

A Thirty-Year Study of Phenotypic and Genetic Variation of Blue Tits in Mediterranean Habitat Mosaics

JACQUES BLONDEL, DONALD W. THOMAS, ANNE CHARMANTIER, PHILIPPE PERRET, PATRICE BOURGAULT, AND MARCEL M. LAMBRECHTS

In recent years, the study of phenotypic and genetic variation has been enhanced by combining genetic, physiological, demographic, and behavioral components of life histories. Using these new approaches, we address the problem of adaptation to environmental heterogeneity by examining in detail the variation of several fitness-related traits in a small passerine bird, the blue tit, which has been extensively studied in habitat mosaics of the Mediterranean region. The response of blue tits to spatial habitat heterogeneity depends on their range of dispersal relative to the size of habitat patches. Dispersal over short distances leads to local specialization, whereas dispersal over long distances leads to phenotypic plasticity. Gene flow between habitats of different quality may produce local maladaptation and a source-sink population structure. However, when habitat-specific divergent selection regimes are strong enough to oppose the effects of gene flow, local adaptation may arise on a scale that is much smaller than the scale of dispersal.

Keywords: gene flow, local specialization, phenotypic variation, plasticity, reaction norm

Habitat heterogeneity is universal, regardless of spatial scales or parameters (Bell et al. 1993). Thus, a basic problem in evolutionary biology is understanding how the balance between local selection and gene flow determines the extent to which populations become adapted to heterogeneous environments (Bohonak 1999). This problem was first addressed long ago by Wright (1940), who stressed the evolutionary interplay between gene flow and local specialization through dispersal, founder effects, genetic drift, and natural selection. Quantifying phenotypic and genetic variation is a prerequisite to understanding how organisms respond to selection in changing environments. However, despite a recent surge of interest in the evolution of local adaptation, particularly regarding the impact of climate change on the evolution of life histories, few studies on animals have investigated the relationship between phenotypic variation and variation of selection pressures at a microgeographic scale. One notable exception is the textbook case showing the evolution of beak and body size in Darwin's Galápagos finch *Geospiza fortis* following episodes of strong directional selection (Grant and Grant 1995). However, we still know little about how selection on quantitative traits in spatially structured populations (those occupying different habitats within a landscape) determines genetic variation among populations (Hendry et al. 2001, Charmantier et al. 2004a, Postma and van Noordwijk

2005). One reason that few studies have adequately addressed the problem of spatial phenotypic variation is that most long-term field projects face a logistical trade-off between (a) the plot size and number of study sites and (b) the intensity of data collection. This trade-off typically results in research that emphasizes detailed studies of single populations and study sites rather than multiple populations scattered across varied landscapes.

The purpose of our study was to investigate phenotypic variation using a small (9- to 13-gram [g]) forest passerine bird, the blue tit (*Cyanistes caeruleus*), which is widespread in forested habitats of the western Palearctic, ranging from southern Scandinavia in the north to the Canary Islands in the south of its breeding range. Our goal was to explore how

Jacques Blondel (e-mail: jacques.blondel@cefe.cnrs.fr), Philippe Perret, and Marcel M. Lambrechts are with the Centre d'Ecologie Fonctionnelle et Evolutive, Centre National de la Recherche Scientifique, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France. Donald W. Thomas is a professor, and Patrice Bourgault is a researcher, with the Groupe de Recherche en Ecologie, Nutrition, et Énergétique, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada. Anne Charmantier is with the Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom. © 2006 American Institute of Biological Sciences.

blue tit populations cope with the extreme habitat heterogeneity found in Mediterranean landscapes, which typically consist of forest patches dominated by broad-leaved deciduous or evergreen tree species. Our fundamental approach was to monitor the movements and reproductive histories of as many marked individuals as possible, for up to 15 generations, from a variety of populations or subpopulations inhabiting divergent habitat types.

The blue tit is a hole-nesting bird that readily breeds in artificial nest boxes and accepts being caught and manipulated without deserting its nest, thus making it possible to collect large data sets on its demography, behavior, morphology, and other phenotypic traits. During the breeding season, blue tits feed on a wide range of invertebrates, but their preferred prey consists of leaf-eating caterpillars, which are available for only two to three weeks in spring (Zandt et al. 1990, Bañbura et al. 1994). When caterpillars are in short supply, tits switch to a large variety of alternate arthropod prey. Nestling tits are host to a panoply of parasites, the most impressive of which are the blood-sucking larvae of blowflies (*Protocalliphora* spp.). These ectoparasites, which may be very abundant in evergreen habitats, can have a marked negative impact on nestling growth and survival. A large spatial variation in infestation rates of *Protocalliphora* parasites is an important contributor to environmental heterogeneity.

We conducted our study in two landscapes located at a similar latitude (between 42 degrees north [$^{\circ}$ N] and 43 $^{\circ}$ N) and altitude (ranging from 80 to 370 meters [m] above sea level) in southern France: a landscape on the mainland near Montpellier, where the blue tit belongs to the continental subspecies *C. caeruleus caeruleus*, and a landscape on the island of Corsica, 80 kilometers (km) off the coast of Italy (figure 1), where the blue tit belongs to the subspecies *C. caeruleus ogliastreae*, which is approximately 15% smaller. Each landscape is a mosaic of habitat patches dominated either by the deciduous, broad-leaved downy oak (*Quercus humilis*) or by the evergreen, broad-leaved holm oak (*Quercus ilex*). The geographical configuration of landscapes was similar in the two regions, but deciduous oak forests were more common than evergreen oak forests on the mainland, whereas the opposite was true in Corsica. This feature will be shown to have important consequences for the spatial structure of populations.

Mediterranean landscapes provide a fascinating opportunity for exploring the consequences of habitat heterogeneity and patchiness on the phenotypic variation of a small bird such as the blue tit. From a bird's perspective, all landscapes are to some extent mosaics of habitats, but Mediterranean landscapes are particularly interesting because they consist of variable proportions of patches dominated by either deciduous or evergreen oak forest. A crucial element of the story is that food chains, starting with the production of young leaves and cascading through herbivorous caterpillars to insectivorous blue tits, follow different temporal trajectories in the two oak forests because of the timing of spring bud burst. Deciduous downy oak produces a large crop of young, tender leaves approximately one month earlier than ever-

green holm oak, which renews only 30% of its foliage in a given year. The one-month offset in bud burst and the differences in spring leaf production result in an early, high-amplitude peak in caterpillar production in downy oak forests and a late, low-amplitude peak in holm oak forests. Because forest types tend to be homogeneous, with more than 95% of the trees belonging to a single oak species, and because the home range and dispersal range of blue tits are generally small relative to the size of oak forest patches, birds typically live and breed in a single habitat type. In downy oak forest, birds have an early and abundant caterpillar supply, but in holm oak forest, food is available only later in the season and in lesser quantities. These differences in the timing and abundance of food have important consequences for fitness features, such as breeding date, clutch size, and number of fledglings, and have been the subject of considerable research in the field of evolutionary ecology over the past 30 years (e.g., Blondel et al. 1993).

