

during face processing<sup>17</sup>. Furthermore, brain-imaging data indicate that even though the amygdala might respond to fearful eyes when they are presented alone, it is activated most in response to whole faces<sup>18</sup>.

Finally, it remains to be determined whether SM's attention to other facial features is normal (only her response to the eye region was recorded), and to explain why she can still recognize expressions of sadness or anger in which eye information is important (normal subjects find it more difficult to recognize these emotions when the eyes are erased)<sup>3</sup>.

The intriguing implications of these new findings need to be explored. What are the neural circuits by which the amygdala might guide eye scan-paths? How does SM judge expressions in composite faces such as those in Figure 1? How does she perform on more implicit tests of fear recognition, or using graded rather than dichotomous measures? Does she orient her eyes normally to emotional visual stimuli other than faces, and to emotional voices? What is the amygdala's normal role in exploring social situations and looking at other people, and are these mechanisms altered in diseases such as phobias or autism that are thought to involve the amygdala? We are just beginning to realize how the brain processes emotionally

relevant cues in the environment, and the unusual features of SM will provide much food for future thought. ■

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## Evolutionary genetics

# Differentiation by dispersal

David W. Coltman

Gene flow between populations — caused by migration, for instance — is most often viewed as a homogenizing force in evolution. But two studies of wild birds and non-random dispersal find otherwise.

Whether or not two separate populations of a species become genetically different is thought to depend largely on gene flow. Classical population-genetics theory predicts that populations that frequently exchange individuals through dispersal will remain genetically similar<sup>1</sup>. Disconnected populations, by contrast, have a greater capacity to become distinct through forces such as genetic drift and adaptation to local conditions. In population genetics, dispersal is often viewed as a diffusion-like, random process, and selection and genetic variation are assumed to be locally homogeneous. Populations of organisms with high rates of dispersal — such as songbirds — are therefore expected to be fairly genetically alike at small spatial scales. But two new independent studies of wild great tits, *Parus major*, challenge this assumption: they show that when dispersal is non-random, genetic differentiation can be produced at surprisingly fine spatial scales (see pages 60 and 65 of this issue<sup>2,3</sup>).

Postma and van Noordwijk<sup>3</sup> studied clutch size in great tits (Fig. 1) on the tiny — 4,022-hectare — island of Vlieland in the Netherlands from 1975 to 1995. They first found that birds that bred in the western part of the island laid, on average, 1.15 more eggs than birds from the eastern part. How much of this difference is determined by the environment, and how much is genetically controlled? Fortunately, 10% of the females born on one side of Vlieland disperse to breed on the other, and this allowed genetic and environmental effects to be teased apart. The authors' analysis showed that birds of eastern ancestry produced consistently smaller clutches in either environment — so there is clearly a large genetic component to the difference in clutch size between the regions. In fact, genetic effects accounted for about 40% of this difference. But, given that the western and eastern regions are separated by only a few kilometres, and they exchange migrants and receive immigrants from outside Vlieland, why does this genetic difference persist?



## 100 YEARS AGO

Writing on the subject of “Greek at Oxford,” a correspondent of the *Times* again expressed the common belief that “Darwin regretted not having learnt Greek.” A letter from Mr. Francis Darwin in the *Times* of December 29, 1904, shows that the statement is altogether opposed to Darwin's views. Darwin says of his education at Shrewsbury School:— “Nothing could have been worse for the development of my mind than Dr. Butler's school, as it was strictly classical, nothing else being taught, except a little ancient geography and history” (“Life and Letters,” i., 31). He was, in fact, a victim of that “premature specialisation” which is generally referred to in a somewhat one-sided spirit, and from which the public schoolboy is not yet freed. Mr. Darwin adds:— “If the name of Charles Darwin is to be brought into this controversy it must not be used for compulsory Greek, but against it. In 1867 he wrote to Farrar, ‘I am one of the root and branch men, and would leave classics to be learnt by those alone who have sufficient zeal and the high taste requisite for their appreciation’ (‘More Letters of Charles Darwin,’ ii., 441).” From *Nature* 5 January 1905.

## 50 YEARS AGO

The expedition organized jointly by the Zoological Society of London and the British Broadcasting Corporation returned to Britain just before Christmas from ten weeks field-work in Sierra Leone, bringing a large collection of animals and a considerable quantity of cinematograph films and sound recordings... One of the main objects of the expedition was to find the nesting habitat of *Picathartes gymnocephala*, a rare passerine bird the systematic position of which is obscure; this bird has seldom been seen alive by Europeans. The habitat was found in difficult hilly bush country, and in spite of the dense shade cast by the forest successful films were made of the birds on and near the nests, of the eggs and of the parents feeding the young by regurgitation. Sound records were also obtained of the voices of the birds in their natural surroundings, and a living specimen was captured and brought to London. Another species never before exhibited in captivity that was successfully sought and found is the brilliantly iridescent emerald starling *Coccycolius iris*. From *Nature* 8 January 1955.



