crease its digestibility for cattle. In this area the combined efforts of chemists, biochemists, animal scientists, agronomists, agricultural and chemical engineers, and economists will be needed to develop more ways to utilize renewable resources for energy and food.

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Plant Chemistry and the Evolution of Host Specificity: New Evidence from *Heliconius* and *Passiflora*

Abstract. *Larval growth rates of* Heliconius *butterflies do not closely parallel host plant choice, an indication that factors other than host plant chemistry are important in evolving host specificity. High growth rate in one species is correlated with reduction in number of palatable host species. This suggests a mechanism by which ecologically restricted species become progressively biochemically specialized.*

Monophagy, defined at the local population level as the feeding of a consumer on just one species of host (*1*), has evolved repeatedly in herbivorous insects. It is particularly common among leaf-eating insects, and is thought to be principally a response to the great diversity of toxic secondary plant compounds found in the leaves of higher plants (*2–4*). While monophagy and plant compounds are undoubtedly related, our results indicate that monophagy may evolve initially as a result of "ecological" factors such as predation or plant abundance, rather than by differences in host palatability (*5*). The results also suggest that, once this type of monophagy is established, selection for increased digestive efficiency may cause the insect to slowly lose the ability to feed on its former host plants. When this happens the insect becomes sensitive to chemical barriers, which are believed to be so important in insect-host plant relationships (*6*). The proposed sequence of ecological monophagy followed by varying degrees of obligate monophagy may help to explain why a given insect group can vary widely in host specificity. It also provides a possible new mechanism for insect-host plant coevolution, the process proposed by Ehrlich and Raven, that results in parallel phylogenies between higher taxa of insects and their host plants (*3*).

In spite of the recognized importance of this phenomenon, the evolution of host specificity in insect-host plant interactions has received only minimal attention. One of the few general texts (*7*) dealing with the evolution of host plant choice concentrates on the effects of host plant chemistry and only very briefly mentions two other contributing factors: searching ability and competitive interactions. Yet, the importance of host plant chemistry remains to be critically evaluated, and other possible selective factors need to be assessed as well. At least three studies on butterfly species have indicated that chemically palatable but unused host species are available in the butterflies' habitat (*8*), which points out the inadequacy of host plant chemistry as being the sole determinant of host plant choice. Also, even when acceptable alternative hosts are not present, a satisfactory model is lacking as to how monophagy could evolve from less specialized ancestors (*3*, *9*).

I investigated this problem by studying oviposition behavior and larval growth ability in three sympatric species of *Heliconius* butterflies. The aim of the study was to determine which host plants were being used by the butterflies in nature and then to compare this with the ability of the larvae of these butterflies to grow on the various host plants. If larval growth ability were exactly parallel to host plant choice in the field, this would indicate that host plant specificity in these butterflies is being enforced by host plant chemistry. If, in contrast, host plant choice were much more restricted than larval growth ability, this would indicate that other factors were promoting host specificity in these butterflies. I also attempted to test the hypothesis that butterflies with host-specific larval growth ability (*10*) would have enhanced growth rate on their chosen host plant. This hypothesis is predicted if insects become host-specific in order to enhance digestive and growth efficiency on one host plant species (*11*, *12*).

Host plant choice was determined in the field by collecting eggs on the various species of *Passiflora* at the field site (*13*). *Passiflora* and related genera are the sole host plants for larvae of the genus *Heliconius* (*4*). The eggs and larvae collected were reared to determine their identity. The numbers in parentheses in Fig. 1 represent these data. Sample sizes are unavoidably small due to difficulties in locating eggs and larvae and also to difficulties in rearing for species identification. Therefore, these data were supplemented by a host plant choice experiment. Females of the three *Heliconius* species were tested. These were descended at least five generations from wild-caught *Heliconius* at the field site, except for the data from *H. erato* which

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were obtained by testing descendants of a Mexican population of the same race (*14*). The host plant species used were the five most common Passifloraceous species at the field site (*15*). In these experiments, butterflies were placed in an insectary devoid of host plants and then host plants were introduced one at a time to observe oviposition behavior. This approximates field conditions, where host plants tend to be widely separated. In at least three cases per host plant, each butterfly species had been prevented from ovipositing for 2 days. Therefore, these data represent host plant choice when the butterfly is highly motivated to oviposit on any acceptable host plant. The results are given in Fig. 1.

