

### CHAPTER 3. HOST PLANT SELECTION IN HELICONIUS

The investigations described in Chapter 2 have made clear the numbers and kinds of host plants which are potentially available to each species of Heliconius. Knowing this, it is of great interest to investigate which of these potential hosts are actually used. For instance, it is possible to test the hypothesis that host plant abundance will be correlated to strategies of host selection. This can be done by comparing the host plant selection of forest-dwelling Heliconius to that of second-growth-inhabiting species. These habitats show marked differences in host plant abundance. It is also possible to investigate the kind and degree of niche differentiation that occurs in these butterflies with regard to host plant use.

This chapter will address these questions primarily by describing which host plant species are selected by Heliconius females under both field and laboratory conditions. In addition, several other aspects of oviposition (or host plant selection) behavior will be discussed, including the effects of host plant size, the part of the plant selected, and the number of eggs laid on each host plant. The following studies are not intended to be definitive descriptions of host plant selection and oviposition behavior in Heliconius: in fact, they barely scratch the surface of what are undoubtedly very complex behaviors.

Most butterflies are excellent subjects for the study of oviposition behavior, which will be defined here as host plant

selection and egg-laying behavior. Oviposition can be studied under caged conditions for many species (Hovanitz and Chang 1964; Wicklund 1975; Copp 1977). It can also be studied by field observations of various kinds (Chew 1975; Singer 1971; Wicklund 1977). In this investigation, Heliconius oviposition was studied by collecting eggs from various Passiflora species in the field and identifying them as to species. This is an indirect method for determining which host plants were selected by each species of butterfly. Given the time available at the field site, it was not feasible to systematically observe host plant searching or oviposition behavior, except in isolated episodes. Therefore, the field data consisting of Heliconius egg collections was supplemented with direct observation of oviposition behavior in insectary females, by (1) observing their behavior when presented with a single host plant or potential host plant, and (2) observing Heliconius when presented with a choice of host plants. Previous work indicates that there is usually a meaningful correspondence between oviposition behavior as observed in the laboratory to that which occurs in the field (Singer 1971), at least with regard to the species of host selected.

It is predicted that a guild of herbivores (Root 1967) such as Heliconius will partition their food plants in such a way as to reduce competition (Benson 1978). There are at least three ways to do this (Gilbert and Singer 1975). One is to increase habitat specificity so that even if the same host plant species is used in common, the same individual plants will not be fed upon by both types

of herbivores. This reduces competition considerably depending on the amount of habitat separation. The data in Chapter 2 indicate that there is a certain degree of habitat separation in the La Selva Heliconius but it is clearly insufficient to eliminate interspecific competition for host plants. A second mechanism for reducing competition is to partition the parts of the host plant fed upon, whether they be stems, roots, leaves, or other parts. The degree of this type of partitioning may depend on the effects that feeding on one plant part will have on another plant part; these effects are at present unknown. However, in Heliconius, which feed either upon new growth or upon mature leaves, depending on the species (Benson et al. 1976), plant tissue partitioning leads often to the exploitation of different individual plants (of different sizes) in which case the degree of partitioning will depend on demographic parameters of the host plant. The third and probably most effective way to reduce competition is for the butterflies to become host-specific on different species of host plant. This will reduce competition for host plant to zero. All three types of host plant partitioning are known in butterflies (Gilbert and Singer 1975) and were investigated in the La Selva Heliconius community. The observed constancy of Heliconius populations indicates that seasonal host plant partitioning is not to be expected.

This chapter begins with a description of the Heliconius eggs collected at the La Selva Field Station, for each species of butterfly. The types of Passiflora host plants from which the eggs

were taken are then summarized for each Heliconius to obtain the patterns of host plant selection. The insectary experiments are then described and analyzed, and their relevance to the field egg collections is discussed. Finally, the overall pattern of host plant selection is related to host plant abundance, possible competitive effects, and differences in the number of eggs laid per host plant.

### 3.2 Egg Collections at the Field Site

Heliconius eggs were frequently found attached to Passiflora vines at La Selva. They are generally elliptical in profile and range from 1.0 to 1.5 millimeters in length. They are covered with ridges between which are indentations, and are yellow in their natural state. The eggs were collected by cutting off the portion of the plant they were attached to, or, in the case of the larger eggs, simply pried off the plant. The species and tag number of the plant were recorded, and the eggs brought back to the field station for rearing. In many cases the eggs would not hatch and subsequently turned black after a period of up to ten days; these eggs were found to be parasitized by micro-hymenopteran parasitoids (see Chapter 5.3a). 5.3a). The eggs that did hatch were provided with Passiflora biflora leaves, which turned out to be an almost universally acceptable food (except for three species; see Chapter 4). The resulting larvae were photographed at various stages of development, as were the pupae. When the adults emerged the butterflies could be

identified as to species. There was 50% or greater mortality in the rearing process due mainly to bacterial infections brought on by unsterile conditions and widely fluctuating temperatures in the station building. The results of identifying the successful rearings are as follows:

1. H. cydno: Eggs of this common species were found on all the common species of Passiflora at La Selva except P. (Tetra-stylis) lobata. The eggs are large (1.5 mm long) and barrel-shaped, and were usually found attached to the tendrils or leaf-tips of the plants.

