S15-5　Population differentiation on islands: a case study using blue tits in habitat mosaics

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Abstract　We hypothesized that changes in life history traits of populations on islands, especially the components of niche enlargement, habitat tenacity and reduced dispersal of the "insular syndrome", would result in greater rather than smaller phenotypic variation in populations on islands as compared to mainland counterparts. We tested these predictions with long term studies of blue tits (*Parus caeruleus*) on Mediterranean mainland and insular habitats. These habitats are particularly suitable for investigating the causes and consequences of phenotypic variation affected by spatially variable selection regimes because they are mosaics of patches in which strongly divergent selection pressures result from major habitat-specific differences in the timing and abundance of food. Considerable inter-habitat phenotypic variation was found in a series of life history traits (demographic, morphometric, behavioral) in the tits, variation that was much higher on the island of Corsica, in particular, than the adjacent mainland. Birds there synchronized their breeding more tightly to local seasonal variations in food than on the mainland as a result of low dispersal and strong site tenacity. Two populations only 25 km apart and subject to strongly divergent resource-based selection regimes became so differentiated that they reached reproductive isolation. Local differentiation in blue tits on Corsica supports the divergence-with-gene-flow model of speciation, which is central to the evolution of reproductive isolation.

Key words　Blue tit, Corsica, Deciduous oak, Evergreen oak, Mediterranean, Phenotypic variation

1　Introduction

Islands and archipelagos are often claimed to present more ecological opportunities for differentiation and speciation than mainland source areas, a claim supported by the spectacular radiation of many groups of plants and animals in such remote archipelagos as Hawaii and the Galapagos. In addition to greater ecological opportunities, birds on islands may also recognize more habitats as a result of behavioral and demographic shifts, leading to phenotypic differentiation within species. Few studies have demonstrated the causal relationships between phenotypic variation and variation in selection pressures at a microgeographic scale (Schluter, 1996; cf. Grant and Grant, 1995). And, as far as we know, no studies have compared such relationships among birds of insular and mainland environments.

Depending on territorial behavior and species-specific dispersal distance between birth and first reproduction, variation in biological traits is determined by their response to environmental heterogeneity. The ratio of scales of dispersal to the scales of selective pressures is crucial. If the range of dispersal is small relative to the scale of environmental heterogeneity, considerable variation can occur over very short distances, especially if the landscape includes habitat types that differ in selection regimes. In that case, local specialization, that is, the evolution of traits that have been selected in a given environment and which do not change if the organism migrates to another environment, is likely to occur.

Island landscapes should provide more opportunities than mainland counterparts for local specialization in response to environmental heterogeneity because niche enlargement, reduced dispersal, strong philopatry and site tenacity, all components of the so-called "insular syndrome" (Diamond, 1983; Grant, 1998; Blondel, 2000), should enhance the micro-evolutionary consequences of natural selection. The many advantages of sedentariness, which eventually lead to flightlessness on islands, include energy saving (McNab, 1994) which is beneficial when food is locally abundant and predictable year-round. Such advantages increase as those of dispersal decrease, with the result that a single large population may become split into several locally-adapted populations that, in turn, differentiate in demographic and morphologic traits (Grant, 1998).

We tested the prediction of greater phenotypic variation on islands as a consequence of higher site tenacity from long-term studies of blue tits (*Parus caeruleus*) in Mediterranean mainland and insular habitats. Mediterranean landscapes are particularly suitable for investigating the causes and consequences of phenotypic variation because they are mosaics of habitats dominated by either deciduous (e.g., *Quercus humilis*) or evergreen (e.g., *Q. ilex*) oaks. A key feature of these habitats is the difference in timing of spring development of leaves and their associated leaf-eating ar-

thropod fauna (caterpillars), the main prey for tits then: it is one month earlier in the former than in the latter (Blondel et al., 1993), generating quite different selection pressures for the tits. Moreover, the abundance of leaf-eating caterpillars is much higher in deciduous than evergreen oaks, which renew only 30% of their foliage yearly. The differences in the timing and abundance of caterpillars are crucial because this food supply has consistently been shown to determine, both proximately and ultimately, such fitness-related breeding traits as laying date and clutch size (Perrins, 1965; van Balen, 1973; Lambrechts et al., 1997).

