

Lawrence E. Gilbert

Department of Zoology
University of Texas
Austin, Texas 78712

INTRODUCTION

Animal-plant mutualisms have been extensively described and yet, to date, we have no clear understanding of the general ecological and evolutionary importance of such interactions. Ecologists have practically ignored mutualism when considering the kinds of population interactions which explain community structure and dynamics.¹ Williamson (1972) accurately reflects the tone of recent temperate zone ecology in relegating mutualisms to the level of interesting curiosity.

In this paper, I present a qualitative and empirically derived model of the various order effects of mutualism between pollen and nectar feeding *Heliconius* butterflies and the cucurbit vines, *Anguria*,² which they pollinate. The model is based first, on the assertion that mutualism between adult insect and plant will make possible the evolution of increased behavioral capabilities by the insect and second, on the logic that such capabilities will influence the rate, intensity and richness of coevolution between the insect, its prey (in this case *Passiflora*, the larval host), its competitors (mainly other heliconiines), its predators, and its mutualistic associates. In this way the mutualism ultimately will help determine the emergent features of an entire coevolved sub-community.

A linear sequence of words is not the best means of explaining such a highly reticulate ecological system. It is difficult to choose a point of departure since one might begin with a particular group of organisms, with a type of interaction, or with an emergent community property for equally good reasons. My approach is first, to briefly characterize the major groups of organisms involved; second, to explore in detail the interaction between *Heliconius* and *Anguria*, and finally, to hypothesize concerning the ways that this coevolved mutualism has shaped individual, population and community properties of *Anguria*, *Passiflora* and *Heliconius*. The resulting model is summarized in skeletal form in Figure 1 which is perhaps useful to have roughly pictured as one reads the text.

BUTTERFLIES AND PLANTS

PASSIFLORA: CATERPILLAR FOOD

Passiflora and several small genera of the Passifloraceae are the only larval host plants for *Heliconius* butterflies. Most of the 350+ species recorded for the New World are tropical vines which display some of the most striking intra- and inter-specific leaf-shape and stipular variation known for plants (Killip, 1938). Locally, *Passiflora* species generally exist as low density populations in which individuals are difficult to find without the aid of egg-laying butterflies. Moreover, because of herbivore damage, plants are rarely in flower or fruiting condition. More interesting however, is the pattern of *Passiflora* diversity among many local habitats. In spite of the vast number of *Passiflora* species available in the neo-tropics, local habitats always have less than 5% and more typically less than 2-3% of the 350 total.³ I will propose causal explanation for both leaf shape variation and apparent limits to species packing in *Passiflora* in a later section of the paper.

As is true of perhaps most plants, *Passiflora* species possess a range of defensive chemicals which remove all but closely co-evolved herbivores from their list of predators and parasites. Though their chemistry is poorly studied, many *Passiflora* are known to contain cyanogenic glycosides and/or alkaloids from which *Heliconius* probably (but not yet certainly) derive their distasteful qualities (Brower and Brower, 1964). Different *Passiflora* species differ in leaf chemistry (they smell different for one thing) and this is undoubtedly one reason that almost every *Passiflora* species is unique from the others with respect to the species or combination of species of *Heliconius* which prefer it for oviposition in a particular area (for example: Alexander, 1961a, Table 1). Other factors may contribute to such host specificity and will be discussed below.

The vast majority of *Passiflora* species possess extrafloral nectar glands on petioles, leaves, stipules, or bracts. These glands secrete nectar which maintains a defense force of predaceous ants, vespid wasps and trichogrammatid egg parasitoids. I believe habitats may differ in the degree to which the resident *Passiflora* use these different hymenoptera as defense against host specific herbivores. In a study of *H. ethilla* in Trinidad it was estimated that over 90% of eggs were killed by parasitoids (Ehrlich and Gilbert, 1973). In other areas ants are so common on the *Passiflora* (e.g. La Selva, Costa Rica) that it is hard to believe that they do not account for most of the mortality of eggs and larvae in spite of the presence of egg parasitoids.

In addition to mutualistic defense against coevolved herbivores, a few species of *Passiflora* have evolved hooked trichomes which are highly effective deterrents against some heliconiine species (Gilbert, 1971a).

*Title in program of the Congress: "Coevolved mutualism between butterflies and plants."

Passiflora species differ with respect to pollinators (various bees, hummingbirds) and seed dispersal agents (birds, bats). On the other hand, the most consistent similarity among species of *Passiflora* is the liability that most, if not all, serve as larval host for at least one heliconian.

