CORRESPONDENCE

Kura makes some calculations which he believes show that the benefits (gained by *C. briggsae* as a result of outcrossing) accrue to the species or to the deme and not to the individual. I fail to see how they lead to the conclusion he draws. Kura then asks why the hermaphrodites intensely resist the X chromosome of males, or something to that effect. I don't see any evidence that they do so. It is difficult to explain why the X chromosome of *C. elegans* is also not selfish; such overtly selfish elements do seem to be rather rare, for reasons that we do not fully understand. But, in any case, I do not see what local mate competition has to do with it.

Kura's question as to which is more advantageous – self-fertilization or meiotic drive – is misleading. Such questions cannot be answered unless we specify from whose point of view we are thinking of the advantage. Moreover, there is probably no meiotic drive here; gametic selection is sufficient to explain the observed phenomenon. I have argued that one should expect the hermaphrodite to cooperate in suppressing the male's nullo-X sperm[6]. This is quite correct, but it does not mean that the cooperation of the hermaphrodite is essential; gametic selection on the male's selfish X chromosome may be sufficient to produce the observed phenomenon even without the cooperation of the hermaphrodite.

Raghavendra Gadagkar

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India; and Animal Behaviour Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur PO, Bangalore 560064, India (ragh@ces.iisc.ernet.in)

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Deep flowers for long tongues: a final word

Ever since it was coined by Ehrlich and Raven[1], the term 'coevolution' has often been used indiscriminately in interpretations of insect–plant relationships, although in the meantime it became more precisely defined. To avoid misleading interpretations, it is advisable to restrict the use of this term to cases in which 'reciprocal evolutionary change in interacting species'[2] can be proved at least by circumstantial evidence. Reciprocal evolutionary changes occur in two interacting organisms, if symmetrical selection pressures act, that is, if a change in the traits of organism A selects the organism B for a corresponding change. This happens if the existence (the overall fitness) of organism A depends on the coexistence of organism B, and vice versa. Fig species and most fig wasp species are the textbook examples of such symmetrical interactions, as neither would exist without the other.

In contrast, the relationship between the orchid *Agraecum sesquipedale* and its pollinator the hawkmoth *Xanthopan morganii predicta*, discussed recently by Nilsson[3] and in subsequent correspondence in *TREE*[4,5] is clearly asymmetrical. There is no mutual dependence between the two partners, since the orchid's existence (fitness) fully depends on the coexistence of the extremely long-tongued hawkmoth, while the moth could exist in the absence of deep flowers because it is also able to feed on different shallow flowers. Nilsson's argument that 'these hawkmoths are particularly susceptible to energy-limitation and thus prone to an evolutionary race in tongue length for more nectar', that is, that *X. m. predicta* has been selected by nectar competitors for a long tongue, is speculation that would need thorough quantitative field studies on the flower-visiting behaviour of the coexisting hawkmoth and other pollinator species before it could be accepted. Wasserthal's[6] hypothesis, questioned by Nilsson, that predation has selected the moth for long tongue also needs more supporting evidence. So, at present there is no convincing explanation for the adaptive significance of *X. m. predicta*'s long tongue – if there is any (see Gould and Lewontin's[7] often-forgotten criticism of the adaptationist view).

Yet, there is an important point that should be considered. The special characteristic of hawkmoth feeding behaviour – sucking nectar while hovering over the flowers – is possible only because the moths have relatively long tongues and, vice versa, long tongues enable the moths to feed during hovering. That means that a long tongue is a fundamental family character of sphingids independent of the morphology of flowers on which the various hawkmoth species feed. This morphological character might have evolved earlier than the flowers with extremely long spurs[6]. (It would be ridiculous to look for the adaptive advantage of hovering over the feeding behaviour of other lepidopterans.) This explains why there are long-tongued hawkmoth species in regions, like Central Europe, where deep-flowered plant species are scarce.

Variation in tongue length among hawkmoth species may result from genetic changes in the process of moth speciation. Extremely long-tongued hawkmoths then could select flowers for extremely long spurs and so provide reproductive isolation among plant lines differing in spur length as expounded by Wasserthal[6]. In the end, this could foster plant speciation without any evolutionary feedback to the moths.

In conclusion, deep flowers are for long tongues, otherwise such flowers could not exist. Long tongues, however, are not for deep flowers, as feeding with long tongues is possible also on shallow flowers. Thus, Wasserthal's opinion that great flower depth is the result of a one-sided plant adaptive evolution is more plausible than Nilsson's evoking the ghost of coevolution past for explaining the origin of this plant–pollinator relationship.

T. Jermy

Plant Protection Institute, Hungarian Academy of Sciences, PO Box 102, H-1525 Budapest, Hungary (h2370sze@ella.hu)

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