

CHAPTER 2. HELICONIUS AND PASSIFLORA:
DISTRIBUTION AND ABUNDANCE AT THE FIELD SITE

Previous studies on butterfly communities indicate that the butterfly ecological niche is partitioned along several dimensions. The host plant niche is emphasized in such studies, but recently other factors have come to be recognized. These include adult resources, predation on adults, and predation on eggs and larvae (Gilbert and Singer 1975). The project described in this thesis investigates the host plant niche as well as some of the other factors. However, one aspect of the insect niche which has received little attention is that of habitat "choice" or specificity. Some insects such as flea beetles are known to be habitat-specific, such that only after the habitat is chosen does host plant selection occur (Tahvanainen and Root 1973). This is also known in Pierid butterflies (Cromartie 1975; Gilbert and Singer 1975). However, general patterns of insect habitat specificity are not well understood (Price 1975).

There are 10 species of Heliconius and 13 species of Passiflora found at the field site, as will be discussed below. With this many sympatric closely-related species some habitat separation is expected to occur due to differences in life histories and ecology. The field site is not a uniform habitat as perceived by this investigator, nor is it uniform with respect to vertebrate communities and plant communities. As will be demonstrated, Heliconius are highly adapted

to specific habitats by mimicry-induced wing coloration and behavioral traits and are probably unable to switch habitats in response to changing host plant resources. Therefore, in this study it is essential to characterize the habitat specificities of the organisms involved. Only with this information is it possible to estimate the kinds and abundances of potential host plant species available to each species of butterfly. Similarly, knowledge of habitat specifications is needed to estimate the degree and kind of Heliconius herbivory to be expected on each host plant species. This chapter is primarily intended to communicate this necessary information.

One representation of an organism's habitat specificity is to list its abundance or population density in each habitat. By definition, the organism can be said to be specific to those habitats where it is commonly found. A useful by-product of this kind of analysis is that these abundances can be used to test hypotheses about insect-host plant population dynamics. For example, in this chapter population densities are calculated for both Heliconius and Passiflora in two habitats at the field site. Treating Heliconius as a "predator" and Passiflora as "prey," the "numerical response" was then estimated. This information may be useful in developing theories about herbivore-plant population dynamics (Southwood 1975). While such tests are strictly peripheral to the overall project, the information is of general interest because so little is known about the dynamics of natural populations of

herbivores and host plants (Price 1975; Southwood 1975).

This chapter is primarily intended to serve as background for the material in later chapters. It is organized into the following four sections. First, a description of the field site is given, along with a climatic summary. The habitats are described, and possible seasonal fluctuations are discussed. Secondly, the distribution and abundance of the Heliconius at the field site is investigated. The different analyses that were employed are discussed, and the results are given in tabular form. There is also a short discussion on the striking correlations between mimicry pattern and habitat choice, and on Elton's hypothesis that competitive exclusion prevents closely related species from sharing the same habitat (Elton 1946). Thirdly, distribution and abundance of the Passiflora species are presented. Elton's hypothesis is discussed for these organisms as well. Finally, the fourth section summarizes certain features of the interaction between Heliconius and Passiflora which can be deduced directly from their abundances in different habitats. Included here is the numerical response analysis discussed above. Also included here is a summary of this chapter with regard to the Heliconius-Passiflora interaction.

2.2 Field Site Description

The La Selva Field Station of the Organization for Tropical Studies (OTS), Costa Rica, was chosen to be the field site for this study for several reasons. One reason is the high diversity of

Heliconius species and Passiflora host plants at the field site which provides a great many opportunities for comparison of ecology and behavior. Another reason is the relative constancy of the physical environment at La Selva in terms of diurnal and annual fluctuations. This constancy is reflected in relatively stable population densities for the organisms (see below) and allows most ecological measurements to be made without regard to seasonality. A third reason is the undisturbed nature of the habitat at La Selva, which allows relatively natural population densities for Heliconius and Passiflora. One disadvantage of this field site is that densities for these organisms are relatively low. However, by preventing concentrated investigation on any one species, this "disadvantage" encouraged the comparative approach.

The climate at the field site is characteristic for a lowland tropical wet forest (Holdridge 1967). Figure 2.1 graphs climatic data taken over the past ten years at the field station. The two most important aspects of climate as represented in the figure are (1) that the driest month of the year, March, consistently receives rainfall, and (2) that seasonal temperature fluctuations are minimal, being less than 20% of the normal diurnal fluctuation. Given the great constancy of temperature and reliability of rainfall at the field site, the most important weather variable with regard to Heliconius populations is the amount of cloud cover. The relatively cool climate at La Selva, a result of nearby mountains, combined with the tendency to be overcast in the wetter seasons

considerably influence the flying behavior of Heliconius butterflies. Seasonal fluctuations in the insects' abundance can therefore be expected. However, fluctuations are probably of relatively small magnitude, as will be shown below (Chapter 2.3e).

The La Selva Field Station comprises about six hundred hectares of virgin tropical forest and another hundred hectares of disturbed vegetation (Figure 2.2). There are no roads on the field site, and this prevents the buildup of high population densities of Heliconius which is characteristic of roadside habitat. Instead, about 20 kilometers of trail cross the field site. The forest habitat consists of hilly upland forest and bottomland alluvial forest ; in the past much of the alluvial forest was cut for plantations. The disturbed habitats at La Selva consist of (1) lawns, which are cut regularly when they reach about 25 cm in height, (2) old cacao plantations, which are being allowed to undergo natural succession, (3) large plots of land which are returning to natural succession after having been cut only once or twice, (4) successional plots with a known history of cutting specifically designed for investigation of natural succession, (5) a Passiflora "garden" in a large mowed clearing near the station buildings, and (6) the boundaries of the property which face on surrounding pastures and plantations. Most of the La Selva Passiflora species are cultivated in the garden area. See Appendix 1 for a more detailed habitat description.

2.3 Heliconius Distribution and Abundance

Heliconius are conspicuous, slow-flying butterflies protected from predation by toxic compounds and bright aposematic coloration (Turner 1971). A long-lived insect, adult Heliconius survive up to six months of age in the field (Ehrlich and Gilbert 1973). These butterflies are very predictable in their habits; each individual has a very predictable home range. The extent of the home range is strongly influenced by the distribution of adult pollen resources (Gilbert and Singer 1971). Determining the distribution of these pollen resources is beyond the scope of this study.

Ten species of Heliconius are found at La Selva. Some species are consistently more abundant than others, with five being common and five uncommon. The ten species are nearly equally divided between the two principal evolutionary radiations of the genus. As shown in Figure 2.3, which includes the phyletic relationships of the Heliconiine species found in Costa Rica, there are two principal radiations, "Granadilla feeders" and "Plectostemma feeders" (Benson et al. 1976; Brown and Mielke 1972). Four of the La Selva species are in the first category, five are in the second. The tenth species, H. doris, distantly related to the rest, is sometimes placed in a separate genus, Laparus. Benson, et al. (1976) discuss the possible evolution of this phylogeny. It is important to note that each Heliconius species consists of many geographic races which may differ widely in behavior and ecology. Therefore,

the following discussion will implicitly refer to the northeastern Costa Rican races of the butterfly species. The names of these races are given in Figure 2.3.