2. H. doris: Eggs of this uncommon species were found only on Passiflora ambigua, laid in large arrays on the underside of fully mature leaves. The eggs are very small (1.0 mm long).

3. H. hecalesia: Eggs of this uncommon species were found only on P. biflora. Laid in groups of three to seven on the upper surfaces of leaves, they are medium-sized (1.4 mm long), and are slender. This species probably also uses P. lancearia, a known host elsewhere in Costa Rica.

4. H. hecale: The eggs of this moderately common species were found on P. vitifolia, P. oerstedii, and P. auriculata at La Selva. They are indistinguishable from H. cydno and H. ismenius eggs, and are laid primarily on leaf tips and tendrils of the host plants.

5. H. sara: Eggs of this abundant species were found only on P. auriculata, in clusters of twenty to forty at the growing tips

of the plant. The eggs are small (1.0 mm long).

6. H. melpomene: Eggs of this common species were found only on P. oerstedii, on the leaves, foliar stipules, or growing tips. The eggs of this species are medium-sized (1.3 mm long).

7. H. erato: Eggs of this common species were found on the growing tips of P. biflora. They are medium to large in size (1.5 mm long).

8. H. charitonia: Eggs of this uncommon species were found only on P. (Tetrastylis) lobata. They are clustered in groups of five to fifteen at the growing tips of the plant and are medium in size (1.3 mm long).

No eggs of H. ismenius or H. sappho were successfully reared. Based on published records (Benson et al. 1976), H. ismenius probably feeds on P. (Granadilla) ambigua at La Selva, and it may also use P. (Granadilla) oerstedii as well. H. sappho undoubtedly uses P. (Astrophea) pittieri at La Selva based on the fact that the closely related H. hewitsoni of Southwestern Costa Rica uses this plant, and it is the only known Central American species in the Astrophea subgenus. Elsewhere, H. sappho uses only Astrophea host plants. H. ismenius eggs are indistinguishable from those of H. hecale and H. cydno, but may be layed on all parts of the host plant, not just the leaf tips and tendrils. Extrapolating from observations on eggs of H. hewitsoni, H. sappho eggs are probably layed ten to twenty to a shoot of host plant and are loosely scattered on leaves

and the stem.

Based on the above information, Heliconius eggs can be classified according to size, number layed per plant, place on plant, and species of plant. Figure 3.1 summarizes this information. The number of Heliconius species' eggs found on each Passiflora species is given in Figure 3.2. In the case of species which lay many eggs at a time the number in Figure 3.2 is the number of different clusters of eggs. Host plant associations which are not represented in the field data but which are thought to occur are indicated by a plus sign. The small sample sizes for some species were one reason why insectary studies were thought to be necessary.

### 3.3 Insectary Studies of Heliconius Oviposition

Laboratory studies of the behavior of caged organisms often reveal information which would be unobtainable under natural conditions. Experimental manipulations can be readily performed and behaviors can be observed in great detail. Caution must be used in extrapolating the observed results to behavior in the natural environment, but field observation greatly adds to the confidence of such an interpretation. The techniques used in the Heliconius insectary studies were repeatedly modified until the procedure appeared to most closely mimic the natural conditions without sacrificing data-gathering efficiency. However, certain aspects of host selection such as long-range searching behavior cannot be studied in the insectary, and this must be kept in mind in interpreting the results.

### 3.3a General Description of Oviposition Behavior in Heliconius

It is beyond the scope of this project to describe Heliconius oviposition behavior in detail. However, the following general outline may be useful in understanding the insectary data.

Female Heliconius appear to be attracted to host plants by olfactory visual cues. Virtually all Passiflora (or passifloraceous) species are attractive from a short distance, regardless of their form, habit, and condition. This is probably good evidence of an olfactory cue. Olfaction in the Heliconiine Agraulis vanillae is known to function in host plant location, and positive anemotaxis in response to Passiflora odor has been demonstrated (Copp and Davenport 1978). Plants in the insectary with the form of a vine growth a vine growth tip, where a stem curves out into the air and droops at the end, appear also to be attractive regardless of their identity (which includes Cucurbitaceae, Aristolochaceae, and Passifloraceae). This is evidence for the functioning of visual cues in host location. It is hypothesized that Passiflora species may also be recognized by their leaf shapes (Gilbert 1975); however the experimental methods used here were not conducive to testing this idea. Thus, both olfactory and visual cues are probably used by the Heliconius in locating their host plants. In addition, Heliconius have a highly developed ability to learn the spatial location of their resources and to return to these places periodically (Ehrlich and Gilbert 1973). The degree to which host plant searching is governed by past experience or is truly random is unknown. In any case, this aspect



of host plant location is probably unimportant in the insectary, where all plants are readily found by the insect.

