CHAPTER 4. LARVAL GROWTH IN <u>HELICONIUS</u>

In Chapters 2 and 3, it was shown that host plant selection in <u>Heliconius</u> correlates with certain characteristics of the host plants. These characteristics--abundance and leaf toughness, are not related to the secondary products chemistry of the plants in any obvious way. This provides evidence that host selection in butterflies is not just a function of leaf chemistry, but varies according to other aspects of host plant ecology. However, the possibility that host plant chemistry is influencing host selection in these butterflies must be investigated. In this chapter, <u>Heliconius</u> larval growth ability is used to assay host plant chemistry.

Benson, et al. (1976) examine broad taxonomic patterns of host plant use in Heliconiines and conclude that these patterns result at least in part from coevolution between Heliconiines and Passifloraceous host plants. Their data are not inconsistent with the results in Chapter 3, but are taken on a much broader taxonomic level. However, the authors cannot specify whether or not the coevolution is biochemical in nature since their data is based on host plant selection by adult females rather than larval growth ability. The data presented in this chapter may be useful in interpreting some of their results and conclusions.

A second reason for studying larval growth ability is to determine the options available to a <u>Heliconius</u> butterfly in terms of host plant selection. It is more feasible for an insect to include

an additional host plant in its diet if that plant is edible. All
that is necessary is a behavioral change in the ovipositing female
such that the plant becomes acceptable. If a plant is not edible to
the larvae despite behavioral changes, alterations in larval feeding
ability are required. Since both types of changes must be carried in
the same individual butterfly for selection to favor using the new
host plant, such an event must be very rare. This will in part depend
on the nature of the "chemical barriers" restricting larval feeding;
are they behavioral or physiological in nature ? (see Chapter 1.3).
A purely behavioral change is much more likely to occur than selection
to overcome the physiological effects of plant toxicity. In addition,
it should be possible to test the hypothesis that species which are
host-specific have more rapid development than the oligophagous
species (see Chapter 1.6).

A third reason for studying Heliconius larval growth is to
discover if host plant acceptability is correlated to larval growth
rates. An exact correlation would indicate that (1) adult females
can accurately assess host plant quality in terms of larval growth
ability; (2) larval growth ability may be the principal criterion used
by the female in host plant selection; i.e. "cryptic" components of
host suitability (Gilbert and Singer 1973) are not recognized; or,
alternatively, (3) larval growth rates may have quickly evolved to
match closely the observed patterns of host plant selection. This
last possibility is unlikely, as will be discussed below.

This chapter describes the results of an investigation of larval

growth in several of the <u>Heliconius</u> species. The following section is a general outline of relevant facts on <u>Heliconius</u> larvae. Next the experimental methods are described and compared to field data. The results are summarized and discussed in the final section of this chapter. The data are given in complete form in Appendix 5.1.

4.2 The Larvae of Heliconius

<u>Heliconius</u> larvae are described in Beebe et al. (1960) and in Alexander (1961). A newly hatched first instar larva usually but not always eats the egg shell as its first meal. After a resting period, the larva seeks out an appropriate site to begin feeding on the host plant, which may or may not be adjacent to the egg, depending on the species. In most of the La Selva <u>Heliconius</u>, the larvae begin feeding on a green tendril or a leaf tip of the host plant, but in <u>H</u>. <u>doris</u>, <u>H</u>. <u>sara</u>, and probably <u>H</u>. <u>sappho</u>, feeding begins on a variety of plant parts. Feeding is not continuous, but occurs in discrete time periods interspersed with periods of inactivity. Inactivity greatly increases before and after the moults and growth is therefore most rapid during the middle of the instars. The larvae of most species will not voluntarily leave the host plant even if it is of poor quality, though they may wander over the plant considerably. The only exception to this is when two <u>Passiflora</u> plants are in contact, in which case the larva may abandon one in favor of the other.

<u>Heliconius</u> have five larval instars, although a sixth instar has been occasionally observed in <u>H</u>. <u>hecale</u> when grown on a poor host

plant. The later instars last longer than the earlier ones, and this is at least partially due to longer moulting times in the later stages (see Figure 4.2). The growth during each instar is roughly a constant multiple of growth in the preceeding instar, the sizes thus following a geometric progression. Moulting tends to take place during the morning hours, but this is not strictly adhered to, for moults have been observed during all hours of the day or night. The most time-consuming part of the moult is forcing off the old head capsule; once this is accomplished the larva walks out of its old skin and consumes it. Moulting larvae cannot be safely manipulated without injuring them because the old skin is firmly attached to a pad of silk laid down prior to the moult. Larvae are delicate at this stage and are highly vulnerable to predation.