HELICONIUS: HERBIVORE AND POLLINATOR

Heliconius or "passion flower butterflies" are common and conspicuous features of low to mid-elevation neotropical forests.⁴ The larval stages feed on leaves of *Passiflora* from which they presumably sequester the chemical products that make the adult butterfly relatively unpalatable to birds (Brower et al., 1963; Brower and Brower, 1964). Adult *Heliconius* have a reproductive life span of up to six months (Ehrlich and Gilbert, 1973), made possible by their ability to extract nutrients from pollen (Gilbert, 1972).

The behavioral complexity of *Heliconius*:

Several lines of evidence suggest that *Heliconius* may have the most behaviorally sophisticated adult phase among butterflies: 1) Adults roost gregariously (Poulton, 1931; Crane, 1957; Turner, 1971) and individuals are highly faithful to the same roosting spot over extended periods (Benson, 1972). 2) Both adult feeding stations and roosting areas are located by visual navigation under the poor light conditions of early morning (ca. 0530 hr) and late evening (ca. 1800 hr), respectively (Gilbert, 1971b and unpublished data). 3) A circadian rhythm in photic (versus color) sensitivity (S. Swihart, 1963, 1964) is nicely consistent with the needs of visual navigation early and late in the day. 4) Adult *Heliconius* can be conditioned to discriminate color associated with nectar rewards (C. Swihart, 1971) and preliminary evidence indicates an ability to learn to associate shape with reward.⁵ 5) In addition to regular return to roosting areas, *Heliconius* show up at particular nectar and pollen sources with a high degree of temporal regularity from day to day (see Fig. 3 below). This strongly indicates that *Heliconius* possess a kind of circadian memory rhythm akin to that known for bees (Koltermann, 1971). 6) *Heliconius* seem to be uniquely qualified for life in greenhouses, insectaries and all manner of artificial environments.⁶ I attribute this to the fact that *Heliconius* orient primarily to learned land marks, one of which, in this case, being enclosure walls. Most other butterflies observed under similar conditions,⁷ except when motivated to feed, mate, or oviposit, orient to sunlight and ignore the enclosure walls. Under such circumstances, fatal damage to the wings occurs in just a few days. 7) *Heliconius* have a very broad visual spectrum - possibly the broadest of all animals (Gary Bernard, personal

communication). 8) For their body size, *Heliconius* have the largest heads of New World butterflies and probably of all lepidoptera.⁸ Given the capability of the *Heliconius* visual system, and given that a butterfly head is mainly compound eyes and optic ganglia, this observation should not be surprising. Indeed, for some other insects, head size and foraging efficiency are known to be positively correlated (Bernstein and Bernstein, 1969). 9) Even in non-visual aspects of behavior, *Heliconius* are highly complex. For instance, female pupae of a number of species in the *hecalesius* and *charitonius* Groups of *Heliconius* (Emsley, 1965) release a pheromone which attracts males, who then sit on the chrysalis waiting for eclosion. This behavior was first noticed by Edwards (1881) in *H. charitonia*.⁹ Other species of *Heliconius* appear superficially to act more like typical butterflies in their mate discovery and courtship. But I have gathered circumstantial evidence that in species such as *H. ethilla* which do not utilize pupal mating, males locate the positions of female prepupae by their odor and return daily to the same areas (Gilbert, unpublished data). Moreover, pupae of *Heliconius* make audible squeaks (Alexander, 1961b) and the adults can hear (Swihart, 1967). Thus, even when pheromones are not released by pupae, communication is possible between pupal and adult stages. 10) Insectary and field observations indicate two ways that the visual system of *Heliconius* enhances the more usual chemosensory modes of host plant discovery.¹⁰ First, as females gain experience in oviposition, they begin to associate the shape and form of the host plant with its chemistry. Circumstantial evidence for this is the frequent insectary and field observation of egg-laying females attracted to visually similar non-host plants. Both form perception and the use of shape by egg-laying females is known in *Papilio democles* L. (Vaidya, 1969a,b).

