CHAPTER 6. SUMMARY AND THEORETICAL IMPLICATIONS

In Chapters 2-5 it has been possible to examine many different aspects of the host plant ecology of a <u>Heliconius</u> butterfly community, including the distribution and abundances of butterflies and host plants, host plant palatability, host-plant-related predation, and butterfly oviposition behavior. The results form a coherent pattern which supports some of the hypotheses discussed in Chapter 1, in addition to suggesting several new hypotheses that have not been considered in the recent literature on butterfly-host plant interactions. This chapter consists of a summary of these results, accompanied by a discussion of theoretical implications. Community composition will be discussed first, followed by butterfly-host plant population regulation, strategies (adaptations) of host plant consumption by butterflies, coevolutionary processes, and finally a brief discussion of host plant adaptations.

6.2 Heliconius-Passiflora Community Composition at the Field Site

The <u>Heliconius-Passiflora</u> community at the La Selva Field Station consists of 10 species of <u>Heliconius</u> and 13 species of <u>Passiflora</u>. As shown in Chapter 2, the community is distrubuted across several habitats ranging from early second growth to mature forest. Six species of <u>Passiflora</u> are abundant in the early second growth study plots, where they are fed upon by three common species

of _Heliconius_, two uncommon species, and a species which varies
erratically in abundance. Six species of _Passiflora_ were also found
in the mature forest study area, all of which were uncommon to rare
as compared to the abundances of the second growth species. Only
one common and one uncommon species of _Heliconius_ feed upon this
forest community of _Passiflora_. In this case it is clear that a low
herbivore diversity is associated with low host plant productivity
(i.e. abundance) rather than low host plant diversity.

Both the early second growth and the mature forest habitats
show an even representation of the two principal taxonomic groupings
of both herbivores and host plants (Figure 2.3 and 2.10). In second
growth there are three _P_. (_Plectostemma_) species and two _P_.
(_Granadilla_) species, fed upon by four "_Plectostemma_ feeding"
Heliconius and two "_Granadilla_-feeding" _Heliconius_. In mature forest
there are two _P_. (_Plectostemma_) species and two _P_. (_Granadilla_) species,
fed upon by one species of "_Plectostemma_ feeder" and one species of
"_Granadilla_ feeder." The results are generally consistent with
Elton's hypothesis that competitive interactions prevent closely
related sympatric species from sharing identical habitats (see
Chapter 2.1, 2.3c, 2.4c). The "_Granadilla_ feeders" generally differ
from the "_Plectostemma_ feeders" by being single-egg layers as opposed
to multiple-egg layers (except for _H_. _erato_; Figure 3.1), which may
provide enough niche-separation for two species to coexist in the
same habitat. Niche-components separating _P_. (_Plectostemma_) from

P. (Granadilla) are less clear in the La Selva data. However, some differences were observed in the type of Heliconius herbivory affecting the two subgenera (see Figures 3.1 and 4.4; see also Benson et al. 1976) and it may be that this along with other unknown niche components can account for the Passiflora composition. Clearly, "historical" or taxonomic diversity is important in determining community composition by providing enough niche-separation for more than one species to coexist in the same habitat.

6.3 Regulation of Heliconius Population Density: Competition and Predation

The numbers of Heliconius in an area are regulated by competition from other Heliconius and by predation from vertebrate and invertebrate predators. At least 95% of Heliconius mortality occurs in the egg and larval stages (Chapter 5.2), and competition for pollen resources may limit egg production in adult female Heliconius (Gilbert 1973, 1975). Other sources of population regulation are probably less important in the relatively benign environment at the field site.

The patterns of host plant partitioning discussed above (Chapter 6.2) indicate that competition for host plant is an important component of community composition. Benson, et al. (1976) and Benson (1978) also have evidence that competitive interactions are important in structuring the Heliconius community. In addition, the

fact that <u>Heliconius</u> diversity and abundance vary with host plant abundance indicates that to some degree, the amount of host plant is a limiting factor to <u>Heliconius</u> abundance. Nevertheless, there does not appear to be any shortage of host plant tissue capable of sustaining larval growth in any of the habitats at the field site. Even in the forest, where host plants are most intensively used, only one <u>Passiflora</u> vine in 12 has a <u>Heliconius</u> egg at any given time (see Chapter 3.4b). Thus, it is very likely that predation on eggs and larvae keeps the butterfly/host plant ratio so low that direct competition for edible host plants does not occur. However, <u>Heliconius</u> abundance and community organization indicate that competition for host plant is prevalent. How can this dilemma be resolved?