Figure 1 The great tit: challenging assumptions about gene flow and genetic differentiation.

To answer this, Postma and van Noordwijk examined the viability and fecundity of birds born in the east or west that breed in the other region, and precisely quantified levels of immigration from outside Vlieland. Immigrants and birds born in the west tended to have larger clutches than birds born in the east, regardless of where they bred. However, female birds born in the east seemed to be better adapted to life on Vlieland, because they were twice as likely to survive as birds born elsewhere (perhaps allowing them to have smaller clutch sizes). So, from the standpoint of clutch size and survival, immigrants seemed most closely related to the birds born in the west. Most interestingly, 43% of first-time breeders in the west were immigrants to Vlieland, compared with only 13% in the east.

There has thus been an influx of genes for relatively large clutches, and the higher rate of immigration to the west has resulted in bigger clutches there. Birds in the east have maintained their locally adapted smaller clutch sizes against an influx of 13% immigration. But the west is swamped by immigrant genotypes. So differing levels of gene flow have maintained large genetic differences at a very fine spatial scale.

Postma and van Noordwijk suggest<sup>3</sup> that differentiation at this scale because of processes such as these may not be rare (as refs 4 and 5 also suggest), but may remain undetected in other populations because few researchers have appropriate long-term data. Results from a 36-year study of nestling body mass in the same species living in woodlands at Wytham in Oxfordshire, UK, would seem to support this suggestion.

Garant *et al.*<sup>2</sup> found that the mean mass of birds in the eastern block of Wytham woods

has decreased since 1965, whereas that of birds in the northern block has remained constant. Quantitative genetic analyses demonstrated a genetic component to these trends, and overall there was 50% more genetic variance in the northern population than in the eastern population. These regions are separated by only about 2 kilometres, and on average are both composed of more than 50% immigrants from other parts of the woods or from outside. How has this differentiation persisted under such high rates of potentially homogenizing gene flow?

Heterogeneous dispersal again seems to be the key. Birds from central regions of Wytham woods and immigrants showed non-random dispersal patterns with respect to their weight. Emigrants to the north tended to be larger over time, whereas emigrants to the east tended to be smaller. Even within families, heavier offspring showed an increased tendency to settle in the north.

So, a markedly non-random settlement pattern drives fine-scale genetic differentiation in Wytham woods. But why is there this non-random settlement? Garant *et al.* suggest that temporal and spatial variations in bird density provide the mechanism. Local density has been, on average, twice as high in the east as in the north, producing greater pressures on habitat in the east. However, density has been increasing in the north, as birds there are more likely to survive and be reproductively successful. Taken together, the results suggest that individuals that are genetically predisposed to be larger and heavier have preferentially settled in the lower-density habitat in the north, and this has driven population differentiation.

These studies<sup>2,3</sup> document remarkable — and quantitatively similar — levels of genetic

differentiation at a very fine scale relative to the birds' dispersal capability. In both cases, differentiation is maintained primarily by non-random dispersal and settlement, and in the absence of major spatial differences in selection. The findings shed new light on the mechanisms of microevolution, because there is no reason to suspect that these phenomena are unique to great tits<sup>4,5</sup>. But the ability to detect such phenomena depends on the availability of long-term data from continuously monitored populations of marked individuals, and on the existence of biotic or abiotic gradients that may drive the underlying microevolutionary processes. In both of these studies there was sufficient pedigree information to be able to compare the performance of individuals with common genetic backgrounds but inhabiting different environments.

With the increasing use of quantitative genetics analyses such as these<sup>2,3</sup> in evolutionary studies of wild animals<sup>6</sup>, we ought to be paying more attention to how quantitative genetic variation is spatially and temporally structured. For example, studies that integrate fine-scaled maps of habitat quality with complex pedigrees can look at how genes are distributed spatially, and how they may interact with the environment.

The great advantage of the quantitative genetic approach is that microevolution can be studied in the wild without knowing exactly which genes are responsible for the variation in the physical traits in question. But this is also a great disadvantage, because it would be ideal to see evidence for spatially associated differences in the genetic loci involved<sup>7</sup>. Indeed, a truly mechanistic understanding of microevolution requires an understanding of genetic architecture (the properties of the individual genes underlying variation)<sup>8</sup>. One way of gaining such an understanding of microevolution in nature will be to apply genomics<sup>9,10</sup> to ecological and evolutionary studies in non-model species, using comparative approaches<sup>11–13</sup>. ■

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