Once a Passiflora is found by a female Heliconius it is closely approached. While butterflies may reject some plants without touching them, as evidenced by flying away from the plant and not returning, in most cases the female "drums" the plant with her foretarsi. This consists of the female hovering in front of a leaf about 1 centimeter away and very rapidly flicking out the white, modified forelegs to tap the leaf surface. The tips of these legs have chemoreceptors which presumably aid in identifying the plant species by its chemical constituency. It is not known whether or not the foretarsi penetrate the leaf cuticle; in several insects (Staedler 1976) and in another Nymphalid butterfly (Chlosyne lacinia) (Calvert 1975), it appears that the cuticle is not penetrated. After the drumming behavior occurs the butterfly then either flies away or proceeds to oviposition. Drumming may be repeated several times in some cases. Drumming behavior appears to be the final step in host plant identification by the butterflies, as evidenced by the fact that most female Heliconius will drum all Passiflora species even though only a select few species are suitable hosts which receive eggs. Most importantly, drumming behavior is an unequivocal indication that the butterfly is searching for a host plant and has in fact "reacted" to the test plant. Thus a simple measure of host plant acceptability is the ratio of tests in which actual ovipositions occurred to the number of tests in which drumming occurred.

In some Heliconius species the time interval between host

plant location and actual oviposition is long, on the order of 15 minutes or more. This is characteristic of those species which lay several eggs per plant, such as H. charitonia, H. sara, H. doris, and H. hecalesia. In contrast, the single-egg laying species such as H. cydno, H. hecale, H. melpomene, and H. erato usually proceed very quickly from drumming to oviposition (or rejection). This difference is probably due to the fact that for the multiple-ovipositing species there is (1) a greater investment in each host plant selected favoring more "choosy" behavior, (2) there is more time available between ovipositions for choosing the host plant, all other things being equal, and (3) the host plant must be determined by the butterfly to be large enough to support the larvae when they hatch; a larger plant is required for the multiple-ovipositing species. The practical result with regard to the insectary data is that the multiple-egg-laying species are not as readily tested in a short time period because they are extremely variable in their short-term responses.

In the single-egg laying species oviposition occurs almost invariably once the butterfly has alighted on the plant and has curved the abdomen to bring it into contact with the host plant. At this stage oviposition may be interrupted before the egg is laid. With the multiple-ovipositing species abdominal contact with the host plant may or may not be followed by oviposition, thus in these species it is not possible to score a positive oviposition response until the eggs are actually laid.

Below, the experimental methods used are discussed in some detail. The results are also discussed in terms of evaluating the methods. However, discussion of the overall results with respect to patterns of Heliconius oviposition are postponed until the next section "Patterns of Host Plant Selection" (Chapter 3.4).

### 3.3b Experimental Methods

All insectary oviposition studies were done in a 4 by 7 meter greenhouse at the University of Texas at Austin. This greenhouse contained various kinds of vegetation including flowering Anguria vines, an important nutritional source for adult Heliconius (Gilbert 1972). Passifloraceous plants were excluded from the greenhouse, however, so that they could be introduced in a controlled manner and the subsequent oviposition behavior observed. The stocks used in the experiments were multi-generation descendents of wild-caught butterflies; the oldest stock used was three years or about 20 generations old, and most were considerably younger. No gross changes have been observed in the butterflies' oviposition behavior during their captivity; however, there is some slight evidence of a loss of larval vigor in certain stocks after long periods (see Chapter 4.3a). The plants used were cuttings or seeds of Passiflora vines collected at La Selva, and propagated in pots containing commercial planting soil. The cuttings used were frequently treated with fungicide during propagation, and it appears that in these

plants normal growth can occur without symbiotic endomycorrhizae. It was found that Passiflora in a non-growing condition, lacking young tissue, were generally unacceptable as host plants. Therefore in all tests only vigorously growing Passiflora vines were used.