A second way that *Heliconius* visual sophistication increases the foraging efficiency for larval host involves learning the position of particular *Passiflora* vines and returning on a regular basis. Although such traplining behavior has been demonstrated only with respect to pollen sources (see below) observations of the same marked female routinely visiting the same vine (W. W. Benson, personal communication; Gilbert, unpublished observations) are good indications that *Passiflora* are incorporated into pollen nectar routes. This is almost certainly the case in populations like the Andrew's Trace *H. ethilla* (Ehrlich and Gilbert, 1973) where the spatial aspect of population structure is governed by the distribution of adult, rather than larval resources (Gilbert, 1971b). 11) Ovipositing females often spend considerable time inspecting the host plant after it has been discovered. It seems reasonable to suggest that this behavior is a visual search for egg predators and for other *Heliconius* eggs or larvae which in many cases are

cannibalistic. The latter hypothesis is supported by the rarity of two or more independently laid eggs on the same growth point even under moderate densities of females in the field. (Random oviposition would lead to occasional clumps which are not found.) W. W. Benson (personal communication) has independently come to similar conclusions.

Heliconius diversity and host specificity:

There are about 45 species of *Heliconius* (Emsley, 1965; Brown and Mielke, 1972), each a specialist on some sub-set of available passifloraceous species. Local habitats, however, typically contain no more than 10 *Heliconius* species, each associated as a rule with a different primary host species. There is, therefore, a correspondence between *Passiflora* and *Heliconius* species diversity at the local level due to a partitioning of host species among the herbivore species.

These patterns of host specificity and partitioning in local *Heliconius* communities may be the ultimate outcome of chemical coevolution between the butterflies and *Passiflora* (see Ehrlich and Raven, 1965). However, indications are that the basis of the observed pattern is more complex than simple chemical interaction between plant and coevolved herbivore. For example each of the six *Heliconius* species¹¹ maintained in the tropical insectaries at Austin has been reared to adulthood on one or more plants not generally chosen by its ovipositing females and even will feed upon, and damage, plants which are unsuitable for normal development. Alexander's (1961a) observations are consistent with this data. Moreover, given the visual component of host location mentioned above, I suspect that non-chemical factors are important in the evolution of host specificity in *Heliconius* as was found to be the case in *Euphydryas editha* (Singer, 1971).

Heliconius population biology:

A two-year population study of *Heliconius ethilla* in Trinidad revealed remarkable constancy of adult numbers in two adjacent sub-populations (Ehrlich and Gilbert, 1973). During the entire period, including two dry seasons, there were no significant changes in the number of adults estimated at 20 day intervals. Moreover, at no time was there a difference in size between adjacent sub-populations occupying similar areas of forest.

The observed spatial structures of *Heliconius* populations, like their dynamic aspects, indicate the operation of strong deterministic elements. The research on *H. ethilla* and Turner's (1971) study on *H. erato* revealed highly sedentary populations which apparently result from individual home range behavior by adults.

Studies of marked butterflies indicate that the daily reproductive effort (eggs or spermatophores) is very constant and may even increase as adults approach their maximum age of 6 months (Gilbert, 1972). The unusually extended reproductive life of *Heliconius* can act to buffer perturbations in larval survivorship (Gilbert, 1971b). For instance, any perturbation in *Passiflora* availability or in intensity of larval predation which is less than 3-4 months will be buffered. Very few natural disasters such as complete defoliation of all possible larval hosts by other insects will last beyond the reproductive life of a female *Heliconius*.

When all these features of population biology, longevity and reproductive activity are viewed as an interacting system, it is a simple step to suspect that the pollen often seen on the proboscis of *Heliconius* has an important nutritive function. Table 1 summarizes the evidence that pollen is an important source of amino acids for egg production and quite possibly for adult maintenance.

ANGURIA: TRADES POLLEN FOR SEX

Ultimately it is the flowering pattern of their pollen plants which provide the option of extended adult life and reproductive effort for *Heliconius*. Although numerous species can be listed as pollen and/or nectar sources for *Heliconius* (Gilbert, 1972), it is the little-known, inconspicuous cucurbit genus *Anguria* and a few species of their relatives, *Gurania*, with which these butterflies have most conspicuously coevolved. Indeed, I have removed pollen from museum specimens of *Heliconius* collected from southern Brazil to Veracruz, Mexico, and have found the characteristic tetrads of *Anguria* to be the only pollen consistently represented over this entire range.

Anguria and *Gurania* are represented by 29 and 73 species, all restricted to the neotropics (Cogniaux, 1924). Like *Passiflora*, the species diversity of these cucurbits is strikingly consistent and low from locality to locality. In each of four rainforest study sites in Trinidad, Panama and Costa Rica the maximum number of sympatric, *Heliconius*-visited cucurbits is either 2 or 3, and no more than 4 even if hummingbird pollinated *Gurania* species are included. Moreover, as was the case with local *Passiflora* populations, individual plants are widely spaced.