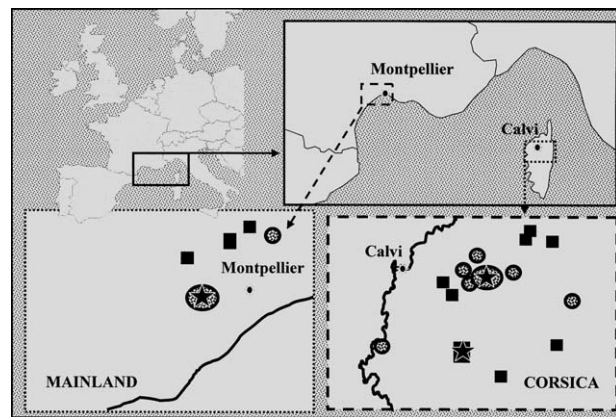


Figure 1. Locations of the two landscapes and study sites. Stippled circles denote deciduous sites (downy oak) and black squares evergreen sites (holm oak). Stars denote the main study sites.

In recent years, the study of phenotypic and genetic variation has been enhanced by the development of new techniques, including mathematical modeling of gene frequency changes, statistical methods to quantify natural selection, experimental manipulation of phenotypes in the wild, and the application of molecular tools to quantify gene flow among natural populations. These techniques have provided new insight into the evolution of breeding traits in blue tits.

In this article we provide a synthesis of our study on phenotypic variation of blue tits in Mediterranean habitat mosaics for over 30 years, highlighting the importance of considering spatial scales when studying an organism's ecological and evolutionary context. We cannot present all of our findings; rather, we focus on questions that are relevant in the context of phenotypic variation, namely:

- How much do breeding performance, foraging patterns, and morphology vary among populations and phenotypes in response to habitat features and constraints?

- To what extent do birds move between habitat patches that differ in the timing and abundance of their food supply? Does mistiming of breeding relative to the period when food is plentiful incur a cost for the birds and their progeny? Are the magnitude and consequences of dispersal across habitats similar on the mainland and in Corsica?
- Is phenotypic variation a reflection of genetic divergence?
- Do blue tits disperse randomly with regard to forest type and exhibit a large degree of phenotypic plasticity, or do they select habitats with a particular type of tree, where they evolve local specialization?

Setting the scene: Habitats, study models, and data collection

In each landscape, one or two main study sites ranging from 50 hectares (ha) to over 200 ha in size have been monitored for many years (since 1975 for the oldest site). These study sites consist of a deciduous habitat dominated by downy oaks on the mainland (hereafter termed “mainland deciduous”), a similar deciduous habitat on Corsica (island deciduous), and an evergreen habitat dominated by holm oak on Corsica (island evergreen). In each landscape, 4 to 10 secondary sites, located less than 40 km from the main sites and dominated by one or more of the other oak species, were included to address specific questions. We use the term “population” in the simple ecological and practical sense to indicate groups of birds that are spatially more or less contiguous in the same habitat type within a landscape.

Habitat factors and constraints. By “constraint” we refer to any environmental feature that might reduce the breeding performance of the tits. Besides patchiness and fragmentation, several factors and constraints characterize Mediterranean habitats for small passerines such as tits, including variation in the timing and abundance of food, parasite loads, and climatic factors. The impact of these factors depends on habitat type, date, and year, giving rise to considerable spatial and temporal variation in blue tit breeding performance. For example, the lower availability of caterpillars late in the season—up to 10 times less in evergreen than in deciduous oaks (table 1)—often results in poor breeding performance.

A second factor that can be a severe constraint is infestation by the blood-sucking ectoparasitic larvae of two species of blowflies in the genus *Protocalliphora* (Hurtrez-Boussès et al. 1997, Simon et al. 2004). A combination of low caterpillar abundance and high *Protocalliphora* infestation can result in a severe reduction in nestling growth and survival, apparently because birds cannot compensate for the detrimental effects of parasites by providing more food to their young.

A third potential constraint is the long, hot, and dry Mediterranean summer, which could be stressful for birds, especially in evergreen habitats where tits breed late in the season. As water-rich caterpillars become increasingly scarce

Table 1. Characteristics of populations in the three main blue tit habitats in this study—mainland deciduous (Rouvière), island deciduous (Muro), and island evergreen (Pirio)—and in the secondary habitats in each region: mainland evergreen (Vic), island evergreen (four woodlots), and island deciduous (Galeria).

Reproductive trait	Mainland deciduous (Rouvière)	Mainland evergreen (Vic)	Island deciduous (Muro)	Island evergreen (four woodlots)	Island evergreen (Pirio)	Island deciduous (Galeria)
Population density (pairs per ha)	0.99 ± 0.29	0.15 ± 0.06	1.28 ± 0.44	0.97 ± 0.20	1.04 ± 0.19	0.35 ± 0.005
Caterpillar abundance (mg caterpillar frass per m ² per day)	22.6 ± 8.8	15.9 ± 11.6	493.2 ± 217.9	—	4.2 ± 21.8	—
Breeding performance						
Laying date (in “Marchdate”; 32 = 1 April)	37.5 ± 8.2 (871)	44.6 ± 7.6 (91)	38.6 ± 7.8 (400)	45.0 ± 6.5 (43)	73.3 ± 3.9 (694)	61.8 ± 7.2 (62)
Clutch size	9.8 ± 1.6 (870)	8.0 ± 0.4 (91)	8.5 ± 0.6 (204)	7.3 ± 0.6 (43)	6.4 ± 0.4 (360)	7.2 ± 1.3 (62)
Number of fledglings	7.5 ± 2.6 (865)	6.3 ± 1.8 (76)	7.3 ± 2.0 (201)	5.6 ± 1.8 (41)	5.0 ± 1.7 (11)	5.0 ± 1.3 (55)
Morphometry						
Male body mass (g)	11.2 ± 0.5 (870)	10.8 ± 0.61 (82)	9.9 ± 0.5 (234)	9.5 ± 0.2 (43)	9.3 ± 0.3 (422)	9.4 ± 0.4 (41)
Female body mass (g)	10.7 ± 0.64 (1094)	10.9 ± 0.58 (74)	9.7 ± 0.5 (278)	9.3 ± 0.5 (52)	9.3 ± 0.3 (437)	9.4 ± 0.5 (47)
Male tarsus length (mm)	17.21 ± 0.44 (843)	16.82 ± 0.56 (79)	16.50 ± 0.49 (231)	16.28 ± 0.53 (41)	16.26 ± 0.48 (389)	16.33 ± 0.53 (37)
Female tarsus length (mm)	16.37 ± 0.48 (1008)	16.39 ± 0.55 (72)	16.00 ± 0.44 (262)	15.98 ± 0.17 (48)	15.85 ± 0.54 (421)	15.69 ± 0.39 (43)
Fledgling mass (g)	10.7 ± 1.24 (850)	9.6 ± 1.11 (139)	10.4 ± 0.5 (357)	9.6 ± 0.4 (66)	9.3 ± 0.8 (448)	9.3 ± 0.9 (49)
Fledgling tarsus length (mm)	16.86 ± 0.60 (850)	16.53 ± 0.48 (133)	16.28 ± 0.40 (304)	16.19 ± 0.18 (39)	15.89 ± 0.61 (211)	15.85 ± 0.64 (33)

g, gram; ha, hectare; m, meter; mg, milligram; mm, millimeter.