2.3b Methods of Study

At the field site adult Heliconius were studied by a mark-release-recapture technique. Because adults of these species show very similar flying behavior they can be sampled with little bias in sampling intensity. This is one advantage of studying a diverse group of closely related, similar species. A butterfly net was carried at all times during work at the field site and every Heliconius observed was chased and caught if possible, with the exception of H. sara. In certain areas at La Selva, this species was so abundant that all individuals were not pursued. When a butterfly was captured a unique number was written on its wing (this technique is described in Ehrlich and Gilbert 1973). The butterfly was then released for possible future recapture. Before release, the date, time of day, species, and individual number were recorded. Also recorded were exact location of capture and data about the butterfly, such as its sex, amount of wing wear, amount of pollen on the proboscis, and three body size measurements. These data, along with appropriate summaries and a more detailed description of the measurement techniques are given in Appendix 2.1. When a Heliconius was recaptured, the same information was taken with the exception of body size measurements. This data made it possible to

obtain information on the longevity and movements of individual butterflies as well as population estimates. Unfortunately, La Selva is a difficult habitat for butterfly capture; most floral resources are high off the ground and thick vegetation impairs mobility to such a degree that the recapture rate was quite low. Thus, with a few exceptions, insufficient data were collected to permit estimation of population sizes. The data is therefore analyzed by listing the number of captures (including recaptures) of each species in each habitat at La Selva, as shown in Figure 2.4.

In those cases when enough captures were obtained, the Lincoln index or the Jolly method was used to estimate local population sizes (Southwood 1966). A "local population" is operationally defined as any series of captures and recaptures in a local area, in which recaptures were frequent, and which had little movement in or out of the area as determined by recapture data. In some cases the local population sampled may be a subset of the true local population of Heliconius. When a single isolated site was sampled, such as an Anguria inflorescence near ground level, the individuals captured could easily be a subset of a larger population in the area. This may result in an unreliable estimate of that species' local abundance. These "less reliable" estimates are represented in Figure 2.7 by open symbols. Fortunately, it was possible to carry out a more thorough sampling program in the succession plots. These plots can be sampled at many points, ensuring that all the Heliconius in the area are included in the sample; they are also relatively isolated

from other similar areas, being surrounded on all sides by forest, pasture, or later successional forest. The population estimates for these areas, represented in Figure 2.7 by solid symbols, are therefore fairly reliable indicators of local abundance. In addition, these estimates may represent the size of local demes for these butterflies, although the amount of migration in and out of the plots may be rather high, in which case they should not be considered true demes.

Given the opportunistic method of sampling Heliconius while engaged in other activities, in most cases difficulty arises in estimating the sampling effort for each habitat. However, in two habitats, the successional plots and the upland forest, long blocks of time were spent (see Figure 2.2). By checking the times of capture for a series of butterflies caught in one day, it is possible to estimate the duration of time spent in these habitats. A "rate of capture" for each species can be calculated by dividing the number of individuals caught by the time spent in the habitat. If it can be assumed that the probability of capture for an individual butterfly is the same in different habitats then the rate of capture will be proportional to population density. Unfortunately, it is difficult to evaluate this assumption. Heliconius in the forest habitat tend to be more visible than their counterparts in the succession plots, due to the sparse understory vegetation. Once they are seen, Heliconius are probably more easily caught in the succession plots than in the forest. Also, for the forest inhabiting species

the proportion of time spent high in the forest canopy is not known. Based on the last factor, it would seem that the rate of capture in the forest is an underestimate of true population density compared to that in the succession plots. Since this underestimate will affect all species approximately equally, it will not alter conclusions based on comparing habitat specificity in the different species of Heliconius.

The area covered in the sampling program can be expressed realistically by the length of trail traversed in each habitat. As shown in Figure 2.2 the length of trail in each habitat is sufficiently large (at least one kilometer) to eliminate biases due to presence or absence of individual floral or host plant resources.

2.3c. Habitat Selection By Heliconius

Habitat selection by the different Heliconius species is shown in Figure 2.4. The numbers represent the total number of captured or recaptured individuals of each butterfly species in different habitats at La Selva. The data clearly indicate that some of these butterfly species have strong habitat preferences. For instance, Heliconius cydno, one of the very common Heliconius at La Selva, is found abundantly in all habitats except the succession plots. In contrast, Heliconius erato is found abundantly in the succession plots but is totally absent from forest habitats. The overall heterogeneity chi-square test indicates that these data are significantly non-random. In addition, butterfly habitat preference is

analyzed for three of the five habitats (see Figure 2.5). The two habitats not examined in Figure 2.5 are very discontinuous since they are essentially edge habitat. Forest, the succession plots, the garden, and the habitat I call "old second growth" are all extensive habitats at the field site, in which the capture frequencies will not be strongly influenced by edge conditions. These habitats also unambiguously represent the stages of succession. To allow the insects to be placed on a gradient of forest affinity, I calculated a "forest affinity index" for each butterfly species by weighting the number of captures in the forest habitat by a value of three, in the "old second growth" habitat by two, and in the succession plot habitat by one, and then calculating the weighted mean. As shown in Figure 2.5, a value of 1 indicates that that Heliconius species was found only in the early-succession habitat, while a value of 3 indicates that captures were made only in the forest habitat.

The data in Figure 2.5 show some very interesting patterns with regard to Heliconius taxonomy and ecology of the different species. As discussed by Turner (1976) Heliconius are remarkable for the complex mimicry patterns within the genus. Among sympatric species of Heliconius, it is very common to find pairs of mimics which resemble each other in detail. Turner (1971) and others (Papageorgis 1975) hypothesize that the two members of each pair should share identical habitat preferences. However, until now this had not been demonstrated with field data. The mimicry pairs at La Selva are indicated in Figure 2.5 by the line connecting pairs of

species. Note that species adjacent in habitat preference with similar "F" values tend to be members of a mimicry pair. Figure 2.6 is a statistical analysis supporting this contention. The values in Figure 2.6 are G-values comparing the habitat frequencies (Sokal and Rohlf 1969). The G-values comparing members of the mimicry pair are very low and in most cases nonsignificant. However, the G-values comparing species from different mimicry pairs tend to be high, and in many cases are extremely highly significant. In the case of two mimicry pairs (H. cydno-H. sappho and H. melpomene-H. erato) the data are conclusive. The evidence for the other two pairs is less strong, especially for H. sara and H. doris, which in any case are not perfect mimics. In the case of H. hecale-H. hecalesia, while H. hecale appears to inhabit early second growth more than H. hecalesia, both species were found to coexist in old second growth areas where the early second growth species were absent (see map, Appendix 2.2).

These habitat preferences also indicate a very interesting pattern with regard to the community ecology of the Heliconius at La Selva. This can be seen by comparing the taxonomic affinities of each member of a mimicry pair as indicated in Figure 2.3 where the mimicry pairs are represented by lines connecting the species. Members of a mimicry pair are invariably unrelated. It seems paradoxical that only relatively unrelated species can mimic each other; one might expect that closely related sympatric species would be preadapted to form mimicry pairs because of similarities

in behavior and general morphology. This data indicates, however, that closely related Heliconius are found in different habitats, perhaps as a result of interspecific competition (Elton 1946; Pianka 1974: 132-154). Consequently, there is no selection for mimicry. In contrast, each member of a mimicry pair is unrelated, and thus is quite different in its host plant use-strategy, as will be shown in Chapter 3.4b. This may minimize competition between the members of the pair and allow them to coexist in the same habitat, where selection for mimicry would be expected to operate. Papageorgis (1975) presents a similar hypothesis, although the supporting data are quite different.

