

Law of the unspecialized: broken?

Specialization has posed crucial problems for evolutionary biologists: What are the benefits of specialization? Is specialization an evolutionary dead end? Theory has long predicted that specialization is favored because of tradeoffs in fitness when organisms utilize different resources. These microevolutionary benefits are thought to be offset by a reduction in macroevolutionary diversification. Again, theory has suggested that the narrow ecology of specialists will result in fewer opportunities for speciation, and, therefore, lower levels of diversification than in less specialized clades. This suggestion dates back to E. Cope in 1896, who coined the idea 'law of the unspecialized'. However, specialization as an evolutionary dead end appears inconsistent with the existence of diverse and highly specialized clades. For example, it is estimated that 80% of phytophagous insects, one of the most diverse groups of organisms, are specialized. Why is this group of specialists so diverse? There are now several phylogenies of groups with more and less specialized clades, and a new study by Termonia *et al.*¹ 'ups the ante' by combining knowledge of the mechanistic basis of specialization in Chrysomelina beetles with a phylogenetic analysis of diversification.

In response to harassment, Chrysomelina beetles produce defensive secretions that are repulsive to predators. The type of defensive secretion produced defines three different types of beetles:

those that synthesize their own defense chemicals; those that are fully reliant on their host plant for such chemicals; and an intermediate group that are only partially dependent on the host plant for their chemical defense. Termonia *et al.*'s phylogenetic analysis reveals that this partially dependent strategy is the most derived of the three, and is descended from the more specialized group, which relies fully on the host plant for defense. In addition to specialization not being a dead end in this system, the authors show that the derived defense strategy has allowed for beetles to move to host plants that are both chemically and phylogenetically distinct.

This paper¹ is part of a new generation of studies that link chemical ecology to evolutionary biology. Conventional wisdom has been that specialization of herbivores is an evolutionary response to plant defenses.



Maurice Laponce and Jacques Pasteels.

However, for the Chrysomelina beetles, specialization is apparently a response to avoid predation. Although it is not clear how frequently specialization in herbivorous insects is driven by predators, host-plant chemistry plays a prominent role in both plant defense and predator avoidance. This still begs the question: why are specialized clades of phytophagous insects so diverse? Does the type of resource used by such insects (i.e. hosts that are defended by chemicals or hosts that provide insect defense) and the spatial scale over which these resources occur delimit opportunities for reproductive isolation? If so, the law of the unspecialized will fail whenever novel specializations promote reproductive isolation. Well-described cases of incipient sympatric speciation (e.g. sticklebacks *Gasterosteus* spp. and Apple maggot fly *Rhagoletis* spp.) and the maintenance of species boundaries in sympatry (columbine *Aquilegia* spp. and monkey flower *Mimulus* spp.) occurring as a result of the evolution of novel specializations for resource use support this view.

1 Termonia, A. *et al.* (2001) Feeding specialization and host-derived chemical defense in Chrysomelina leaf beetles did not lead to an evolutionary dead end. *Proc. Natl. Acad. Sci. U. S. A.* 98, 3909–3914

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Rearguard action: why do some butterflies have false heads?

Most readers of *TREE* will know that some butterfly species have developed colour patterns that make them look as though they have another head at the posterior end of their body. This phenomenon is a classic example used in adaptive coloration lectures. The standard explanation for the false head is that it confers an anti-predatory advantage to the butterfly. It is suggested that this has developed because predators preferentially attack the head of butterflies, as this is a particularly vulnerable part of the body. The false head acts to increase the chance that an attack is

directed to the less vulnerable posterior, providing the butterfly with an increased chance of surviving an attack.

This explanation has now been challenged by Cordero¹, who argues that the 'vulnerable head' hypothesis has not been subjected to critical examination that would allow testing between this standard hypothesis and plausible alternatives. The author goes on to introduce just such an alternative. Under the new hypothesis, predators preferentially target the posterior end of butterflies, because butterflies are more able to detect and react to impending

attacks on their head, as this is where their eyes are. Under this alternative hypothesis, the false head acts to increase the likelihood that an attack will be directed to the real head.

Cordero argues that it should be possible to differentiate between these two hypotheses empirically. The first hypothesis suggests that attacks directed to the head are more successful than are those directed to the rear, whereas the alternative hypothesis predicts the opposite. In addition, the standard hypothesis predicts that evolution of a false head will induce a