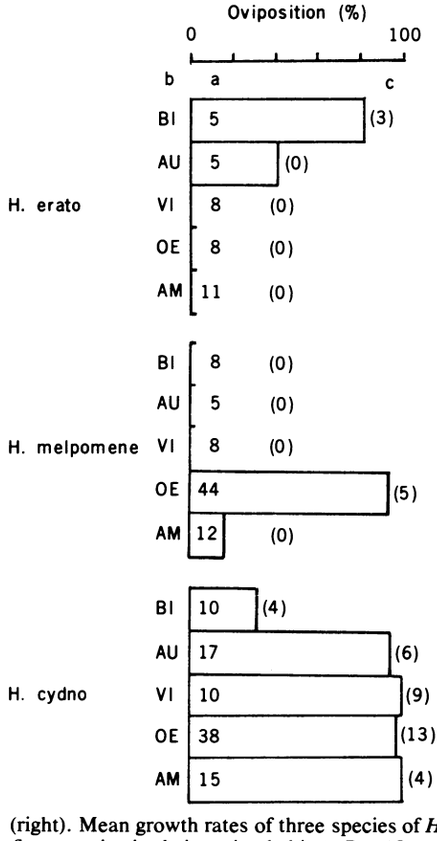
The data in Fig. 1 demonstrate that two of the *Heliconius* species are principally monophagous. However, a third species, *H. cydno*, is oligophagous (*1*), ovipositing on all five host plant species tested. These differences in host plant preference are genetically inherited behaviors, as demonstrated by the fact that over five or more generations descendants of wild-caught females show the same behavior pattern as that exhibited in the field.

Larval growth rates were obtained for these butterfly species by rearing them from egg to pupa on vigorously growing plants cultivated in greenhouses (*16*). Larval growth was measured on live plants that were moved to a constant environment chamber (*17, 18*). Growth rate was measured by weighing eggs and the resulting pupae and the time from hatching to pupation was recorded. Results are given in Fig. 2 in terms of a measure of growth rate that takes into account the relative values of the weight and time measurements. This measure eliminates most effects of interspecific size differences (*19*).

Larval growth rates indicate that one species, *H. erato*, is digestively specialized on its host plant. The other two species of *Heliconius*, including the monophagous *H. melpomene*, are not digestively specialized, but grow about equally well on all five species of *Passiflora*. The digestive efficiency hypothesis would predict that *H. erato*, the digestively specialized species, would have enhanced growth rate on its host plant when compared to the unspecialized *Heliconius*. When the mean growth rates are compared (Fig. 2), *H. erato* is seen to have a slightly faster growth rate than the other two species, and this difference is statistically significant (*20*). Thus the hypothesis is supported by the data. However, the difference is surprisingly slight, and would not have been observed at all under less controlled conditions. This may in part be the reason that the digestive efficiency hypothesis has received such mixed experimental support (*21*).

The *Heliconius* data also point out another difficulty in testing the digestive efficiency hypothesis. Figure 1 oviposition data indicate that *H. melpomene* is host-specific; and if, on this basis, it was considered to be digestively specialized, the prediction of the digestive efficiency hypothesis would have been that *H. melpomene* should have an enhanced growth rate on its host plant. The hypothesis would not have been supported for that species. Thus, it is insufficient to rely on host plant choice as an indicator of digestive specialization.

The data for *H. melpomene* unequivocally demonstrate that an insect can evolve to be monophagous without any noticeable increase in digestive specialization. Taxonomically, *H. melpomene* is closely related to *H. cydno* and several other *Heliconius* species forming the "Granadilla-feeding" species group. None of these are as host-specific as *H. melpomene*, at least among the Costa Rican species, and all of these "Granadilla-