Two experimental techniques were used to study oviposition behavior. The first was a single plant presentation method, originally suggested by Newton Copp of the University of California at Santa Barbara. Heliconius of many species (including some non-Costa Rican species and including Dryas julia, a La Selva Heliconiine) were placed in the insectary on a permanent basis, where they fed, mated, and gathered pollen. To observe oviposition behavior a potted Passiflora plant is introduced into the center of the greenhouse for a twenty minute period. Under favorable conditions of bright midday sunlight most of the female Heliconius will approach the plant and "drum" the leaves. The behaviors of the different individuals are then recorded. This method has several advantages:

1. The observer need only watch one host plant at a time.
2. Single-plant presentation approximates natural conditions because in nature the plants are widely-spaced and would be encountered only one at a time.
3. Single plant presentation avoids the problem of females which may be stimulated to oviposit by one plant species and yet lay the egg on an adjacent plant. Possible problems of odor-mixing between adjacent plants are avoided as well.

4. The method is efficient in that the number of female butterflies can be adjusted so that data is obtained relatively continuously.
5. Oviposition is observed directly, and detailed observations can be made.
6. By sequestering in cages the females which attempt to oviposit it is possible to prevent oviposition during the experiment, thus preventing the butterflies from laying all their eggs and becoming "unmotivated" to participate in further testing.
7. It is possible to record the egg outputs of individual females and to collect their eggs individually.

In August 1975 this method was used to test the oviposition responses of six La Selva Heliconiines which had been prevented from ovipositing for at least 48 hours. This was done in order to test host plant acceptability when the butterflies were highly motivated to oviposit on any acceptable host. Eight Passiflora species were presented for 20 minutes each, and one female of each species responded to each presentation. Oviposition was prevented during the three replicates of the experiment, which were done on three successive days; therefore on the third replicate the butterflies had not oviposited for 100 hours or more. The results are shown in Figure 3.3.

In May and June, 1976, this same method was used except that oviposition was allowed to occur normally. Four La Selva Heliconius

species and H. erato from Tamaulipas, Mexico, were used in testing the acceptability of 26 Passiflora species, including 10 La Selva Passiflora. The Mexican H. erato is of the same race (petiveranus) as the Costa Rican form. Two H. cydno females, one H. melpomene female, one H. hecale female, three H. charitonia females, and one H. erato female responded consistently to the Passiflora presented. Eggs were removed as soon as they were laid and placed in labelled containers. The place on the plant where the eggs were laid was recorded as well as the plant. The results are given in Appendix A4.1. The results are also shown in condensed form in Figure 3.4. Here the taxonomically closely-related species of Passiflora are grouped to make the results clearer, and the non-Costa Rican Heliconius (with the exception of H. erato) are left out.

The second experimental technique (June-July 1977) used was designed to discover any relative preferences the butterflies might have for different types of host plant. About 20 female Heliconius of the same species were removed from the insectary in which that species is propagated and placed for two hours in the experimental insectary. Up to ten plants of various Passiflora species were placed in a ring in the center of the experimental insectary; as before there were no other Passiflora present. The order of plants in the ring was random, and different in each replicate. The eggs laid on each Passiflora were collected every half hour and the number recorded. The results are given in Appendix A4.2, and in Figure 3.5 in condensed form.

In all experiments individual identities of the butterflies

and the

In all experiments individual identities of the butterflies and the plants were recorded. However, there is a substantial amount of experimental variation even when experiments are repeated on the same individuals, and this variation is of the same order of magnitude as the overall experimental variation. Therefore the individual identities of butterflies have been ignored in the following analysis, except to indicate the numbers of butterflies involved.

### 3.3c Significance of Insectary Studies

The results of the August 1975 tests where females of five species were prevented from ovipositing for 48 hours prior to the test are highly consistent among the three replicates. In 19 out of 48 butterfly-plant interactions there was a consistent positive reaction; in 17 out of 48 the reaction was negative; and only in 11 interactions were the three replicates inconsistent (Figure 3.3). Under these conditions of host plant deprivation, selection of host plant appears to be an all-or-nothing phenomenon, at least among the plants tested. I believe this testing method to be a good indicator as to which plants should be considered "host plants," including primary or "always used" host plants and secondary or "alternative" host plants (Singer 1971).

The results of the May-June 1976 tests where females were allowed to oviposit have much greater variation in the results than the tests described above. However, the proportion of tests with

positive reaction may be a fair indicator as to how "preferred" a host plant is to the butterfly, defined as the probability of ovipositing given that the plant is encountered. Within the set of "host plants," as defined above, this procedure indicates which are primary and which are secondary host plants, and to what degree. In Heliconius tested under these conditions it appears that the primary hosts are highly "acceptable," with 80% acceptability or better, as evidenced by the results for H. melpomene on P. oerstedii and H. erato on P. biflora (Figure 3.4). This number probably varies according to the variation in the condition of the test host plants and in this case indicates that the plants were in uniformly acceptable condition. The Passiflora species can thus be ranked according to their percent acceptability to each Heliconius, information which may be useful in deriving ecological models of resource utilization (Schoener 1971; Pyke et al. 1977; Levin 1977).