2.3d Home Range of Individual Heliconius

In their Trinidad study of Heliconius ethilla, Ehrlich and Gilbert (1973) found that individual butterflies have highly restricted home ranges. An analysis of movements of recaptured Heliconius at La Selva shows that these species also have relatively restricted movement patterns. The histogram in Figure 2.8 indicates that over 90% of all recaptures were within 100 meters of the previous capture site, and that 95% were within 200 meters. Fully 100% were within 1000 meters. It is particularly significant that H. cydno has a low percentage of long range movements. The individuals of the forest-inhabiting species could potentially range over large areas of uninterrupted habitat at La Selva. Of the 41 recaptured H. cydno, only 3 were over 200 meters away from the point

of capture. Thus, even this forest-inhabiting species has restricted home ranges.

of previous capture. Thus, even this forest-inhabiting species has restricted home ranges. Among the other species of Heliconius, very little movement was observed between the garden area by the station buildings and the successional plots. These areas are isolated from each other by intervening forest. Of 105 recaptures in these areas, only 3 were movements between them, a journey of about 1000 meters. I conclude from this that, like the H. ethilla of Ehrlich and Gilbert (1973), these butterflies' home ranges do not extend across large gaps of unsuitable habitat.

There are statistically significant differences among the species with respect to the distances moved (Figure 2.8); however, this may be due to sampling biases rather than real differences in home range. For instance, butterflies in the successional plots were readily sampled 100 meters away from their point of capture, whereas the Heliconius marked on the East Boundary trail line 1800 could only be sampled either in the same spot or 200 meters away, there being no suitable sites in between. Thus, it is not possible to realistically estimate inter-species differences in home range using these data.

2.3e Population Density

In the study cited above, Ehrlich and Gilbert (1973) discovered a remarkably constant population density from month to month over a three year period. They postulate that this was due to long adult life spans and highly density-dependent mortality in

the immature stages, conditions which tend to buffer short-term fluctuations in environmental quality. The data in Figure 2.7 are roughly in agreement with the results of the Ehrlich and Gilbert study. At La Selva, three of the five species keep local population sizes consistently around the value of 10 in all seasons. A fourth species, H. sara, probably also has constant population sizes, but at a much higher density. The fifth species, H. hecale, appeared to be variable in abundance in the succession plots, where one abundance peak was estimated at a value of 30 individuals. This does not appear to correlate with seasons. With the exception of H. hecale, therefore, stable population sizes seem to be characteristic for these butterflies, at least at the level of resolution of the estimates in Figure 2.7.

The species which was best sampled, H. erato, clearly shows a stable population size of approximately 10 individuals in the succession plots area ($\bar{x} = 10.1$, s.e. = 1.5). Since the captures are heavily male-biased, this value is probably an underestimate of the total number of H. erato adults. The true number should range from 10 to 20 (see Appendix 2.5 for discussion).

The estimated numbers of H. sara adults in the succession plots are much higher than the estimated number of H. erato adults. However, only during October, 1976 was this H. sara population sampled intensively enough to obtain recaptures. At other times, these butterflies were marked at about the same rate as the other species, but no recaptures occurred. The population estimate in

October 1976 was approximately 100 males and 100 females, estimated separately in this case. Possible reasons for this unusually high population density will be discussed below.

Except for H. sara and H. hecale, the La Selva Heliconius appear to have relatively stable, low density populations. Even relatively rare species such as H. hecalesia and H. sappho are regularly found in certain areas at La Selva. Under the assumption that rate of capture (Figure 2.9) is proportional to local abundance, H. sappho shows a population density of only .3/hectare in its preferred forest habitat, or one individual per 3 hectares. This is actually not much smaller a value than the 1.5/hectare value estimated for H. cydno, the most abundant forest species.

2.4 Passiflora: Distribution and Abundance

Passiflora are small to medium-sized vines which reach their greatest diversity in the neotropics. They are characterized by showy flowers and a wide variety of leaf-shapes. Twelve species of this large genus have been found at La Selva along with a closely related species in the genus Tetrastylis, making a total of thirteen passifloraceous species at La Selva. The two principal subgenera of Passiflora are well-represented at La Selva, with five species apiece (see Figure 2.10). These two subgenera, Granadilla and Plectostemma, comprise the bulk of the genus Passiflora. Two other subgenera are represented at La Selva, Astrophea and Distephana. Both are thought to be primitive (Benson et al. 1976). Tetrastylis lobata

lobata is so similar to members of the subgenus Plectostemma in several characteristics that the above authors consider it to be a Passiflora and not a true member of the genus Tetrastylis. I will therefore for convenience refer to Tetrastylis lobata as "Passiflora" lobata in the following discussion, though this name change is not formalized (Benson et al. 1976).

Larvae of the genus Heliconius are restricted to feeding on host plants in the family Passifloraceae (Benson et al. 1976). The only representatives of this family found at La Selva are the aforementioned Passiflora species. Consequently, these thirteen species represent all potential hostplants for the Heliconius at La Selva. Therefore, in studying the host plant ecology of these butterflies it is sufficient to restrict the investigation to thirteen species of host plant.

All but one of the La Selva Passiflora species possess extrafloral nectaries which function to attract ants and other nectar-feeding insects (see Chapter 5.3d for further discussion). There are striking differences not only in the leaf shape of the different species of Passiflora but also in the general habit and appearance of the different species. As illustrated in Figure 2.10, the leaves range from typical "shade-tolerant" entire-leaved plants with woody stems and thick, leathery leaves to herbaceous plants with thin, membranous leaves. Many species are intermediate between these two extremes. See Appendix 3.1 for more information on Passiflora vegetative characteristics.

2.4b Methods of Study

Passiflora species were identified according to the treatments of Killip (1939) and Standley (1937). All Passiflora vines discovered along the trails at La Selva were tagged with a unique number. However, in the succession plot area the vines grew so abundantly that individual plants were not tagged in most cases (see Appendix 3.2 for distribution map). Because most Passiflora along the trails have been enumerated, it is possible to calculate relative abundances of Passiflora species in the different La Selva habitats. In Figure 2.11 the number of different Passiflora species found in different habitats is given.

Two additional Passiflora censuses were made in order to better estimate absolute densities in different habitats. The first method was to map one hectare of virgin forest, being careful that no Passiflora vines were overlooked. The area mapped is part of a forest study plot which has been gridded and mapped by the University of Washington. The grids are 20 meters across and by mapping 25 such grids, one hectare of forest can be covered. The grids were chosen so as to form 20 meter-wide transects through the forest (see Area III on map in Figure 2.2). Approximately one hour was spent in each grid to insure that no Passiflora vines were overlooked. The size, species, and number of visible growing shoots were recorded for each Passiflora vine. The results are given in Figure 2.12.