The data in Chapter 5 on host-plant-related predation indicate that the various <u>Passiflora</u> species attract different types of insects which prey on <u>Heliconius</u>. If the different types of predation are density-dependent with respect to the number of <u>Heliconius</u> eggs and larvae found on the host plants, then <u>Heliconius</u> species A could have a negative effect on the population of <u>Heliconius</u> species B which is minimized when the two species use different host plants and maximized when they share the same host. This negative effect is caused through the buildup of density-dependent predators, fewer of which will be common to two host plants of different species as opposed to two hosts of the same species.

B will also have a negative effect on A. The two Heliconius will thus "compete" (competition being generally defined as two populations having mutually negative effects on each other (MacArthur 1972: 21), and the "competition" will be greater when host plants are shared than if they are partitioned. This type of "predator-mediated competition" could well produce the observed patterns of host plant partitioning discussed above. It could also account for the maintenance of a low butterfly/host plant ratio. For further discussion of this topic, see Brower 1958.

Another, perhaps simpler way of looking at this "predator-mediated competition" hypothesis is to reason that (1) predators keep the butterfly/host plant ratio low, so that the butterflies have enough host plant that they can be relatively "choosy" in selecting the best host, and (2) density-dependent predation prevents two species of butterfly from using the same host and encourages them to select different host plants. One way to test this hypothesis would be to search for density-dependent predation by minipulating the number of eggs and larvae.

The overall butterfly/host plant ratio is about equal in both second growth and forest habitats (Chapter 2.5). However, 90% of the increase in Heliconius in the more abundant second growth habitat is due to one species. This species, H. sara, is a cluster egg-layer, which suggests that predation affecting cluster-layers is quite different from that affecting the other Heliconius,

allowing them to build up very high population densities.
Considering only the species which lay one egg at a time, the
butterfly/host plant ratio decreases at high population density by
an order of magnitude (Figure 2.17). The data on eggs collected
(Chapter 3.4b) also supports this conclusion, as does the data on
predators found in the two habitats (Chapter 5.3e). This decrease is
undoubtedly a result of higher-intensity predation when there are
greater population densities. Butterflies in the early second growth
can avoid this higher predation pressure by being much more selective
in their choice of host plant, which leads to the greater host
specificity found in that habitat (see Chapter 3.4a). This is made
possible by the higher abundance of host in early second growth. In
contrast, the predation pressure in the forest habitat is lower as
a result of the low-density populations there, which allows Heliconius
such as H. cydno to successfully feed upon a wide variety of
Passiflora species. It is important to note that at equilibrium the
overall survivorship is expected to be the same in both habitats;
the butterflies have adapted to the difference in predation pressure
by evolving different oviposition behavior.

6.4 Strategies of Host Plant Consumption

As shown in Chapter 3.4b, host plant selection in Heliconius
is correlated to two aspects of host plant quantity, Passiflora
abundance and size of the plant. As shown in Chapter 4.4d for

H. cydno, host plant selection also depends on plant nutritional quality as measured by larval growth ability on the host plant. It is also likely that host selection depends on host plant-related predation as discussed in Chapter 5. This is another component of host plant quality as viewed by an ovipositing butterfly. How can these components of host quantity and quality be modelled so as to predict host plant selection in any given butterfly population?

6.4a Host Plant Quantity

From the ovipositing butterfly's point of view, host plant abundance may be expressed as the encounter rate of host plants during the searching period. However, those species which lay many eggs at a time do not require as high a minimum encounter rate to lay all their eggs as the single-egg-laying species (see Chapter 3.4a), and the "effective host plant density" will be higher for those species. "Effective host plant density" may be defined as the number of host plants encountered (per unit time) divided by the number of host plants required for oviposition (per unit time).

As discussed in Chapters 3.4b, 4.2, and 4.4e, multiple-ovipositing species have specialized behavior, morphology, and digestive physiology which enable them to efficiently consume large, tough-leaved Passiflora. Therefore, the tendency for multiple-egg laying is expected to be a relatively fixed property of any given Heliconius. Once this tendency is quantified the "effective host

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plant densities" can be scaled for each species by (1) host plant
abundance, (2) encounter rate of host plant, which depends on
searching ability, and (3) the mean number of eggs layed at a time
(clutch size). Potential as well as actually used host plants can
be each assigned an "effective density." If searching ability is
assumed to be the same for different butterfly populations then it is
not necessary to know the actual encounter rates in comparing
populations; (1) and (3) above are all that is necessary.

6.4b Host Plant Quality

To predict which host plants are actually selected it is also
necessary to know host plant quality for the different plants. In
theory, this may be expressed as the "host-plant-related fitness"
of eggs layed on that plant. This fitness will consist of (1)
survivorship on the host plant of eggs and larvae, and (2) any other
fitness differences caused by host plants, such as adult size and
fecundity. The survivorship component will depend on (1) host-plant-
related predation pressure, and (2) larval development time, with
slower larval development exposing the larva to higher risks of
predation. Adult size is influenced by larval growth ability on
the host plant. In H. hecale, female fecundity may depend on pollen
gathering ability, and in insectary populations does not correlate
to adult size, but in H. charitonia adult size is correlated to
fecundity (H. Dunlap-Pianka, personal communication).