Note: Data are plus or minus one standard deviation. Sample sizes are in parentheses.

as the season progresses, water may not always be readily available to invest in thermoregulation through evaporation.

Data collection. More than 5000 breeding attempts have been recorded from our nest boxes in 27 main and secondary study sites over 30 years. Only some of the most relevant approaches and results relating to the theme of phenotypic variation will be summarized here. More details and results, including statistical procedures, can be found in the relevant references. Our nest boxes, placed at densities of approximately two per ha, were routinely checked at least once a week to collect basic data on breeding traits such as laying date of the first egg, clutch size, hatching date, number of hatchlings, and number of fledglings. Chick body mass and tarsus length were measured at day 15 posthatching, when they had reached their asymptotic mass. Chicks were banded at 6 days, and parents were captured for identification (ring number, sex, age) and measurement of morphometric data when chicks were at least 10 days old. Only genuine first clutches (i.e., excluding repeat clutches and the very rare second clutches) were considered. Because various experiments were carried out, population statistics refer only to unmanipulated broods. Food abundance was routinely measured by collecting the frass of leaf-eating caterpillars in 0.25-m² trays placed under the forest canopy and collected twice a week (see Zandt et al. 1990). The proportion of caterpillars in the nestlings' diet positively correlated with the amount of frass collected in trays, indicating that frass is a reliable indicator of the caterpillars' abundance (Bañbura et al. 1994).

How do phenotypes vary across habitats?

Since we first discovered that blue tits may start breeding more than three weeks apart, depending on the type of habitat they settle in (Blondel and Isenmann 1979), we examined many other traits and found that they also varied considerably within and among habitats and landscapes.

Breeding time and clutch size. In seasonal environments, the breeding date of small insectivorous birds must be tightly synchronized with the narrow temporal window of the spring peak in insects, which itself depends on the spring development of vegetation. The caterpillar peak date occurred at approximately the same date in the mainland and island landscapes for each of the deciduous or evergreen habitat types. As a result, the seasonal differences in leaf development between the two species of oaks translates into an optimal laying date, illustrated by the dotted lines in figure 2a. Ideally, chicks should be about 9 to 11 days old at the peak of caterpillar abundance, because chicks raised before or after this peak date are in poor body condition and have low prospects of survival (Dias and Blondel 1996, Blondel et al. 2001, Thomas et al. 2001a). The selective advantage of timing the breeding process relative to local food abundance can be portrayed as the ratio of the amount of food available in the habitat to the quantity of food and energy that parents must harvest to meet the growth requirements of their young (Tremblay et al.

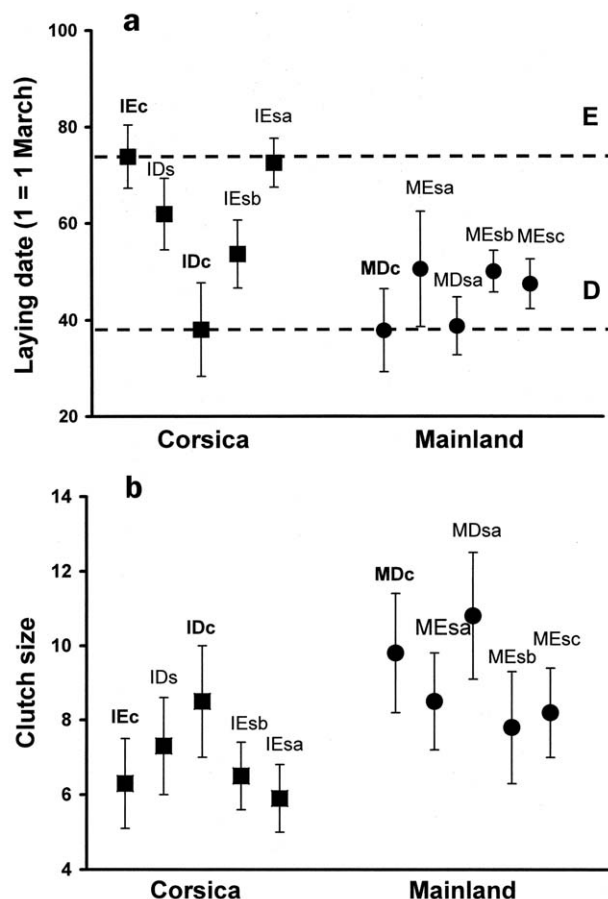


Figure 2. Phenotypic variation of laying date (a) and clutch size (b) for blue tits, plus or minus one standard deviation. The horizontal dotted lines in panel a indicate the best date for the onset of breeding relative to food availability in deciduous (D) and evergreen (E) habitats, respectively. Abbreviations: IDc, main island deciduous habitat; IDS, secondary island deciduous habitat; IEc, main island evergreen habitat; IEsa and IESb, secondary island evergreen habitats; MDC, main mainland deciduous habitat; MDsa, secondary mainland deciduous habitat; MEsa, MEsb, and MEsc, secondary mainland evergreen habitats. Modified from Blondel and colleagues (2001).

2003). Blue tits breeding in the mainland deciduous and island evergreen habitats optimize this ratio by timing egg laying such that their peak nestling food demand occurs when caterpillars are the most plentiful. The later and smaller food peak in the island evergreen habitat makes populations breeding there lay three to four weeks later and produce clutches 30% to 40% smaller than those in the mainland deciduous oak forest (table 1, figure 2b). Breeding success, estimated as the proportion of eggs producing surviving offspring, is similar in the two populations.

If birds that settle and breed in patches of the less common oak type in each landscape (evergreen on the mainland,

deciduous on Corsica) equally optimized the supply–demand ratio of food, they would start to lay eggs approximately one month later in the evergreen than in the deciduous habitat on the mainland, and one month earlier in the deciduous than in the evergreen habitat on the island. However, this is not the case: Three mainland populations (secondary mainland evergreen, populations MEsa, MEsb, and MEsc in figure 2a) and one island population (secondary island evergreen, IESb in figure 2a) breeding in evergreen habitats near the main deciduous habitats started laying earlier than would be expected if their breeding were optimally timed. In addition, one Corsican population breeding in a deciduous habitat (secondary island deciduous, IDs in figure 2a) near the evergreen habitat started to breed too late. As a consequence of this offset between the time of peak caterpillar abundance and nestling demand, their breeding success was lower and fledglings were lighter, with lower prospects of being recruited into the population.

On average, blue tits produced larger clutches in deciduous than in evergreen habitats, and larger clutches on the mainland than on Corsica (table 1, figure 2b). In addition, clutch size was lower in the less common evergreen habitat on the mainland and higher in the less common deciduous habitat on Corsica than in the respective main habitat of each landscape. For both laying date and clutch size, phenotypic variation between habitats was much larger on the island (figure 2a, 2b), a feature we will discuss later. In the mainland landscape, birds started laying eggs within a range of 9 days, as compared with 29 days in Corsica.

