unconstrained females to produce as a response to this level of constrained oviposition is 0.4 under the simplifying assumptions of Godfray's model[14]. This value can be compared to the mean sex ratio produced by females brought into the laboratory that were unconstrained, which was 0.34. The theory of responses to constrained oviposition therefore explains over 60% of the deviation from a sex ratio of 0.5 as predicted by fisherian frequency-dependent selection on the sex ratio under panmixis.

Ode *et al.*'s[6] test of the constrained-oviposition hypothesis is, to my knowledge, the first study to provide an explanation for female-biased sex allocation under panmixis by an arthropod in the field. Just how widespread are sex-ratio shifts in response to constrained oviposition is unknown at this point, but constrained oviposition has been found in a number of species of parasitoid wasps that exhibit a broad range of mating structures[14,17,18]. Whether or not responses to constrained oviposition turn out to be prevalent, Ode *et al.*'s study has given impetus to an expanded view of sex allocation behaviour that includes non-hamiltonian responses to mating structure.

George E. Heimpel

Dept of Entomology, University of Wisconsin, Madison, WI 53706, USA

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Speciation and signal trait genetics

To understand the process of speciation, we need to measure traits contributing to reproductive isolation and if possible identify their genetic basis. A particular problem with signal traits is that they tend to be difficult to measure repeatably. Insect cuticular hydrocarbons, used by numerous species as close range chemical signals, are a rare exception since they can be quantified precisely using gas chromatography[1-3]. Two new studies have exploited this potential[4,5].

Cuticular hydrocarbons operate in mate recognition in many groups. The best studied are the female hydrocarbons of the *Drosophila melanogaster* complex which stimulate male courtship behaviour[6]. Investigation of the genetic basis of this system has recently begun to answer some important questions about the origin of species. In particular, the opportunity to identify particular genes involved in isolating traits allows us to make inroads into the questions of how many genes need to change to isolate a new species, and where these genes are located in the genome.

Drosophila melanogaster and *D. simulans* are cosmopolitan human commensals while *D. mauritiana* and *D. sechellia* are endemic to Indian Ocean islands. Biogeographical and geological evidence estimates the divergence between the outgroup species *D. melanogaster* and the other species at 2–4 million years ago, and divergence within this ingroup at 1–2 million years ago[7]. *Drosophila melanogaster* and *D. sechellia* are sexually dimorphic for their main cuticular hydrocarbons, while *D. mauritiana* and *D. simulans* are sexually monomorphic (see Fig. 1). Cuticular hydrocarbons contribute to asymmetric reproductive isolation between the species: males of sexually dimorphic species will court females of all species, whereas monomorphic males will only court conspecific females. Genetic analysis reveals that the main hydrocarbon difference between *D. melanogaster* and *D. simulans* is largely controlled by five non-overlapping regions on chromosome III, with no effect of the rest of chromosome III or the remaining 60% of the genome[4]. This suggests a minimum of five genes on a single chromosome account for most of the change in the isolating trait.

Whether five genes is a small or large number as a basis for reproductive isolation is controversial[8]. Different proposed modes of speciation require different numbers of genes. A small number of genes of large effect suggests the involvement of natural selection since each locus is likely to have a big impact on fitness. On the other hand, traits controlled by large numbers of genes may be more likely to change as a result of genetic drift. The apparently small number of genes involved in the *D. melanogaster–D. simulans* difference suggests that selection has played a role in their divergence. The number of genes involved in traits responsible for divergence is also interesting because some models suggest that large changes in a signal trait may be more likely if controlled by a small number of genes of large effect[9]. This may enable traits to cross adaptive valleys where minor changes might receive greater opposition from selection.

In considering these hypotheses it is worth bearing in mind that the number of genes contributing to the difference at the time of speciation may have been less than the number contributing at present. Furthermore, although their present role is well established, the involvement of hydrocarbons in the speciation event relative to other factors such as song and courtship behaviour is unknown[10,11].

As well as providing insights into the genetics of speciation, cuticular hydrocarbons may also allow us to reconstruct speciation histories. The main hydrocarbon of *D. melanogaster* and *D. sechellia*

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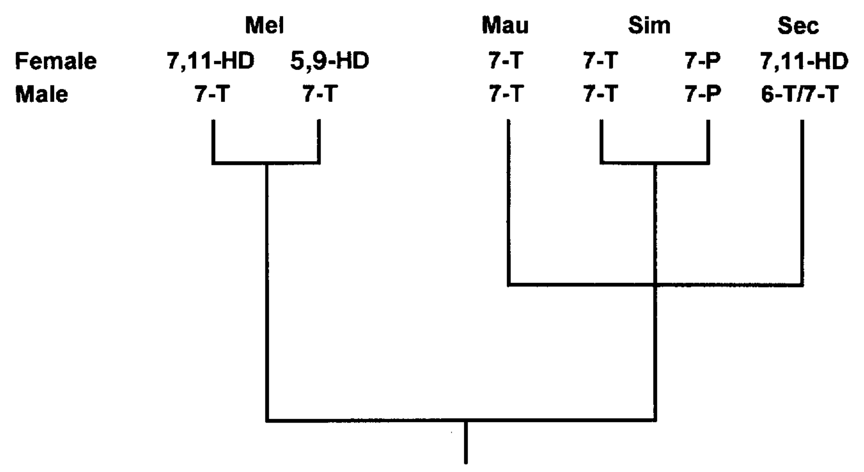