Heliconius larvae are occasionally cannibalistic when given the opportunity. Cannibalism usually consists of a large caterpillar consuming a smaller caterpillar or an egg, but even large caterpillars may be eaten during a moult. It is possible to raise H. cydno from the egg to the third instar by feeding it nothing but Heliconius eggs, although growth in the second instar is retarded. Thus, other Heliconius are the only non-passifloraceous food known to be acceptable to the larvae of these butterflies.

At the end of the fifth instar the larvae change color somewhat and wander off the host plant in search of a pupation site. When a site is found by the larva it makes a pad of silk on a stem or under a leaf, and it then hangs from this by its hind pair of prolegs. The

next day pupation occurs. Thus, the last two days of the fifth instar
is a non-feeding period.

Like oviposition behavior, larval feeding behavior can be
classified according to the number of individuals found together. With
H. doris, H. sara, and probably H. sappho, groups of larvae feed,
rest, and moult synchronously. It is interesting to note that the
larvae of these species are black and yellow, and are difficult to
distinguish. The larvae of H. hecalesia and H. charitonia also feed
gregariously but are not as coordinated in their activities. H. hecal-
esia larvae are dark brown and black and somewhat resemble the above
species. H. charitonia larvae are white with black spots, and thus
resemble the larvae of the single egg-laying species. These species
feed solitarily, and are all white or cream-colored with black spots.
Since larval coloration does not follow taxonomic lines but is
correlated to degree of gregariousness, it must be concluded that some
unknown form of mimicry or protective coloration is operating. Figure
4.1 summarizes the above data for each species.

4.3 Experimental Methods

4.3a Facilities and Experimental Stocks

Larval growth rates in Heliconius were measured using insectary
populations of butterflies and host plants. The experimental technique
developed from the standard laboratory procedure of raising larvae on
cut leaves in containers (Waldbauer 1968). However, the standard
technique was found to yield growth rates which were slow compared to

growth under more natural conditions, and it became clear that it was necessary to (1) raise the larvae on live plants for normal growth rates to be obtained, and (2) that temperature had to be controlled so that growth rates could be compared between different rearings. This was accomplished by placing the larvae on potted _Passiflora_ plants which were put in a controlled-environment chamber for the duration of the measurements.

The _Heliconius_ and _Passiflora_ were propagated under natural light in seven 4 by 7 meter temperature-controlled greenhouses, located on the roof of Patterson Laboratories at the University of Texas, Austin. About 80 species of _Passiflora_ and 10 species of _Heliconius_ are maintained in these facilities on a permanent basis. The larvae were grown in a "Hotpack" controlled-environment chamber, with controlled temperature and humidity. Lighting in the chamber consisted of alternate bulbs of "soft-white" and "gro-lux" flourescent lights.

Thirty-two species of passifloraceous host plant were used in these measurements, including most of the La Selva species. As with the plants used for oviposition tests these plants are either cuttings or seeds of wild-type plants and thus are at most one generation removed from the natural population gene pool. The plants are propagated in 15 to 30 centimeter diameter pots in commercial potting soil, and are kept to a relatively small size by either pruning or _Heliconius_ herbivory. A typical vine used for testing has about five branches with new growth points and is 1 to 2 meters long. The branches are trained around sticks for convenience in handling. Every two weeks the

plants are fed a solution of minerals (Peters 20-20-20 plant food) and are watered daily with distilled water. All the La Selva *Passiflora* species are derived from La Selva populations except *P. quadrangularis*, *P. menispermifolia*, *P. lancearia*, and *P. laurifolia*. *P. pittieri* was not available for testing.

Nine of the La Selva *Heliconius* were tested, along with three other Heliconiines. Only *H. sappho* was unavailable. Of these, three species were not derived from La Selva stock: *H. hecalesia*, *H. ismenius*, and *H. doris*, taken from another part of Costa Rica, Northern Mexico, and Costa Rica, respectively. *H. erato* is represented by two stocks, one from Northern Mexico and one from San Jose, Costa Rica. The remaining four species, *H. hecale*, *H. cydno*, *H. sara*, and *H. melpomene*, are from La Selva. The oldest stock used was two years or approximately twelve generations removed from the wild populations. At the time there was no indication of changes in the characteristics of the stocks; however, after 2.5 years the *H. melpomene* population began to die out and it appeared that this was correlated to a loss of larval vigor, as evidenced by slow growth and eventual death on normally palatable host plants. This also happened one year later to the *H. cydno* population (aged 3.5 years). The causes of the decline of these populations are not known.

4.3b Procedure for Measuring Growth Rate

Larval growth rate was measured in the following way. Eggs were collected, weighed, and stored in small plastic cups in a controlled

environment chamber at 85% relative humidity, a temperature of 24.5 degrees C., and a 14-10 hour light-dark cycle. When eggs of most species were stored together the first one to hatch would often eat the other eggs, therefore the eggs were stored one to a cup. The egg weights were used to calculate a species mean, which could then be used in place of individual weighings when necessary. There is a considerable amount of variation in egg weight due to drying out during egg maturation as well as to variation in the condition of the mother at the time of oviposition; the overall within-species coefficient of variation is about 10%.