The June-July 1977 choice tests resulted in patterns of host selection which are consistent with the results of the other tests. In the case of H. cydno, if the plants are ranked (with the Passiflora receiving the most H. cydno eggs as rank number 1), the results are significantly positively correlated to the ranking based on the "percent acceptability" to H. cydno discussed above (Kendall's tau coefficient,  $p = .05$ ). In Chapter 4.4d it will be shown that these rankings are also correlated to the H. cydno larval growth ability on the host plant.



All three of the experimental techniques tested yielded meaningful results. The 48-hour oviposition deprivation experiment is useful in determining which plant species are acceptable host plants. The other two methods show the relative acceptabilities of these host plants. The single plant presentation method is advantageous in that several species of butterflies can be tested simultaneously, while the multiple plant method tests many host plants at the same time. At the present unrefined level of analysis, both methods seem equally useful in describing patterns of host plant selection.

The results of the insectary experiments are fully consistent with the field data on host plant selection, as may be seen by comparing Figure 3.2 and Figure 3.4. The only discrepancy discovered is that H. melpomene occasionally oviposits on P. ambigua in the oviposition-deprivation experiment (Figure 3.3), and that H. erato may oviposit on P. auriculata, as seen in Figure 3.4. In addition, H. charitonia may oviposit on a wide variety of species of Passiflora but strongly prefers to use P. lobata or P. adenopoda, species which were not available for much of the testing (see Gilbert 1971 for further discussion).

### 3.4 Patterns of Host Plant Selection

The ten La Selva Heliconius species fall into two distinct patterns of host plant selection. Three species, H. cydno, H. hecale, and H. ismenius, appear to be oligophagous or (relative) "generalists,"

as they will be called herein. The "generalist" H. cydno is remarkably unselective as to the host species chosen, while H. hecale seems to prefer three species and may accept several others occasionally. Little information is available on H. ismenius, other than the fact that the insectary population derived from Mexico is very similar in response to H. hecale. H. cydno is found in a habitat with low host plant abundance, and this supports the hypothesis that in such an environment the insects are selected to be "generalists." H. hecale is found in a high Passiflora-density habitat but successfully penetrates some of the lower-density habitats as well (see Figure 2.5 and Appendix A2.2). This Heliconius species apparently does not build up stable high population densities in the early second growth areas, suggesting that it cannot successfully compete there. The mimic of H. hecale, H. hecalesia, is very definitely uncommon in the early second growth, and is found with regularity only in edge and old second growth areas. It appears that H. hecale is primarily adapted to areas of old second growth where host plant abundance is much lower, but can use early second growth areas occasionally. More field work is required to fully understand the habitat preferences of this species.

#### 3.4a Host Specificity

Seven Heliconius species at La Selva are host-specific, primarily ovipositing on one species of Passiflora. Of these, five

species lay clusters of eggs (see Figure 3.1). As discussed above (Chapter 3.3a) these species are normally very "choosy" in selecting their host plant and need to find an acceptable host plant only infrequently. By laying several eggs at a time, these butterflies can effectively use a much lower density of host plant than the single egg-ovipositing species. In addition, once a plant is found, the larvae of the multiple-ovipositing species are much more efficient in converting it into butterfly biomass, by virtue of the fact that the larvae can successfully feed on mature leaves as well as new growth (see Chapter 4.4a). These properties should in theory enable these species to use widely scattered, large host plants. This may account for the ability of H. sappho to persist as a host specialist in an area of extremely low host plant abundance. In general terms, the multiple-egg ovipositing species have much lower minimum requirements for maintaining themselves on a given host plant abundance, and hence remain host-specific even when host plants are rare and scattered.

The two remaining species H. erato and H. melpomene, are single-egg ovipositing host specialists which are adapted to early second growth habitat which characteristically has high densities of host plant. They are able to maintain stable, relatively high-density populations by this strategy. Judging by the small number of eggs collected at the field site (Figure 3.2), these species probably compete effectively in this habitat by scattering their eggs in relatively hidden places. Their oviposition search behavior

of flying slowly through dense vegetation, close to the ground, corroborates this supposition.

It appears that for the single-egg ovipositing species of Heliconius butterflies, the degree of host plant specialization is positively correlated to host plant abundance, as was initially hypothesized. This correlation cannot be explained as a spurious artifact of the butterflies' habitat preferences. For example, it could be argued that the forest species' host plants are chemically more uniform than the second-growth species' hosts, as predicted by the theories of Feeny or Rhodes and Cates (Chapter 1.5). However, the data in Chapter 4 directly refute this contention.