In H. cydno a slow larval growth rate results in both slower development and a smaller adult (see Appendix A5.4). In general, host plant acceptability to ovipositing H. cydno females is correlated to larval growth rate on the host plant. However, because of egg placement strategy H. cydno is expected to especially prefer those host plants which are primarily ant-defended as opposed to parasitoid-defended (see Chapter 5.4). This may explain why P. vitifolia and P. auriculata are slightly more favored by ovipositing females than their larval growth rate values would indicate, since these plants are very attractive to ants (Figures 4.8 and 5.3). Similarly, P. costaricensis may be less preferred for oviposition than the growth rate values would indicate because this species has dense pubescence causing larvae to fall from the plant.

In contrast to H. cydno behavior, H. melpomene has a very strong preference for ovipositing on P. oerstedii, an egg-parasitoid-defended host plant. Since H. melpomene has rapid growth on several other Passiflora, this preference for P. oerstedii is best explained as a response to the type of host-plant-related predation to which the butterfly is adapted (Chapter 5.1 and 5.4). Thus, both larval growth ability and host-plant-related predation combine to determine host plant quality, as "assayed" by acceptability to ovipositing Heliconius females.

6.4c Host Plant Selection

Given that the effective density and the host-related-
fitness are known for each type of host plant, it would be predicted
that the host plant yielding the highest fitness would be used by
the butterfly. If the effective density of this type of host plant
is less than one, then the second-best host plant category (in
terms of host related fitness) should be used as well. If the sum
of the effective densities of these two types does not add to at
least one, the third best plant category should be used. In general,
as many of the better plants will be used as required to make the
total effective density equal to one.

This model qualitatively fits the observed patterns of host
plant selection in Heliconius. Effective densities of host plant are
high for multiple-ovipositing Heliconius in all habitats, leading
to a high degree of host plant specificity. In early second growth
effective host plant density is high for single-ovipositing species,
which again predicts a high degree of host specificity. In mature
forest the effective host plant density for a single-ovipositing
species is low, which predicts that several host plants will be
selected. Every Heliconius (except possibly H. hecale) fits this
patter, as discussed in Chapter 3.4.

6.4d Egg Placement

As shown in Chapter 5.4, egg placement in Heliconius,
defined as the part of the plant selected for oviposition, is

correlated to the habitat in which that butterfly is found. This
difference in behavior may well be a response to the type of
predation affecting the eggs and larvae in that habitat.

6.5 Coevolution Between Heliconius and Passiflora

As discussed in Chapter 4.4b, there is a certain degree of
correlation between larval growth ability and host plant taxonomy,
when the different Heliconius larvae are raised on different species
of Passiflora. The "Plectostemma feeding" group of Heliconius are
able to grow and develop at normal rates only on P. (Plectostemma)
and a few other species of Passiflora, which supports the hypothesis
that this group of Heliconius is biochemically coevolved with the
Plectostemma subgenus. However, the "Granadilla feeding" group of
Heliconius show little if any feeding specialization on P. (Granad-
illa) species, which indicates that any coevolution which occurs
in these species is not based on leaf chemistry. Since on a broad
taxonomic scale both groups of Heliconius show equal "fidelity"
(in terms of host plant choice) to their supposedly coevolved
Passiflora subgenus (Benson, et al. 1976), this finding demonstrates
that the type of butterfly-host plant coevolution referred to by
Brues (1920) and Ehrlich and Raven (1964) can occur independently
of host plant defensive chemistry. Therefore, a reassessment is
needed of the applicability of the "gene-for-gene" model to butterfly-
host plant coevolution, as discussed in Chapter 1.4.

The taxonomically-correlated patterns of growth rates in
Heliconius indicate that among new-growth-feeding _Heliconius_, larval
growth rates are _very_ slow to evolve (Chapter 4.4e). In contrast,
host plant selection behavior and oviposition behavior are much
more variable and quick to evolve, as demonstrated by comparing the
closely related _H. cydno_ and _H. melpomene_ in terms of host plant
choice (Chapter 5.4). This suggests the hypothesis that insect-
host plant coevolution may operate in stages, only the last stage of
which is biochemical specialization on the host plant. The
proposed changes occur both in temporal sequence and in order of host
plant taxonomic distance, as will be made clear below. They are not
mutually exclusive, but represent points along a continuum.

1. Establishment of a preference hierarchy among _acceptable_
host plants, as discussed above (Chapter 6.4b). This preference
hierarchy will depend on host plant quality. Even at this stage
there may be some subtle influence of host plant chemistry. If
two species are otherwise equal in quality and one is slightly more
palatable, then it should be favored.