The eggs usually hatched during the morning hours, therefore at about mid-day all the newly hatched larvae were put on Passiflora plants in the same controlled environment chamber described above. The young larvae are very delicate and must be handled with a soft brush or coaxed into walking onto the host plant of their own accord. The species of larva, its weight, and the species and identification number of host plant were then recorded. The larvae are then allowed to feed undisturbed on the host plant until after pupation. They are checked daily and their instar number recorded, along with notes on the part of the plant being consumed. When a larva reaches the fifth instar the plant is placed on a stand surrounded by water so that the wandering caterpillar will not leave the plant. After pupation, the pupa is pried off the plant still attached to its pad of silk, weighed, measured, and hung in a cup. The pupal length is measured in milli-meters, from the tip of the cremaster to the "forehead," i.e. the

anterior tip of the pupa excluding the two irregular lateral pro-
tuberances or "horns." The cup is placed in the constant-environment
chember while the pupa develops, and is checked daily. When the adult
ecloses and after its wings have hardened, it is measured using the
same technique as for field-caught adults, described in Appendix 2.1.
The adults were then used for various purposes. The resulting data is
summarized in Appendix 5.

The growth rate of each larva was calculated using the formula:

$$R = \frac{\left(\dfrac{\text{Pupal weight}}{\text{Egg weight}}\right)^{1/5} - 1}{\text{Days}/5} \qquad (\text{Days} = \text{days from hatching to pupa})$$

This measure gives the rate of relative size increase during an aver-
age instar, and thus is approximately an instantaneous or "physiolog-
ical" measure of growth. This has the advantage of taking into account
the differences in mean egg and pupal size in the different species,
which would otherwise strongly bias interspecific comparisons. A
discussion of this and other growth rate measures is given in Appendix
5.2. The growth rate data is summarized in Figure 4.4. Here only
those growth rate values were used that were obtained from healthy
larvae, as determined by successful eclosion of the adult. By excluding
larvae which were unhealthy, the sample size of some species rearings
was reduced. However, this was more than compensated for by decreasing
the experimental variation due to disease, outbreaks of which occurred
on several occasions.

4.3c Comparison With Field Conditions

The above rearing technique was compared to growth under natural conditions. Since the instar number and moults were recorded for each larva, it is possible to reconstruct the life-history of an "average" larva grown in the constant-environment chamber. This can then be compared to field notes on the time required for a larva in nature to develop from instar 'A' to instar 'B'. This was done for two species, H. cydno and H. hecale, as shown in Figure 4.2. The results are remarkably consistent, indicating that a steady temperature of 24.5 degrees is physiologically equivalent to the natural temperature regime with regard to development rates. This temperature is the mean annual temperature at La Selva, which indicates that the diurnal temperature fluctuations are not so severe that the larvae cannot buffer the effects on growth rate (for general discussion see Eubank et al. 1973).

One further check on the experimental technique is to compare the body size measurements of laboratory-reared individuals and wild-caught individuals. The data in Figure 4.3, taken from Appendices 2.4 and 5.3, indicate that the body sizes are comparable for several different species. Apparently the experimental rearing conditions used in this investigation mimic natural conditions very closely from the standpoint of growth and development.

4.4 Larval growth rates in La Selva Heliconius

4.4a Results

Growth rate results are summarized in Figure 4.4. The numbers in the figure are R-values (Chapter 4.3b) multiplied by 100 for clarity. When more than one measurement was taken the mean was calculated, as represented in the figure by underlined numbers. These results will first be discussed species by species.

1. H. melpomene: This species oviposits only on P. oerstedii and P. menispermifolia (and occasionally P. ambigua) of the 14 Passiflora species tested. Surprisingly, growth is rapid on several kinds of non-acceptable Passiflora, including the most common species available to it at La Selva, P. biflora, P. auriculata, and P. vitifolia. However, the results on P. vitifolia are from one successful rearing and many other attempts failed to produce viable adults. Thus, there may be a mortality component not reflected in the growth rates obtained in this species. Alternatively, this result may be attributable to disease.

2. H. cydno: This "generalist" (oligophagous) species was the most extensively tested Heliconius. Not surprisingly, growth was rapid on most species of Passiflora tested and only 6 out of 28 species were unsuitable for complete larval development. In those cases death occured after feeding for some time on the plant, which means that the response is probably a result of toxicity and is not a purely behavioral response.

