

## Evolution

## Responses to chemical warfare

J. S. Jones

SPECIES, like states, often indulge in arms races; and their economy may become so involved in the process that it determines the course of evolution. The struggle between humans and insect pests has such a history. After some initial easy victories, mutual escalation has meant that many crops now demand repeated spraying and that 3 per cent of a pest's proteins may be devoted to detoxification. This race has gone on for only as long as that between the West and the Warsaw Pact. There has been much more prolonged chemical warfare between insects and plants, and an equivalent coevolution of natural pesticides and of means of detoxifying them. Indeed, some insects have evolved methods of dealing with plant toxins which make them resistant to chemical control. At a recent meeting in Australia\* — where most organisms seem to have evolved the ability to bite, sting or poison their fellows — the parallels between the genetics of resistance in pests and that of the use of toxic resources by fruitflies were discussed. There is a real prospect of economically valuable results emerging from fundamental research.

Many *Drosophila* grow on poisonous plants. Local adaptation to a toxin may lead to rapid genetic change. *D. mojavensis* lives on agria cactus on the Baja California peninsula, but on organpipe on the Mexican mainland. Flies choose a medium supplemented with a chemical cocktail close to the toxins of their natural host (J.C. Fogelman, Univ. Rochester). There are also differences in the rate of development on each host (W.J. Etges, Univ. Arkansas), and the beginnings of reproductive isolation between the races. Mainland females discriminate against Baja males when given a choice of mates by using chemical cues in the cuticular hydrocarbons (T.A. Markow, Arizona State Univ.). There may be a balance between sexual and natural selection, as lower-molecular-weight hydrocarbons increase male attractiveness but are less effective at retaining moisture. Attractiveness decreases at high temperature, as this increases the proportion of long-chain hydrocarbons. Males with heavyweight waterproofing are impervious but impotent. In *D. melanogaster*, resistance to desiccation is achieved only at the cost of evolving a lower metabolic rate (P.A. Parsons, Griffith Univ.) and the shift to a new toxic host by *D. mojavensis* may have been forced on the flies as the Mexican

climate dried. The process is going on apace in the cactus *Drosophila* of the Caribbean, where it has led to speciation (W.B. Heed, Univ. Arizona).

The interaction between fly and toxin involves some third parties: the bacteria and yeasts which produce the cactus rots upon which the flies feed. Many of these are restricted to a particular cactus, and by detoxifying poisons speed the growth of the *Drosophila* (W.T. Starmer, Syracuse Univ.). In return they are transported from plant to plant by the flies.

Some cacti have themselves become pests. The prickly pear *Opuntia* has been accompanied by *D. buzzatti* in its spread across the world. Although the dependence of the flies on yeast and cactus is just as rigid as in *D. mojavensis*, the interaction between host choice and fly fitness is much more complex (J.S.F. Barker, Univ. New England). In other *Drosophila* that feed on toxic plants such as fungi, the genetics of host specialization is also complicated and may be modified by experience (J. Jaenike, Univ. Rochester). *D. melanogaster* uses a wide range of foods. Many contain ethanol, a toxin to which this species, like its human commensal, is well adapted. The genetics of host preference in *D. melanogaster* has proved subtle and elusive (A.A. Hoffman, La Trobe Univ.). New population genetic theory shows that any tendency of animals of a particular genotype to choose a habitat in which they are relatively fit could be a potent mechanism of maintaining genetic diversity, as long as the same gene influences habitat selection and fitness (P.W. Hedrick, Pennsylvania State Univ.). There is as yet no clear evidence of such pleiotropy in the genes for toxin resistance and for host selection. As is so often the case in population genetics, the theoretical cart is well ahead of the empirical horse.

Much is known of the biochemistry of detoxification of natural and artificial poisons. The alcohol dehydrogenase gene is central to ethanol detoxification, and genotypes which increase flux through this pathway are more common in wineries and survive better on alcohol (B.W. Geer, Knox College.). *D. melanogaster* has one structural gene with two promoters active at different times during development; but in the cactus-fly species the structural gene has been duplicated, and each copy has a promoter homologous to that of *D. melanogaster* larvae (D.T. Sullivan, Syracuse Univ.). There may be a parallel here with the gene amplifications often involved in insecticide resistance.

Detoxifying esterases have also undergone gene duplication in *Drosophila*. The duplicated esterases within cactus *Drosophila* species show more sequence similarity than does each of them among species, suggesting that concerted evolution is involved (P.D. East, Univ. New England). The *Est-6* locus in *D. melanogaster* has more than 20 alleles differing in amino-acid sequence. The commonest allele has the same DNA sequence throughout the world, although other alleles show sequence divergence. This common allele may represent a new esterase which has spread so rapidly that there has been no time for sequence change (J.G. Oakeshott, CSIRO, Canberra). Although the nature of selection on this allele is unknown, sexual selection is a possibility as esterases secreted by males act as molecular contraceptives which inhibit female remating (R.C. Richmond, Indiana Univ.).

Modern genetic technology means that cloned genes in one species can be used to search for their homologues in others. The evolution of *Drosophila* in response to natural toxins may therefore have practical use in studying insecticide resistance. The sheep blowfly *Lucilia coprina* in Australia is resistant to organophosphates because of the evolution of new esterases. At least two loci are involved and, as in *Drosophila*, they are part of a gene family. The chromosomal positions of these genes and their activity during development are the same as in *Drosophila*. A search for the *Lucilia* resistance genes using a *Drosophila* esterase probe is the first step in cloning these genes and perhaps in developing new methods of combating their effects (R. Russell, CSIRO, Canberra). *Lucilia* eye-colour genes also have amino-acid sequences similar to those of their equivalents in *D. melanogaster*. But this homology conceals considerable divergence in DNA sequence. *Lucilia* and *Drosophila* have very different codon preferences, and the transcription unit for the eye mutants in *Lucilia* is several times longer than in the more widely studied species because of the presence of much longer introns (A. J. Havells, Australian National Univ.).

More than 500 insect pests are now resistant to chemical control and there is even evidence of a recent spread of resistance through the world's *D. melanogaster*. Most of the genes involved are single mutants of large effect, which are just the sorts of genes which can now be genetically manipulated in *Drosophila*. It is inconceivable that new weapons in the war on pests will come from an understanding of insects' own defences against natural chemicals. Perhaps this arms race will be the last in human history to end in the destruction of only one of the antagonists. □

J.S. Jones is in the Department of Genetics and Biometry, University College London, London NW1 2HE, UK.

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