2 Methods

Blue tit populations were studied in two landscape mosaics of similar geographic configuration, one in southern France, near Montpellier, and the other on the island of Corsica. Each landscape includes habitat patches of either deciduous or evergreen trees. Within each landscape, five study areas, dominated either by deciduous (*Quercus humilis*) or by evergreen (*Quercus ilex*) oaks, were chosen within 40 km of one another on the mainland and 60 km on Corsica. This scale is much narrower than the usual scale for interpopulation variation in passerine birds (Avise, 1994).

Breeding and morphometric parameters were collected from birds breeding in nest-boxes, which were erected at a density of *ca* 2 nest-boxes ha^{-1} in each study area. Thus a total of 600 nest-boxes were available across the ten study sites. Nest-boxes were routinely checked at least once a week, and laying date (first egg), clutch size (first clutches), hatching date, number of hatchlings and fledglings were recorded. Adults were caught when nestlings were close to fledging, identified from their ring number if ringed, sexed, and aged. All adult birds were measured (body mass, wing length, tarsus length, bill length), as well as young birds just prior to fledging (see Blondel et al., 1993; Lambrechts et al., 1997 for details).

3 Results

Considerable inter-landscape (mainland vs. island) and inter-habitat (deciduous vs evergreen oakwoods) varia-

tion was found in all the traits examined, including breeding traits (Blondel et al., 1993; Lambrechts et al., 1997), behavior (e.g., social tolerance and territorial behavior: Perret and Blondel, 1993), song structure (Doutrelant et al., 1999), and morphology (Blondel et al., 1999, 2001). In this paper we only consider laying date which is crucial for breeding success because birds which best synchronize the nestling stage with the short period of maximal caterpillar abundance raise more and better quality young which, in turn, have a better chance of recruitment. Corsican populations, on average, started laying later than mainland populations (Table 1), though, crucially, with much greater interpopulation variation than on the mainland. A comparative analysis of within-landscape variation in laying date between the mainland and Corsica using Bartlett's test of equality of variance (Snedecor and Cochran, 1980) revealed remarkably higher differentiation in laying date on Corsica than on the mainland ($\chi^2 = 165.24$, $P < 0.0001$): the five mainland populations started laying within 12 days of one another compared to 36 days on Corsica (Table 1).

Since the timing of food availability was coincident in the two regions, with caterpillars becoming available one month later on evergreen oaks in both (Blondel et al., 1993), the smaller inter-habitat variation in laying date on the mainland necessarily resulted in a greater mismatching of resource supply and demand across populations than on Corsica. Mismatched populations were found to be those breeding in evergreen oaks which are prevented from adapting to the local peak in food availability by gene swamping from deciduous oakwood populations where birds are rightly timed (Dias and Blondel, 1996). These differences in degree of adaptation to the timing of food availability result in a source-sink system (Dias et al., 1996).

Breeding pattern differed strikingly on Corsica where phenotypic variation was higher. In two populations in habitats only 25 km apart, one dominated by evergreen oaks ("evergreen 1" in Table 1) and the other by deciduous oaks ("deciduous 2" in Table 1), both were rightly timed to the peak of caterpillar abundance, effected by a difference of one month in their laying dates (Table 1). In contrast to the pattern on the mainland, both populations had adapted their

Table 1 Mean laying dates, with standard deviation in parenthesis, of blue tits in ten deciduous and evergreen Mediterranean mainland and insular habitats, taken from "March-date" (e.g., 32 = 1st of April)

	Mainland	*N*	Island	*N*
Deciduous 1	37.8 (8.6)	380	61.9 (7.4)	45
Deciduous 2	42.0 (6.0)	43	38.0 (9.7)	183
Evergreen 1	50.5 (11.9)	54	73.8 (6.6)	256
Evergreen 2	50.0 (4.3)	28	53.6 (7.0)	15
Evergreen 3	47.4 (5.1)	25	72.5 (5.1)	28
Mean	39.8 (9.9)		59.6 (18.3)	
Range	38 – 50		38 – 74	

Record series range between 3 and 15 years, depending on habitats. *N* = sample size.

breeding phenology to local variation in food supply (Lambrechts et al., 1997; Blondel et al., 1999). Furthermore, they differed significantly in all measured demographic and morphometric traits as well, e.g. wing length, body mass, tarsus length and bill length (Blondel et al., 1999). Yet a genetic analysis of population structure using microsatellite loci (Charmantier, 2000) showed that genetic differentiation between the two populations was small, albeit significant ($F_{st} = 0.0072$ to 0.0108 depending on years, $P<0.01$).

