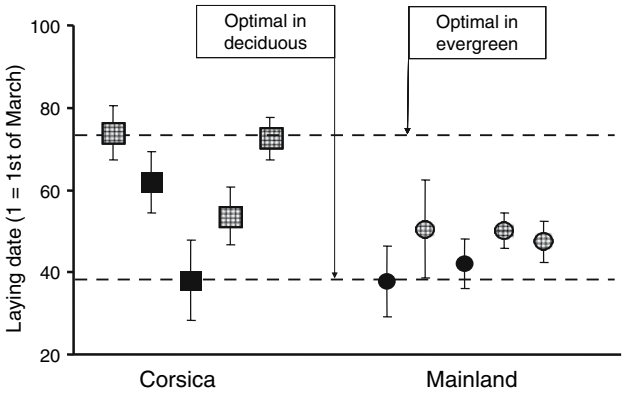

Fig. 4 Phenotypic variation of laying date for blue tits (±1 SD). *Horizontal dotted lines* denote the best date for starting breeding relative to food availability in deciduous and in evergreen oakwood, respectively. *Black symbols* deciduous habitats, *squared symbols* evergreen habitats. Note the much higher variation of laying dates in Corsica than on the mainland (modified from Blondel et al. 2006)

(Lambrechts et al. 1997b; Blondel et al. 1999; Fig. 3c). In addition, the two populations differed in a number of traits including demographic, morphological and behavioural traits as a response to consistent differences in habitat quality (Table 1).

Thus, these two populations of blue tits only a few kilometres apart have evolved specialisation to local habitats, which is a demonstration that adaptive responses to habitat-specific selection regimes may operate on a scale which is much smaller than the scale of potential dispersal and gene flow. What makes Corsican populations differ so much from those on the mainland, and explains a larger phenotypic variation of traits with tighter habitat-specific adaptations at a small spatial scale, is reduced dispersal in island birds which is a component of the so-called insular syndrome (Diamond 1983; Blondel 2000) which has been shown to occur in Corsican birds (Blondel et al. 1988). In the gene flow/selection tension, stronger habitat fidelity combined with habitat-specific associative mating (Blondel, unpublished) results in lower dispersal rates and hence lower gene flow in Corsica than on the mainland. These patterns are conducive to local specialisation and population structuring, whereas high dispersal on the mainland leads to phenotypic plasticity and, possibly, local maladaptation.

Local adaptation to Mediterranean-specific constraints

This pattern in Corsica with two populations facing very different environmental features to which they seem to be equally well adapted provides a quasi-experimental and fascinating opportunity for investigating the ecological and

Table 1 Differences in ecology and morphometry between two populations of blue tits *Cyanistes caeruleus* living in evergreen holm oaks and in deciduous downy oaks on the island of Corsica

	Evergreen	Deciduous	*P*
Population density	1.04 ± 0.19 (30)	1.38 ± 0.44 (18)	***
Mean peak caterpillar frass (mg/m^2)	172 ± 102 (21)	1347 ± 327 (15)	***
Laying date	73 ± 4.0 (694)	41 ± 11.8 (400)	***
Clutch size	6.4 ± 0.4 (360)	8.5 ± 0.6 (204)	***
Breeding success	0.52 ± 0.13 (310)	0.82 ± 0.04 (195)	**
Fledging mass	9.3 ± 0.83 (448)	10.4 ± 0.53 (357)	***
Body mass of males	9.4 ± 0.30 (422)	10.0 ± 0.53 (234)	***
Body mass of females	9.3 ± 0.43 (437)	9.8 ± 0.52 (278)	*
Tarsus length of fledglings	15.89 ± 0.61 (211)	16.28 ± 0.40 (304)	***
Tarsus length of males	16.26 ± 0.48 (389)	16.50 ± 0.49 (231)	***
Tarsus length of females	15.85 ± 0.54 (421)	16.00 ± 0.44 (262)	*
Proportion of yearlings	0.23 ± 0.13 (35)	0.41 ± 0.14 (16)	***

Samples sizes in parentheses (years for population density, caterpillar frass and proportion of yearlings; after Blondel et al. 1999, 2006)

Population density in breeding pairs per ha, laying date in "March-dates", i.e. *1* = 1 March, breeding success = no. fledgings/clutch size

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

evolutionary responses of birds to habitat-specific features and constraints. Adaptation to two constraints will be briefly described.