The other Passiflora census was made in the successional plots. Due to the high density of vegetation in this area, a very different censusing technique was required. Growth shoots of each Passiflora species, rather than plants, were enumerated because it was frequently impossible to determine whether or not two shoots belonged on the same or different individual plants. Also, from the point of view of most of the Heliconius species, the new shoot is a more relevant unit of host plant quantity. Five different successional plots were sampled, ranging in age from ⁰.5 to 4.5 years since the last cutting. These censuses were repeated in two successive years, comprising ten censuses in all. The method used was to enumerate all Passiflora shoots found between the trail's edge and one meter back into the vegetation, extending up in a column to the vegetation canopy, which ranged from one to three meters in height. This column flanked either side of the trail traversing the succession plots. Thus the overall sample consisted of two 1-meter wide "walls" of vegetation parallel to the trail. The species of each shoot was recorded along with its height above ground. The presence of eggs and/or larvae were recorded as well. The data are given in Figure 2.13. When the vegetation was over 3 meters tall it invariably "roofed" over the trail. In this case, any shoots over the 1-meter wide trail were counted. The absolute densities of Passiflora shoots were estimated for each plot by dividing the number of shoots less than 3 meters in height by twice the length of trail in that plot, and adding the number of

shoots over three meters in height divided by three times the trail length. In this way the shoots over the trail are accounted for. The resulting densities are given in shoots/m² in Figure 2.13.

The above three measures of Passiflora distribution and abundance can be analyzed by a method analogous to the Heliconius habitat analysis. As before, "edge" habitats are eliminated from the analysis. The "early second growth" data was obtained by scaling the species totals in the succession plot census so as to add up to a total of 50 "plants." The "forest" habitat data was obtained by adding the numbers of Passiflora plants in the forest study area to the number of tagged plants along the upland forest trails. The "old second growth" category includes all tagged Passiflora interior to patches of that habitat. The results are tabulated in Figure 2.14.

The Passiflora abundance data is summarized in Figures 2.15 and 2.16. In Figure 2.15 all species are lumped and the overall abundance of Passiflora is given for six stages of succession. The .5, 1.5, 2.5, 3.5, and 4.5 year-old succession plots and the forest study area are represented. In Figure 2.16 the results are presented by species, comparing the two habitats, forest and succession plots. In this figure the different succession plots are considered together as a unit. The "forest" abundance values are taken from all the data in Figure 2.12, not just the forest study area census. The resulting total is scaled so as to add up

to 30 shoots/hectare, the Passiflora abundance in the forest study site.

2.4c Passiflora Distribution and Abundance

Like the habitat preferences of the Heliconius species the Passiflora distribution at La Selva is highly significantly non-random (Figures 2.11 and 2.16). As might be predicted from leaf morphology and degree of woodiness, the "shade-tolerant" species tend to be found in the forest habitat, while the more herbaceous "fugitive" species are found in the second growth habitats. Two Passiflora species are found commonly in both habitats, P. vitifolia and P. auriculata. It is interesting to note that these species are intermediate in their leaf morphology and degree of woodiness.

There is a pattern in the above Passiflora distribution data which is reminiscent of the Heliconius distribution patterns. The two main Passiflora subgenera, as shown in Figure 2.14, have representatives in all habitats at La Selva, just as do the two main groups of Heliconius. The "forest" habitat contains two Granadillas and two Plectostemmas, while the "early second growth" habitats contain one Granadilla and three rather dissimilar Plectostemmas. While the sample sizes are too small to significantly distinguish among most species of Passiflora, there appears to be a trend in which closely-related Passiflora species have evolved different habitat "preferences," while more distantly related species can coexist in the same habitat. An exception to this is the case of P. "laurifolia" and

P. ambigua, which appear to coexist in the same habitat and are very closely related. However, P. biflora and P. lancearia are closely related and have very different habitats, as do P. oerstedii and P. ambigua. The three Plectostemma species in the early successional areas which coexist are rather dissimilar in habit. P. costaricensis has very tomentose leaves and no extrafloral nectaries. P. auriculata has large petiolar nectaries and is a rather woody species with thick subcoriaceous leaves. P. biflora is herbaceous with photosynthetic stems and thin, membranous leaves; the nectaries are on the leaf blades. Although more information is necessary to establish the pattern firmly, it appears that some kind of competitive exclusion principle is operating among the more closely-related, similar species.

The data on Passiflora density are summarized in Figure 2.15. The abundance of Passiflora growth tips is relatively much higher in the succession plots with an average density of about $.23/m^2$ or 2300 shoots per hectare. This value is two orders of magnitude higher than the value obtained in the forest study area where densities are on the order of $.003/m^2$, or 30 shoots per hectare. The abundances of individual Passiflora species will be discussed in Chapter 3, when actual host plant use by the butterflies will be discussed.

2.5 Passiflora Availability to Heliconius

Even though the Heliconius and Passiflora species at La Selva

have significant habitat "preferences," nearly every Heliconius species comes into contact with nearly every Passiflora species at some locality, at least for the five most common species in both genera. Only P. ambigua of the common La Selva Passiflora appears to be unavailable to the early second growth Heliconius, and even this species is artificially available in the garden area. It is therefore possible to at least qualitatively observe the interactions of most of the principal species of insect and host plant.

As stated above, Passiflora abundance varies greatly with habitat. Forest-inhabiting Heliconius depend on a greatly reduced host plant resource base as compared with the second growth-inhabiting species. This provides a test for the effects of host plant abundance on insect host plant choice, which will be discussed in the next chapter. Using the knowledge that Heliconius are completely restricted in their larval food plants to species of Passiflora (including "Tetrastylis") at La Selva, the data for all the species can be lumped together, and a crude analysis can be made of Heliconius numerical response to changes in Passiflora abundance. Figure 2.17 illustrates the numerical response of the butterflies in the forest and the succession plot habitats. The solid dots and lines represent the response to an 85-fold increase in the number of Passiflora shoots per hectare. The response is an approximately 65-fold increase in the density of Heliconius. While the possibility remains that the density of forest-inhabiting Heliconius has been slightly underestimated, the overall response

appears to be roughly in proportion to the amount of host plant. This would support the hypothesis that in some sense these butterflies were "host plant limited." This result may be misleading, however, because 90% of the increase in Heliconius abundance is due to one species, H. sara. If this species is excluded (open dots and dotted lines in Figure 2.16), there is only a five-fold increase in Heliconius abundance. Thus it is possible that one species, H. sara, is "host plant limited" in the sense discussed above, while the other species are limited by other factors.

In summary, each Heliconius butterfly at La Selva probably has a home range less than one kilometer in diameter. In this home range it may encounter between ten and twenty individuals of the same species, although one species is more common than that figure would indicate and several may be less common. Seasonal fluctuations in abundance appear to be minimal, though butterfly flying activity is curtailed during overcast weather. The home range chosen is located in a characteristic habitat for the species. Some habitats possess a greater abundance of host plants than others, but in all habitats a wide range of Passiflora species are available to each individual Heliconius. The host plants actually selected are the subject of the next chapter.