#### 3.4b Niche Overlap and Competition for Host Plants

The observed patterns of host plant selection in Heliconius (Figure 3.2) indicate that partitioning of the Passiflora resource occurs to a great degree along species lines. Most common Passiflora species at La Selva (and one uncommon species, P. pittieri) have a host-specific species of Heliconius that uses it. Only P. biflora appears to have more than one associated specialist Heliconius species, and in this case there is a marked separation by habitat, plant size, and number of eggs laid per plant (see H. hecalesia and H. erato in Figure 3.1). The two "generalist" species, H. cydno and H. hecale, overlap with each other and with the other Heliconius species at La Selva in preferred host species, but differ somewhat in habitat preference. However, strong overlap

in host plant use by these two species is definitely occurring, as illustrated by the fact that in old second growth and edge habitats both types of eggs were frequently collected from the same Passiflora plants.

If host plant specialization and the resulting partitioning were a direct result of competition for host plants, as has been predicted (Dethier 1947, Price 1975), specialization should occur in those habitats where host plants tend to be "limiting," that is, in short supply. An obvious measure of the degree of host plant scarcity is to calculate the ratio of eggs collected per host plant per day in the two habitats at La Selva. In the forest habitat, 12 eggs or clusters of eggs were collected from 144 Passiflora shoot/days, for a ratio of .08 eggs/shoot/day, while in the second growth areas only five eggs or clusters of eggs were found on 750 shoots of Passiflora, for an egg/shoot/day ratio of .0067. This reaffirms the assertion in Chapter 2.5 that most of the Heliconius (excepting H. sara) were not strongly "host plant limited," and that there is a superabundance of Passiflora in the early second growth habitat. It is in this habitat that host specialization is most prevalent, whereas it is in the forest and old second growth (where host plants are scarce) that the "generalists" are to be found. This argues against the idea that host plant specialization and niche partitioning is a result of direct competition for host plant. Instead, it may well be that host plant partitioning results from indirect competitive effects caused by host plant-specific predators and

parasitoids. This will be discussed in Chapter 6.3. Host plant specialization itself is best explained as a result of host plant abundance, as discussed above.

There is an interesting correlation between the number of eggs laid per plant and the size of the host plant. As would be predicted, the single-ovipositing species H. erato, H. melpomene, and H. cydno tend to oviposit on small host plants, while the multiple-ovipositors select larger host plants. However, there appears also to be some correlation to leaf toughness. It has been demonstrated in Pierid butterflies that gregarious larvae can grow and develop much more rapidly on a tough-leaved host than single larvae, probably due to a mechanical advantage in chewing (Jordan in prep.). In the La Selva Heliconius the host-specific species which feed on the tough-leaved P. ambigua, P. pittieri, and P. auriculata are all cluster layers with twenty to several hundred eggs per cluster. In addition to P. biflora, H. hecalasia feeds on P. lancearia or (probably) P. talamancensis, which are large, tough-leaved species closely related to P. biflora. This Heliconius species also lays several eggs per plant. P. oerstedii, P. biflora, P. vitifolia, and P. (Tetrastylis) lobata never develop tough leaves, even though the last two species may reach large size. The first of the above three species are fed on only by single-ovipositing species of Heliconius, while P. ("Tetrastylis") lobata is attacked by a multiple-ovipositor. However, this latter may be a special case (Gilbert 1971, see also Chapter 4.4a). Thus, the

number of eggs laid per host plant correlates well with the leaf toughness and size of the host plant. Of course, the "generalist" species, which are single-ovipositors, use only the tender new growth of their hosts. This topic will be discussed further in Chapter 4.4e.

If the correlation between host plant leaf toughness and number of eggs laid per host plant is valid then it is possible at least in theory to account for the observed patterns of host plant selection based on (1) host plant abundance, and (2) host plant leaf toughness and size. I deduce that in a herbivore community such as this,

(1) all tough-leaved host plants will have host-specific multiple-ovipositing herbivores, regardless of the abundance of plants,

(2) tender-leaved host plants will have host-specific single-ovipositing herbivores only in areas of high host plant abundance,

(3) tender-leaved host plants (including tender parts of tough-leaved plants) will have "generalist" single-ovipositing herbivores in areas of low host plant abundance.