Early systematic treatments of *Anguria* and *Gurania* indicate that all species are dioecious and that natural populations have male biased sex ratios (Cogniaux, 1924; Cheesman, 1940). All of the seven species¹² which I have studied in the field and grown in the insectary fit this pattern except for *G. leviana*, a hummingbird pollinated species, which is monoecious.

Anguria flowers are produced in an inflorescence on a long peduncles if male, in pairs at each node if female. Male flowers

Table 1. Evidence for pollen feeding in *Heliconius* (summarized from Gilbert, 1972).

1. Distinctive pollen collecting behavior in *Heliconius*.
2. Other species do not accumulate pollen loads when visiting *Heliconius* pollen plants.
3. *Heliconius* possess elaborate pollen-processing behavior which includes mixing of dry pollen with exuded nectar.
4. Morphological details of *Heliconius* proboscis that are involved with pollen collecting are lacking in non-pollen gatherers.
5. In experiments with artificial flowers, glass beads are chosen over sugar water.
6. Active release of amino acids and protein by pollen soon after mixing in sugar solution eliminates need for chewing or digesting.
7. *Heliconius* assimilate free amino acids and use them in egg production.
8. Pollen feeding increases egg production as much as 5 X over that observed in straight nectar diets.

last only one day, then drop off of the inflorescence. Daily production by one inflorescence is typically .3 to .5 flowers per day, although some species of *Anguria* (e.g. *Limonense*) produce 1.0 flowers per day for the first few days of flower production. By counting the scars of previous flowers and dividing by estimated daily rate of production, it is possible to estimate the total time that any particular *Anguria* has had flowers available to pollinators.

Field and insectary observations indicate continuous flowering by male plants for periods ranging from 6 months to 3 years. Amazingly enough, a single inflorescence may have a life span of from 3 months to over a year. A single inflorescence of *A. grandiflora* Cogn. collected in the Carare Valley, Columbia, (deposited in the Chicago Field Museum of Natural History) showed evidence of 410 past flowers and at least 35 buds waiting to

BUTTERFLIES AND PLANTS

flower when pressed. This represents at least 1 year, probably more, of continuous pollen and nectar production at one point in space, as well as life-long feeding stations for any *Heliconius* fortunate enough to locate this scattered and highly inconspicuous resource.

But, in spite of such long term predictability in flower production, there can be great day to day variation in total flower production on any particular male plant. This fact results from little or no correlation between the flowering patterns of the different inflorescences on a plant. To illustrate, Table 2 summarizes flower production for 16 inflorescences of an *A. umbrosa* male for a 16 day period. Notice that daily flower production varies from 2 to 10 with an average deviation of 1.57 flowers/day from the mean of 6.06 flowers/day. At the same time, the variation between inflorescences over the 16 days is much less (an average deviation of .71 flower/inflorescence from a mean of 6.06 flower/inflorescence).

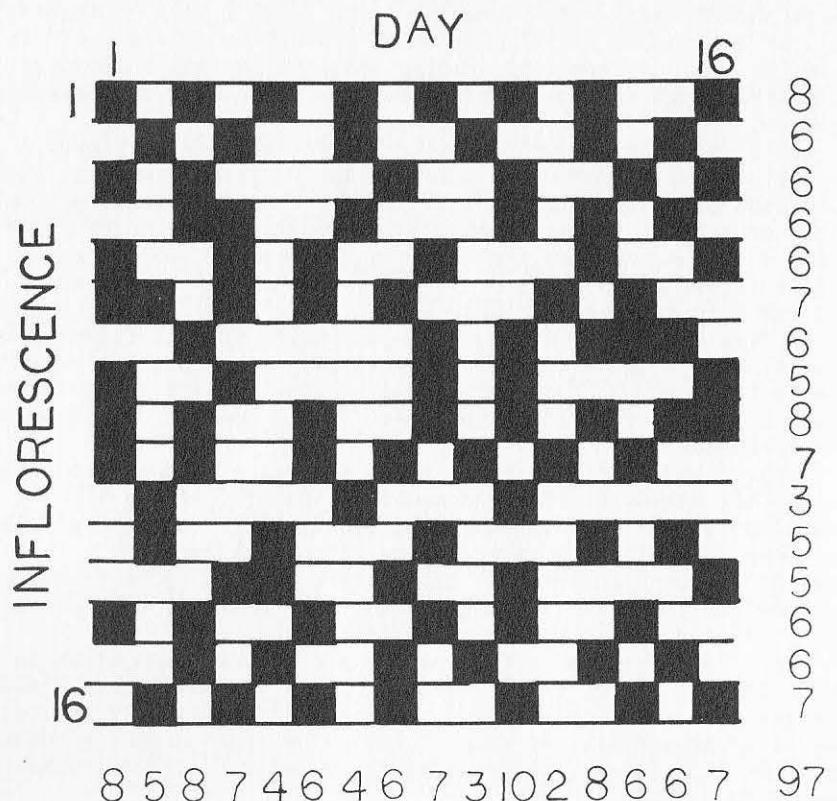
Other important variables in the pattern of flower production include the number of inflorescences per plant (1-20 in *A. triphylla*; 5-100 in *A. umbrosa*) and the distances between adjacent flowering male vines (typically from .1 to .5 kilometer). The implications of such temporal and spatial patterning in resource availability for understanding the foraging behavior of *Heliconius* will be discussed in the following sections.