The first constraint is food supply. Large differences in the tempo and mode of food resources between evergreen and deciduous oaks make the relationship between food and breeding performance of tits quite different in the two habitats. Breeding performance is expected to increase as the supply/demand ratio of food increases, saturating at some level of supply below which food is expected to be limiting and above which it is expected to be superabundant. From data on breeding performance in relation to food availability, Tremblay et al. (2003) empirically estimated the food saturation point at about 500 mg of caterpillar frass per square metre and per day. Indeed, in the caterpillar-poor evergreen habitat of Corsica, breeding performance (scaled as the proportion of maximal performance for whatever trait, for example fledging success or fledging mass) strongly increases as the supply demand ratio increases. But above the saturation point, food becomes superabundant so that parent birds can easily compensate for any variation in local food abundance. Tremblay et al. (2003) used three surrogates for measuring the effect of food variation on breeding success, namely (1) the peak of caterpillar frass production, (2) the offset between the caterpillar peak and the peak of food demand, and (3) clutch size which is an indication of the workload of parents tending their chicks. In the poor evergreen oakwood, all three variables had significant effects on breeding performance but not in the rich deciduous oakwood. A steep slope of fledging mass and fledging success as a function of caterpillar abundance showed that both mass and success were sensitive to changes in food supply when food is limiting. On average, peak brood biomass varied from ca. 59 g in poor evergreen habitats (6.3 chicks × 9.3 g) to ca. 86 g in rich deciduous habitats (8.3 chicks × 10.3 g), but at the same time the supply–demand ratio increased from 1.6 to 16.2 over the same gradient (Tremblay et al. 2003). In evergreen habitats, various combinations of constraints including food shortage, high parasite loads and high temperatures make breeding conditions of these late-breeding birds much more variable and sometimes extremely poor (Blondel et al. 1999; Tremblay et al. 2003; Simon et al. 2004). Therefore, any deviation of the offset between supply and demand will have strong effects on breeding performance below this saturation threshold but hardly any effect above it.

These different patterns of food availability allowed the investigation of how tits worked for providing a similar amount of energy to few chicks in a poor habitat and many chicks in a rich habitat. Tremblay et al. (2005) radio-tagged a sample of tits and followed them while they foraged. Tits have been found to forage much closer to their nest in deciduous oaks (25.2 ± 12.3 m) where caterpillars were plentiful than in evergreen oaks (53.2 ± 22.9 m) where they were much scarcer. They also made twice as many foraging trips (36.5 ± 10.5 vs 17.0 ± 4.5 visits), hence travelling similar distances in the two sites, i.e. 1,840 and 1,809 m h^{-1}, respectively. Many short trips in one site and fewer longer trips in the other led to birds patrolling over four times larger surface areas in the evergreen habitat (7,854 m^2) than in the deciduous habitat (1,963 m^2). However, quite interestingly, prey size was 77% higher in the evergreen habitat than in the

deciduous habitat (0.19 ± 0.05 cm^3 compared to 0.11 ± 0.04 cm^3). We do not know whether larger size of caterpillars in evergreen oaks is because tits select larger prey or because caterpillars grow faster when ambient temperatures increase as the season progresses. But, all in all, larger prey size and fewer chicks made the total amount of food provided to each chick similar in the two habitats (0.36 ± 0.012 cm^3 h^{-1} chick^{-1} in the deciduous compared to 0.39 ± 0.09 cm^3 h^{-1} chick^{-1} in the evergreen habitat). Because brood size and chick mass were higher in deciduous than in evergreen oakwood, parents in the former had to provide food for a greater chick biomass (39% higher in a 3-year study by Tremblay et al. 2005), which was not a problem for them since caterpillar abundance was 581% higher than in evergreen oaks.