3. H. hecale: This generalist species appears to be poten-
tially even more oligophagous than H. cydno. Two plants, P. foetida
and P. pedata, are palatable to H. hecale but lethal to H. cydno, and
no species were found to be unsuitable to H. hecale except P. serra-
tifolia, which kills every Heliconiine tested except H. ismenius and
Mexican Euides isabella (see also Benson et al. 1976).

4. H. ismenius: This species has growth rates similar to
H. hecale, to which it is very closely related. The only difference
seen is that H. ismenius is able to feed on P. serratifolia, and is
thus likely to be the most generalist species of all. However,
further experimentation may reveal that H. hecale and H. ismenius
are unable to feed on as yet untested species. (host: P. "

5. H. charitonia: This host-specific species (host: P.
"Tetrastylis" lobata, P. adenopoda; see Gilbert 1971) is very general-
ist in its ovipositon behavior in the absence of its preferred hosts.
Observations in the insectary indicate that larvae of this species
can grow and develop on a wide variety of host plants, even though
such growth may be very slow. What little data there is in Figure 4.4
indicates that H. charitonia is similar in response to H. erato, with
rapid growth on Plectostemma and slow growth on Granadilla.

6. H. erato: This host-specific species (host: P. biflora)
may also oviposit on P. auriculata occasionally, but never on most
other Passiflora. The growth rates are consistent with this behavior in

that the above two species support rapid growth while the majority

of Passiflora do not.

7. H. hecalesia: This host-specific species (host: P. biflora,

probably also P. lancearia) has not yet been tested except on P.

biflora. However, observations in the insectaries indicate that this

species can feed on P. auriculata successfully, but not on most other

Passiflora. Thus, its response is similar to that of H. erato.

8. H. sara: The results in Figure 4.5 show that this host-

specific species (host: P. auriculata) can grow successfully on the

host plant only, feeding on young and fully mature leaves. The larvae

seem to be more tolerant in the later instars, however.

9. H. doris: As seen in Figure 4.5 this species is similar

to H. sara in that growth is only possible on the host plant (host:

P. ambigua), but that the later instars are less restricted. Mature

leaves are fed upon by this species.

The above results fall into three categories. Four species

have oligophagous larvae that can feed on a wide variety of Passiflora

species with equal growth rates; these are the "Granadilla feeders."

Three species grow rapidly only on the Plectostemma subgenus and a few

other species of Passiflora, and grow slowly or not at all on the

Granadilla; these are the "Plectostemma feeding" group of Heliconius.

Two species have larvae which in the younger stages can only feed on

the host plant and all other Passiflora are lethal; these are the species with yellow and black, highly gregarious larvae. H. sappho, the species not tested, probably falls into this category as well. Except for these latter species, which have clearly converged in terms of their larval biology, the patterns of larval growth rate correlate very well to the taxonomy of Heliconius.

4.4b Heliconius-Passiflora Biochemical Evolution

What bearing do these results have on the conclusions of Benson, et al. (1976), regarding Heliconiine-Passifloraceae coevolution? They conclude that the "Granadilla feeders" are principally coevolved with the Granadilla species of Passiflora. The data given in Figure 4.4 suggest that the tendency for "Granadilla feeders" to use Granadilla is not due to any "chemical barriers" that might result from biochemical coevolution between herbivore and host plant (Erickson and Feeny 1971). The fact that nearly all Passiflora are highly edible to the larvae implies that, with respect to these butterflies, there is little chemical diversity among host plants and that biochemical coevolution is not occurring at the present time. Thus, any wide-scale coevolution of "Granadilla feeders" and the subgenus Granadilla must be on other types of traits than host chemistry.

In contrast, the data for the "Plectostemma feeders" (Figure 4.4) is not inconsistent with the hypothesis that these species are bio-chemically specialized on the subgenus Plectostemma. Why should the two groups of Heliconius differ in this respect? One possible hypothe-

sis is that, for some as yet unknown reason, feedin on the <u>Granadilla</u>
subgenus preadapts the butterflies to feed on other <u>Passiflora</u>, as
might occur if the chemicals in the leaves of <u>Granadilla</u> included the
chemicals in the leaves of all other <u>Passiflora</u> species. A second
hypothesis is that the "<u>Granadilla</u> feeders" have on the average
evolved in habitats with low host plant abundance, which has selected
for the ability to be "generalist." Indeed, three of the four species
tend to be forest-inhabiting, and even <u>H</u>. <u>melpomene</u> is not found far
from forest in Costa Rica. Thus, the "<u>Granadilla</u> feeders" seem to
occupy a low-host-plant-abundance habitat on the average. In contrast,
the "<u>Plectostemma</u> feeders," <u>H</u>. <u>erato</u> and <u>H</u>. <u>charitonia</u>, are second
growth-inhabiting species to a much greater degree, inhabiting fence-
rows and plantations all over Central America. The more forest-
inhabiting species in the "<u>Plectostemma</u> feeders" are multiple-
ovipositors. Therefore, this group of <u>Heliconius</u> probably experiences
a much higher "effective host plant abundance" (see Chapter 6.4a) than
the "<u>Granadilla</u> feeders." This makes the second hypothesis quite
plausible. However, neither hypothesis can be rejected at present.