Both temporal and spatial patterns of flower production in female *Anguria* differ greatly from those of the male vines. Not only are the female plants less frequent and more widely spaced, they also cease flowering when a cluster of fruit begins to develop. There are thus several reasons for the relative rarity of female flowers in nature.

Mature *Anguria* fruits resemble small cucumbers and each contains 50-60 mature seed. Entire fruits are sometimes found on the forest floor after being dropped by parrots (beak marks are distinctive). Squirrels also eat the fruits and may also carry them away whole since fruits often disappear completely, without a trace. Green fruits are often destroyed by an unidentified lepidopteran larva which bores into the fruit.

BUTTERFLY EGGS AND CUCURBIT SEEDS

Mutualisms are those interspecific relationships for which benefits clearly outweigh costs for each species involved, and for which net profits to individuals of each species can be translated into an increase in Darwinian fitness.



ANGURIA UMBROSA

Table 2. Each row represents the flowering of a single inflorescence of *A. umbrosa* over a 16 day period. Each column represents a day's flower production by the 16 inflorescences. Solid boxes represent flowers. The average number of flowers per day and the average number per inflorescence over 16 days is 6.06.

Benefit versus cost for the butterfly:

The advantage to *Heliconius* of its pollen collecting visits to *Anguria* are clear (Gilbert, 1972). Studies on the nitrogen budget of this system show that a large (no. 3 on a scale of 0 to 3) load of *Anguria* pollen contains sufficient nitrogen to account for the production of 5 eggs of *H. charitonius*,¹³ which approximates the daily egg production of many *Heliconius* species.

What are the costs to *Heliconius*? One kind of cost is the time and energy required for foraging; another is the increased risk of predation which is itself a function of time exposed while foraging. Because *Heliconius* are relatively unpalatable and warningly colored I assume the latter cost to be small.

Although *Anguria* flowers all year-around in rain forests, with individual male plants flowering constantly for as much as one year, there is still the previously discussed day to day uncertainty in the number of flowers available per plant. This uncertainty in the daily availability of resources at one point in space is further compounded a) as average number of inflorescences per plant decrease and/or b) as the number competing *Heliconius* per inflorescence increase. The greater the uncertainty per plant, the more plants a *Heliconius* must incorporate into its trapline to obtain, with high certainty, a given quantity of pollen.

Cost-benefit analysis would predict that whenever the cost of visiting *Anguria* plants exceeds the benefits of the pollen collected, foraging should ultimately cease. A comparison of female versus male foraging behavior strongly supports this prediction. Early morning pollen foragers (ca. 0530-0630 hr) are about 90% female in Trinidad *H. ethilla* (Gilbert, 1971b). Consequently, in a total sample of 794 pollen loads, 93% ($N = 44$) of all large pollen loads were borne by females (Gilbert, 1972) because early individuals get most of the pollen. Males, for reasons discussed by Gilbert (1972), benefit less from daily pollen collectings than do females. One possible exception to this rule occurs on the day following a mating when males would benefit from rapid replacement of spermatophore material.¹⁴

Benefit versus cost for the cucurbit:

Turning now to the plant point of view: what are the benefits in *Anguria* feeding pollen to *Heliconius*? The obvious answer is that seed-set requires an animal pollen vector in dioecious plants. However, if one examines the cost of pollinator service to *Anguria*, it is seen first, that male plants bear the burden of this responsibility¹⁵ and second, that because females are rare much more pollen is produced than appears necessary for pollinating the occasional female plants which come into flower. Furthermore, nectar

production, which occurs primarily after pollen removal (see Fig. 4 below), is an added cost to the plant which is even more difficult to relate to benefit since the majority of post-pollen nectar visits come from males not bearing pollen (Gilbert, unpublished data).