2. Complete avoidance of palatable but other wise low
quality host plants, as demonstrated by _H. melpomene_'s rejection of
P. auriculata, _P. ambigua_, and _P. vitifolia_; by _H. cydno_'s rejection
of _P._ (_Tetrastylis_) _lobata_, or by _H. erato_'s rejection of _P._
vitifolia. Host plants which are taxonomically distant from the
preferred host should have a much higher probability of this type

of rejection.

    3. Evolution of larval feeding specialization, as evidenced
by the "_Plectostemma_ feeding" group, or by the restriction of
Heliconius to Passifloraceae. Taxonomically distant plants should
on average yield much slower or nonexistent growth rates for
Heliconius larvae than closely related plants, as exemplified by
_H_. _erato_ (Figure 4.6), or _H_. _cydno_ when raised on passifloraceous
Adenia species (Figure 4.4). The rate of evolution of feeding
specialization should depend on at least two factors, as discussed
below and in Chapter 4.4c.

    These stages, in conjunciton with host plant diversification
and evolutionary radiation, logically result in the "coevolved"
patterns of host plant selection in butterflies discussed by Ehrlich
and Raven (1964). As a relatively small host plant taxon evolves,
it undergoes changes in leaf chemistry and ecological setting. The
longer and more pronounced the evolutionary radiation of the taxon,
the more distinct and subdivided it becomes both ecologically and
chemically, which in turn provides increased opportunities for
behavioral and feeding specialization, respectively. The result of
this process after several subsequent host plant radiations could
well be the parallel taxonomic associations which gave rise to the
theory of butterfly-host plant coevolution. Note that "gene-for-
gene" coevolution need not occur. In fact, the only requirement for
plant "coevolution" is that the plants diversity in terms of

secondary products chemistry. Thus, the term used by Brues, "parallel evolution," may be more appropriate when discussing the evolution of host plant chemistry than the widely accepted "coevolution" adopted by Ehrlich and Raven. The appropriateness of the latter will depend on how much the host plant's chemical differentiation is directed by butterfly herbivory, which is at present unknown.

In some cases larval feeding specialization may evolve rapidly so as to closely match host plant selection in a host-specific species (Chapter 4.4e). In *Heliconius* this has occured in the gregarious-feeding species which consume tough-leaved host plants. As discussed in Chapter 4.4e, this specialization may be a result of the greater host-specificity resulting from high effective host plant density (see Chapter 6.4), or from a lower nutrient/toxin ratio which may occur in mature as opposed to young host plant tissue. It would be interesting to know if this is a general pattern among herbivorous insects.

6.6 Passiflora Antiherbivore Adaptations

As discussed in Chapter 2.4c, there is a tendency for the forest-inhabiting species of *Passiflora* to have thick, tough leaves that are generally oval in shape, while the early-second growth-inhabiting species have thin, membranous leaves of various outlines. The two principal exceptions are *P. vitifolia* and *P. auriculata*,

which are the only two species found commonly in both habitats.

When H. cydno larvae are raised on the new growth tissues of four

tough-leaved species, the mean growth rate is five to ten percent

lower than when raised on four thin-leaved species (data in Figure

4.4), indicating that even the new growth of these tough-leaved

species is better protected than that of thin-leaved Passiflora.

The mature leaves of the tough-leaved species are inedible to all

except the gregarious-feeding specialist larvae of Heliconius, in

contrast to the mature leaves of the thin-leaved plants which may

be consumed by solitary-feeding larvae of many species. Thus,

leaf-toughness appears to function as an anti-herbivore defense

in these plants, effective against all Heliconius except very

specialized species. However, larvae in the Heliconiine genus

Euides may also feed upon mature, tough leaves, although such growth

appears to be very slow.

There is no tendency in the La Selva Passiflora for the

tough-leaved species to support generalist herbivores as opposed

to the ephemeral thin-leaved species supporting specialists, as

the theories of Feeny (1976) predict (see Chapter 2.5). In fact,

the patterns of feeding specialization indicate that the greatest

feeding specificity is in tough-leaved plants, as discussed above.

It appears that in general, late-successional plants in the tropics

have both types of antiherbivore defenses, "quantitative" as well

as "qualitative," which in combination should select for greater host specificity than either strategy alone (Southwood 1973).

The different _Passiflora_ species attract different kinds of insects to their extrafloral nectaries, as shown in Chapter 5.3d. The type of insect attracted appears to be at least partially a result of nectary structure; the effects of nectar flow rate or composition were not determined. Since the type of insect attracted also appears to depend on the plant's habitat, the strategy of biotic defense adopted by a _Passiflora_ should be integrated with many other plant life-history factors.