

Herbivore host choice and optimal bad motherhood

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When theory predicts which phenotypes are well adapted to a given environment, the data do not always match the predictions. Host-plant selection by herbivorous insects is one such example. Herbivorous insects often appear to make poor choices about where their offspring should develop. New evidence presented by Scheirs *et al.* suggests that adult insects can choose oviposition sites that enhance their own long-term fitness at the expense of their individual offspring. This suggests that herbivorous insects might be genuinely bad mothers, that host choice is nonetheless adaptive, and that theory needs to incorporate new assumptions about host effects on adult performance.

It is a textbook cliché that the behaviour of organisms often seems highly adapted to the environment in which they live. The modern approach of studying adaptation is based on developing theoretical models, with explicit assumptions, which make predictions about the best-adapted, or evolutionarily stable, phenotypes¹. The models are then tested against empirical evidence. The approach can claim some notable successes; for example, explaining biased sex ratios, altruistic behaviour and certain foraging traits; in such instances there can be an impressive match between theory and data^{1,2}. But the match is not always impressive. When it is poor, a detailed look at the theory and the data is required to ask what went wrong³. The solution to such a problem is the subject of a recent study by Scheirs *et al.*⁴, which provides important new evidence surrounding the problem of why herbivorous insects seem to be such poor mothers.

Herbivore host-plant choice
Predicting the choice of host plant by herbivorous insects would be an impressive scoop for behavioural ecology and the adaptationist research programme. Approximately one quarter of all described species on earth are herbivorous insects, and many of them are specialists, feeding on only one or a limited range of host species⁵. The choice of hosts

by herbivorous insects is, therefore, not without ecological and evolutionary significance. Unfortunately, past attempts to understand the adaptive basis of host-selection decisions have been rather disappointing^{6,7}. Numerous optimization models have been used to try and answer the question⁷, following in the wake of diet selection models in predator-prey, and other similar, systems. In the simplest predator-prey models, parameters, such as the abundance of different prey items, their energetic value, and the time cost of handling and subduing prey, are investigated⁸. A common prediction is that predators should always accept, and often show a preference for, food which is of high energetic value, or which is easy to subdue and handle. The prediction has been upheld almost ubiquitously in experimental tests⁸. There are analogous predictions made under host-selection models for herbivorous insects, which differ in that parents are not choosing their own diet, but rather that of their offspring. Herbivorous insects, however, very frequently show a preference for the host which is not the best for their offspring^{6,7} and often reject those which are the best. In essence, they appear to be bad mothers.

The problem of a poor match between theory and data has many possible solutions (Table 1). It could be that the

behaviour genuinely makes little adaptive sense, in which case reasons must be found. Or the behaviour might actually be well adapted but the data are inadequate to show how. Finally, the behaviour might be well adapted but the theory is inadequate at explaining how. The solution provided by Scheirs *et al.*⁴ falls most easily into the second category. Using experiments on a leaf-mining fly, they show that the phenotypic variation in adult preference for different plants is highly correlated with adult performance, rather than with offspring performance. The somewhat sinister implication is that at least some herbivorous insects are bad mothers for their own selfish gain.

Adults matter too

Chromatomyia nigra is a small fly, common throughout Europe, which lays its eggs into the leaves of several grass species. The offspring develop to adulthood by mining through the leaf, feeding as they go. Like many other leaf-mining flies, the adults also feed from plant leaves by puncturing the leaf and consuming the exuded plant sap (Fig. 1). Following previous herbivory researchers, Scheirs *et al.* measured the performance of developing offspring in the laboratory. Development time, survival and pupal size were noted on four common plant

Table 1. Some ways in which herbivorous insects might appear to be poor at host-plant selection

Broad mechanism	Specific mechanism	Example	Ref.
Behaviour genuinely makes little adaptive sense	Little genetic variation	Restricted taxonomic range of hosts	11
	Host novel	Not enough time for adaptation	6
	Physical constraints	Hosts difficult for adults to lay eggs on	13
	Physiological constraints severe	Decision making difficult or costly	12
Data inadequate	Measurement of oviposition preference flawed or incomplete	Hosts not encountered during preference test as in nature	14
	Measurement of offspring performance flawed or incomplete	Natural enemies excluded in experiments	6
Theory inadequate	Tradeoff between adult and offspring performance	Best larval host is bad for adults	4
	Host availability variable in time and space	Best host now might not always be available to offspring	6
	Oviposition site not the major influence on larval performance	Larvae can move from host to host	6

hosts. No one host species appeared to be optimal for offspring: development time was very similar on all species; survival produced a clear performance hierarchy, whereas pupal size produced a slightly different performance hierarchy. In simultaneous choice tests, adults produced a clear oviposition preference hierarchy, but preference was not significantly correlated with any of the measured offspring performance indicators.

