

Reply from M. Heino, J.A.J. Metz and V. Kaitala

Éva Kisdi clarifies the relationships between frequency dependence, optimization and ESSs. We basically agree with all her comments.

However, some further clarification may be useful.

In the first paragraph of Kisdi's letter, ESSs and optimal strategies are seemingly opposed by saying that 'finding an optimal strategy is a considerably stronger result than finding an ESS'. Although this statement is factually correct, it might engender a suggestion that is slightly wrong. Conceptually, ESSs are always primary: only ESSs matter from the viewpoint of long-term evolution. Optimization is secondary only, and must be justified by an ESS argument that explicitly accounts for the ecology in which the evolutionary problem is embedded. When we approach the problem from this angle it is found that there exist special ecological circumstances for which the ESSs satisfy an optimization principle (that is, the rather exceptional one-dimensional environments).

Kisdi characterizes one-dimensional environments by assuming that 'fitness is an increasing function of a single environmental factor'. Since precision matters here, mainly for technical reasons¹, we suggest rephrasing this statement as 'fitnesses depend uniformly monotonically on a single environmental factor'. Dependence on the environment is 'uniformly monotonic' only if it is monotonic in the same direction for every possible value of the evolutionary trait. This condition is both necessary and sufficient for the ESS to be characterizable by an optimization principle.

To conclude, we agree that the analysis of certain simple models can be done by optimization arguments in place of an ESS analysis. Since optimization tools are usually easier to use, such methods are preferable whenever they are appropriate. But considerable care is needed, as the conditions under which optimization methods apply are ecologically a lot more restrictive than is commonly realized.

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Deep flowers for long tongues: reply from L.A. Nilsson

The core of disagreement about the tongue-flower elongation, coevolution versus non-coevolution, is whether a long hawkmoth tongue is used primarily for feeding or for predator avoidance. Wasserthal¹ considers his predation hypothesis for tongue length confirmed, but his three cited papers lack quantitative data on natural predation. Svensson *et al.*² argue in support of his interpretation by anecdotal evidence. They miss the flight-elongation focus. However, I agree with them and with Samways³ that major predation on large hawkmoths is expected from flying vertebrates, not arthropods in ambush *à la* Wasserthal.

Nectar-extracting mouthparts have attained impressive extremes in euglossine bees (4 cm), nemestrinid flies (8 cm) and hummingbirds (10 cm), each set of taxa using/pollinating a unique guild of deep-flowered plants^{4,5}. Nothing suggests that predator avoidance has influenced the elongation (co)evolution. Long-tongued hawkmoths and their deep flowers, although displaying world records (30 cm and 40 cm, respectively), are hardly exceptions in this respect. The various very deep-flowered angiosperms (e.g. *Epiphyllum* in neotropical Cactaceae) are probably coevolved with hawkmoth tongues.

Hawkmoth flight repertoires include 'on-the-spot' hovering as well as 'swing-hovering' during flower-visits. Also, hummingbirds, long-tongued solitary bees (euglossines, anthophorids) and long-tongued flies (horseflies, nemestrinid and bee flies) hover on-the-spot. No doubt this behaviour favours targeting and insertion precision with the extended mouthparts into narrow nectariferous structures. Extremely long-tongued hawkmoths probably require even more precision control. Added swing-hovering may increase visual and/or olfactory information about the position of the flower. Anti-predator adaptations, on the other hand, are to be expected among other traits.

Basal hawkmoth clades contain the long-tongued taxa⁶. But modern phylogenetic analyses (so badly needed!) are likely to show a very long tongue to be a derived, relatively late trait within several lines (e.g. *Amphimoea*, *Coelonia*). Furthermore, very long-tongued hawkmoths might not be true generalists but instead might have guild constancy under natural, undisturbed conditions. Their opportunistic exploitation of pantropical weedy *Lantana*⁷, a lepidopteran-adapted species, is hardly surprising.

Wasserthal's argument that 'obligate synchrony and syntopy' of *Xanthopan morgani praedicta* and *Angraecum sesquipedale* would have been required

for coevolution is flawed. These interactors are participants of coevolving guilds⁸. Various pollinator shifts may well have occurred, as are commonplace in the history of orchids and other angiosperms^{9,10}. Coevolution and shifting occur by relatively 'better' pollinators. The basis for Darwin's reciprocal-effect model is that a competitive visitor with a non-bottom-reaching tongue better contacts the flower's pollination organs¹¹. The depth of spur and the length of reward-extracting organ become inter-dependent and matching at the population level¹². A consistently bottom-reaching, although competitive, hawkmoth tongue excludes pollinator shifts, as indicated by *Xanthopan* on *Angraecum compactum*⁷. Some 100 Madagascan angraecoids have demonstrably retained adaptation to medium-tongued hawkmoths. *Angraecum sesquipedale*, guild-member angiosperms, *Xanthopan* and major hawkmoth competitors are evidently coevolved.

The intention of Wasserthal's study has not been overlooked, nor has the difficulty of obtaining natural interaction data. Our team still recorded frequent pollination of *A. sesquipedale* in 1983 and 1986. Wasserthal's study of the same populations, species and systems in Madagascar has partly led to more questions than answers, and he has yet to adopt a plausible evolutionary interpretation of his observations.

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