Breeding success and the growth and development of chicks.

Comparing breeding success between deciduous and evergreen habitats that are close to one another revealed that blue tits fledged on average 10% to 15% more offspring in the caterpillar-rich island deciduous habitat than in the caterpillar-poor island evergreen habitat (table 1, figure 3). In addition, nestlings in the island deciduous habitat were 0.5 to 1.0 g heavier at fledging. A consistently better breeding performance in deciduous oak forests than in evergreen ones has been explained by Tremblay and colleagues (2003), who demonstrated that the relationship between breeding success and food abundance is not linear but follows a saturation curve. Fledgling mass and survival reach a plateau above a certain level of food abundance, which corresponds to the highest ratio of food supply to de-

mand (that is, as much food as the nestlings can process; figure 3). Up to about 500 milligrams (mg) frass per m^2 per day, fledgling mass is tightly correlated with the number of caterpillars available, but above this value, which is usually met in deciduous oakwoods, food is superabundant. The food-processing capacity of fledglings appears to saturate, with the result that fledgling mass is independent of food abundance (Thomas et al. 2001b).

Three parameters were used to measure the effect of variation in food abundance, namely (1) the peak in caterpillar frass production, (2) the offset between the caterpillar peak and the peak nestling demand, and (3) clutch size, which is an indication of the workload of parents tending their chicks. Any variation of these variables had significant effects on breeding performance in the caterpillar-poor island evergreen habitat, but not in the caterpillar-rich island deciduous habitat. An illustration of this effect is the steep slope of fledging success and fledgling mass (figure 3) as long as caterpillar abundance is below 500 mg frass per m^2 per day. On average, the maximum biomass of the brood varied from approximately 59 g in the poor evergreen habitat (6.3 chicks $\times$ 9.3 g) to approximately 86 g in the rich deciduous habitat (8.3 chicks $\times$ 10.4 g), but at the same time the supply–demand ratio increased from 1.6 to 16.2 over the same habitat gradient (Thomas et al. 2001b, Tremblay et al. 2003).

Because correlation does not necessarily imply causation, we experimentally enlarged a sample of broods to test the causal nature of these differences in habitat quality on breeding performance and nestling growth and survival. In the caterpillar-poor evergreen forest, adding three chicks to nests significantly decreased chick growth and survival, and also

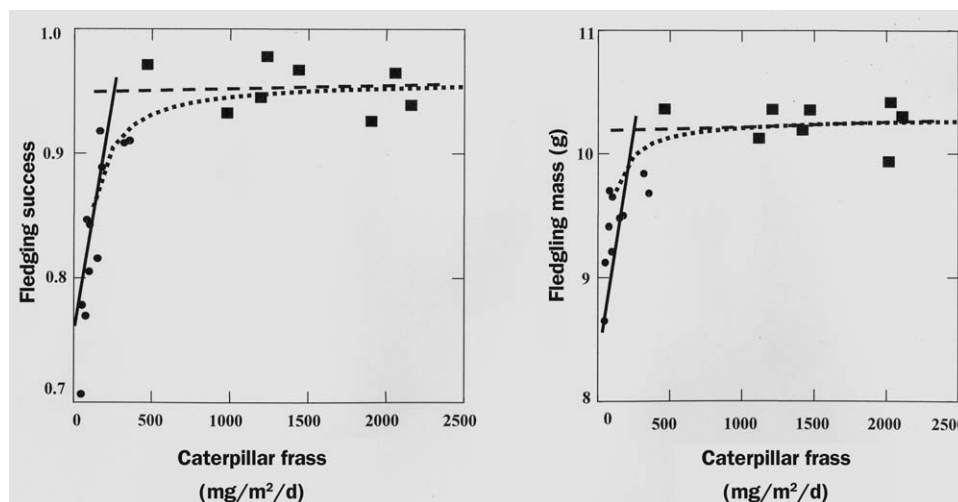


Figure 3. Variation in mean annual fledging success and fledgling mass (in grams) with increasing food supply in deciduous habitats (squares) and evergreen habitats (dots). Curves indicate saturation functions fitted to the combined data for evergreen and deciduous habitats. The intersection of linear regressions through data for island evergreen and island deciduous habitats indicates the level of caterpillar abundance (about 500 milligrams per square meter per day) at which fledging success and fledgling mass are maximized. Modified from Tremblay and colleagues (2003).

decreased the body mass of the parents, which had to work harder to feed these extra chicks. By contrast, brood enlargement had no effect, either on chicks or on adults, in the caterpillar-rich downy oak forest (Tremblay et al. 2003).

Food and foraging patterns. Caterpillars are the preferred prey of blue tits, presumably because they are easier than many other invertebrates to manipulate and ingest, and possibly because they contain more water (85% for caterpillars, as compared with 73% for spiders, for example), which may be important in the hot, dry Mediterranean environment. Video recordings inside nest boxes when nestlings were 9 to 13 days old provided data on the nature and size of prey in 26 nests (8 in island deciduous and 18 in island evergreen habitats), as well as on provisioning rates. Caterpillars constituted the bulk of prey, amounting to 82.4% ($\pm 9.9\%$) and 73.6% ($\pm 16.2\%$) of prey items in the deciduous and evergreen habitats, respectively. Whenever caterpillar abundance falls below a value of approximately 160 mg frass per m² per day, blue tits diversify prey items and switch to other, less profitable prey, such as spiders, grasshoppers, homopterans, or even ants (Bañbura et al. 1994).

When food is plentiful, tits forage within a short distance, usually not farther than 100 m from their nest (Naef-Daenzer et al. 2000, Tremblay et al. 2005). Because food is much scarcer in evergreen habitats than in deciduous ones, we expected a larger foraging range in the former than in the latter, along with a decrease in provisioning rates as foraging distances and search times increase. Tremblay and colleagues (2005) radio-tagged a sample of birds and showed that parent tits indeed foraged much closer to their nest in the deciduous habitat (25.2 ± 12.3 m on average) than in the evergreen habitat (53.2 ± 22.9 m). However, they made more foraging trips in the deciduous than in the evergreen habitat (36.5 ± 10.5 versus 17.0 ± 4.5), resulting in similar commuting distances per hour in the two sites (1840 and 1809 m, respectively). Birds in the evergreen habitat, which made fewer but longer trips, were forced to patrol surface areas over four times larger (7854 m²) than those covered by birds in the deciduous habitat (1963 m²).

Interestingly, prey size was 73% larger in the evergreen habitat (0.19 ± 0.05 cubic centimeters [cm³], as compared with 0.11 ± 0.04 cm³ in the deciduous habitat). All in all, larger prey size and fewer chicks made the total amount of food delivered to each chick similar in the two habitats (0.36 ± 0.12 cm³ per hour for each chick in the deciduous and 0.39 ± 0.09 cm³ per hour for each chick in the evergreen habitat). The similar biomass of prey provided to nestlings, due to larger prey size in the poor habitat, suggests that foraging parents increase prey selectivity as caterpillar abundance decreases. However, because the peak in caterpillar abundance occurs four weeks later at the evergreen site, when mean ambient temperatures are 2 degrees Celsius (°C) to 4°C higher, faster growth may result in a larger average size of caterpillars there. Parent tits have to provide food for a much greater chick biomass in the deciduous than in the evergreen habitat (39% higher in a three-year

study by Tremblay and colleagues [2005]), but this is not a problem for them, since the caterpillar abundance was 581% higher there than in the evergreen habitat during the years of the study.

