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The herbivores of Passiflora: comparison of monophyletic and polyphyletic feeding guilds

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Abstract

Two types of insects commonly attack the new shoots of Central American *Passiflora* vines. These are *Heliconius* butterflies and flea beetles. All *Heliconius* attack Passifloraceae, and they constitute a monophyletic feeding guild; i.e. a guild which is descended from a common ancestor, probably ancient, which also fed on Passifloraceae. In contrast, the *Passiflora*-feeding flea beetles form a polyphyletic feeding guild, in which beetles in different genera independently (and more recently?) evolved a preference for *Passiflora*. The host plant preferences in these two guilds were compared, and were found to be remarkably similar except for a tendency for the butterflies to be more host-specific. Both guilds had two generalist species, as well as one specialist which fed on *P.* subgenus *Granadilla* hosts, and four specialists which fed on *P.* subgenus *Plectostemma* species. Both guilds had highly similar diversity indices in two habitats, and both guilds responded similarly in feeding trials using *P.* subgenus *Plectostemma* and *P.* subgenus *Granadilla* hosts. These results indicate that the superficial pattern of feeding preferences and species diversity was not strongly influenced by the type of ancestry in the insect-plant association, but was instead determined by characteristics of the host plants.

Key-words: evolution, Chrysomelidae-Halticinae, *Heliconius* species, *Passiflora* species, food preferences, generalists, insect diversity, plant diversity, specialists, speciation

Ehrlich & Raven (1964) proposed that evolving insect-plant associations have been a major force in the generation of diversity in plant and animal communities. Although this idea was very influential in stimulating interest in coevolutionary processes and insect-plant interactions (Gilbert & Raven, 1975), it has proven to be very difficult to test. For example, at the present time there is very little evidence that groups of insects such as the butterflies have strongly affected plant diversification, as Jermy (1976) and Janzen (1981) have recently discussed. Given the difficulty of testing the Ehrlich & Raven hypothesis, it may be of interest to investigate the related hypothesis that a guild (i.e. functionally related group; Root, 1967) feeding on a taxon of plants will be more diverse if they have had a long evolutionary association with that group of plants. This result is to be expected if the insects evolve greater specialization in host plant use, which would then allow more diversification among the insects in the guild. This hypothesis may be tested by comparing guilds of insects which vary in the degree of evolutionary association with their host plants, and observing whether the guilds with the closer evolutionary associations are more specialized and/or more diverse. Because host plant diversity, abundance, and geographic distribution also affect herbivore diversity (Gilbert & Smiley, 1978), it is desirable to eliminate these effects by comparing guilds which feed on the same host plants. In this paper I compare two such feeding guilds which both consume the new shoots and leaves of *Passiflora* (Passifloraceae).

Central American *Passiflora* species are eaten by several types of herbivorous insects (Gilbert, 1977). At the La Selva Field Station of the Organization for Tropical Studies (10°25′N, 84°0′W), two guilds of insects feed upon the new shoots and new leaves. These are the *Heliconius* butterflies (Lepidoptera: Nymphalidae) and several species of flea beetles (Coleoptera: Chrysomelidae, Alticini). The *Heliconius* guild is monophyletic, that is, it is derived from a common ancestor which also fed on Passifloraceae: in fact the entire tribe Heliconiini probably derived from a Passifloraceae-feeding ancestor (Ehrlich & Raven, 1964; Benson et al., 1976). In contrast, the flea beetle guild is polyphyletic, i.e., the flea beetles have independently and probably more recently evolved a preference for *Passiflora* at least four times, as evidenced by the fact that each of the four identified *Passiflora*-feeding genera are known to feed on other families of plants than Passifloraceae. For example, the *Altica* species which, like the other *Passiflora* feeders, appears to be a *Passiflora* specialist (Smiley, unpublished observations), is a member of a large genus which is known to feed upon 18 plant families in the Northeastern United States alone (Wilcox, 1979). The other flea beetle genera I have collected from *Passiflora* are also known from many plant families: *Disonycha*, at least ten families including monocots and gymnosperms; *Monomacra*, on Phytolaccaceae as well as Passifloraceae; and *Strabala*, on five families including Gramineae and Leguminosae (Wilcox, 1979; Blake, 1953). This pattern indicates that the flea beetles have had a much looser evolutionary association with the *Passiflora* than the *Heliconius*, and by comparing the two groups it may be possible to observe the effects of such differences. Of course, observed differences could be due to differences in life-history between butterflies and beetles. Nevertheless, such comparisons may at least set an upper limit as to the importance of long-term evolutionary associations. If the two guilds were found to be nearly identical in diversity and host specialization it would be a strong argument that long-term evolutionary association has had little direct influence on the generation of insect diversity in the *Heliconius*.