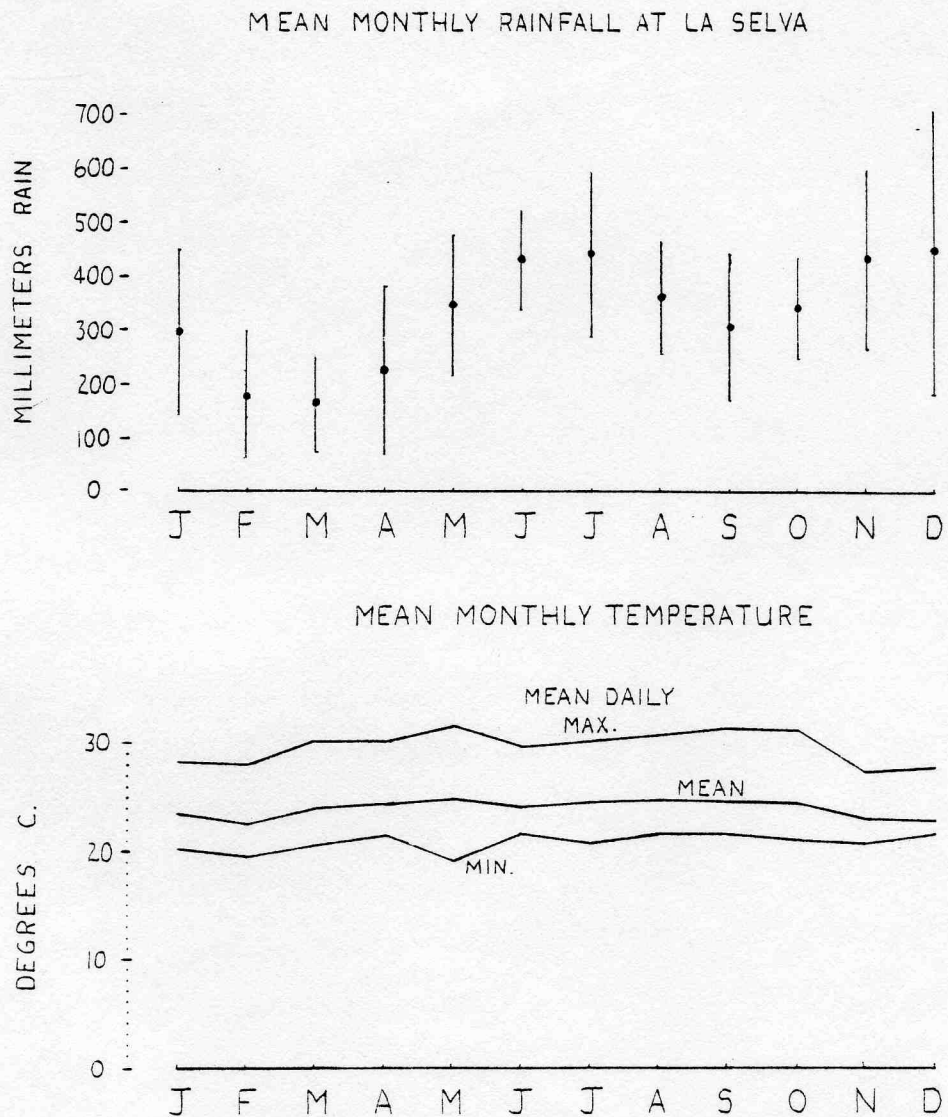


Figure 2.1 La Selva Climate. Based on rainfall from 1957 to 1975 and temperatures from August 1969 to October 1971. (Compiled by G.S.Hartshorn.)

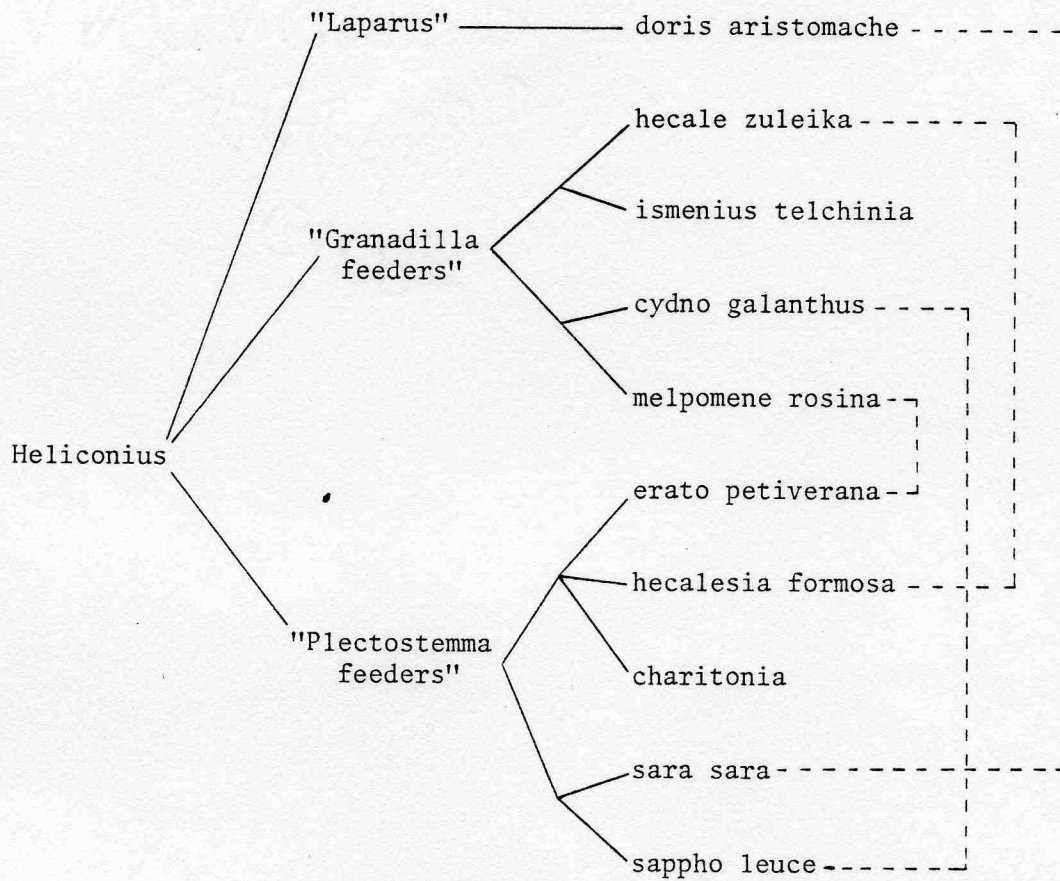


Figure 2.3 Phylogenetic and mimetic relationships of La Selva Heliconius. Dotted lines connect mimics.

<u>Heliconius</u> <u>species</u>	CTF	Other For	OSG +Edge	PG	SP	Total
doris	0	0	1	0	1	2
hecale	0	0	13	28	24	65
ismenius	0	3	5	0	0	8
cydno	18	66	72	12	8	176
melpomene	0	0	23	26	34	83
erato	0	0	9	11	74	94
hecalesia	0	0	4	0	1	5
charitonia	0	0	3	4	1	8
sara	0	1	45	8	179	233
sappho	5	1	1	1	0	8
Total	23	71	176	90	322	682

Figure 2.4 Heliconius captures in five habitats at La Selva. CTF=Central forest area; OSG=Old second growth area; PG=Garden area; SP=Successional plot areas. Contingency table G-statistic: $G=536$, $df=36$, $p<.005$.

Species	Succession plots + garden	Old second gr.	Forest	Total	'F'
ismenius	0	1	3	4	2.8
— sappho	1	1	6	8	2.3
— cydno	20	31	84	135	1.9
— hecalesia	3	3	0	6	1.5
— doris	1	1	0	2	1.5
— hecale	50	6	0	56	1.2
— sara	192	9	1	202	1.1
— melpomene	60	1	0	61	1.0
— erato	85	1	0	86	1.0
charitonia	5	0	0	5	1.0
Total	417	54	94	565	1.4

Figure 2.5 Number of captures of Heliconius in three habitats at La Selva. 'F' is index of forest affinity, found by weighting forest values by 3, old second growth by 2, succession plots + garden by 1, and then calculating the weighted mean. See text for habitat descriptions. Lines connect mimicry pairs. Contingency table G-statistic: $G=424$, $df=18$, $p<.005$.