4.4c The "Digestive Efficiency" Hypothesis

The growth rates in Figure 4.4 generally support the hypothesis
that host-specific species have an advantage in growth rate as compared
to less specialized feeders. The fastest growth rates observed in
<u>Heliconius</u> are in <u>H</u>. <u>hecalesia</u> and <u>H</u>. <u>charitonia</u>, two "<u>Plectostemma</u>

feeders" which are relatively specialized digestively. Also, the mean growth rate value of "Plectostemma feeders" on Plectostemma, as shown in the box in Figure 4.4, is much higher than the means in any of the other boxes, indicating that this digestively specialized group of Heliconius does indeed have an advantage in growth rate as compared to the less specialized "Granadilla feeders." When the growth rates are compared from just three species, H. cydno, H. melpomene, and H. erato (Figure 4.6) the specialized species (H. erato) has a significantly faster growth rate than the two unspecialized species when raised on P. biflora, the host of H. erato. However, this value is roughly equal to the growth rates of the unspecialized species when raised on some of the other Passiflora. This points out a problem with this method of testing the hypothesis. If the "unspecialized species" are in fact slightly specialized, as the data in Figure 4.4 indicate, then the difference in growth ability on P. biflora may be due to a loss of feeding ability in H. cydno and H. melpomene rather than to an increase in the growth rate of H. erato. The problem originates from the fact that there is no objective way of determining the "baseline" or "unspecialized" growth rate for each plant species, and there is no reason to expect the different plant species to be equal in this respect. Nevertheless, the balance of the data support the hypothesis that there is a positive growth rate advantage accruing from becoming digestively specialized. The advantage appears to be slight, however, which may explain why the hypothesis has received such mixed experimental support (see Chapter 1.6).

The data in Figure 4.6 point out another difficulty in testing the digestive efficiency hypothesis. Oviposition data indicate that H. melpomene is host-specific. If, on this basis, it was considered to be digestively specialized, the prediction of the hypothesis would be that H. melpomene should have an increased growth rate on its host plant. In this case the hypothesis would have been refuted since H. cydno has an equal growth rate to H. melpomene when raised on P. oerstedii, the host of H. melpomene. Of course, H. melpomene is actually unspecialized digestively even though it is host-specific in nature, and hence the hypothesis is not actually refuted. Thus, it is insufficient to rely on host plant choice as an indicator of digestive specialization.

4.4d Correlation of Oviposition Preference to Larval Growth Ability

If the growth rates obtained for H. cydno when raised on various Passiflora species are compared to the results of oviposition testing, a consistent relationship is seen. In Figure 4.7 it is shown that H. cydno always reject a lethal Passiflora but usually accept a Passiflora yielding a growth rate of 1.0 or over. This indicates that this species can correctly assess the palatability of at least 18 species of Passiflora. What is more, the relative palatabilities (growth rate values) are significantly positively correlated to the relative acceptabilities to the ovipositing female (Figure 4.8), even when the lethal Passiflora are not considered. Clearly, oviposition preference is strongly correlated to the larval growth ability on the

host plant in this species.

In H. erato the correlation between oviposition preference and larval growth ability also appears to hold. The acceptable but unpreferred P. auriculata supports growth at a slower rate than P. biflora, the preferred host, while the unacceptable species support very slow growth or none at all. Curiously, one striking exception to this is the tendency for H. erato to oviposit on P. quadrangularis, an invariably lethal host plant.

4.4e Evolution of Larval Growth Ability

In H. melpomene there is a great discrepancy between larval growth ability and host plant choice by the ovipositing female. In view of this species' close relationship to the "generalist" H. cydno it is likely that (1) H. melpomene has only recently evolved host specificity, and that (2) there is little selective pressure to evolve digestive specificity. Turner (1976) has suggested that H. melpomene and H. cydno evolved from common stock in the recent geologic past based on geographic patterns of race-formation. In contrast, the "Granadilla feeders" and "Plectostemma feeders" probably diverged in the very distant past (Emsley 1965), and consequently the differences in larval growth ability are not surprising. The overall pattern suggests that in the new-growth-feeding Heliconius, larval growth rates are slow to evolve changes.