Morphology. Independent of the differences in size between the mainland and insular subspecies of blue tit, adult birds are usually larger and heavier in caterpillar-rich deciduous than in caterpillar-poor evergreen habitat patches both on the mainland and on the island of Corsica (table 1). The question arises of whether these differences are genetically determined or are a proximate response to differences in conditions during development. Body condition, estimated by fledgling mass and hematocrit levels, differed depending on the levels of parasite infestation. We suspected that these differences between parasite-free and heavily parasitized chicks were the result of genetically determined responses to parasite-mediated selection, allowing birds to evolve developmental traits that buffered the negative effects of parasites (Simon et al. 2005).

To test this hypothesis, we partitioned phenotypic variation into genetic and environmental components by using cross-fostering experiments, with the resulting broods containing chicks from the two study sites, evergreen and deciduous. Half of the experimental broods were deparasitized. Although the chicks from the deciduous woodland were significantly heavier than those from the evergreen woodland at the beginning of the cross-fostering experiment (day 4), mean asymptotic mass and hematocrit levels of deparasitized experimental broods did not significantly differ between chicks from the two habitat types. This experiment showed that environmental constraints, primarily the abundance of caterpillars and parasites, rather than adaptive genetically determined differences underlay differences in the size and hematocrit of nestlings. Similarly, Braillet and colleagues (2002) noticed that differences in body mass between adults from these two populations disappear when they are maintained with food ad libitum in an aviary environment. Thus, the most likely factor for explaining higher mass and larger size in deciduous habitat is the difference in food that favors growth in the richer habitat, leading to environmentally induced phenotypic plasticity.

Subtle mechanisms may influence body size and shape. In a study of sexual size dimorphism, small adult males were shown to have a higher breeding success than large males in the evergreen Corsican site, whereas the opposite was true in the deciduous site on the mainland (Blondel et al. 2002). This pattern was attributed to the advantage for males of being small when food is scarce, since small size is a means of saving energy and favoring maneuverability while foraging (Mosher and Matray 1974). Small males could be especially favored in the heavily parasitized populations, where chick provisioning is their prime responsibility, while females spend a considerable amount of time on nest sanitation.

These patterns suggest that in evergreen habitat, natural selection acts in opposite directions depending on life stages,

with higher recruitment for larger male chicks, but higher reproductive success for smaller breeding males. This would result in fluctuating selection through different life history components, making it unlikely that an evolutionary response to selection on body size would be observed (Charmantier et al. 2004a).

Parasitism as a factor of phenotypic variation. Different kinds of parasites occur in all our study populations, but rates of infestation and their consequences vary extensively both within and between populations, adding one more cause of phenotypic variation. The most common and aggressive parasites are the blood-sucking larvae of the blowflies *Protophormia azurea* and *Protophormia falcipar*, with some blue tit populations living in evergreen holm oak habitats on Corsica suffering the highest prevalence and intensities of these parasites so far recorded in Europe. Parasite prevalence in our island evergreen population usually reaches more than 90% of the nests, and infestation levels can reach as many as 15 larvae or 3 g per chick (Hurtrez-Boussès et al. 1997).

These larvae attach to the edge of the wing, leg, or bill of a chick and rasp a hole in its skin to feed on blood. They have various detrimental effects on chicks, including reduced body mass, tarsus length, hematocrit, postfledging survival (Hurtrez-Boussès et al. 1997), and aerobic or metabolic capacity (Simon et al. 2004). Video recording inside the nest box revealed that parasite-free nestlings spend most of their time resting quietly and preening while waiting for food, whereas infested nestlings constantly move, scratch, and apparently try to escape the bites of parasites by perching on the nest margins. The frequency of parental visits is approximately 65% higher in parasitized nests, with an unbalanced contribution of the two parents. Males strongly accelerate their feeding rates (from 4.5 visits per chick per hour in unparasitized nests to more than 7.5 visits in parasitized nests; Hurtrez-Boussès et al. 2000), while females spend a large amount of time on nest sanitation (increased from 5% in unparasitized broods to more than 17% in infested nests). Parasites are especially harmful when food is scarce, but their effects are partially or totally alleviated when food is abundant, which always occurs in the deciduous habitats (Simon et al. 2004). Stressful conditions imposed by parasites may have additional effects, such as decreasing the heritability of size-related traits, as shown in several species of birds (Merilä 1997). Van Noordwijk and colleagues (1988) demonstrated that heritability of body size is higher under good conditions, and, in a nine-year manipulation of parasite loads in our heavily parasitized population of Corsica, Charmantier and colleagues (2004b) demonstrated that the heritability of tarsus length was significantly higher in deparasitized broods ($h^2 = 0.91 \pm 0.09$) than in control parasitized broods ($h^2 = 0.53 \pm 0.14$). This finding provided the first evidence that host quantitative genetics can be influenced by parasitism. Although heritability does not necessarily mean evolvability, this effect illustrates the potential for parasitism to constrain an evolutionary response to selection.

Moving across habitat patches

Environmental heterogeneity raises the question of how, why, when, and to what extent individuals move and disperse between habitat patches that differ in structure and quality. While an individual's ecological context might be the habitat within which it grew or currently lives, its evolutionary context includes all the habitats experienced by its ancestors at the scale of a landscape (Holt and Gaines 1992). Dispersal was expected to differ between the mainland and Corsica because it is well known that dispersal is usually reduced in islands, potentially reducing gene flow and increasing the potential for local specialization. Movements of blue tits within and across landscapes may be addressed by various approaches, including the response of traits to habitat-specific features, recruitment, habitat selection, genetics, and dispersal, a key trait for analyzing issues on phenotypic variation. Given the average dispersal range of small forest birds such as tits, which is about 1 to 2 km from their natal site, the distance between habitat patches within our study landscapes is often shorter than the potential natal dispersal range of birds. In landscapes characterized by woodlots interspersed with crop fields or pastures with clear-cut boundaries, blue tits are usually reluctant to fly over open spaces, but our Mediterranean landscapes are mixtures of woodland, scrubland, and edges connecting habitats so that tits can freely disperse over very large distances.

What are the causes, the costs, and the consequences of a mismatch between peak food demand and the peak of local food resources?