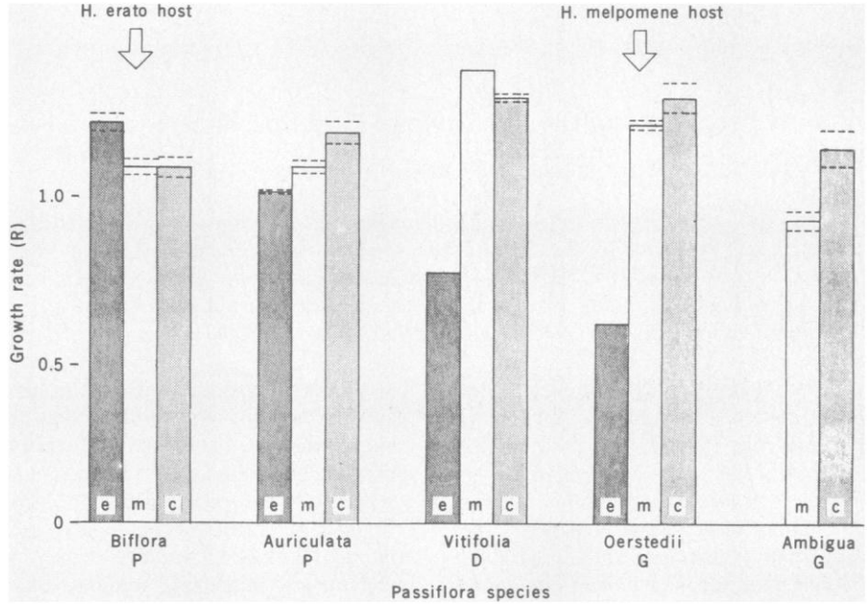


Fig. 1 (left). Percent oviposition in three species of *Heliconius*. Percent oviposition represents the number of tests in which oviposition was attempted as determined by abdomen extension and contact with the host plant, divided by (a) the number of separate 20-minute tests in which the insect was observed to drum the *Passiflora* foliage, × 100. Foretarsal drumming behavior is an indicator of willingness to oviposit. (b) Five *Passiflora* species, *P. biflora* (BI), *P. auriculata* (AU), *P. vitifolia* (VI), *P. oerstedii* (OE), *P. ambigua* (AM), respectively. (c) Number of eggs (in parentheses) collected at the field site on the respective *Passiflora* species. *Heliconius erato* and *H. melpomene* are principally monophagous (*1*), while *H. cydno* is oligophagous. Fig. 2 (right). Mean growth rates of three species of *Heliconius*: e, *H. erato*; m, *H. melpomene*; c, *H. cydno*; when raised on the most common *Passiflora* species in their native habitat. *Passiflora* subgenera are P, *Plectostemma*; D, *Distephana*; G, *Granadilla*; the ordering reflects their phylogenetic relationships (*14*). See (*19*) for definition of *R*. Dotted lines represent standard errors of means. *Heliconius erato* is digestively specialized on its host plant, while *H. melpomene* and *H. cydno* are not.

feeders'' have larval growth abilities similar to *H. melpomene*'s (*15*). Thus, the Costa Rican *H. melpomene* appears to have evolved from a group of *Heliconius* species that are characteristically oligophagous. It seems likely that this evolution has occurred recently (*22*), and that perhaps there has not been time for the evolution of digestive specialization. In contrast, *H. erato* has several closely related species, all of which are apparently host-specific on the same group of *Passiflora* host plants (*4, 14*). Thus, *H. erato* has probably been evolving host specificity for a relatively long time (*23*). This implies the lack of a strong selective pressure to evolve digestive specialization (*24*).

An alternative hypothesis would be that the host plant of *H. melpomene* just happens to contain all the possible *Passiflora* defensive chemicals, and that, by feeding on *P. oerstedii*, the insect is preadapted to feed on all the other species. This seems unlikely, yet, without phytochemical data, the hypothesis cannot be dismissed (*25*).

Why should a species such as *H. melpomene* evolve monophagy in the midst of four palatable alternative host plant species? One hypothesis can be rejected, that *H. melpomene* has somehow evolved a preference for the most common host species in its habitat. At the field site *H. melpomene*'s host plant is the least common of the five species of *Passiflora*, and in the butterfly's favored microhabitat, second growth vegetation, the plant ranks fifth in abundance (*15, 26*). Other hypotheses are more promising. At least two other studies on butterfly species have revealed that some host plants are avoided, not because they are unpalatable, but because eggs laid on these plants suffer heavy predation from ants (*5*). Similarly, data from the *Heliconius* field site indicate that host plant-specific predation pressure from ants and parasitoids may be responsible for host specificity in *H. melpomene* (*15*). Other possible selective forces favoring monophagy could be competition from other *Heliconius* (*15, 27*) or some subtle aspects of the female butterfly's searching strategy (*7*).

These results suggest the following scheme for the evolution of host plant specificity in these insects. First, among a set of approximately equally palatable host plants, one may yield the highest fitness (per unit of female reproductive effort) to the butterfly, because of differences in the ''ecological'' factors discussed above. The insect will be selected to oviposit on that host plant as often as possible. Under certain ecological conditions, the butterfly may be selected to oviposit only on that host plant, as is exemplified by *H. melpomene*. This would be a case of ecological monophagy (*5*). Second, if the above ecological conditions persist long enough, selection will act on the insect to increase growth efficiency on the host plant. By the digestive efficiency hypothesis, this will happen at the expense of the ability to feed on the formerly used host plant species. Thus, obligate monophagy will evolve. *Heliconius erato* appears to be a species which has partially evolved obligate monophagy. Four other species of *Heliconius* in Costa Rica apparently have evolved completely obligate monophagy (*15*). It may be significant that three of the four species are related to *H. erato* (*4*).

