IS COEVOLUTION DEAD?

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Bernays and Graham pose two main alternative explanations for the commonness of host specialization in herbivorous insects: coevolution, and variability among plant species in the abundance of associated predators and parasitoids. Their suggestion that predator/parasite pressure deserves more consideration as a cause of specialization is laudable and should stimulate research in this underexplored area. However, their arguments against coevolution as a major cause of specialization raise several questions that need examination.

There seem to be two ways by which the process of coevolution can favor specialization. The first is that coevolution inhibits broadening of the host range and thus keeps specialist species specialized. The argument here is presumably that by becoming more and more finely tuned to exploiting a single host plant, an insect may sacrifice the ability to broaden its host range in the future because it becomes less and less adapted to using other hosts. This loss of adaptation to one host in conjunction with increased adaptation to another implies the existence of trade-offs in adaptation to different hosts (Gould 1979, Rausher 1984, Via 1984, Futuyma and Philippi 1987).

The second possibility is that coevolution actively narrows host range. Under this scenario, coevolution occurs between a somewhat generalized insect and one of the plants it uses. Selection imposed by the herbivore leads to the evolution of defenses in that plant, to which the insect can in turn respond in any of three ways: (1) by evolving counter-resistance; (2) by evolving avoidance of that plant; or (3) by doing neither (1) nor (2). Alternatives (1) and (3) involve no change in degree of behavioral specialization. Alternative (2), however, results in greater specialization.

Bernays and Graham seem to argue that accumulating evidence indicates neither of these possibilities commonly occurs in nature. I believe that the three arguments they put forward are not entirely convincing.

Their first argument is that coevolution has not commonly led to avoidance because many feeding deterrents have no harmful physiological effects when ingested. That a compound is a deterrent means that an insect has evolved behaviorally to interpret that compound as a signal that the plants(s) containing it are poor substrates for survival and reproduction. They may be poor substrates for several reasons: (1) the deterrent itself is toxic; (2) some other chemical in the plant is toxic or inhibits growth; (3) some other non-chemical character of the plant (e.g., toughness, trichomes) renders it a poor substrate; or (4) some aspect of the plant's microenvironment (microclimate, enemy load) is inimical to the herbivore. Situations 1–3 may all arise as a result of coevolution, i.e., as a result of the herbivore selecting for resistance factors. Even situations of type 4 could be caused by coevolution, as when selection for extrafloral nectaries increases the number of predators/parasites in the vicinity of a plant. Simply ruling out situation 1 does not, therefore, rule out coevolution as a major factor leading to reduction in the quality of a particular host and consequent evolution of avoidance of that plant by the herbivore (specialization).

Bernays and Graham's second argument is that coevolution cannot commonly cause behavioral specialization, because insects seldom impose strong selection on plants and therefore co-evolution seldom occurs. It may be true, as they argue, that herbivorous insects are relatively rare. However, rarity may often be a result of the prior evolution of resistance mechanisms by plants. Remove those resistance mechanisms and herbivorous insects might become much more common, sufficiently so to generate the selection required for the evolution of resistance factors (Janzen 1979). Moreover, many studies have documented substantial reductions in plant growth rate, survivorship, and reproductive success caused by insects (Cantlon 1969, Morrow and Lamarche 1978, Rausher and Feeny 1980, Parker and Root 1981, Louda 1983, Marquis 1984). These studies do not demonstrate selection, since they do not demonstrate that plant genotypes that differ in susceptibility to herbivores also differ in fitness. However, they do indicate that the potential for intense selection by insects on plants is frequently present in nature.

The only way to support or refute the contention that herbivores commonly exert important selection pressures on resistance traits is to measure selection and determine its causes directly. Such attempts are
beginning to be made and are suggesting that such selection may in fact be quite common (Berenbaum et al. 1986; E. L. Simms and M. D. Rausher, personal observation). It is thus still an open question whether reputed defenses have evolved because of selection imposed by herbivorous insects, and there is no solid basis for concluding, therefore, that coevolution does not commonly cause narrowing of host range in insects.

Finally, Bernays and Graham argue that trade-offs in performance across hosts are uncommon in herbivorous insects. If this claim is valid, two inferences follow: (1) increased physiological and morphological adaptation to using a particular host does not limit the ability of an insect to evolve characters needed to expand its host range to include a novel host; and (2) the evolution of avoidance behavior by a generalist confronted with a newly evolved toxic host is less likely than the evolution of counter-resistance (i.e., maintaining a broad host range). Inference 2 is suggested by analyses of two-locus models of the evolution of preference and performance in herbivorous insects (Castillo-Chavez et al. 1988, Rausher 1989). In these models, physiological and behavioral specialization is not a stable equilibrium to which a herbivore population could evolve unless trade-offs in performance exist.