About half of the birds breeding in our study sites each year were not locally born. We have few indications of where they come from, but it is likely that many birds born and raised in one habitat type disperse to the other. This could result in local maladaptation if breeding traits that evolved in one habitat type are not plastic enough to cope with the characteristics of the other habitat type. Is it possible that the time lag between food demand and food supply that results in a low supply–demand ratio and in food shortage produces a source–sink population structure? In that case, more birds would emigrate from the more common to the less common habitat than the reverse, as a result of poor breeding performance in the latter. This question was addressed using fingerprinting of minisatellite loci that allowed us to estimate the degree of genetic differentiation of individuals within and between local populations. Using samples from several supposedly source (deciduous) and sink (evergreen) habitats over a landscape of 20 km² in the mainland landscape, Dias and colleagues (1996) found greater genetic differentiation of individuals between different source habitats than between sources and sinks. This was an indication that birds from the two habitat types, sources and sinks, belonged to the same local population, and that these habitats are linked through dispersal. Indeed, asymmetrical dispersal, from more common habitats where birds are locally specialized to less common habitats where birds do not breed at the best time because of gene flow, is the most parsimonious

hypothesis for explaining the observed patterns. Even if half the offspring born in a sink habitat remained in their natal habitat, their number would not compensate for the continuous flow of birds immigrating from sources and thus preventing adaptation to the sink (Holt and Gaines 1992). However, whatever the extent of the mismatch between food demand and food supply in the maladapted populations, there is some evidence of habitat tuning in the less common habitat patches of each landscape, because birds start to breed slightly later in the evergreen mainland sites (secondary mainland evergreen, populations MEsa, MEsb, and MEsc in figure 2a) and slightly earlier in the secondary island deciduous study site (IDs in figure 2a) than in the corresponding commoner habitats of each region. The same is true for clutch size, which is always larger in deciduous than in evergreen habitats, with intermediate values in the less common habitats of each landscape (figure 2b). These shifts in breeding time and clutch size are an expression of phenotypic plasticity within a window that allows birds to compensate, but only to a limited extent, for the large offset between food supply and demand.

The pattern in which early-breeding phenotypes overflow from deciduous oak woods into less common patches of evergreen oaks, where birds miss the best time to breed, provides a unique, quasi-experimental opportunity to explore the energetic and fitness costs of supply–demand offset. Since an offset between food supply and demand must be mediated by parents that have to work harder to meet their own requirements and those of their young, we also measured the physiological cost of this offset for adults in terms of metabolic effort. This effort of adults has been assessed by measuring the amount of energy needed for rearing chicks, while their metabolic effort has been assessed through an estimation of the ratio between field metabolic rate (FMR) and basal metabolic rate (BMR), using doubly labeled water ($^2\text{H}_2^{18}\text{O}$) with joules as a currency of energy. This ratio, calculated as FMR/BMR over time periods of 24 hours, was shown to increase strongly as the offset between breeding date and caterpillar peak increased (Thomas et al. 2001a).

Comparing well-synchronized pairs in the main evergreen site on Corsica with unsynchronized pairs in a mainland secondary evergreen site, the daily unit cost for rearing young (per gram of nestling mass) was on average 1.01 kilojoules (kJ) per adult per day in Corsica and 2.59 kJ per adult per day in the unsynchronized continental broods, an increase of more than 100%. The metabolic effort of adults increased from 4.91 $\times$ BMR in the most synchronized to 6.96 $\times$ BMR in the most unsynchronized continental birds, but averaged only 3.45 $\times$ BMR in Corsica. This high metabolic effort of unsynchronized birds was associated with low survival and persistence in the breeding population and with lower future reproductive prospects for breeding pairs in unsynchronized populations (1.35 years for both males and females) compared with synchronized pairs (females, 2.16 years; males, 2.23 years; Thomas et al. 2001a). Whenever tits adequately synchronize their breeding time to the peak of caterpillar abundance, they

work at a level that is typical for breeding birds when provisioning their young, around 3 to 4 $\times$ BMR (Nagy 1987). In contrast, birds that miss this optimal breeding time have to work far beyond what appears to be their sustainable limit.

Why is there higher phenotypic variation in Corsica than on the mainland?

Imagine that Corsica were not an island. Because the geographic configuration of habitat patches within landscapes is similar on the mainland and in Corsica (figure 1), phenotypic variation in both breeding and morphometric traits would be expected to be similar in the two regions (table 1, figure 2). In Corsica, one might expect a pattern of mismatching between the breeding time and the peak of caterpillar abundance similar to that on the mainland, but tending in the opposite direction, with populations in deciduous habitats being maladapted because evergreen oaks dominate the landscape on the island (whereas the reverse is true on the mainland). However, this is not the case, because the breeding time of tits is closely synchronized with the caterpillar peak date in both the deciduous and the evergreen insular habitats, which are only 25 km apart. In addition, birds from these two populations differ in a number of traits (table 1; Lambrechts et al. 1997a, Blondel et al. 1999). Thus, with a one-month lag in their breeding time, these two island populations differ exactly as did the genetically isolated mainland deciduous and island evergreen populations discussed above. This provides a striking example of an adaptive response of life history traits to habitat-specific selection regimes that operate on a scale much smaller than the scale of dispersal and potential gene flow. This finding is especially interesting because there is no barrier to dispersal in these landscapes, which do not include open spaces that birds would be reluctant to fly over.

The most likely explanation for this difference between the mainland and island patterns is that dispersal rates strongly differ between the two regions. What sets Corsican populations apart from those on the mainland, and explains their larger variation in phenotypic traits, is the reduced dispersal in island birds, a component of the so-called insular syndrome that has been shown to occur in Corsican birds (e.g., Blondel et al. 1988, 1999). Stronger habitat fidelity in Corsica than on the mainland, combined with presumably habitat-specific assortative mating, results in lower dispersal rates and lower gene flow on this island.

Is genetic variability geographically coherent with phenotypic variation?

The large phenotypic variation observed in so many traits raised two questions. First, what is the extent of genetic variation between these populations at both interregional and intraregional spatial scales? Second, how do populations respond to the contrasting selection regimes they experience in the two habitat types?

The first question was addressed by exploring the genetic structure of populations in five evergreen and four deciduous habitat patches on Corsica, and eight deciduous patches

on the mainland. Using DNA amplification techniques with seven microsatellite loci, which proved to be highly polymorphic (13 to 26 alleles), Charmantier (2000) genotyped 314 blue tits and found several patterns of genetic differentiation. With a Wright's statistic (F_{st}) of 0.031 ($P < 0.0001$), which reflects the degree of differentiation among populations, Corsican populations are clearly differentiated from those of the mainland. Within Corsica, a significant, albeit small, differentiation was found between our main island deciduous and island evergreen sites ($F_{st} = 0.007$ to 0.011 , depending on years; all $P < 0.02$), and annual F_{st} within nine Corsican populations varied from 0.015 to 0.021 (compared with 0.0086 for eight mainland populations; Dias et al. 1996). Thus, although the F_{st} values remain small, the prediction of some genetic structuring in Corsica as a result of low dispersal on the island is supported.

Although significant, the genetic differentiation between the main deciduous-dwelling and evergreen-dwelling Corsican populations did not exceed 1%, a very small value that contrasts with the large interpopulation phenotypic variation described above. A likely explanation for this weak genetic differentiation is that neutral markers have not yet tracked the evolution of diverging phenotypic traits because it has been too recent, too rapid, or both. Although microsatellites are rapidly evolving markers and hence are sensitive for detecting intraspecific differentiation, adaptive evolution at gene combinations determining fitness-related traits may have occurred exceptionally quickly, with potentially little change occurring in the neutral regions of the genome. This finding is not surprising, because an increasing number of studies from a wide range of taxa show that natural selection can produce rapid adaptive morphological divergence in the absence of discernible differentiation at neutral DNA loci (Orr and Smith 1998).