In contrast to the above conclusion, the gregarious-feeding species which feed on tough-leaved host plants have converged on a

high degree of digestive specialization. In the case of H. sara (and probably H. sappho), this specialization is probably secondarily derived from the general "Plectostemma feeding" pattern. The reason for this difference is not known, but there may be something about feeding on mature as opposed to young leaves that selects for increased specialization. Perhaps the nutrient/toxin ratio is much lower, favoring specialized detoxification mechanisms. Alternatively, it may be that these species are so host-specific that their populations have never been forced to rely on a secondary host plant, and thus have never been through an evolutionary "bottleneck" selecting for "generalist" feeding ability.

Heliconius species	Number of larvae feeding together:	Appearance:
doris	many	Black head capsule, yellow body in earlier stages, black body later.
hecale	one	Yellow head capsule, white body with black spines and small row of spots along side. Spots may be absent.
ismenius	one?	Identical to H.hecale, spots larger.
cydno	one	Yellow head capsule, white body with black spines and spots on back and sides.
melpomene	one	Like H.cydno but spots fainter.
erato	one	Yellowish head capsule with black facial markings, cream-colored body with faint yellowish stripe along side, black spots on back and sides.
hecalesia	5-10	Black head capsule, dark reddish-brown body with black spines.
charitonia	5-10	White head capsule with black facial markings, white body with black spots on back and sides.
sara	many	Black head capsule except in first two instars, yellow body in younger instars, black body later.
sappho	many?	Like H.sara?

Figure 4.1   Coloration and degree of gregariousness in Heliconius larvae. Note that the gregarious species are dark while the solitary species are whitish with black spots and spines.
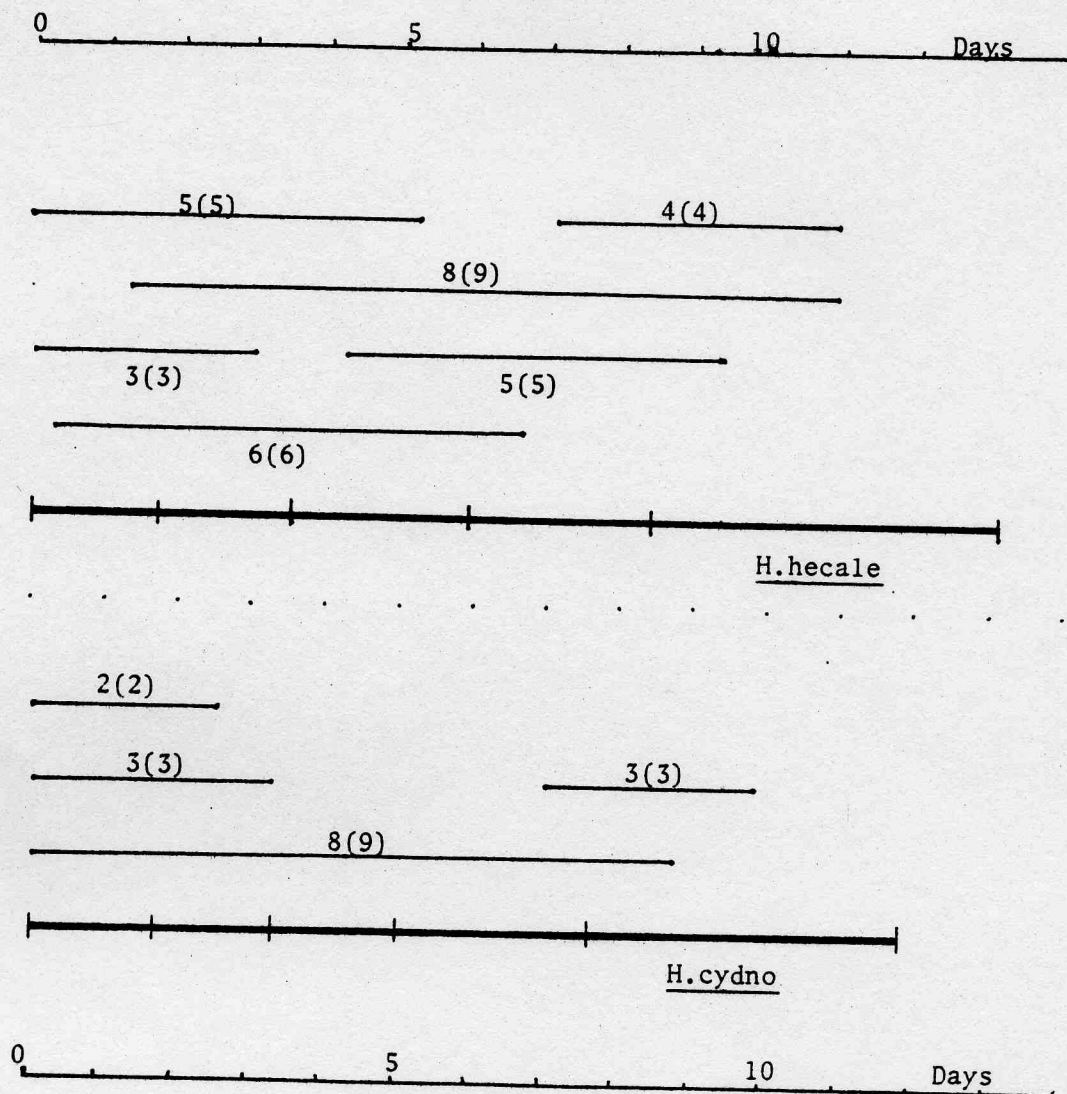
Figure 4.2   Comparison of development times in field and laboratory *Heliconius* larvae. Heavy line is average development time in laboratory larvae; vertical bars represent moults. Light line is corresponding development observed in naturally occurring larvae; number is observed developmental time. The number in parentheses is the expected developmental time based on laboratory growth rates.