Fig. 1. The phylogeny of the *D. melanogaster* complex, showing main male and female cuticular hydrocarbons. The outgroup species *D. melanogaster* (Mel), and the three ingroup species *D. mauritiana* (Mau), *D. simulans* (Sim), and *D. sechellia* (Sec) are illustrated as are the polymorphisms in *D. melanogaster* and *D. simulans*.

females, 7,11-heptacosadiene (7,11-HD), acts as a potent inhibitor of male *D. simulans* courtship. The unwillingness of *D. simulans* males to mate with high 7,11-HD females can be taken to imply[10] that dimorphic *D. melanogaster* hydrocarbons must be ancestral to the monomorphic *D. simulans* hydrocarbons. The main hydrocarbon of *D. simulans*, 7-tricosene (7-T), may have evolved as a new female signal, followed by changes in the male preference away from 7,11-HD and towards 7-T. However, the alternative transition is also possible. A small change, such as might result from genetic drift, in the level of 7,11-HD may not seriously inhibit *D. simulans* male courtship. A series of small drifts in female cuticular hydrocarbon, each followed by a change in male preference, could have led to the evolution of the *D. melanogaster* trait from *D. simulans*[12]. Genetic analysis shows the *D. simulans* and *D. sechellia* hydrocarbon difference is also under the control of chromosome III with only a few genes or even a single locus involved[10]. This adds to the evidence that 7,11-HD is the ancestral hydrocarbon, retained by *D. sechellia* but lost by *D. simulans* and *D. mauritiana*.

Interspecific studies have recently been complemented by investigation of the genetic basis of cuticular hydrocarbon variation within a single species. A worldwide study of 63 *D. melanogaster* strains reveals a polymorphism in their major hydrocarbon (see Fig. 2), which is also under the control of chromosome III[5]. Although the majority of strains have 7,11-HD as their main female hydrocarbon, females from sub-Saharan Africa and the Caribbean differ quantitatively, having low levels of 7,11-HD and high levels of the position isomer 5,9-heptacosadiene (5,9-HD). Intriguingly, crosses between these strains revealed that females with high levels of 7,11-HD mate more rapidly than females with low levels, regardless of male strain. The consequences of this behavioural difference remain unexplored. Although there is little evidence for assortative mating, the authors suggest that it may have contributed to the development or maintenance of genetic differences between strains from sub-Saharan Africa and the rest of the world. However, if more rapid mating conveys a selective advantage for the 7,11-HD form, this could lead to the introgression of genes into the 5,9-HD form.

A similar polymorphism has been identified in *D. simulans*[13]. Most strains have 7-T as their major female hydrocarbon, with the exception of individuals from the Gulf of Benin, which show low levels of 7-T, and high levels of 7-pentacosene (7-P). The control of this polymorphism has been narrowed down to a single locus (*Ngbo*) on chromosome II. The two less common forms of *D. melanogaster* and *D. simulans* (high 5,9-HD and high 7-P) are controlled by semidominant alleles. In *D. melanogaster* the semidominance of the 5,9-HD form could hinder the spread of the potentially advantageous 7,11-HD form.

In contrast to interspecific studies, the pattern of hydrocarbons within *D. melanogaster* supports the idea that high 5,9-HD is the ancestral form, since the diversity of the complex in Africa suggests its origins lie in that continent. If the high 5,9-HD trait is ancestral, then all males prefer derived females. This may be contrary to Kaneshiro's hypothesis – that females from populations that have passed through bottlenecks will be discriminated against[14]. Since expansion is associated with repeated founder events, it may lead to loss of courtship behaviours through genetic drift and reduced mate discrimination at low population density. Alternatively, if mates are rarely encountered this might lead to selection for more attractive females. The 7,11-HD trait may have evolved to induce more vigorous male courtship behaviour in low density populations. A number of scenarios can be envisaged to explain the similarity between strains from the Caribbean and sub-Saharan Africa. The authors speculate that they may be the result of colonization with the movement of the slave trade, but since hydrocarbons are involved in waterproofing the insect cuticle, adaptive explanations may also be possible. Hydrocarbons in other *Drosophila* species have been shown to adapt rapidly to environmental differences[15].