Materials and methods

To compare these guilds I collected three types of data from the field site at La Selva. Data on host plant use were obtained in all months of the year between March 1975 and December 1979 by collecting *Heliconius* eggs, larvae, and flea beetle adults from approximately 250 *Passiflora* vines belonging to 14 species in 4 subgenera (Smiley, 1978a). These plants were all well-mixed among each other, not occurring in patches, such that an insect travelling from one plant to another of the same species would be highly likely to encounter several other species on the way. Larval flea beetles were uncommon and appeared to cause less herbivore damage

Table 1. *Heliconius* eggs and flea beetle adults collected on *Passiflora* at La Selva. A: *Passiflora* subgenus *Astrophaea*; D: *P.* subgenus *Distephana*; G: *P.* subgenus *Granadilla*; P: *P.* subgenus *Plectostemma*; PIT: *P. pittieri*; VIT: *P. vitifolia*; AMB: *P. ambigua*; QUAD: *P. quadrangularis*; OER: *P. oerstedii*; LOB: *P. lobata*; COR: *P. coriacea*; AUR: *P. auriculata*; BI: *P. biflora* COST: *P. costaricensis*.

Herbivore species	Number of plants[2]	*Passiflora* species									
		A	D	G			P				
		PIT	VIT	AMB	QUAD	OER	LOB	COR	AUR	BI	COST
		Number of eggs									
Heliconius cydno		24	9	4	2	13	0	2	6	4	0
H. hecale		0	15	0	0	3	0	0	1	0	0
H. melpomene		0	0	0	0	10	0	0	0	0	0
H. ismenius		0	0	1	0	0	0	0	0	0	0
H. charitonia		0	0	0	0	0	5	0	0	0	0
H. erato		0	0	0	0	0	0	0	0	13	0
H. hecalesia		0	0	0	0	0	0	0	0	8	0
H. sara[1]		0	0	0	0	0	0	0	16	0	0
H. sapho[1]		1	0	0	0	0	0	0	0	0	0
H. doris		0	0	0	0	0	0	0	0	0	0
		Number of flea beetle adults									
Altica sp.	20	1	0	1	0	6	33	0	8	17	3
Monomacra sp.	19	0	6	0	7	17	3	0	4	2	1
Strabala sp. 1	10	0	2	19	0	5	0	0	0	0	0
Disonycha sp.	3	0	0	0	0	0	0	0	1	4	0
Alticini sp. 1	8	0	0	0	0	0	0	0	4	4	0
Strabala sp. 2	7	0	0	1	0	0	12	0	0	0	0
Alticini sp. 2	5	0	0	0	0	0	4	0	0	3	0
Alticini sp. 3	1	0	0	0	0	0	0	0	0	0	1
Alticini sp. 4	1	0	0	0	0	0	1	0	0	0	0

1. Egg masses collected.
2. Number of different individual plants from which flea beetles were collected.

than the adults. Flea beetles were identified to the lowest taxonomic level possible by the staff of the U.S. National Museum. These data on host plant use are presented in Table 1.

Data on guild diversity were collected during the same time period in primary forest, secondary forest, forest edge, and a 2- to 3-hectare artificial clearing. In these habitats the *Passiflora* plants were counted, *Heliconius* adults were captured with a net, and flea beetle adults were collected, so that relative abundances and therefore diversity indices could be calculated, as shown in Table 2.

Feeding trials, the third type of data collected, were done so as to compare patterns of feeding specialization in the two guilds. *Heliconius* feeding trials were conducted by rearing the larvae from hatching to pupation as described in Smiley (1978b), while flea beetle feeding trials were performed by confining the beetles in small cages with circular wire screen sides approximately 20 cm high and clear plas-

Table 2. Diversity of *Heliconius*, flea beetles, and *Passiflora* host plants. Diversity index (e^H; Hill, 1973) calculated for *Heliconius* captured, flea beetles collected, and *Passiflora* tagged and counted in three habitats at La Selva. Original data from Smiley (1978b) and Table 1.