Recent experiments designed to detect trade-offs in performance across hosts have, in general, failed to reveal the negative genetic correlations that are thought to be indicative of such trade-offs (Gould 1979, Rausher 1984, Via 1984, Weber 1985, Hare and Kennedy 1986, Futuyma and Philippi 1987). However, there are some limitations to all of these studies: (1) Most probably did not have the statistical sensitivity needed to detect weak negative correlations. Since theory has not been developed sufficiently to enlighten us as to whether weak correlations are sufficient to favor the evolution of specialization, it remains possible that specialization commonly results from as yet undetected, weak correlations. (2) Only a few components of fitness are usually measured (most commonly growth rate and pupal size; seldom fecundity or survivorship in the field). Negative genetic correlations could thus exist in unmeasured fitness components. (3) In most studies, genetic correlations were measured in laboratory environments, which could give rise to artificial patterns of correlations (Service and Rose 1985). Genetic variants that are unexpressed in nature could conceivably cause significant differences in general vigor under laboratory conditions due to genotype–environment interactions (e.g., Parsons 1977, Murphy et al. 1983, Luckinbill and Clare 1985). These differences would tend to yield positive correlations across hosts for characters like growth rates and pupal size, and would tend to obscure any negative correlations arising from trade-offs. (4) All studies except that of Gould (1979) have sought trade-offs in performance among plants that the study insect normally uses. It is possible that an absence of trade-offs in these insects is what permits the use of multiple hosts. However, an alternative explanation is that trade-offs once existed, but were not of sufficient magnitude to overcome disadvantages associated with specialization. The insects thus remained polyphagous; over time, however, natural selection has eliminated the trade-offs by eliminating the overlap in genes affecting performance on different hosts. If this explanation is correct, inability to detect trade-offs in these studies may indicate not that they are generally absent in herbivorous insects, but only that they tend to be eliminated when they are not strong enough to cause narrowing of the host range. (See Uyenoyama 1986 for a similar, more extensive argument concerning lack of detectable costs associated with pesticide detoxification. See also Lenski 1988a, b for evolutionary reduction in costs of resistance to virus in bacteria.)

Reports of genetic correlations between preference and performance (Tavormina 1982, Via 1986, D. Ng, personal communication) provide positive evidence of the existence of trade-offs in performance across hosts. The most likely manner in which these correlations arise is via linkage disequilibrium between fitness and preference loci, which in turn is likely only if trade-offs exist. In view of this evidence and the above considerations, concluding that trade-offs across hosts are generally nonexistent in herbivorous insects seems somewhat premature.

Although there are problems with Bernays and Graham’s contention that coevolution is seldom an important cause of behavioral specialization, this contention may nevertheless be true. However, even if true, chemical and other intrinsic characteristics of plants may still cause the evolution of specialization. As has been suggested by others (Jermy 1976, 1984, Nowacki et al. 1976, Moran and Hamilton 1980), chemical, physical, and physiological properties of plants that reduce insect fitness may evolve because of ecological functions unrelated to deterring herbivores. Resistance to insects would then be an accidental side effect, but one that may impose tremendous selection pressures on insect behavior and physiology. Variation in host quality due to variation in natural enemy load is thus not the only alternative to coevolution as an explanation of specialization in herbivorous insects.

In closing, I would like to suggest a way by which plant chemistry and insect natural enemies might in combination favor specialization. Consider an herbivorous insect that uses two host plant taxa that are chemically very different. The herbivore possesses at least two different adaptations that permit detoxification of the secondary compounds produced by each plant. Suppose that plant taxon A harbors more enemies of
the herbivore and that therefore herbivore survivorship is lower on these plants than on taxon B. Various genetic (Rauscher 1985) and optimality (Levins and MacArthur 1969, Jaenike 1978, Courtney 1983) models suggest that under these conditions the herbivore will often evolve to become behaviorally specialized on plant B. Once this occurs, adaptations that permit detoxification of chemicals produced by taxon A may be lost, either because nonfunctional, though neutral, mutations accumulate, or because trade-offs in performance across hosts ensure that selection for improved adaptation to taxon B results in a correlated decline in adaptations to taxon A. Selection imposed by natural enemies thus facilitates the evolution of both behavioral and physiological specialization. Suppose now, however, that changes in environmental conditions cause a great reduction in the abundance of herbivore natural enemies of taxon A. The original selective factor favoring specialization will have been removed. But recent two-locus models of the joint evolution of preference and performance in herbivores (Castillo-Chavez et al. 1988, Rauscher 1989) suggest that the herbivore may not be able to re-expand its host range. In effect, the herbivore is trapped in an Evolutionary Stable State of specialization because it cannot simultaneously put together genotypes that detoxify the secondary compounds of host A and that modify behavior to permit the insect to use host A. Thus, under this scenario, natural enemies are responsible for the herbivore becoming specialized, while plant chemistry is responsible for it remaining specialized. Unfortunately, current empirical evidence is insufficient for determining how commonly this, or any other process, is responsible for the commonness of specialization in herbivorous insects.

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Literature Cited