<u>Heliconius</u> species:	isme	sapp	cydn	hsia	dors	hecl	sara	melp	erto	char
ismenius	---	1.0	1.3	6.6	4.9	24	29	27	30	12
sappho	1.0	---	.7	8.0	4.5	33	43	37	41	12
cydno	1.3	.7	---	7.9	3.9	114	267	144	184	18
hecalesia	6.6	8.0	7.9	---	.4	8.1	13	15	17	7.0
doris	4.9	4.5	3.9	.4	---	1.8	3.5	4.8	5.4	3.0
hecale	24	33	114	8.1	1.8	---	3.2	4.7	6.8	1.1
sara	29	43	267	13	3.5	3.2	---	1.8	3.1	.5
melpomene	27	37	144	15	4.8	4.7	1.8	---	.1	.2
erato	30	41	184	17	5.4	6.8	3.1	.1	---	.1
charitonia	12	12	18	7.0	3.0	1.1	.5	.2	.1	---

Figure 2.6 Table of values of the G-statistic. Each value is a G-test of a 2x3 table of contingency, comparing capture frequencies in three habitats for a pair of Heliconius species. A value of 6.0 or greater indicates a difference in habitat preference at the .05 level of significance. Lines connect mimicry pairs.

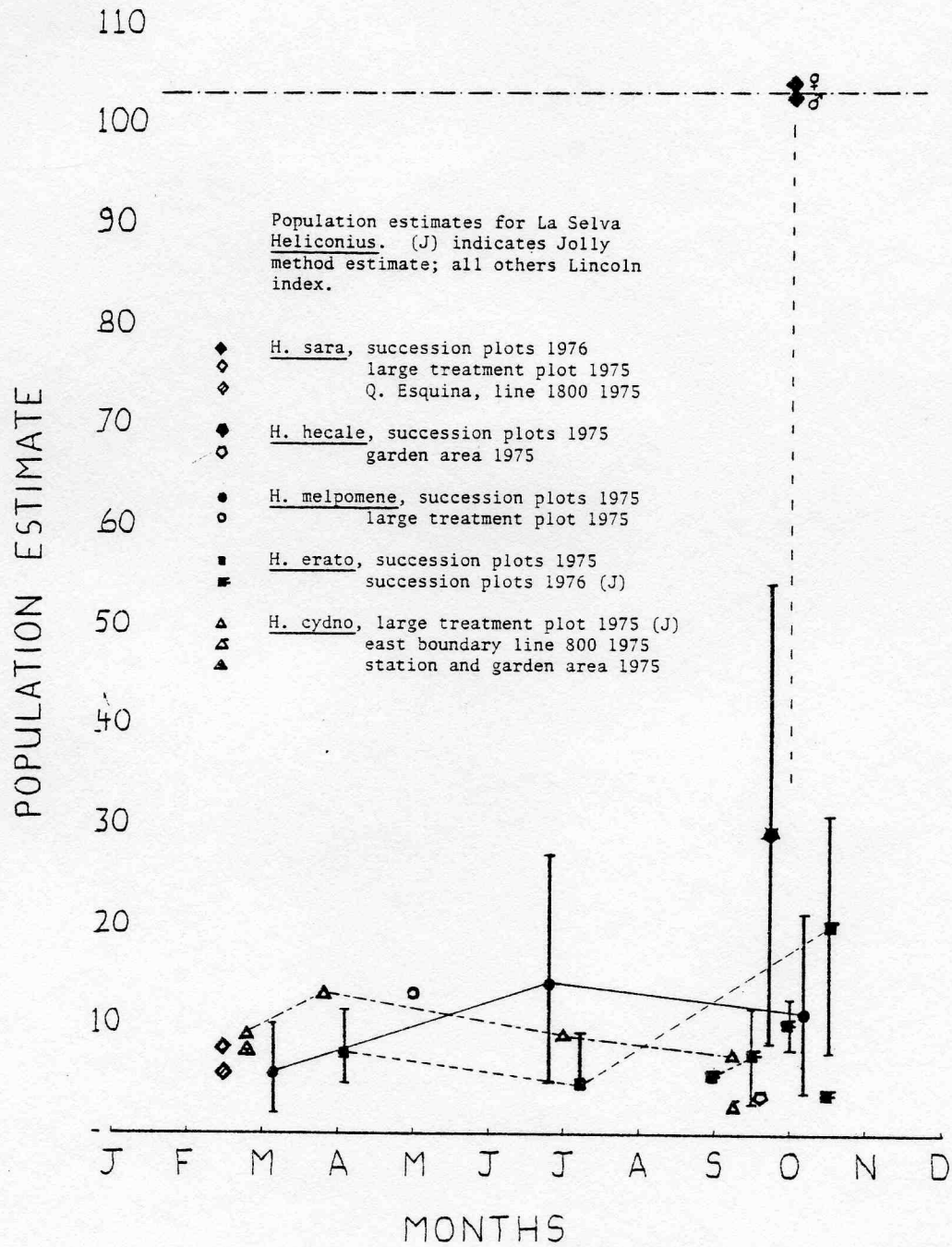
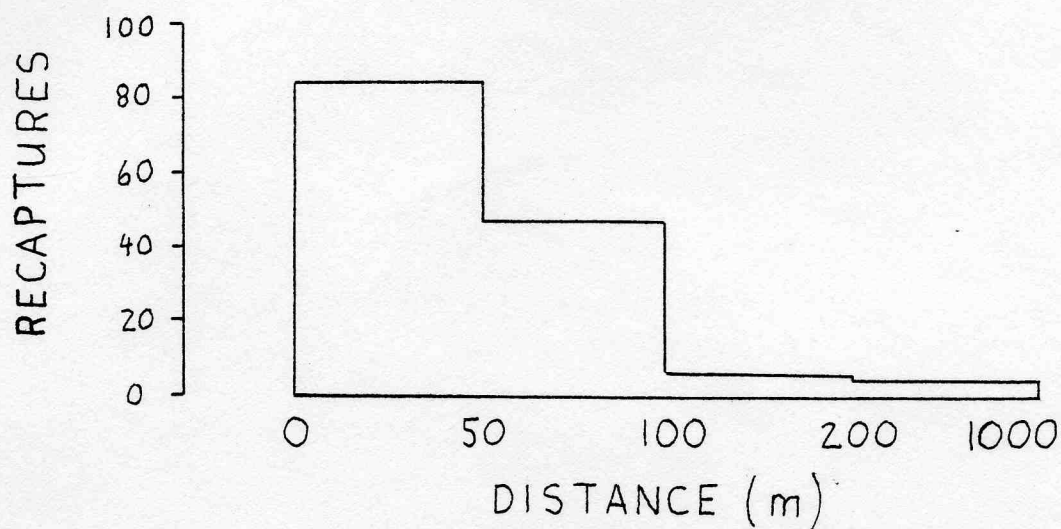


Figure 2.7 Population estimates for La Selva Heliconius. See text for further explanation.