This hypothesis explains most of the patterns of host plant selection in the La Selva Heliconius. Unexplained is why P. vitifolia and P. costaricensis do not have host-specific single-ovipositing Heliconius feeding on them in the early second growth, and why P. coriacea, a tough-leaved species, does not have a multiple-ovipositing specialist Heliconius feeding upon it. See Chapter 6.4 for further discussion.

| <u>Heliconius</u><br>species | Egg size | Number per plant | Where layed on plant                        | Host species   |
|------------------------------|----------|------------------|---|--|
| doris                        | small    | several hundred  | under mature leaf                           | <u>P.ambigua</u> (prob.<br><u>P."laurifolia"</u> )<br><i>as well</i>   |
| ismenius                     | large    | 1?               | scattered on new growth tissue              | <u>P.ambigua</u><br><u>P.oerstedii?</u><br>many other<br><u>Passiflora?</u>  |
| hecale                       | large    | 1                | leaf tip or new tendril                     | <u>P.vitifolia</u><br><u>P.oerstedii</u><br><u>P.auriculata</u><br><u>P.biflora?</u>   |
| cydno                        | large    | 1                | leaf tip or new tendril                     | <u>P.vitifolia</u><br><u>P.pittieri</u><br><u>P.oerstedii</u><br><u>P.quadrangularis</u><br><u>P.ambigua</u><br><u>P."laurifolia"</u><br><u>P.biflora</u><br><u>P.lancearia</u><br><u>P.costaricensis?</u><br><u>P.coriacea</u><br><u>P.auriculata</u> |
| melpomene                    | medium   | 1                | meristem leaf cluster, stipules, leaf blade | <u>P.oerstedii</u><br><u>P.menispermifolia</u>   |
| erato                        | medium   | 1                | meristem leaf cluster                       | <u>P.biflora</u>   |
| charitonia                   | medium   | 5-10             | meristem leaf cluster                       | <u>"Tetrastylis"</u><br><u>lobata</u>  |
| hecalesia                    | medium   | 5-10             | scattered on new growth tissues             | <u>P.biflora</u><br><u>P.lancearia?</u>  |
| sara                         | small    | 20-40            | meristem leaf cluster                       | <u>P.auriculata</u>  |
| sappho                       | small    | 20-40?           | scattered on stem?                          | <u>P.pittieri</u>  |

Figure 3.1 Egg characteristics of Heliconius species at La Selva.



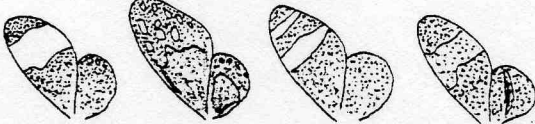






| FIELD - COLLECTED EGGS  |                        |   |  |   |   |   |   |   |   |
|---|------------------------|---|--|---|---|---|---|---|---|
| <br>HELICONIUS | sappho (G)             | .   | .  | .   | .   | .   | .   | . | + |
|   | cydno (S)              | 4   | 13   | 6   | 9   | 4   | 24  |   |   |
|   | hecalesia (G)          | 8   | .  | .   | .   | .   | .   | . | . |
|   | hecale (S)             | +   | 3  | 1   | 15  | .   | .   | . | . |
|   | doris (G)              | .   | .  | .   | .   | +   | .   | . | . |
|   | sara (G)               | .   | .  | 16  | .   | .   | .   | . | . |
|   | melpomene (S)          | .   | 5  | .   | .   | .   | .   | . | . |
|   | erato (S)              | 3   | .  | .   | .   | .   | .   | . | . |
|   | (G): Gregarious larvae | bi  | oer  | aur   | vit   | amb   | pitt  |   |   |
|   | (S): Solitary larvae   |  |  |  |  |  |  |   |   |
| PASSIFLORA  |                        |   |  |   |   |   |   |   |   |

Figure 3.2 Egg collections at La Selva from six Passiflora species. bi=biflora  
 oer=oerstedii aur=auriculata vit=vitifolia amb=ambigua pitt=pittieri.

| <u>Passiflora</u><br>species | <u>Heliconius</u> species |           |        |          |                    |   |
|------------------------------|---------------------------|-----------|--------|----------|--------------------|---|
|                              | cydno                     | melpomene | hecale | ismenius | charitonia (Dryas) |   |
| biflora                      | 2                         | 0         | 0      | 0        | 3                  | 3 |
| coriacea                     | 3                         | 0         | 0      | 0        | 3                  | 3 |
| auriculata                   | 3                         | 0         | 2      | 2        | 3                  | 3 |
| costaricensis                | 2                         | 0         | 1      | 2        | 2                  | 2 |
| vitifolia                    | 3                         | 0         | 3      | 3        | 2                  | 0 |
| quadrangularis               | 3                         | 0         | 0      | 2        | 3                  | 0 |
| ambigua                      | 3                         | 2         | 0      | 2        | 0                  | 0 |
| oerstedii                    | 3                         | 3         | 3      | 3        | 3                  | 0 |