Habitat	*Heliconius*	Flea beetles	*Passiflora*
Successional plots	3.46	3.36	2.96
Secondary forest and forest edge	5.88	5.50	6.91
Primary forest	1.54	4.56	5.46
All habitats	5.36	5.53	9.45

tic dishes for the top and bottom. Host plant cuttings with stems immersed in water were introduced into the cage for 2 days with wild-caught beetles, and the amount of feeding recorded. Three species of beetle were tested in this way (Table 3), along with six species of *Heliconius*.

Comparison of feeding guilds

Comparison of the two guilds in Table 1 indicates that *Heliconius* appear to be more specialized in terms of host plant use than the flea beetles, since 5 out of 7 species were found to use one species of host as opposed to 0 out of 7 for the flea beetles (ignoring species with fewer than 5 host records). However, aside from this

Table 3. Herbivore feeding trials on *Passiflora* foliage. Results of feeding trials using newly hatched *Heliconius* larvae and adult flea beetles on La Selva *Passiflora* species. + indicates that substantial feeding took place, – that little or no feeding occurred. *Heliconius* data from Smiley (1978b). See legend Table 1 for further explanation.

Herbivore species	*Passiflora* species									
	A	D	G			P				
	PIT	VIT	AMB	QUAD	OER	LOB	COR	AUR	BI	COST
H. cydno	+	+	+	+	+	–	+	+	+	+
H. hecale		+	+		+	–		+	+	+
H. ismenius	+	+	+	+	+	–	+	+	+	+
H. melpomene		+	+		+	–		+	+	+
H. charitonia	+	+	–	–	+	+	+	+	+	+
H. erato	+	+	–	–	–	–	+	+	+	+
Alticini sp. 1		–	–		–	–		+	+	
Strabala sp. 1		+	+		+	–		+	+	
Strabala sp. 2		–	–			+			–	

difference, the two feeding guilds showed remarkable similarities. Both guilds possessed two relatively generalist species which use *Passiflora* in the two primary subgenera *Granadilla* and *Plectostemma*, and both possessed several additional species which were more specialized. Of these, one species was relatively abundant which specialized on *Granadilla*, while four species were found to specialize on *Plectostemma*. Both groups were also found to have 2-3 rare species whose host plant relations were not evident in the data.

Diversity comparisons (Table 2) also indicated remarkable similarity between the two groups. In the clearing habitat, *Passiflora*, *Heliconius*, and flea beetle diversities were quite comparable, as were diversities in secondary forest and edge habitats. In primary forest the flea beetle and *Passiflora* diversities were comparable, but the *Heliconius* diversity was greatly reduced. The diversity of *Heliconius* and flea beetles summed over all habitats was nearly identical, although somewhat less than the calculated *Passiflora* diversity. Overall, the two guilds were almost identical in diversity in each habitat, except for the *Heliconius* in primary forest where only two species were common.

Extensive data from *Heliconius* feeding trials (Smiley, 1978a), summarized in Table 3, indicate that *Granadilla* specialists can also consume *Plectostemma* successfully, but that the reverse is not true. This same result was observed in the flea beetle feeding trials. *Strabala* sp. 1, a *Granadilla* specialist, was observed to feed readily on *Plectostemma* as well as *Granadilla*, whereas Alticini sp. 1 and *Strabala* sp. 2, both *Plectostemma* specialists, were found to be unable to consume *Granadilla* host plants. Therefore it appears that both guilds are subject to similar constraints in the evolution of feeding tolerances.

Conclusions

The *Heliconius* were found to be somewhat more specialized in their host plant use than the flea beetles, which tended to use 2-3 species of host rather than the one host used by most *Heliconius*. Although this might be expected in the guild with the strongest evolutionary association to the host plants, it may also be an artifact of the much greater mobility of butterflies in seeking out host plants. A female butterfly such as *Heliconius melpomene* may pass over many edible host plants in searching for just the right species (Smiley, 1978b), but a flea beetle with its reduced powers of movement may be forced to occasionally consume any plant that is edible to it.

In spite of the observed difference in host specificity, the other characteristics of the two feeding guilds were remarkably similar. In diversity measures, in host plants used, in the response to host plant subgenera, the two guilds were nearly identical. The data indicate strongly that detailed characteristics of herbivore guilds may be determined by the host plant community, regardless of the degree of evolutionary association between insect and host plant. Therefore, long-term evolutionary associations such as those described by Ehrlich & Raven (1964) and Benson et al. (1976), do not necessarily have a major direct effect on the development of herbivore communities. However, an indirect effect, such as might be caused by coevolution acting to increase host plant diversity, has not been ruled out and must still be considered a strong possibility in this system.

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