Species	Distance moved (meters)				
	0-50	50-100	100-200	200-1000	1000+
sara	18	22	0	0	0
cydno	27	5	6	3	0
hecale	10	0	0	2	0
melpomene	17	4	1	1	0
erato	13	18	0	0	0
other <u>Heliconius</u>	3	0	0	0	0
Total	88	49	7	6	0

Figure 2.8 Analysis of Heliconius movement using recapture data.
(Contingency table G-statistic: $G=54$, $df=12$, $p<.005$)

Species	Succession plots	Forest
ismenius	0	0
sappho	0	.1(5)
cydno	.17(4)	.5(24)
hecalesia	rare(0)	0
doris	rare(0)	0
hecale	.34(8)	0
sara	6.03*(141)	rare
melpomene	.47(11)	0
erato	1.67(39)	0
charitonia	rare	0

Figure 2.9 Capture rate of Heliconius species in two habitats at La Selva. Sample size is in parentheses. 23.4 hours were spent in the successional plot sample, 48 in the forest sample. *Capture rate for H.sara underestimates true population density (see text).

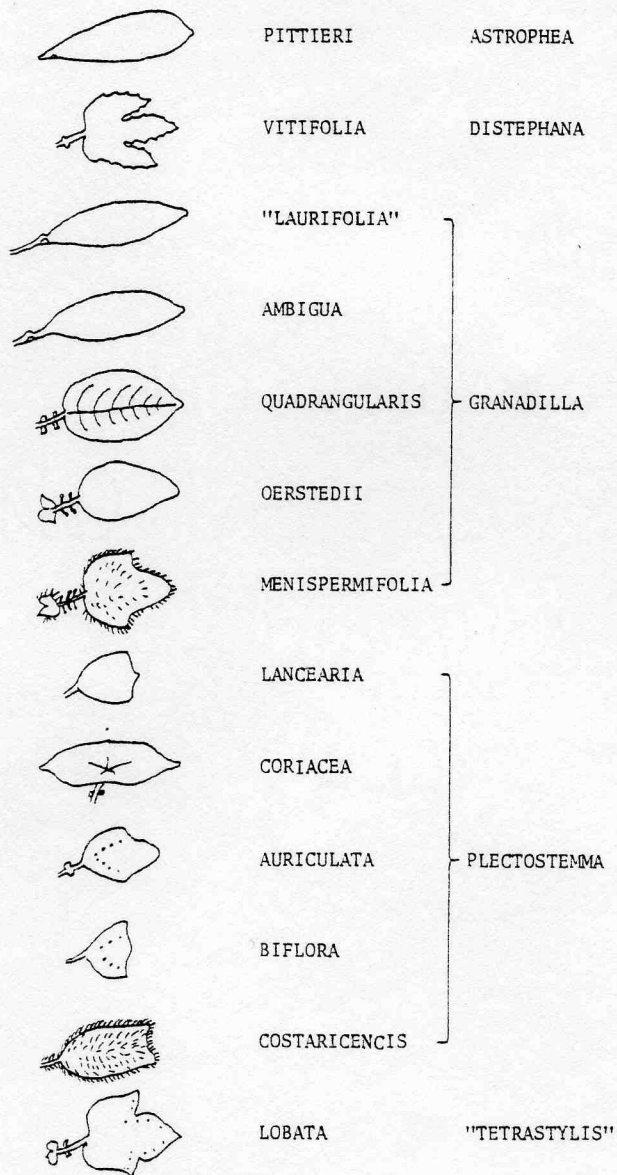


Figure 2.10 Passiflora species and subgenera at La Selva. "Tetrastylis" is of uncertain affinity.

<u>Passiflora</u> <u>species</u>	CTF	Other For	Edge	SP	OSG	Total
pittieri	4	0	0	0	0	4
vitifolia	13	5	7	2	6	33
"laurifolia"	4	0	0	0	0	4
ambigua	4	6	0	0	4	14
quadrangularis	0	0	0	0	1	1
oerstedii	0	0	1	3	5	9
menispermifolia	0	0	0	0	1	1
lancearia	4	0	0	0	0	4
coriacea	0	3	0	0	3	6
auriculata	3	2	6	8	11	30
biflora	0	0	0	3	10	13
costaricensis	0	0	0	3	1	4
lobata	0	4	0	3	4	11
Total	32	20	14	22	46	134

Figure 2.11 Number of tagged Passiflora species in five habitats at La Selva. CTF=Central forest area; SP=successional plot area; OSG=Old second growth areas. Contingency table G-statistic: $G=127$, $df=48$, $p<.005$.

Species	Size class			Total	Number of meristems
	seedling	medium	large		
"laurifolia" ^a	0	2	1	3	8
vitifolia ^a	0	4	2	6	12
auriculata ^a	0	0	2	2	7
Total ^a	0	6	5	11	27
pittieri ^b	0	2	1	3	6
"laurifolia" ^b	0	0	1	1	10
lancearea ^b	1	3	0	4	6
ambigua ^b	2	1	1	4	8
vitifolia ^b	4	1	2	7	15
auriculata ^b	0	1	0	1	3
Total ^b	7	8	5	20	48

Figure 2.12 La Selva Forest Passiflora Census

- a. All Passiflora vines in one hectare area, searched thoroughly.
- b. Passiflora vines along Central and West Loop Trails.

Plant sizes: 0-3m long, seedling; 3m+ long or less than 5mm stem diameter, medium; greater than 5mm stem diameter, large. Number of meristems: understory meristems only were counted.

Species	AGE OF PLOT												Density (meristems/m ²)	
	.5		1.5		2.5		3.5		4.5		total			
	a	b	a	b	a	b	a	b	a	b	a	b		
	55c	98	50	55	107	50	140	107	45	140	397	450	847	
<i>auriculata</i>	14	37	4	9	47	16	17	22	18	30	100	114	214	.150
	0	0	2	4	13	6	19	17	6	3	40	30	70	
<i>vitifolia</i>	8	2	0	1	18	0	0	0	2	1	28	4	32	.025
	0	0	0	3	11	0	0	0	0	1	11	4	15	
<i>biflora</i>	2	0	0	1	8	1	13	1	1	7	24	10	34	.022
	0	0	0	0	1	0	4	0	0	0	5	0	5	
<i>costaricensis</i>	0	0	0	0	5	0	11	2	1	3	17	5	22	.015
	0	0	0	0	4	0	1	0	0	0	5	0	5	
<i>oerstedii</i>	1	1	0	0	7	0	0	0	2	1	10	2	12	.007
	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>lobata</i>	0	0	0	0	0	3	0	0	0	0	0	3	3	.003
	0	0	1	0	0	0	0	0	0	2	1	2	3	
Total	25	40	4	11	85	20	41	25	24	42	179	138	317	.230
	0	0	3	7	29	6	24	17	6	6	62	36	98	
Density (meristems/m ²)	.23	.20	.06	.14	.49	.04	.20	.17	.31	.16	.28	.18		
	.21		.10		.41		.19		.20					

Figure 2.13 Succession plot *Passiflora* census. (a='76 census, b='77 census, c=transect length, d=height above ground, "meristem"=*Passiflora* growth shoot)

Species	Succession plots	Old second gr.	Forest	Total	'F'
pittieri(A)	0	0	3	3	3.0
lancearia(P)	0	0	4	4	3.0
" laurifolia"(G)	0	0	4	4	3.0
ambigua(G)	0	6	4	10	2.4
vitifolia(D)	5	4	13	22	2.4
coriacea(P)	0	3	0	3	2.0
quadrangularis(G)	0	1	0	1	2.0
menispermifolia(G)	0	1	0	1	2.0
lobata(T)	2	4	0	6	1.7
biflora(P)	5	10	0	15	1.7
oerstedii(G)	2	5	0	7	1.7
auriculata(P)	33	10	3	46	1.4
costaricensis(P)	3	1	0	4	1.3
Total	50	45	31	126	1.9

Figure 2.14 Number of Passiflora vines in three habitats at La Selva. 'F' is index of forest affinity, found by weighting forest values by 3, old second growth by 2, succession plot by 1, and then calculating the weighted mean. (A)=Passiflora subgenus Astrophea, (D)=Distephana, (G)=Granadilla, (P)=Plectostemma, (T)="Tetrazyllis". See text for habitat descriptions. Contingency table G-statistic: G=109, df=24, p .005.