Heliconius species:	Rearing Conditions	
	Field	Laboratory
cydno female	41.2±1.5 (20)	40.0±3.1 (12)
cydno male	41.5±1.8 (38)	40.7±1.8 (31)
hecale female	43.0±1.9 (6)	44.9±1.6 (8)
hecale male	42.7±1.8 (6)	45.0±2.0 (20)
melpomene female	36.3±3.2 (11)	38.9±1.5 (9)
melpomene male	37.1±2.8 (18)	38.9±1.3 (14)
erato female	36.8±1.7 (4)	34.2±1.5 (9)
erato male	39.3±3.8 (4)	34.2±2.0 (14)
charitonia	44.4±2.3 (9)	42.0±3.0 (3)

Figure 4.3   Comparison of body size (length of forewing in millimeters) in laboratory-reared and wild-caught Heliconius. Numbers are mean ± standard deviation. Sample size is in parentheses.

	melpomene	cydno	hecale	ismenius	ethilla	charitonia	erato	clysonimus	hecalesia	Dryas
pittieri										
foetida 18,19*		0	86			0	0			
vitifolia 3	134	109	116	133	106	125	86			0
near subulata (Gran.) 32	0	93	98							
jamesoni 23		98			118					
mollissima 25	96	114				98				
Granadilla										
quadrangularis	0	114					0			
alata 9				120			0			
triloba 36		89								
laurifolia 38		127					75			
ambigua 5	90	111	101	96			0			0
serratifolia 28,29	0	0	0	85						
pedata 27		0	104							
edulis 16,17		122				0				
oerstedii 4	118	126	111			0	59			0
cyanea 15		98								
caerulea 12,13	111	137		122	116		87			
menispermifolia 24	106									
					110.2				73.7	
Plectostemma										
coriacea 6	0	102	109		48	0				81
suberosa 30			75		61					
tuberosa 33		121						126		
biflora 1	106	111	113	116	98		122		147	126
talamancensis 31		133						128		
helleri 22		124					114	124		
lancearia 40		113					87			0
auriculata 2	105	115	107				102			113
costaricensis 7	80	113	89		95	0	81			106
capsularis 34		114			114	140				
brevifolia 26	0	96								
membranacea 39		0								
					102.4				117.6	
T. lobata 8		0				135				0
T. dioscoreifolia 41						105				
Adenia manii 11	0	0								

Figure 4.4 Heliconius larval growth rates (x100). Underline indicates average value when N 1. (*See Appendix 5.1 for localities.)

Heliconius species:	Passiflora species:	Early instars:	Later instars:
sara	auriculata	+	+
	ambigua	−	
	quadrangularis	−	
	oerstedi	−	
	(coccinea)	−	
	(allardi)	−	
	caerulea		+
doris (green morph)	quadrangularis		−
	vitifolia		+
	oerstedi		+
	serrato-digitata		+
	laurifolia		+
	ambigua		+
	biflora		?
	auriculata		−
	coriacea		−
doris (red morph)	laurifolia		+
	ambigua		+
	serrato-digitata		−