The second constraint is parasitism. Several populations of blue tit are heavily parasitised by the blood-sucking larvae of two species of blowflies (*Protocalliphora azurea* and *P. falcozi*), especially in evergreen habitats of Corsica where parasite prevalence usually reaches more than 90% of the nests. A large spatial variation in infestation rates of these parasites is an important contributor to environmental heterogeneity. There may be up to 150 of these larvae swarming in a single nest, i.e. 30 g, more than half the total mass of the six chicks (Hurtrez-Boussès et al. 1997). Blowfly larvae live in the nest material and, three to four times a day, climb up the chicks, attach to the edge of their wing, leg or bill and feed on blood, pumping more than one-third of the blood of the brood each day. This makes chicks quite uncomfortable in their nest, spending much of their time moving, grooming and trying to escape the bites of the parasites (Simon et al. 2005). Parasites do not attack adult birds but they have many detrimental effects on chicks: they reduce fledging mass, tarsus length, hematocrit values, post-fledging survival and metabolic capacity, resulting in an overall metabolic depression which reduces all anabolic processes including growth (Hurtrez-Boussès et al. 1997; Simon et al. 2004, 2005). As a result, fitness costs of parasites could be particularly harmful after fledging, when birds are relieved of them but at a time when they need most energy for moulting and escaping predators. In addition, Charmantier et al. (2004b) showed that parasitism reduces the additive genetic variance of traits, hence their heritability, for example tarsus length, potentially constraining an evolutionary response to selection.

To sum up, compared to blue tits breeding in rich deciduous oaks on Corsica, tits which breed in poor evergreen oaks differ in a number of traits: (1) they are smaller in size and forage over larger areas, (2) they have developed various behavioural and evolutionary defences against parasites including a different sharing of parental care, with females spending much time in nest sanitation, which is compensated by a considerable increase in chick provisioning by males (Hurtrez-Boussès et al. 2000), (3) these changes are associated with a higher sexual size dimorphism, with selection for smaller males, presumably linked to increased foraging activities (Blondel et al. 2002), (4) response to selection pressures could be constrained by lower heritability of traits in heavily parasitised populations (Charmantier et al. 2004b), (5) mating systems include more extra-pair young during a current breeding attempt (Charmantier and Blondel 2003) and higher divorce rates at the next breeding attempt (Blondel et al. 2000), and, finally, (6) on the whole breeding in evergreen oaks results in a reduced fecundity, higher adult survival, lower proportion of yearlings in the breeding population, but also a high year-to-year variation in response to high variation of limiting food resources and parasitic loads.

This case study of Corsican blue tits shows that close habitat-specific adaptations involve suites of traits including body size and shape, life history and demographic traits that do not necessarily evolve independently from one another. Theory predicts that if the environment is relatively constant in space, which is true in the two types of Mediterranean oakwoods, maximising mean fitness results in a specialised phenotype because environmental constancy favours the evolution of specialisation (Futuyma and Moreno 1988) even if gene flow is in excess of a few migrants per generation (Stearns 1992). In vertebrates, differentiation of phenotypes on a microgeographic scale has rarely been proven to be adaptive although local variation of fitness-related traits as a result of resource-based divergent selection expresses the process of adaptation (Reznick et al. 1990; Garland and Adolph 1991). Corsican populations of blue tits provide a striking example in birds of adaptive response of suites of life history traits to habitat-specific selection regimes that operate on a scale which is much smaller than the scale of potential gene flow. A large body of theoretical work shows how selective variation can be maintained because of spatial heterogeneity (e.g. Maynard-Smith 1966; Felsenstein 1976; Hedrick 1986) giving support to the "divergence with gene flow" model of speciation according to which reproductive isolation can evolve between populations connected by gene flow whenever divergent selection is strong relative to gene flow (Rice and Hostert 1993).

Does phenotypic variation reflect genetic variation?

One may expect that the large amount of observed phenotypic variation in Mediterranean blue tits reflects a large amount of underlying genetic variation. However, geographically structured intraspecific variation has