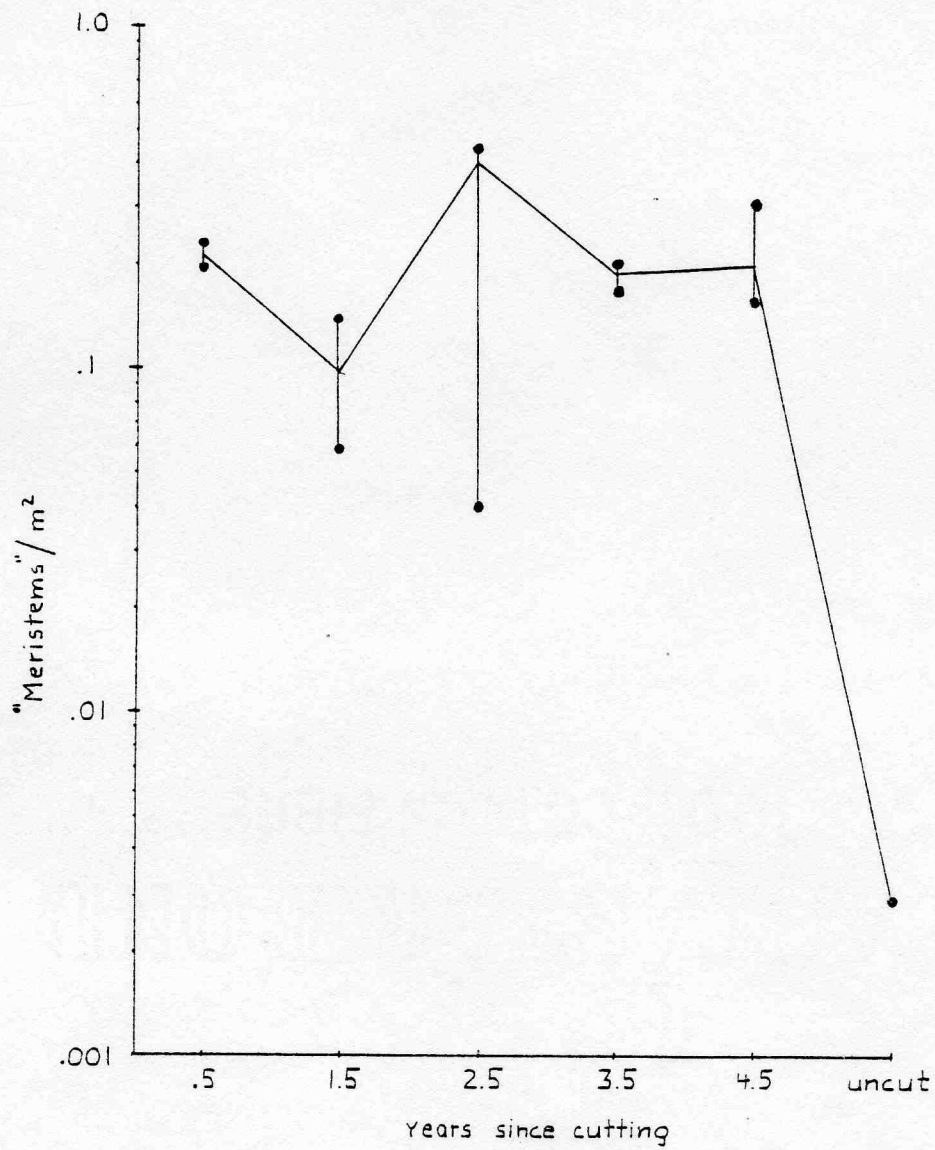


Figure 2.15 La Selva *Passiflora* abundance, measured in terms of the number of growing shoots per square meter ("meristems/m²").

<u>Passiflora</u> species	Succession plots	Central forest
pittieri	0	2
lancearia	0	2
"laurifolia"	0	6
ambigua	0	3
vitifolia	250	10
lobata	30	0
biflora	220	0
oerstedii	70	0
auriculata	1500	4
costaricensis	150	0
Total	2300	27

Estimated abundance of *Passiflora* shoot tips per hectare, in two habitats at La Selva.

Figure 2.16 Estimated abundance of *Passiflora* shoot tips, per hectare, in two habitats at La Selva.

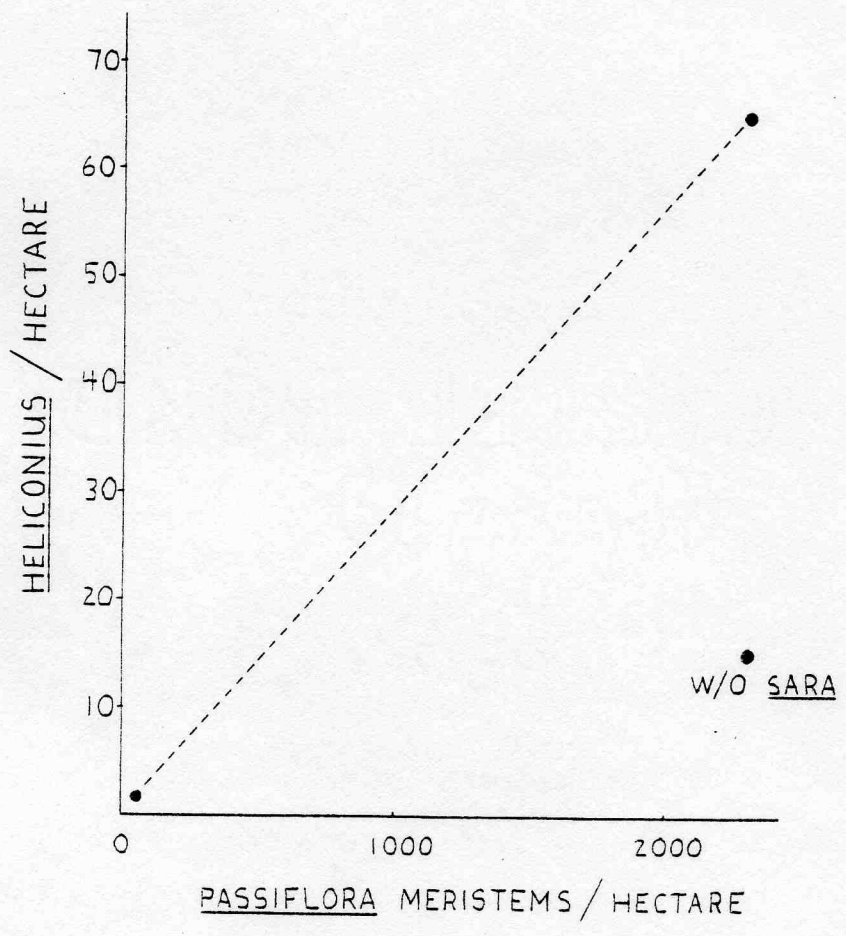


Figure 2.17 Numerical response of Heliconius to Passiflora abundance.