

Dispatches

Sympatric Speciation: Perfume Preferences of Orchid Bee Lineages

Female attraction to an environmentally derived mating signal released by male orchid bees may be tightly linked to shared olfactory preferences of both sexes. A change in perfume preference may have led to divergence of two morphologically distinct lineages.

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Sympatric speciation may occur when there are barriers to gene flow between divergent populations that are in contact [1]. Sensory preferences, particularly those affecting signal choice, have been hypothesised as a mechanism that could result in reproductive isolation and assortative mating within populations [2]. There is good evidence supporting a mechanism for speciation through such sensory drive, especially where mates are recognised by visual cues which vary quantitatively [3]. The best known examples are found in fish, sticklebacks and cichlids [2,4]. For many animals, however, mate choice is mediated in large part by pheromonal signals and the narrow species-specificity of pheromones is assumed to place them under a high degree of stabilizing selection [5]. Selection could act to prevent mating between sympatric species, which often leads to the production of less viable hybrids, but the evolution of recognition signals to initiate that reproductive isolation has been viewed as problematic. Preferences for particular odours by subsets of populations have been proposed as a mechanism for sympatric speciation by sensory drive. In a new study published in this issue of *Current Biology*, Eltz *et al.* [6] found that volatile perfumes acquired from the environment by the orchid bee *Euglossa viridissima* differed between two morphotypes, which genetic analysis showed were reproductively isolated lineages.

Pheromone composition is hugely diverse with remarkable convergences occurring across taxa, and we are only beginning to understand the evolution of this diversity. A major difference between pheromones and other signals is that pheromones are

categorical, rather than graded, and the presence or absence of one component fundamentally changes the signal [7]. The evolution of pheromone composition is suggested [8] to have progressed by two possible routes: a slow and gradual change of components, such that related species share closely related or identical compounds; and major changes leading to saltational shifts with very divergent phenotypes. Examples of the first process are noted where pheromone functionality is under environmental constraints, such as in the pheromone trails of *Pogonomyrmex* spp. and *Myrmica* spp. ants. We find examples of saltational change in sex pheromones [5,9], which is surprising given that signals mediating mate attraction are usually highly species-specific and narrowly tuned. It is expected that even a slight change in a mating signal would make the bearer unattractive and change should therefore be selected against. Sex pheromones are often blends of components and slight changes in a species blend can nullify attraction responses in one species but elicit a strong response in another. The mix of pheromone components is thus crucial and blends should be under a strongly symmetrical male–female stabilizing selection. Recent studies of moths [5], however, have contradicted this assumption, showing that selection pressures are asymmetrical with lower pressure resting on female signalling systems, allowing greater variation in blends, with a correspondingly higher pressure in males. There is also evidence of selection for flexibility in male responsiveness in a subset of the population, allowing tracking of major variations in female pheromone blends. For example, in European and Asian corn borer moths a change in sex pheromone

blend has underpinned speciation [10]. A small proportion of European males can still respond to the sex pheromone produced by females of the Asian species, as well as their own.

A change in pheromone production must be matched by the capacity to attract at least a proportion of the population with broadened responsiveness. We can see that odorant production and reception must be tightly coupled, but what of situations where odour signals are pheromone analogues derived from environmental sources? For example, male *Bactrocera* fruit flies collect plant volatiles which they release to attract mates [11]. Geographical factors are expected to result in differing abundances of odorant sources or even the absence of particular sources in some environments, thus providing a route to reproductive isolation and allopatric speciation. However, individual preferences for particular odours could facilitate sympatric speciation by sensory drive. Eltz *et al.* [6] found that, in Mexico, two morphotypes of the orchid bee *E. viridissima* collect blends of volatile perfumes from the environment and that these blends differ greatly between the two morphotypes, as does responsiveness to the components of these blends. Microsatellite analysis confirmed that the two morphotypes are reproductively isolated lineages. As with *Bactrocera* fruit flies it is also the male orchid bee who collects the attractant perfumes.