traditionally been considered not to occur at the scale of landscapes in birds because dispersal and gene flow are assumed to prevent evolutionary differentiation (Slatkin 1985; Bohonak 1999). Using seven highly polymorphic microsatellite loci, Charmantier (2000) showed that mainland populations of the *caeruleus* form are differentiated from Corsican populations of the *ogliastrae* subspecies ($F_{st} = 0.031$), but this value is low for two subspecies that have been isolated for a long time. Interestingly but not unexpectedly given their large phenotypic differences, populations in evergreen oaks on Corsica are genetically differentiated from those breeding in deciduous oaks, which is not the case on the mainland. Thus, although the F_{st} values remained small albeit still significant (0.015, $P < 0.01$), the prediction of some genetic structuring within Corsica as a result of low dispersal on the island is supported. However, the very small value of genetic divergence (0.011) between the two populations we studied in detail contrasts with the large inter-population phenotypic variation we observed in many traits. This is one more example that natural selection can produce rapid and sometimes strong adaptive morphological divergence in the absence of discernable differentiation at neutral DNA loci and that weak genetic differentiation does not necessarily mean phenotypic resemblance. An increasing number of studies from various groups of animals show that natural selection can produce rapid adaptive morphological divergence in the absence of discernable differentiation at neutral DNA loci (Merilä et al. 2001). In this context, one interesting example is that of Crossbills in the western Palaearctic and North America. The four species of crossbill, *Loxia curvirostra, L. scotica, L. pytyopsittacus* and *L. leucoptera* have been separated mostly on the basis of the size and shape of their bill (Cramp and Perrins 1994). But Questiau (1999) and Piertney (2001) have shown from molecular phylogenetics that, except for the two barred crossbill *L. leucoptera* which is clearly differentiated from all other populations, genetic variation is not greater between the other three species than within them. Therefore, the various crossbill lineages over Europe must be included in only two species, the two-barred well differentiated crossbill *L. leucoptera*, and the common crossbill *L. curvirostra* which encompasses in a single polytypic species all European and North American populations. These populations are linked by gene flow but they keep phenotypic differences in bill size as a response to persistent directional selection pressures from the highly variable size and hardiness of the seeds of conifers the different populations feed upon. Such discrepancies between high morphological differentiation and weak genetic differentiation at small geographical scales have also been found in several species of fish (Nagel and Schluter 1998) and birds (Smith et al. 1997). They indicate that divergence results from directional selection counteracting gene flow rather than from geographic isolation.

Although all the morphological traits examined in our blue tits showed significant heritabilities and several of them are under consistent directional selection, most of them failed to show the expected evolutionary responses (Charmantier et al. 2004a). Another similar example has been provided by Garant et al. (2004) on fledging mass in the great tit. Many factors may explain why traits have considerable additive genetic variance, appear to be under directional selection and yet do not evolve (Price et al. 1988; Kruuk et al. 2001; Merilä et al. 2001). They include, among others, environmental causes, biasses in estimating heritabilities, gene swamping across habitats, divergence in selection regimes in two neighbouring habitats (Lande and Arnold 1983), and genetic correlations between sexes for a given trait or with other targets of selection.

Reaction norms

To summarise from a reaction norm approach applied to the onset of breeding, two sets of blue tit populations evolved local specialisation to the commoner habitat in each landscape (Fig. 5). The two parallel lines that do not cross correspond, so to speak, to a "deciduous genotype" in mainland forests mostly dominated by deciduous trees, and to an "evergreen genotype" in Corsican oak forests mostly dominated by evergreen trees. They express reaction norms of populations, that is the range of phenotypes

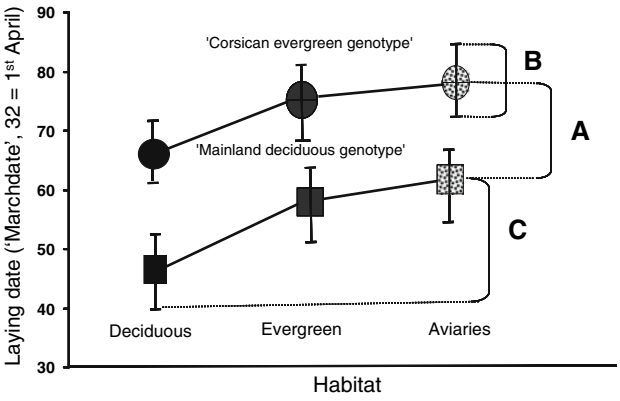

Fig. 5 Reaction norms for the onset of breeding for each set of populations of blue tits breeding on the mainland and in Corsica. The *two distinct lines* correspond to "evergreen" and "deciduous" genotypes in Corsica and the mainland, respectively (*A*). The variation of laying date around the mean (standard deviation, *B*) and across habitats (deciduous, evergreen, aviaries, *C*) is an expression of the phenotypic plasticity of the populations in time and in space (modified from Lambrechts and Dias 1993; Blondel et al. 2006)