We addressed the second question using analyses based on selection and quantitative genetics in the three main study areas on the mainland and in Corsica, where long series of pedigrees were available. We estimated directional (and stabilizing or disruptive) natural selection on morphometric traits (tarsus length and body mass) using local recruitment as a measure of fitness (Charmantier et al. 2004a). Expected responses to selection (R) were predicted using heritability estimates (h^2) and selection differentials (S), from the equation $R = h^2S$. Following the rationale of Hoffmann and Merilä (1999), we expected the variance components of morphometric traits to vary between populations, with heritability values decreasing as environmental conditions became more constraining. In the three populations, heritability values were significant for tarsus length and body mass, with a trend of higher h^2 for body mass as habitat quality increased. Significant selection differentials on tarsus length and body mass were found in two study areas, with a predicted increase of 0.18 g per generation in the mainland site. However, despite significant heritability and selection, no significant change was found over time on this trait or on tarsus length in any population (Charmantier et al. 2004a).

Many factors may explain why traits have considerable additive genetic variance, appear to be under directional selection, and yet do not evolve (Kruuk et al. 2001, Merilä et al. 2001). One bias in estimates of heritability may come from the occurrence of extrapair paternity, which proved to be fairly common in these populations, ranging between 12% and 29% of the chicks. However, recent simulations have shown that heritability of morphometric traits, typically above 0.20, will not be seriously biased by this range of misassigned paternities (Charmantier and Réale 2005). At most, extrapair paternity would make the discrepancy between expected and observed response to selection stronger. Another potential explanation for the stasis of heritable selected traits is gene flow across habitats, which can constrain evolution if selection on the focal trait operates in opposite directions in two neighboring habitats. A genetic correlation might also constrain evolutionary response when the two sexes are subject to opposite selection pressures. This could happen in some of our populations, for example, in the evergreen island population, where the determination of sexual size dimorphism results in selection for small size in males and large size in females (Blondel et al. 2002). Finally, the absence of evolutionary response to selection on body size could result from genetic correlation with other targets of selection, for example, other unmeasured traits (Lande and Arnold 1983).

One approach for extending our understanding of the differentiation between populations would be to compare the genetic differentiation for neutral markers (F_{st}) with the degree of differentiation for quantitative traits, using Q_{st} statistics, which are the counterparts of F_{st} for quantitative traits (see, e.g., Merilä and Crnokrak 2001). Higher values of Q_{st} (phenotypic variation) than of F_{st} (genetic variation) would confirm that the quantitative trait differentiation we observe does not result from genetic drift alone, but is the outcome of natural selection.

Phenotypic plasticity or local specialization, or both?

Two mechanisms may produce variation of phenotypes. First, phenotypic plasticity occurs when genetically identical organisms reared in different environments display quite different phenotypes. Second, variation of phenotypes can result from local specialization, which is the evolution of traits that have been selected in a given environment and that do not change if the organism migrates to another environment. Both phenotypic plasticity and local specialization 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.

Demonstrating adaptive responsiveness to local environmental cues. Our study system represents an extreme case of habitat heterogeneity and divergent selection regimes at the landscape scale for small passerines in temperate habitats. The most fascinating feature of the story, with a cascade of consequences on life histories, is the one-month difference in blue

tits' breeding time depending on which oakwood morphotype they settle in. Experiments were necessary to determine whether this difference in the onset of breeding was a plastic response of phenotypes or resulted from genetic differentiation in response to local selection regimes. We undertook four experiments in aviaries in Montpellier, in which we submitted hand-raised chicks of late-breeding tits from evergreen Corsican habitat and early-breeding tits from deciduous mainland habitat to different artificial or natural photoperiods (figure 4; Lambrechts et al. 1997b).

The timing of the first clutches of our captive tits differed between different treatments as follows: (a) The one-month

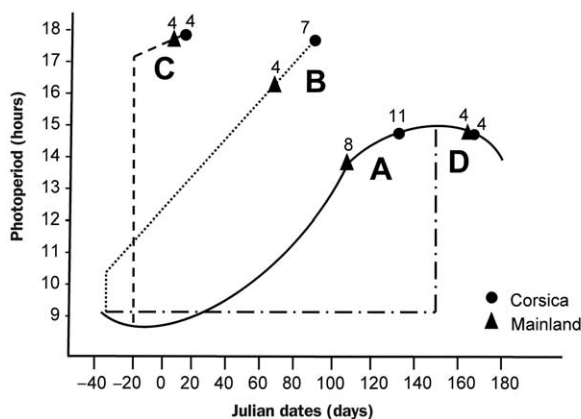


Figure 4. Onset of egg laying (mean in Julian dates; 1 January = 1, 1 February = 32) of captive blue tits from mainland (mainland deciduous) and Corsican (island evergreen) habitats breeding in outdoor aviaries. Birds were submitted to four different changes in photoperiod, starting at different periods in the year. Treatment A consisted of natural light and was used as a control. In treatment B, a progressive increment of artificial light simulating spring development was initiated in November. In treatment C, birds were submitted to a step change in artificial photoperiod, simulating the long day length prevailing in Corsica when the population starts to breed. In treatment D, birds were kept indoors with a nine-hour photoperiod and then placed in outdoor aviaries with natural photoperiodic conditions. Numbers represent sample size. Data are from Lambrechts and colleagues (1997b).

difference in laying date remained when these captive birds were allowed to breed under natural spring photoperiods, suggesting that populations differed in their response to photoperiod. (b) Birds advanced their breeding time but still kept their one-month difference in laying date when they were exposed to an artificially early spring photoperiod beginning in November. (c) When birds were exposed in December to an artificially long day length exceeding that at which they normally breed, they responded by advancing their breeding date, but the one-month difference in laying date disappeared. This shows that the one-month offset was not due to

a difference in the rate of gonadal development. (d) The same treatment performed in summer instead of winter gave a similar result. These experiments showed that mainland and island blue tits can start breeding at any time of the year when submitted to a suitable photoperiod, whether artificial or natural, and that differences in the timing of breeding are due to a genetic difference in their photoperiod response that corresponds with the one-month offset in the timing of food availability in the natal habitat.

The antagonism between selection and gene flow. Intraspecific variation at small spatial scales has long been thought not to occur in such mobile organisms as birds, because dispersal and gene flow across habitats were assumed to prevent evolutionary differentiation (Slatkin 1987). Our blue tits on the island of Corsica are particularly interesting because they exhibit cases both of maladaptation and of local specialization. Blue tits in the deciduous and evergreen main habitats, which are only 25 km apart, behave as though they were locally specialized and genetically isolated. This is a striking avian example of the adaptive response of a series of life history traits to habitat-specific selection regimes that operate on a scale much smaller than the scale of potential gene flow. Supporting a large body of theoretical work (e.g., Hedrick 1986), this case study supports 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). The contrast between a weak genetic differentiation of molecular markers between these two populations of tits and the local structuring of several phenotypic traits suggests that divergence results from directional selection counteracting gene flow, rather than from geographic isolation. In the tug-of-war between gene flow and local specialization, which has also been found in fish (Nagel and Schluter 1998) and bird species (Smith et al. 1997), the intensity of selection determines the outcome of the two opposing forces. This explains why local, genetically based specialization can occur despite gene flow, but only when directional selection acts on a trait with high selective value. Recently, Garant and colleagues (2005) elegantly demonstrated in the great tit (*Parus major*), a close relative of the blue tit, that nonrandom gene flow can sometimes maintain and reinforce phenotypic and genetic differentiation.