Figure 4.5   Experiments on larval growth in H.sara and H.doris. A '+' indicates feeding and growth occurred, a '−' indicates 100% mortality.
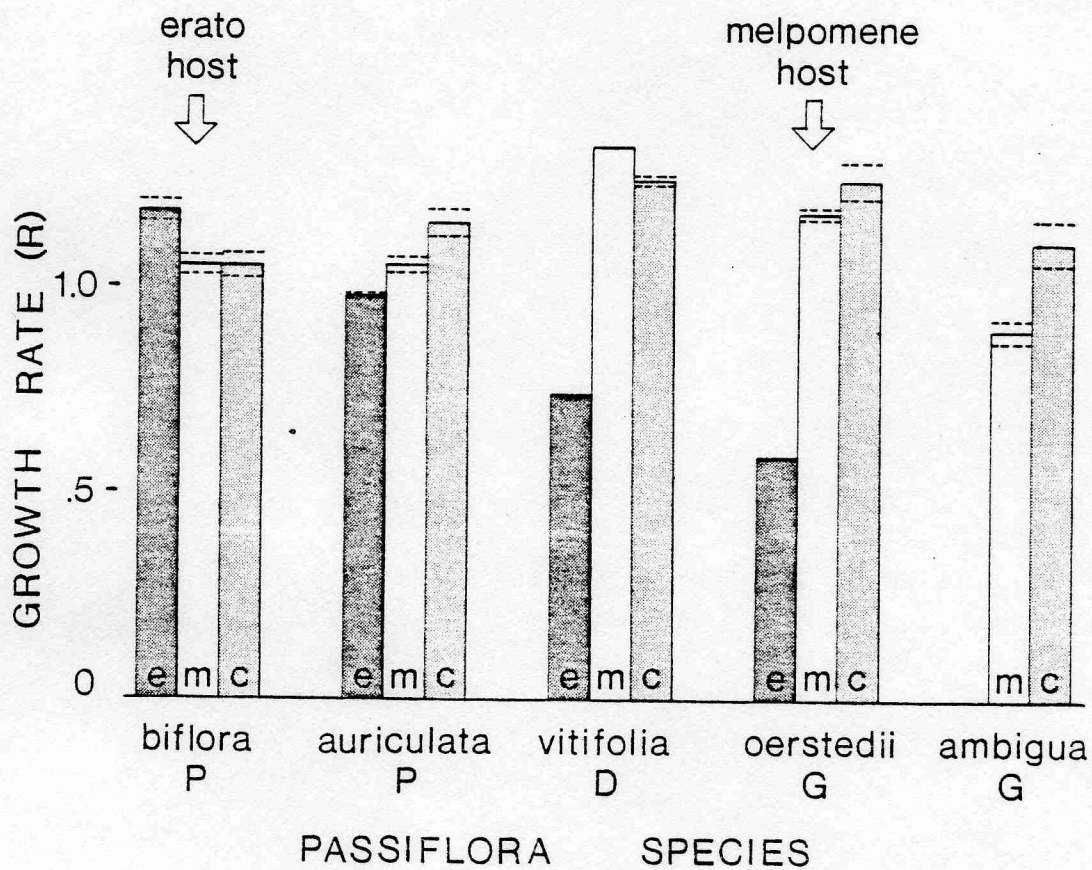
Figure 4.6 Larval growth rates of three Heliconius species when raised on five Passiflora species. P=Passiflora subgenus Plectostemma, D=Distephana, and G=Granadilla. See text for definition of R. Heliconius species: c=cydno, m=melpomene, e=erato.

	Host Acceptability	Growth Rate (R)
coriacea	+ (3/6)	1.02
auriculata	+ (16/17)	1.15
biflora	+ (3/10)	1.11
tuberosa	+ (2/2)	1.21
costaricensis	+ (2/2)	1.13
adenopoda	–	0
foetida	– (0/8)	0
vitifolia	+ (10/10)	1.09
quadrangularis	+ (3/3)	1.14
ambigua	+ (15/15)	1.11
laurifolia	+ (1/2)	1.27
serratifolia	– (0/3)	0
pedata	– (0/2)	0
edulis	+ (1/2)	1.22
oerstedii	+ (37/38)	1.26
caerulea	+ (2/2)	1.37
cyanea	+ (1/1)	.98
"T." lobata	– (0/2)	0

Host Plant Acceptability V/S Palatability to Larvae:
Heliconius cydno

Figure 4.7   Host plant acceptability virsus host plant palatability in H. cydno. A '+' indicates that a host plant is acceptable. The number in parentheses is the ratio of ovipositions to number of times plant was tested (see Chapter 3). The growth rate 'R' is approximately the relative size increase on any given day (see Appendix 5.2).

PASSIFLORA SPECIES

Desirability of Host Plant		Growth Rate on Host Plant	
18	auriculata	laurifolia	1.27
14	laurifolia	oerstedi	1.26
(12)	quadrangularis	auriculata	1.15
10	oerstedi	quadrangularis	1.14
9	vitifolia	costaricensis	1.13
7	ambigua	ambigua	1.11
6	costaricensis	biflora	1.11
3	biflora	vitifolia	1.09
2	coriacea	coriacea	1.02
0	menispermifolia	menispermifolia	(slow)

Kendall's tau = 2.62, p<.005

Figure 4.8   Correlation of host plant acceptability and larval growth rate in H.cydno. Passiflora acceptability is determined by multiple-plant choice test (see Chapter 3). The growth rate 'R' is approximately the relative size increase on any given day (see Appendix 5.2).