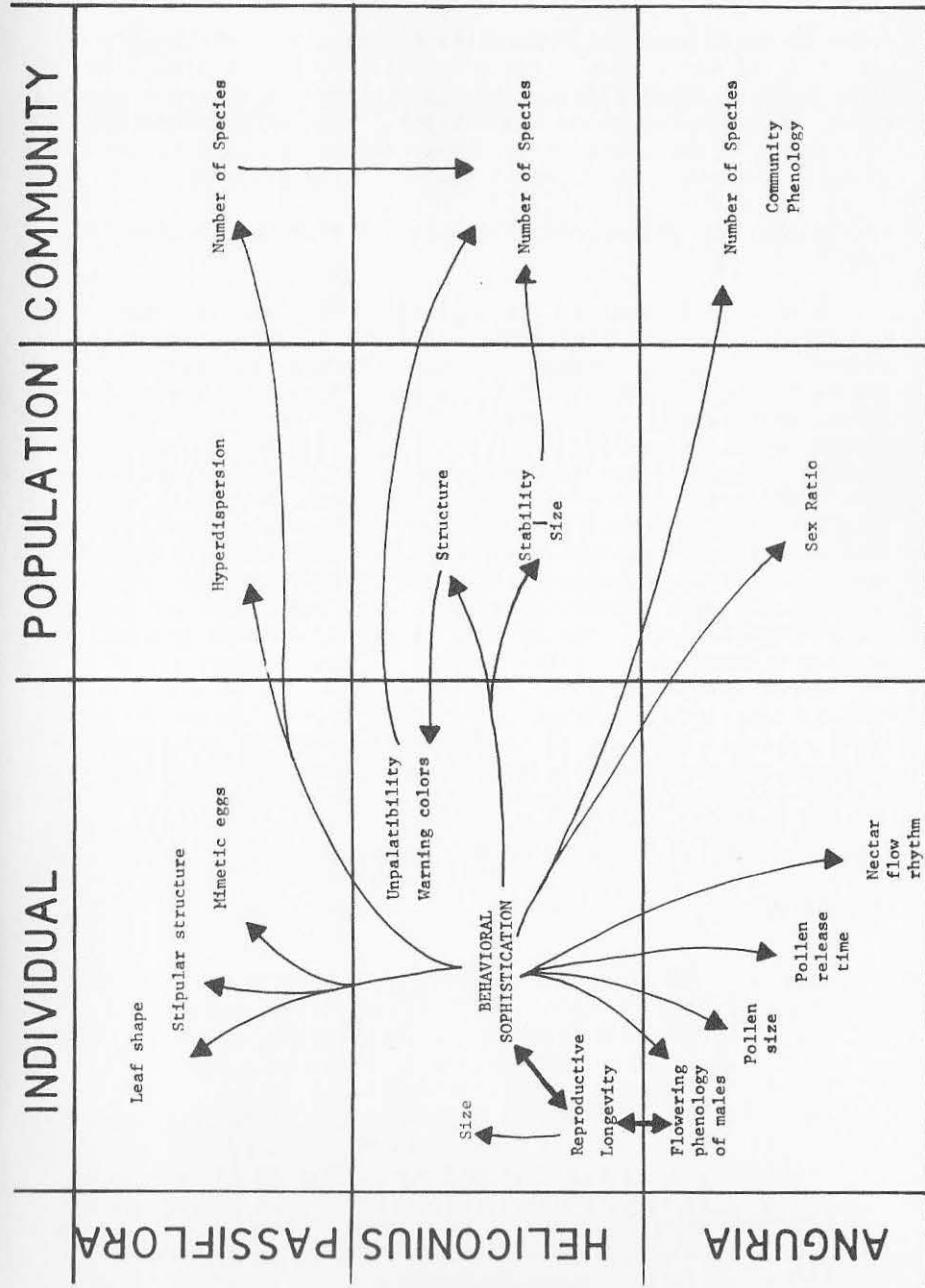
I suggest that the prodigious pollen and nectar production by male *Anguria* and possibly the evolution of larger, more efficiently collected pollen grains¹⁶ have evolved by a botanical version of sexual selection, whereby the *Anguria* male genotype which most consistently keeps *Heliconius* stocked with pollen is the one most likely to have its pollen land on the rare female stigmas which sporadically appear throughout the year. In general, any trait of the male which would enhance the plant's attractiveness to *Heliconius* would be selected for the same reason (assuming that *Heliconius* can discriminate the different genotypes). Since pollen collecting by *Heliconius* takes place in semi-darkness for many *Anguria* species, the function of subsequent nectar production during the brighter hours might be to help train the butterflies to the male plant's position. Nectar production by the female flower, to be discussed below, may serve a similar function.