Male orchid bees collect volatile compounds from flowers and other sources, which they store as blends in pockets found on their hind legs (Figure 1). These compounds are released at display sites and females have been observed to approach males from downwind, before copulation [12]. The two types of *E. viridissima* differ morphologically in that one form has two mandibular

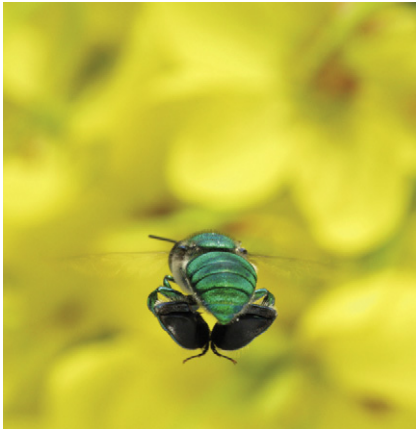


Figure 1. Rear view of orchid bee, *Euglossa viridissima*, showing the hind leg pockets used for collection of perfumes (photo courtesy of Thomas Eltz).

teeth (bidentate) whilst the other has three (tridentate). Both morphotypes were found at all 15 sites sampled in the Yucatan peninsula of Mexico, although tridentates were most abundant overall. The two morphotypes were equally responsive to the same compounds, but Eltz *et al.* [6] found a characteristic compound, 2-hydroxy-6-[(1E, 3E)-non-1, 3-dienyl]benzaldehyde (HNDB), which was present in the hind leg extracts of tridentate males but always absent from bidentate males. This compound, and its three stereo-isomers, comprises 67% of total ions in the perfume pockets of tridentate males. HNDB was attractive only to tridentate males in bioassays and exclusively elicited a response from tridentate antennae in electroantennogram (EAG) tests. Thus, HNDB is the only compound known to be collected by *E. viridissima* which is exclusively attractive to one of the two lineages.

Context-specific behavioural constraints meant that Eltz *et al.* [6] could not demonstrate that tridentate females were exclusively attracted by the odours of their cognate males. But there is ample evidence that male orchid bees release their perfumes only at mating sites, so a male preference for collecting a specific perfume should be matched by a similar female odour preference when seeking a mate. These results suggest that a shift in olfactory preference might have led to divergence and subsequent reproductive isolation of the bidentate and tridentate lineages in

E. viridissima. A change in olfactory receptor expression or abundance could modify olfactory preferences in males and determine which perfumes they prefer to collect, but this change must be matched by a similar change affecting female perfume preference. Thus, genetic change influencing sensory preferences could have led to assortative mating and driven the differentiation of the two *E. viridissima* lineages.

A major question in evolution is how mating signals and responsiveness are narrowly attuned in a single species but diverge during speciation. Research into linkage between signal production and reception has shown that the two characters are rarely linked, with pheromone production and response in insects typically being under the control of genes located on different chromosomes [13]. If signal and receiver are not linked, then changes in the mating signals of females, which are a limited resource for males, will mean there is a greater selection pressure for males to keep a broader responsive range than for females to maintain a narrow pheromone blend [14]. Such asymmetric tracking could lead to assortative mating and speciation. For *E. viridissima*, however, the situation is markedly different, because males are not tracking female odours and instead both exhibit a preference for an odour blend determined by genes influencing their olfactory receptors. The perfume collected by males and thus the blend released at mating sites must be under the control of their expressed odour receptors, making for a tight linkage between the perfume blend released and female preference for an odour.

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Kinetochores Attachment: How the Hec Can a Cell Do It?

Creating stable yet flexible attachments of spindle microtubules to the kinetochores is critical for facilitating chromosome congression, segregation, and checkpoint signaling. Two new studies have elucidated the molecular details of how the Ndc80 complex mediates this dynamic attachment.

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To generate two genetically identical daughter cells during mitosis the

duplicated chromosomes need to attach to the spindle microtubules to establish bi-oriented connections to microtubules emanating from opposite