In a novel departure, however, Scheirs *et al.* also measured adult feeding preference on the four plants, as well as the performance of adults when isolated with individual plant species. Adult feeding preference followed exactly the same hierarchy as oviposition preference. Both adult longevity and fecundity, however, followed an identical hierarchy and were highly correlated with ovipositional and adult feeding preference. Scheirs *et al.* argue that, in essence, the flies oviposit where they feed, and they feed on the plants which best enhance adult rather than larval performance. The implication is that, by enhancing their own survival and fecundity, herbivorous insects might be able to have more offspring. When the best larval food plants are not the same as the best adult food plants, the added quantity of offspring gained by choosing the best plants for adults might be sufficient to override the costs of reduced offspring quality and survivorship.

The suggestion that factors, other than host effects on larval performance, might influence oviposition decisions is not new. Even the simplest optimization models predict that the opportunity cost of rejecting suboptimal hosts when optimal hosts are rare can sometimes be great enough to favour a very generalist strategy⁷. Such models, however, usually predict that the most favourable hosts should still be accepted when encountered so they cannot in themselves explain rejection of hosts that return high offspring performance. Incorporating the effects of different hosts on adult performance into studies is an important step in our understanding of this behaviour, because it is easier to envisage cases where hosts that are optimal for offspring might actually be rejected by ovipositing parents if they have negative effects on adult performance and, therefore, future reproduction. An



Fig. 1. An example of a leaf-mining fly. Leaf-mining flies of the genus *Chromatomyia* puncture plant leaves, into which they oviposit, and from which they feed on exuded plant sap.

analogous case in predator–prey systems is when predators are themselves at risk of becoming prey when gathering high value food. Models that consider adult performance consequences do exist for ovipositing organisms such as parasitoids^{9,10}, although the ideas have not been applied to herbivorous insects. Scheirs *et al.*⁴ show, for the first time, that effects of the host plant on adult herbivore performance can influence their oviposition decisions. The other source of intuitive appeal of this study is that the majority of herbivorous insect species undergo complete metamorphosis, leading to very different selection pressures on immatures and on adults. We would, therefore, expect conflict of interest between adult and offspring to be quite widespread. The implications for host-plant evolution are important because, for plants that are susceptible to herbivory, deterring adults even in rather subtle ways could have big effects on oviposition behaviour and might be just as important as classical defences, which reduce the effectiveness of larval attack.

Alternative solutions

Realistically, given the enormous variety of herbivore natural histories, it is unlikely that optimization of adult performance is the sole explanation of why bad motherhood appears to be so common. Several other lines of inquiry also appear to be bearing fruit (Table 1). Behaviour might often make genuinely little adaptive sense. There might be considerable constraint on reaching the optimal phenotype of a sort which is difficult to include in traditional model frameworks: recent work has shown that species might lack suitable genetic variation in key traits¹¹, hosts might be too recent (evolutionarily speaking) for

new adaptations to have arisen⁶, and the physiology or morphology required for host-selection might be limiting in some way^{12,13}. It is probable that the data have been deficient in many previous studies. Measuring offspring performance in convincing ways is not easy, as the apparent performance hierarchy can depend on the fitness components measured. Measurements carried out in the laboratory omit the influence of natural enemies and other selective forces. Field studies, however, are more convincing if they are long term, but long-term studies are all too rare. Even measuring oviposition preference is not as straightforward as it might first appear, for the variable can be measured in many different ways¹⁴ and different methods can return different results¹⁵. Progress is being made with the methodological difficulties¹⁶ and time will reveal if they can account for the past mismatch between data and theory. Model assumptions might sometimes be inappropriate in other ways: some herbivores, including well-studied species, conform to a parasite-like lifestyle through much of their development but graze on several plants later in their development⁶. They might also experience a fluctuating range of plant species both between generations and within generations⁶ so that what looks like a poor strategy in the short term or under local conditions might be a very good way of making the best of a larger, uncertain world.