that are produced by a single genotype along an environmental gradient which includes three habitats, deciduous oak forest, evergreen oak forest, and aviaries (Blondel et al. 2006). In addition, each of these genotypes can be expressed through some degree of phenotypic plasticity both in time and space. In time, variation of laying date around the mean is the year-to-year proximate response of birds to variation of several factors such as temperature or food which may operate within the window of photoresponsiveness (Fig. 5b). Phenotypic variation in space is a response to habitat-specific features with birds starting to breed consistently earlier in deciduous habitats than in evergreen habitats and in aviaries (Fig. 5c). For evolving local habitat-specific specialisation, the niche or habitats to which different sub-populations adapt should be markedly different and display a long-term persistence even if ecological factors such as food or parasites may fluctuate enormously from year to year. One factor of great importance suggested by theoretical investigation as well as by some studies, for example the studies of Grant and Grant (1989) on the large cactus finch *Geospiza conirostris* of the Galapagos, is the way in which the environment is heterogeneous. Only when heterogeneity is strong is the difference between the extremes large and persistent so that population variation is large with selection being strong enough to produce divergent differentiation. This is obviously the case in Mediterranean blue tits.

Conclusion and future prospects

One message of this study is that environmental heterogeneity has to be of a special kind to foster such a high degree of population differentiation at the scale of landscapes. Our study system represents an extreme case of habitat heterogeneity and divergent selection regimes at the scale of landscapes for small passerines in temperate habitats. The most fascinating feature of the story, with a cascade of consequences on life histories, is the 1-month difference in tits' breeding time depending on which oak morphotype they settle in. Contrasting directional selection pressures that characterise the two kinds of oakwood for tits produced a range of adaptive phenotypic responses and were strong enough to make the process of adaptation easier to dissect for analysis. These large habitat-specific differences in local selection regimes make gene flow potentially producing local maladaptation and a source-sink population structuring depending on the extent of dispersal. However, local specialisation of blue tits in Corsican habitat mosaics supports the "divergence with gene flow" model of differentiation: gene flow does not necessarily prevent local adaptation if opposing selection regimes favour niche-specific adaptations. Finally, comparing the responses of less-dispersive island birds and highly dispersive mainland birds to the same spatial diversity of habitats gives us a practical demonstration of the relationships between dispersal, spatially variable selection, and local adaptation. Spatially structured populations on Corsica illustrate that increased biodiversity at the intra-specific scale on islands compensate to some extent for the decrease of biodiversity at the inter-specific scale which is a common feature on islands.

Several additional studies on this model are in progress or should be addressed. They include the following: (1) try to decipher the relative roles of isolation, gene flow, selection and random drift on the phenotypic variation of traits by comparing the degree of differentiation of molecular markers (F_{st}) with that of quantitative traits of which the genetic basis is estimated (Q_{st}; e.g. Merilä and Crnokrak 2001), (2) investigate the degree of habitat-specific tightness using stable isotopes and/or trace elements (Hobson and Wassenaar 1997) to examine to which extent tits are specialised to each oak morphotype, (3) find at which threshold of frequency and size of habitat types selection regimes will shift from specialisation to one habitat type to specialisation to the other—this point could be approached from a landscape genetics perspective which, through an amalgamation of molecular population genetics and landscape ecology, provides information about the interaction between landscape features and microevolutionary processes (Manel et al. 2003), and, finally, (4) by advancing the phenology of budding, leaf production and food supply, climate warming is expected to exacerbate the mismatching between food supply and nestling demand for a broad spectrum of terrestrial birds until directional selection adjusts laying date to new optimal dates. Breeding time is one of the many traits that will be affected by global change. The tempo and mode of all the microevolutionary processes that will be associated with our changing world will be worth studying in detail if we are to predict the consequences of these changes on the distribution and abundance of animals.

Acknowledgments I warmly thank many colleagues and friends who participated for many years to this long term project, especially Philippe Perret, Don Thomas, Marcel Lambrechts, Paula Dias, Anne Charmantier, Claire Doutrelant, Patrice Bourgault, Adèle Mennerat, Marie Maistre, Mireille Cartan-Son and Marie-José Galand. Many students, research and technical staff, as well as postdoctoral researchers, also contributed in some way to this programme. The blue tit project also benefitted from many people in Montpellier and elsewhere within the informal hole-nesting birds study group in Europe. Financial support has been generously provided over the years by the Centre National de la Recherche Scientifique, the European Union, the Association pour l'Etude Ecologique du Maquis, the Parc Naturel Régional de la Corse, the Natural Sciences and Engineering Research Council of Canada, and the National Geographic Society. Arie van Noordwijk made very useful comments on a first version of this paper. Warm thanks to all of them.

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