4 Discussion

This case study provides a striking, and as far as we know the first, example in birds of an adaptive response of suites of life history traits to habitat-specific selection regimes that operate on a scale much smaller than the scale of potential gene flow. A strong interpopulation variation in laying date is particularly meaningful because suites of other traits, including morphometric traits, are likely to co-vary with laying date.

Because mainland and Corsican landscapes are well matched in geographic configuration and proportion of habitat types, something other than landscape structure must be involved to explain the patterns. The most likely is that dispersal distances are lower and habitat fidelity, as well as habitat-specific assortative mating, higher on the island, supporting our prediction about the role of dispersal and habitat selection in population differentiation on islands.

In vertebrates, population differentiation on a microgeographic scale has rarely been proven to be adaptive (Schluter, 1996), even though local variation in fitness-related traits resulting from divergent resource-based selection expresses the process of adaptation (Reznick et al., 1990; Endler, 1995; McKinnon and Rundle, 2002). Examples of genetically-based micro-geographic variation that relates suites of covarying traits to environmental factors within species have been found in fishes (Endler, 1995), mammals (Nevo, 1986; Daly and Patton, 1990), and lizards (Losos et al., 1997). Yet in such mobile organisms as birds, local population differentiation in response to divergent selection pressures is supposed to be rare on a scale smaller than the dispersal range of individuals because of the homogenizing effects of gene flow.

Theory predicts, nevertheless, that if the environment is relatively constant in space, maximizing mean fitness results in adaptive differentiation of specialized phenotypes because environmental constancy favors the evolution of specialization (Futuyma and Moreno, 1988), even if gene flow is in excess of a few migrants per generation (Barton and Whitlock, 1997). Corsican blue tits support these predictions because their specialization to local habitats results from divergent selection pressures which are presumably sufficiently strong to outweigh the effects of gene flow, if any (Slatkin, 1994; Endler, 1995). This is an illustration of the 'divergence-with-gene-flow' model of speciation (Maynard Smith, 1966) whereby reproductive isolation can evolve between populations connected by gene flow whenever divergent selection stemming from environmental differences is strong relative to it (Rice and Hostert, 1993; Schluter, 2001). Moreover, the overall pattern of differentiation between the two Corsican populations is consistent with Rice and Hostert's (1993) claim that speciation proceeds most rapidly when several traits covary under divergent selection, as is the case here (Blondel et al., 1999). Whatever the extent of dispersal between the two populations, gene flow between them must be low because of premating isolating mechanisms, whether physiological or behavioral, which depend on traits that diverge in association with the exploitation of different habitats and resources.

Given their large phenotypic variation, the small degree of genetic differentiation between the two Corsican populations is surprising and suggests substantial gene swamping. Genetic differentiation across conspecific populations, nevertheless, does not necessarily parallel patterns of morphological variation (Lovette et al., 1998). Neutral markers may have not yet tracked the evolution of diverging suites of traits because it has been too recent and/or too rapid. Although microsatellites are among the most rapidly evolving repetitive markers, and hence sensitive detectors of intra-specific differentiation, adaptive evolution of gene combinations determining fitness-related traits may presumably occur still more rapidly, ahead of change in neutral regions of the genome.

Such an explanation has been proposed to explain the low genetic differentiation among well-differentiated populations of cuckoos (egg color of cuckoo gentes) (Gibbs et al., 1996) and among sympatric morphs of the Arctic charr (*Salvinus alpinus*) in Iceland (Danzmann et al., 1991). The relatively recent structure of Corsican landscapes, which results from long-lasting human impact on the vegetation (Reille, 1992), supports the interpretation of low genomic differentiation in spite of the evolution of distinct ecological morphs. Comparing the responses of less dispersive island birds and more dispersive mainland birds to similar spatial diversity of habitats provides a practical demonstration of the relationships between dispersal, spatially variable selection and local adaptation which may be conducive to speciation (Via, 2001). One consequence of the 'insular syndrome' favoring local differentiation is compensation for the lower inter-specific diversity in impoverished insular communities by greater intra-specific diversity.

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