This scheme is generally consistent with the theory (*3*) of butterfly-host plant coevolution. As a relatively new host plant species or taxon evolves, it undergoes changes in chemistry and ecological setting. The longer and more pronounced the evolutionary radiation of the host taxon, the more distinct it may become both ecologically and chemically; thus, there would be increased opportunities for ''ecological'' and eventual ''obligate'' specialization, respectively. The result of this process after several subsequent host plant radiations could be the parallel phylogenies of insect and host plants observed by Ehrlich and Raven (*3*). Indeed, ''gene for gene'' coevolution (*28*) need not occur; the only evolutionary effect of the herbivores on the plants that is necessary is a general tendency toward chemical and ecological differentiation among the plant taxa. The requirements for this type of coevolution to occur may be much more easily satisfied than the ''gene for gene'' model of coevolution.

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References and Notes

1. The terms monophagy, oligophagy, and polyphagy have been used differently by different authors. In this report, monophagy has the strict definition given here, while oligophagy will be taken to mean the use of more than one species by the local population of herbivores. However, in much of the discussion ''monophagy'' could be replaced by the more general term ''host-specialization'' without loss of meaning.
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10. That is, larvae which would only grow and develop on one host plant species.
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12. R. I. Krieger, P. P. Feeney, C. F. Wilkinson, *ibid.* **172**, 579 (1971).
13. The study site was at the La Selva Field Station of the Organization for Tropical Studies, near Puerto Viejo de Sarapiqui, Heredia Province, Costa Rica.
14. The Costa Rican *H. erato* insectary population died out before I could use it for experiments, hence the use of Mexican populations instead. These were from southern Tamaulipas, Mexico, near the town of Gomez Farias. There is good evidence that the Costa Rican and Mexican *H. erato petiverana* are very similar in their responses. First, the same host plants, *P. biflora* and close relatives in the *Passiflora* subgenus *Plectostemma*, are used in both areas (*4*). Second, all the close relatives of *H. erato* that I have tested, including *H. charitonia*, *H. hecalesia*, and *H. clysonimus* from Costa Rica, have qualitatively the same growth response as *H. erato*, namely, slower growth on *P. auriculata* than *P. biflora*, and still slower (or no) growth on *Passiflora* subgenera *Distephana* and *Grenadilla*. Third, four Costa Rican *H. erato* were tested on three of the *Passiflora* species in Figs. 1 and 2 with the following R values: 1.32, 1.20, 0.93, for *P. biflora*, *P. auriculata*, and *P. vitifolia*, respectively. These are similar to the Mexican *H. erato* data and reinforce the trends.
15. J. Smiley, in preparation.
16. The *Heliconius* greenhouse facilities at the University of Texas consist of seven temperature-controlled Lord & Burnham glass houses (5 by 8 m) which double as plant propagation and insectary facilities. *Heliconius* and *Passiflora* species are maintained on a permanent basis for laboratory studies.
17. Temperature in the controlled environment chamber was kept at 24°C, the mean annual temparature of the field site. To prevent overcrowding and possible cannibalism (*4*) only one larva at a time was raised on each plant. Larvae that did not metamorphose into healthy adults were not included in Fig. 2.
18. Plants all descended from populations collected at the field site (*13*).
19. The growth rate measure used is: $R = G/T$, where R is the growth rate, $G = [(W_p/W_e)^{1/5}] - 1$, and $T = t/5$; W_p is the pupal weight, W_e is the egg weight, t is the time from hatching to pupation, and 5 is the number of instars. In words, R is the amount by which the insect increases its size within an instar, divided by the time spent in the instar, averaged over the entire larval period. If absolute developmental times (t) are considered, the same pattern holds within species; by equating the fastest rates for each species, I find that the relative values are simply the inverse of those in Fig. 2.
20. P is less than .05, t (one-tailed) = 2.3, d.f. = 9, comparing mean R for *H. erato* against the pooled mean for *H. melpomene* and *H. cydno*.
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24. Considering the slight growth rate enhancement for the digestively specialized *H. erato*, this hypothesis is not unreasonable.
25. Adequate phytochemical data are not available for most of the species. However, *P. ambigua* (see Fig. 2) is probably a generally more toxic plant than *P. oerstedii*, the host of *H. melpomene*. For instance, both *H. erato* and *H. charitonia* can grow and develop (albeit slowly) on the latter, whereas the former plant appears to be 100 percent lethal in the tests I have attempted.
26. Neither *H. melpomene* nor its host plant *P. oerstedii* are common in Costa Rica, as compared to other species of *Heliconius* and *Passiflora* (personal observation).
27. W. W. Benson, *Evolution*, in press.
28. C. J. Mode, *ibid.* **12**, 158 (1958); C. P. Da Costa and C. M. Jones, *Science* **172**, 1145 (1971).

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