Figure 3.3 Oviposition tests (single plant presentation) on six Heliconiine species which were prevented from ovipositing for at least 48 hours before each test. The numbers represent tests during which oviposition was attempted by the butterfly: actual oviposition was prevented. Each plant was tested on each of three different days.

| <u>Passiflora</u><br>species:        | <u>Heliconius</u> species |                    |                 |                |                     |
|--------------------------------------|---------------------------|--------------------|-----------------|----------------|---------------------|
|                                      | <u>cydno</u> 2            | <u>melpomene</u> 1 | <u>hecale</u> 1 | <u>erato</u> 1 | <u>charitonia</u> 3 |
| coriacea                             | 3(6)                      | 0(3)               | --              | 2(3)           | 2(2)                |
| auriculata                           | 7(8)                      | 0(1)               | --              | 1(2)           | --                  |
| biflora (incl.<br>helleri, tuberosa) | 2(8)                      | 0(3)               | --              | 1(2)           | 1(2)                |
| costaricensis (incl.<br>rubra)       | 2(3)                      | 0(1)               | 0(1)            | 0(1)           | 0(1)                |
| vitifolia                            | 4(4)                      | 0(2)               | 1(1)            | 0(3)           | --                  |
| quadrangularis                       | 4(4)                      | 0(1)               | 0(1)            | 2(2)           | --                  |
| ambigua (incl.<br>laurifolia)        | 8(8)                      | 0(4)               | 0(1)            | 0(5)           | --                  |
| oerstedii                            | 14(14)                    | 10(11)             | --              | 0(5)           | 0(1)                |
| menispermifolia                      | 0(1)                      | --                 | 0(1)            | 0(1)           | --                  |
| lobata                               | 1(3)                      | 0(2)               | --              | 0(1)           | --                  |

Figure 3.4. Single plant presentation oviposition tests (May-June 1976). The number in parentheses is the number of tests in which the butterfly was observed to "taste" the plant (foretarsal drumming); the other numbers are the number of tests in which oviposition occurs. The number of individual butterflies tested is underlined at the top.

| <u>Passiflora</u><br>species: | <u>(20)</u> (19) (20) (11) (9) |    | <u>cydno</u><br>(20) (11) (9) |    | <u>ismenius</u><br>(9) |    | <u>hecale</u><br>(8) |    | <u>erato</u><br>(3) |    | <u>charitonia</u><br>(10) (5) (3) |    |
|-------------------------------|--------------------------------|----|-------------------------------|----|------------------------|----|----------------------|----|---------------------|----|-----------------------------------|----|
|                               | --                             | -- | --                            | -- | 0                      | -- | 0                    | 0  | --                  | 5  | --                                | -- |
| pittieri                      | 1                              | 1  | 2                             | -- | --                     | -- | --                   | -- | 5                   | 6  | 5                                 | -- |
| coriacea                      | 6                              | 12 | --                            | -- | --                     | 0  | 0                    | 0  | --                  | 0  | --                                | -- |
| auriculata                    | 3                              | 0  | --                            | -- | --                     | 0  | 1                    | 1  | --                  | 8  | --                                | -- |
| biflora                       | --                             | -- | --                            | -- | 0                      | -- | --                   | -- | --                  | -- | --                                | -- |
| lancearea                     | 1                              | 5  | 2                             | -- | --                     | -- | --                   | -- | 0                   | 0  | 0                                 | -- |
| costaricensis                 | 7                              | 2  | --                            | -- | 5                      | 9  | 11                   | -- | --                  | 0  | --                                | -- |
| vitifolia                     | --                             | 6  | 12                            | -- | --                     | 26 | 1                    | 1  | 1                   | 0  | 17                                | -- |
| quadrangularis                | 1                              | 6  | 14                            | 8  | 1                      | 0  | 0                    | 0  | 0                   | 0  | 0                                 | 0  |
| ambigua                       | 6                              | 8  | --                            | 26 | 10                     | -- | --                   | -- | --                  | 0  | --                                | 10 |
| laurifolia                    | --                             | -- | --                            | -- | --                     | 1  | 1                    | 1  | --                  | -- | --                                | -- |
| serratifolia                  | 4                              | 6  | --                            | -- | --                     | 33 | 17                   | 17 | --                  | 0  | --                                | -- |
| oerstedii                     | 0                              | 0  | 3                             | -- | --                     | -- | 0                    | 0  | 0                   | 0  | 0                                 | -- |
| menispermifolia               |                                |    |                               |    |                        |    |                      |    |                     |    |                                   |    |

Figure 3.5 Multiple plant oviposition choice tests (June-July 1977). Numbers in parentheses indicate number of females participating in test; the other numbers indicate the number of eggs collected from each plant. Heliconius species are underlined at top. The same individual plants were used throughout.