Tradeoffs between larval and adult performance might not be the only reason why herbivorous insects are bad mothers, but the idea is an intuitively appealing solution, the tradeoffs are potentially widespread, and Scheirs *et al.*'s study have shown that it can be realized in nature⁴. The work reveals two exciting prospects: first, modelling the severity of the tradeoff should reveal quantitative predictions about when adults should sacrifice larval performance for the sake of themselves, hence, when mothers should be bad parents. Second, the measurement of host effects on adult performance should become more routine in host-selection studies and should reveal how widespread the adult–offspring performance tradeoffs are. Host choice in herbivorous insects might finally be making adaptive sense after all, but not in the way we first thought.

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Doubly duped males: the sweet and sour of the orchid's bouquet

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Flowers of the orchid genus *Ophrys* resemble female insects, and thereby sexually deceive, attract and are pollinated by male insects. Floral bouquet is thought to play a major role in this sexual mimicry, although the search for functional odour components has been something of a chemical ecologist's Holy Grail. Two new papers unravel the exquisite intricacy of the chemical deception by the orchid.

Noteworthy to Linnaeus¹ and puzzling for Darwin², the visual similarity between *Ophrys* flowers and female insects can be striking. *Ophrys* attract pollinating insects, often only males (usually bees and wasps) of a single species^{3,4}, which 'pseudocopulate' with the flowers, resulting in pollination. For example, early spider orchid *Ophrys sphegodes* flowers are only pollinated through pseudocopulation by males of the bee *Andrena nigroaenea* (Fig. 1). Understanding the chemistry behind this example of sexual deception has been the aim of new work by Ayasse *et al.*^{4,5}, with the power of their approach deriving from their combination of high resolution lab-based analyses [gas chromatography coupled to mass spectrometry (GC-MS) and gas chromatography coupled to electroantennography (GC-EAG)] with elegant field-based bioassays.

In 1999, the group demonstrated that hydrocarbons (C21 to C29 alkanes and

alkenes) were both the sex pheromone of the female bee and the sex attractant of the flower⁷. One-to-one plant-pollinator relationships are generally considered uncommon⁸, although this is understandable in the case of an *Ophrys* species if it employs the species-specific sexual communication channels of its pseudocopulator. Although the chemistry might be somewhat mundane, this⁷ was the first conclusive demonstration of the chemical basis for sexual odour deceit in any *Ophrys*-pollinator pair, and, incidentally, one of the clearest

characterizations of the sexual attractant and copulation releaser pheromone of any bee species⁴. Insect cuticular hydrocarbons have long been known to function in diverse pheromonal roles, including sex attraction⁹ and, therefore, it might not come as a surprise that this class of compounds is implicated as a sex pheromone in *A. nigroaenea* and has been co-opted by *O. sphegodes*.

The sweet: how to attract a male – repeatedly
Although usually able to mate repeatedly, a male bee or wasp is generally highly

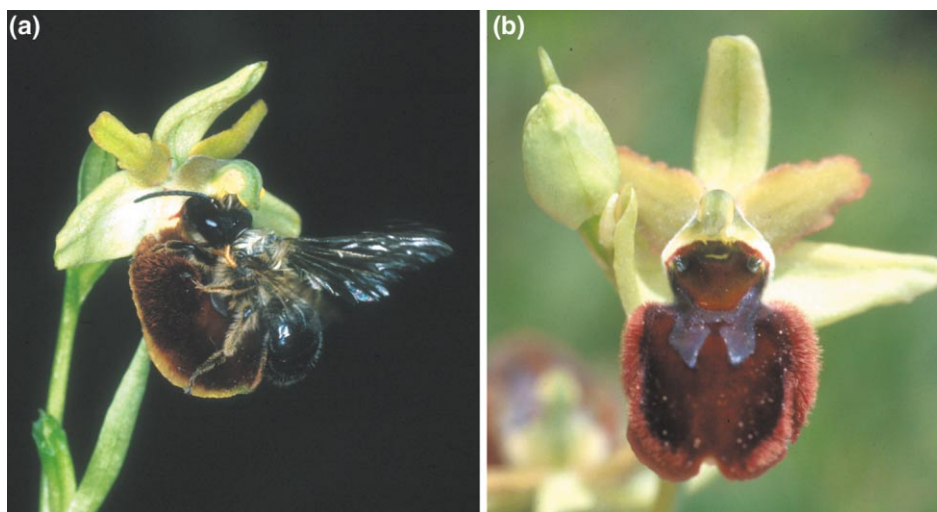


Fig. 1. Examples of bee orchids and their interaction with pollinators. (a) A male *Andrena nigroaenea* pseudocopulates with a flower of *Ophrys sphegodes*. (b) The flower of *Ophrys sphegodes*. Photographs reproduced, with permission, from Manfred Ayasse.