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populations actually undergo an 'adaptive suicide'. A degrading environment can obstruct the evolutionary path of a dispersal trait towards more viable rescue states. From within such an 'adaptive trap', gradual evolution of dispersal can no longer prevent population extinction.

In this workshop, the recent rise of adaptive dynamics theory was very apparent, with many speakers using this tool to explore different aspects of dispersal evolution. In the real world, however, detailed knowledge about dispersal in many organisms remains scarce. Some contributions suggested that new techniques, such as those from molecular biology, might help to overcome this shortage. It will remain a challenge to integrate the various approaches presented, so that more theoretical predictions can be tested in the field. A forthcoming symposium\* in France will provide the next opportunity to see how close we are to finding a unifying approach in the study of dispersal.

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The fruit flies *Drosophila simulans* and *D. mauritiana* are probably the best-studied pair of sibling species. The former is a cosmopolitan human commensal, whereas the latter is an island endemic, presumably isolated half a million years ago<sup>4</sup> (Mya). When crossed, the males suffer spermatogenic defects and are sterile, whereas the females retain normal fertility. This has allowed geneticists to map the putative speciation genes by backcrossing hybrid females with parental males and thus introgressing portions of the genome of the one species into the genetic background of the other.

A particularly impressive series of such introgressions has been carried out by a group led by Chung-I Wu at the University of Chicago. Having located a range of speciation genes, they conclude that hybrid male sterility is caused by no less than 120 genes, scattered across the genomes of both species<sup>8</sup>. Most of these appear to have relatively small effects individually but exhibit strong epistatic interactions<sup>9</sup>. An X-linked locus called *Odysseus* is such an example. Like its mythological namesake, it causes havoc when introduced in the foreign genetic environment: it induces approximately a 40% reduction in male fertility. But its effect can be moderated or aggravated if it is accompanied by nearby co-introgressed genes.

### Homeobox divergence

In a paper in *Science*, Ting *et al.* now report the cloning of *Odysseus*<sup>4</sup>. Having narrowed down the locus to an 8.4 kb region, they found it to possess three open reading frames, the 349 amino acids long transcript of which unexpectedly contained the 60 or so amino acids that characterize homeobox genes.

The group then sequenced part of the gene in all four species that make up the *melanogaster* clade, to which *simulans* and *mauritiana* belong. The homeobox turned out to be highly divergent among the four species, the largest difference being 15 amino acid substitutions between the sibling species *simulans* and *mauritiana*. Homologues of the gene are found in mouse, rat and the worm *Caenorhabditis elegans*, where it is expressed in neural, rather than reproductive, tissues, and where it is extremely conserved. For example, the sequence difference between *simulans* and *mauritiana* (diverged 0.5 Mya) is twice as large as that between mouse and *C. elegans* (diverged c. 700 Mya)!

The authors convincingly argue that the sequences compared in *Drosophila* are true homologues. For example, the difference in the introns between *simulans* and *mauritiana* is only 1.4%, exactly

conforming to the neutral rate. In addition, they sequenced multiple alleles per species, which means that the differences between the species are not the result of sampling within-species polymorphisms.

The gene (which Ting *et al.* refer to as *OdsH* - *Odysseus*-site Homeobox gene) thus appears to have undergone a dramatic increase in evolutionary rate in this species group. The increase has been driven by directional selection rather than a relaxation of stabilizing selection, as is proved by the overwhelming prevalence of substitutions that cause an amino-acid change over those that do not (at least in the lineage leading to *mauritiana*). What remains is the tantalizing question: what sort of selection could have propelled an otherwise strongly conserved regulatory gene across long mutational distances to cause hybrid male sterility?

Rapidly evolving homeobox genes that are expressed in male reproductive tissues have been found before. A gene called *Pem* is expressed in the testes of rat and mouse and its homeobox differs by 24 amino acids between these two species<sup>10</sup>. Sperm proteins in *Drosophila* and a mollusc are also known to evolve uncharacteristically fast<sup>11,12</sup>.

These observations form a molecular extension of the taxonomists' old rule of thumb that male genitalia and secondary sexual traits are the best characters to distinguish otherwise similar species<sup>13</sup>. Such morphological traits are obviously the product of sexual selection by male competition and female choice. It is becoming increasingly clear, however, that sexual selection does not only act on gross reproductive morphology, but on all aspects related to competition for mates, including the chemistry of the ejaculate<sup>14</sup>.

Sexual selection can cause reproductive traits to change rapidly and unpredictably. In allopatric populations, this can lead to large differences in mate-recognition, which can cause behavioural incompatibility, such as in the various

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