Reaction norms. On a regional scale, each population of blue tits is specialized to the more common habitat, with, so to speak, a “deciduous oak genotype” on the mainland and an “evergreen oak genotype” in Corsica (figure 5). In the less common habitats within each landscape, birds are clearly maladapted, because they mismatch breeding with the peak of caterpillar supply—with the remarkable exception of Corsica discussed above, where blue tits are equally well adapted locally to the two species of oak. In all the mismatched populations (three on the mainland and two in Corsica, with their laying date falling between the two dotted lines shown in

figure 2a), the “window” of phenotypic plasticity appears not to be wide enough to allow immigrating individuals to fully compensate for the large (one-month) difference in the local timing of food resources. Thus, wherever habitat patchiness is a mixture of deciduous and evergreen patches, the resulting reaction norm includes local specialization, phenotypic plasticity, or local maladaptation, depending on the size of habitat patches relative to the average dispersal range of the birds. Although there must be high selection pressures in suboptimal habitats for either local specialization or phenotypic plasticity, response to selection is weak, because habitat patches and tit population sizes are too small to prevent the effects of gene flow from nearby source habitats (Postma and van Noordwijk 2005). Figure 5 summarizes the patterns resulting from a reaction norm approach applied to laying date: The two parallel lines, which correspond to a deciduous genotype for blue tits on the mainland and an evergreen genotype on the island of Corsica, are reaction norms of locally specialized populations. In addition, each of these genotypes can be expressed through some degree of phenotypic plasticity both in time and space. Variation in laying date around the mean is the year-to-year proximate response to variation in various factors such as temperature or food. 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 aviaries.

Future prospects

The example of blue tits in Mediterranean landscapes shows that the potential for selective spatial differentiation is greater than is usually appreciated. This gives support to the contention of Holt (1987) that habitat patches that differ strongly in quality and phenology form temporally stable but spatially heterogeneous environments in which theory predicts selection for habitat fidelity, reduced dispersal, and the evolution of specialization. Geographic proximity does not necessarily imply similar adaptations, so that adjacent populations may be ecologically different, albeit genetically quite similar, or may even be genetically dissimilar, as recently shown by Garant and colleagues (2005).

The recent impetus in integrative biology, which combines evolutionary ecology, behavioral ecology, molecular genetics, endocrinology, and evolutionary ecophysiology, offers many avenues for future research on this model. A number of specific points are worth addressing. First, it is important to analyze whether philopatric and immigrant birds constitute two distinct groups with different strategies. Do birds move randomly as a proximate consequence of density effects, or directionally as a strategy for improving their fitness in a new appropriate habitat? Similarly, examining the degree of habitat–phenotype matching using stable isotopes (e.g., Hobson and Wassenaar 1997), trace elements, or both would allow us to examine to what extent tits are specialized to oak morphotypes, based on chemical signatures within the food web.

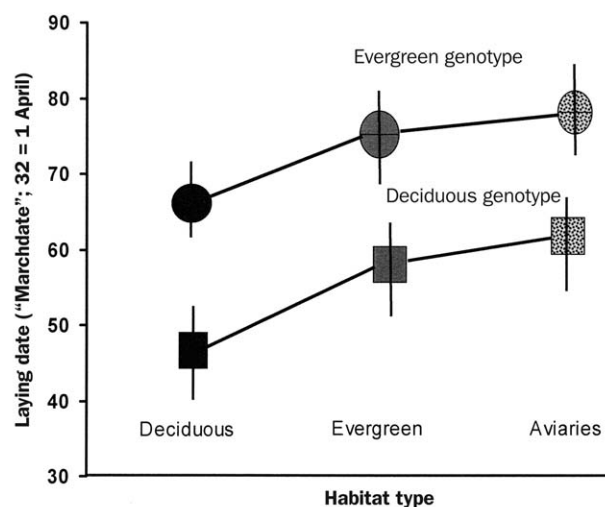


Figure 5. Reaction norms, specialization, and phenotypic plasticity of blue tits for the onset of breeding. The two distinct lines obtained for the mainland and the island birds when the average laying date is plotted against habitat type can be interpreted as the mean reaction norm for each set of populations. The upper line corresponds to an “evergreen genotype” and the lower line to a “deciduous genotype.” The variation of laying date around the mean (standard deviation) and across habitats (deciduous, evergreen, aviaries) is an expression of the phenotypic plasticity of the populations in space (habitats) and time (year-to-year variation expressed by standard deviation). Modified from Lambrechts and Dias (1993).

Second, to explain the discrepancy between phenotypic variation and its genetic expression, it is useful to explore the Q_{st} values of fitness-related traits. Comparing the degree of differentiation of polymorphic molecular markers (F_{st}) with that of quantitative traits (Q_{st}) should give an insight into the relative roles of isolation, gene flow, selection, and random drift on the phenotypic variation of traits (Merilä and Crnokrak 2001). Another objective is to develop a genetic map of the species in order to develop a QTL (quantitative trait loci) approach to identify key genes contributing to phenotypic variation.

Third, habitat quality and the response of organisms to environmental variation, including global warming, should be assessed using an analysis of interhabitat developmental instability (i.e., fluctuating asymmetry), which is often considered to be a biological monitor of environmental and genomic stress (Parsons 1992).

Fourth, an interesting question is whether differences in life history measures between individuals are explained by processes occurring over short-term or longer-term timescales. For example, how much variation is due to behavioral plasticity, and how much to environmental, parental, or origin-specific effects? Detailed analyses of habitat-specific responses of traits to selection, using quantitative genetics, should help

answer these questions. If heritability decreases under stressful conditions (see Charmantier and Garant 2005), responses to selection should be weaker in constraining environments.

A fifth point of interest is the size and geographical configuration of habitat patches, because understanding the conditions and scale under which spatial heterogeneity promotes or inhibits species diversity is a challenge of great importance. One crucial point will be to determine the threshold of frequency of habitat types and population sizes above which selection regimes will shift from specialization to one habitat to specialization to the other. New tools from landscape genetics (Manel et al. 2003) that combine landscape ecology and population genetics may provide information about the interaction between landscape features and microevolutionary processes such as gene flow, genetic drift, and selection.

Finally, by advancing the phenology of budding, leaf production, and food supply, climate warming is expected to exacerbate the mismatch between food supply and nestling demand for a broad spectrum of terrestrial birds, until directional selection potentially adjusts laying date to new optimal dates (Visser et al. 2004). 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 this changing world will be worth studying in detail if the consequences of these changes on the distribution and abundance of animals are to be predicted.

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