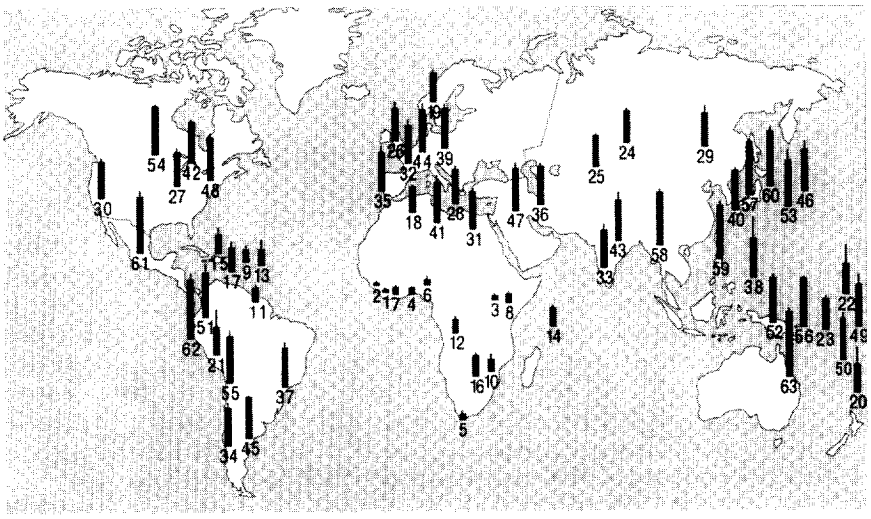

Fig. 2. A worldwide survey of levels of the *D. melanogaster* main cuticular hydrocarbon 7,11-HD in 63 strains. Histograms show mean % 7,11-HD ± s.d. ranked in ascending order. *Modified, with permission, from Ref. 5.*

The components needed to study the role of signal traits in speciation are clearly available in the *D. melanogaster* complex. The combination of within- and between-species studies with an easily measured isolating trait provides a powerful model system. Determination of the genetic basis of these traits is already well advanced and ultimately it should be possible to identify and sequence the genes involved. The next step will be to investigate the selection pressures operating on hydrocarbon differences, through further population comparisons and study of possible areas of contact between the two hydrocarbon forms.

Stuart H. Buckley
Tom Tregenza
Roger K. Butlin

Dept of Biology, University of Leeds,
Leeds, UK LS2 9JT

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Global biodiversity: is it in the mud and the dirt?

Links between soil and sediment biodiversity and ecosystem function were the topic of a symposium organized by Diana Wall Freckman, at the American Association for the Advancement of Science (AAAS) annual meeting in Seattle in February 1997. The goal of the symposium was to highlight the vast unexplored biodiversity of the soil and sediment biota and the importance of these biota to ecosystem function at small and large spatial and temporal scales. Areas were highlighted where a lack of information on the soil and sediment biota critically limits our ability to understand and manage terrestrial and aquatic ecosystems.

Soil has been called 'the poor man's tropical forest'. In a square meter of soil, there are tens of millions of bacteria, tens of meters of length of fungal mycelia, millions of protozoa and nematodes and up to a million arthropods, reported Valerie Behan-Pelletier (Research Branch, Agriculture Canada, Ottawa). But what do these creatures do? And perhaps more mysteriously, does each of these creatures have a unique functional role in the soil ecosystem? If the biodiversity of the soil declines, because of human use for agriculture or forestry, or deposition of acid rain or heavy metals, will the ability of soil to support plant growth, store carbon and cleanse pollutants from water decline? If we cut down the poor man's tropical forest, will we lose a vast reservoir of biodiversity and critically affect soil functions?

The nature and extent of our ignorance of the soil biota are staggering. Freckman (Colorado State University, Ft Collins, USA) presented conceptual food web diagrams for soil systems, emphasizing that there were few data on the specifics of these food webs. This ignorance is frightening, because we know that the soil and sediment biota are responsible for processing c. 80% of the organic material that is produced by plants globally, converting this production into CO_2 and other atmospheric trace gases (e.g. methane, nitrous oxide) and into soil organic matter, which is critical to maintaining the physical, chemical and biological integrity of the soil ecosystem. Research is indicating that extreme environments and low diversity systems, such as those found in hot and cold deserts, could be used as models for understanding the linkage between ecosystem function and biodiversity of soil communities. There, the linkages between diversity and function are not masked by the overwhelming diversity found in other terrestrial ecosystems. Freckman was able to demonstrate that many of the ignored components of the soil community, such as nematodes, are important to organic matter processing, are controlled by soil properties (e.g. salinity, nutrient availability), are highly sensitive to disturbance and are amenable to management.

Behan-Pelletier described recent efforts to directly address links between soil biodiversity and ecosystem function questions, using mites as a model for the soil fauna. Mites are ideal for exploring relationships between biodiversity and ecosystem function because they are phylogenetically diverse, ubiquitous in soil, and are a practically tractable group to address. Though globally only about 15% of mite species are taxonomically described, diversity of mites in any single temperate habitat rarely exceeds about 350 species, most of which are morphologically distinct, so that an ecologist can recognize morphospecies. And, most importantly, there are systematists in North America who work on mites, can develop identification keys to species, and can interact with ecologists. Behan-Pelletier suggests that studies of relationships between mite diversity and ecosystem function can serve as a model for studies of other soil and

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