5-25-2005

Nonrandom dispersal and local adaptation

Jay F. Storz

University of Nebraska - Lincoln, jstorz2@unl.edu

Nonrandom dispersal and local adaptation

J. F. Storz

School of Biological Sciences, University of Nebraska–Lincoln, 314 Manter Hall, Lincoln, NE 68588, USA; email: jstorz2@unl.edu

Two recent studies of wild bird populations provide new insights into mechanisms of microevolutionary change by revealing how variation in fitness-related traits may be maintained over very small spatial scales.

When a population is distributed across a heterogeneous environment, the prospects for local adaptation depend on the spatial scale of fitness variation relative to the spatial scale of dispersal. If the patchiness of environmental conditions is too "fine-grained," the spatial acuity of natural selection may be severely diminished by the homogenizing effects of gene flow (García-Ramos and Kirkpatrick, 1997; Lenormand, 2002). For example, habitat variation over a scale of several square kilometers may be sufficiently "coarse-grained" to permit local adaptation in animals with weak dispersal capabilities like snails, but certainly not in more vagile animals like birds. So when fine-scale patterns of trait differentiation are observed in high gene flow species, some form of ecological or evolutionary explanation is required.

These two new studies (Garant *et al*, 2005; Postma and van Noodwijk, 2005) involved long-term, longitudinal studies of free-ranging great tits (*Parus major*) in different parts of Europe. The study by Postma and van Noodwijk (2005) documented microgeographic variation in clutch size between subpopulations of great tits that inhabit opposite sides of the tiny (4,022 ha) island of Vlieland in the Netherlands. Similarly, the study by Garant *et al* (2005) documented microgeographic variation in fledgling mass between two ecologically distinct sectors of a contiguous woodland in Oxfordshire, England that are separated by less than 4 km.

One possible explanation for the fine-scale patterns of differentiation is that the phenotypic variation between different habitats is environmentally induced. Indeed, a role for phenotypic plasticity in causing geographic variation in avian morphology would not be without precedent (James, 1983). Another possible explanation is that the genetically based trait differences reflect the cumulative effects of divergent natural selection toward different trait optima in the different habitats. In both studies, the authors were able to test these alternatives by tracking the natal dispersal and settlement of individually marked birds with known pedigrees: basically, the birds performed their own reciprocal transplant experiments. This allowed the authors to separate out the genetic and environmental components of trait variation. Importantly, the reciprocal transplant experiments also provided the opportunity to assess the fitness consequences of genetically based trait variation in each of the different habitats. In both studies, results of pedigree-based analyses revealed that the observed patterns of trait differentiation were not attributable to phenotypic plasticity, nor did they reflect habitat-specific differences in selection regimes.

So how are these persistent differences in morphology and life history maintained over such small spatial scales? In both cases, nonrandom dispersal appears to be the key. In the case of the great tits on Vlieland (Postma and van Noodwijk,

2005), the microgeographic differentiation in clutch size can be explained by differences in the extent to which local subpopulations are prevented from attaining the island-specific phenotypic optimum. Small clutches are favored on both the eastern and western sides of the island, but the subpopulation on the western side of the island receives a proportionally greater number of immigrants from outside the island that tend to carry genes for large clutch sizes. Consequently, the subpopulation on the western side of Vlieland receives a continual influx of maladaptive migrant alleles that contribute to an increase in average clutch size that exceeds the island-specific optimum. By contrast, the subpopulation on the eastern side of the island receives proportionally less immigration and the average clutch size remains closer to the island-specific optimum.

In the case of the great tits in Oxfordshire (Garant *et al*, 2005), the microgeographic differentiation in fledgling mass can be explained by two factors. One factor is the habitat-specific differences in the expression of genetically based trait variation, and the other, patterns of natal dispersal between habitats that are highly nonrandom with respect to phenotype. Since the evolutionary response to selection on a particular trait is directly proportional to the level of genetic variation in the trait, population differences in trait values could reflect differences in heritability (*i.e.,* the fraction of trait variation that is attributable to genetic differences between individuals) even if the populations are subject to the

same selection pressures. This is the case in the woods of Oxfordshire: the heritability of fledgling mass is considerably higher in the northern sector of the forest than in the eastern sector, such that the expected response to selection is roughly twice as high in the north. However, it seems likely that any trait variation caused by the habitat-specific differences in heritability would be swamped by gene flow, given that >60% of the breeding birds in a given area are born outside that area. It turns out that habitat-specific differences in the heritability of fledgling mass are reinforced by nonrandom dispersal, as larger-than-average birds tend to settle in higher quality habitat in the northern sector of the forest. Thus, levels of genetically based trait variation and patterns of natal dispersal are both strongly influenced by fine-scale variation in habitat quality.

The studies by Garant *et al* (2005) and Postma and van Noodwijk (2005) are noteworthy because they demonstrate how nonrandom dispersal can promote genetic differentiation in fitness-related traits even in the absence of spatial variation in the selection regime. In population genetic models, gene flow is typically viewed as a purely homogenizing force because the rate at which migrant alleles are introduced into a given population is assumed to be independent of their effects on fitness. However, in the case of great tits, dispersal between different habitats appears to be highly phenotype dependent. So the alleles that influence fledgling mass and clutch size may be characterized by rates of migration that are nonrandom with respect to their effects on fitness in different environments. Both of these studies should change the way we think about mechanisms of microevolutionary change. Geographic patterns of variation in fitness-related traits are often assumed to reflect the interplay between the diversifying effects of local selection and the homogenizing effects of gene flow (Hendry *et al*, 2001). In contrast to this conventional view, the patterns of trait differentiation observed in great tits appear to reflect the interplay between the diversifying effects of nonrandom dispersal and the homogenizing effects of spatially uniform selection.

References

Garant, D., Kruuk, L.E.B., Wilkin, T. A., McCleery, R. H., and Sheldon, B. C. (2005) *Nature* **433**: 60−65.

García-Ramos, G., and Kirkpatrick, M. (1997) *Evolution* **51**: 21−28.

Hendry, A. P., Day, T., and Taylor E. B. (2001) *Evolution* **55**: 459−466.

James, F. C. (1983) *Science* **221**: 184−186.

Lenormand, T. (2002) *Trends Ecol Evol* **17**: 183−189.

Postma, E., and van Noodwijk, A. J. (2005) *Nature* **433**: 65−68.