Thus, traits of *Anguria* males which might have been hazily interpreted as "mechanisms to keep the pollinator in the system" are more plausibly interpreted as traits evolved to maximize individual fitness.

CONSEQUENCES OF THE *HELICONIUS X ANGURIA* MUTUALISM

Pathways by which the *Heliconius x Anguria* mutualism influence both component and emergent properties of a restricted, coevolved community are shown in Figure 1. The heavy line connects those features of *Heliconius* and *Anguria* most likely evolved in context of the mutualism: the reproductive longevity and associated behaviors of *Heliconius* and the flowering pattern of *Anguria*. Specifically the innovation of pollen feeding by *Heliconius* and the constant availability of *Anguria* pollen and nectar has, by shifting the burden of reproductive effort from larval to adult stages, increased the reproductive longevity and reproductive value of adults (Gilbert, 1972). Any physical or behavioral trait which increases adult foraging efficiency or

Figure 1. Pathways by which *Heliconius x Anguria* mutualism influence individual, population and community level features in a system of interacting species. See text for explanation.



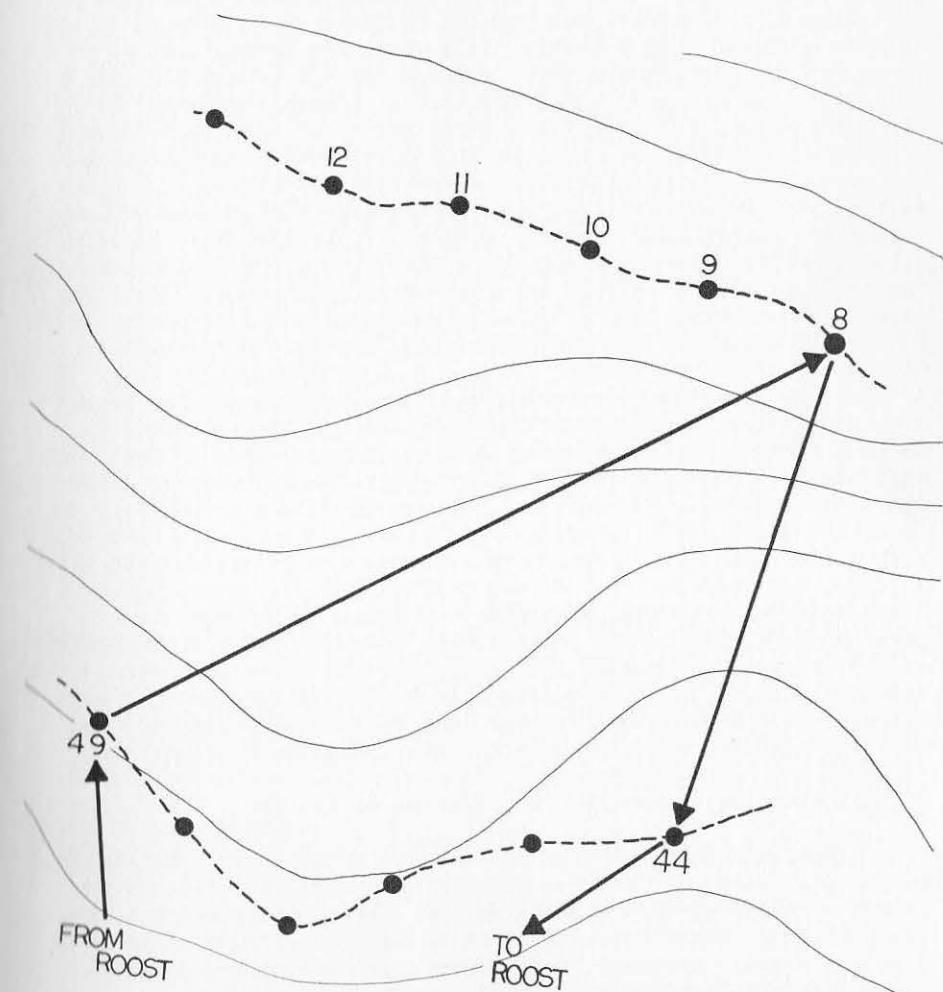
competitive ability will therefore be selected. The highly developed visual system, related head size, learning ability, and early morning flight, etc., are all traits, previously discussed, which can be explained in these terms. Many other properties of the system depend directly on these behavioral capabilities of the butterfly, as will be shown in the following paragraphs.

Navigation, gregarious roosting, kin selection and *Heliconius* diversity:

Since pollen sources are spatially constant over many weeks but inadequate and unpredictable on a daily basis, traplining is clearly an optimal foraging strategy. Perhaps the best evidence for traplining behavior in insects comes from a female *H. ethilla* (#466) whose daily movement patterns can be reconstructed from extensive recapture data (Fig. 2). Notice the close correspondence between time and space in the movements of this *H. ethilla* female. Mate-seeking males have been found to behave in similar fashion (Gilbert, 1971b). Such faithfulness to time windows has been described for tropical bees (Janzen, 1971). Although there has been no experimental demonstration of circadian memory rhythm in *Heliconius*, these observations are highly suggestive of such a mechanism. Moreover, the pattern of nectar flow in sympatric *Anguria* is also consistent with this hypothesis (see below).

Roost site fidelity by an individual would improve its ability to locate the first points on traplines under the poor light of early morning. I have hypothesized that gregarious roosting has evolved in *Heliconius* as the result of young individuals following, then roosting, near experienced individuals to enhance their chances of locating scarce, inconspicuous, pollen sources (Gilbert, 1971b). Evidence that experience enhances pollen acquisition is provided in a contrast of pollen load size between young (1 month old) and middle aged (1-3 months old)

Figure 2. Part of the trapline of *H. ethilla* female #466 (from Gilbert, 1971b). On 20 August, 1970, this female was recaptured three times: 1) Station 49, *Gurania spinulosa*, 0550 hr; 2) Station 8, *Palicourea crocea*, 1150 hr; 3) Station 44, *Anguria triphylla*, 1345 hr. On the following day (21 August) #466 was once again seen early at Station 49, and was seen or taken there on two other early morning visits. It was also taken at 49 at 1025 and 1125 hr. The *Anguria* at Station 44 was always visited late by #466: 1410 hr, 1450 hr, and 1345 hr. Stations are 50 yards apart; the line from Station 8 to 12 runs along a ridge; the contour intervals are 100 ft. A map of the entire area is found in Ehrlich and Gilbert (1973).



individuals. In a sample of observations from the Trinidad study area, the young and middle aged individuals were equally abundant (40 vs 41%, N = 305) yet among the older individuals large (no. 3) pollen loads were 6X more frequent (Gilbert, unpublished data).

Because individuals are regular in their daily movements, and because of their long potential life span, the butterflies on a roost probably include several generations of closely kin individuals.¹⁷ Benson (1971) and Turner (1971) have suggested that the apparent small size and sedentary nature of many *Heliconius* populations would allow kin selection to operate, accounting for the evolution of unpalatability and warning coloration in *Heliconius*. Here then is a possible pathway by which *Heliconius* diversity is influenced by increased behavioral sophistication. Richard Levins (1974) has concluded that, in theory, selection for predator avoidance will increase prey populations. Thus, on a given resource base more *Heliconius* individuals can be packed into a habitat because of warning coloration, and more rare species will persist at equilibrium.

Figure 1 indicates other pathways by which increasing behavioral sophistication might determine levels of species diversity for *Heliconius*. Many butterfly species disperse from an area when host plants, nectar sources or other individuals disappear (Gilbert and Singer, 1973). In contrast, because they have the ability to learn the locations of previously visited resources and because of strong roost fidelity, *Heliconius* are less likely to leave an area during temporary shortages of ovipositional sites, mates, etc. This would decrease the probability of local extinction at any given population size and increase the potential number of species at equilibrium. Note that another factor which would enhance *Heliconius* diversity by reducing probability of local extinction was discussed above: namely, the long reproductive life allowed by pollen feeding which acts to buffer population fluctuations.

Circadian isolation and cucurbit species diversity:

Numerous *Heliconius* were observed to visit *Anguria triphylla* in the afternoon and ignore a *Gurania spinulosa* (visited earlier in the morning) clearly visible nearby. These observations stimulated a study of the time course of anther dehiscence and nectar flow in several insectary grown species of *Gurania* and *Anguria* taken from the Trinidad study area.

A striking separation occurs between the sympatric *Anguria* species both in pollen release and nectar flow (Fig. 3). *Gurania spinulosa* (not figured), which releases pollen early with *A. umbrosa*, flows its nectar in the mid day minimizing overlap with the *Anguria* (Gilbert and Golding, in preparation). Whether this temporal displacement is due to selection for increased reproductive isolation or for decreased overlap on the pollinator resource

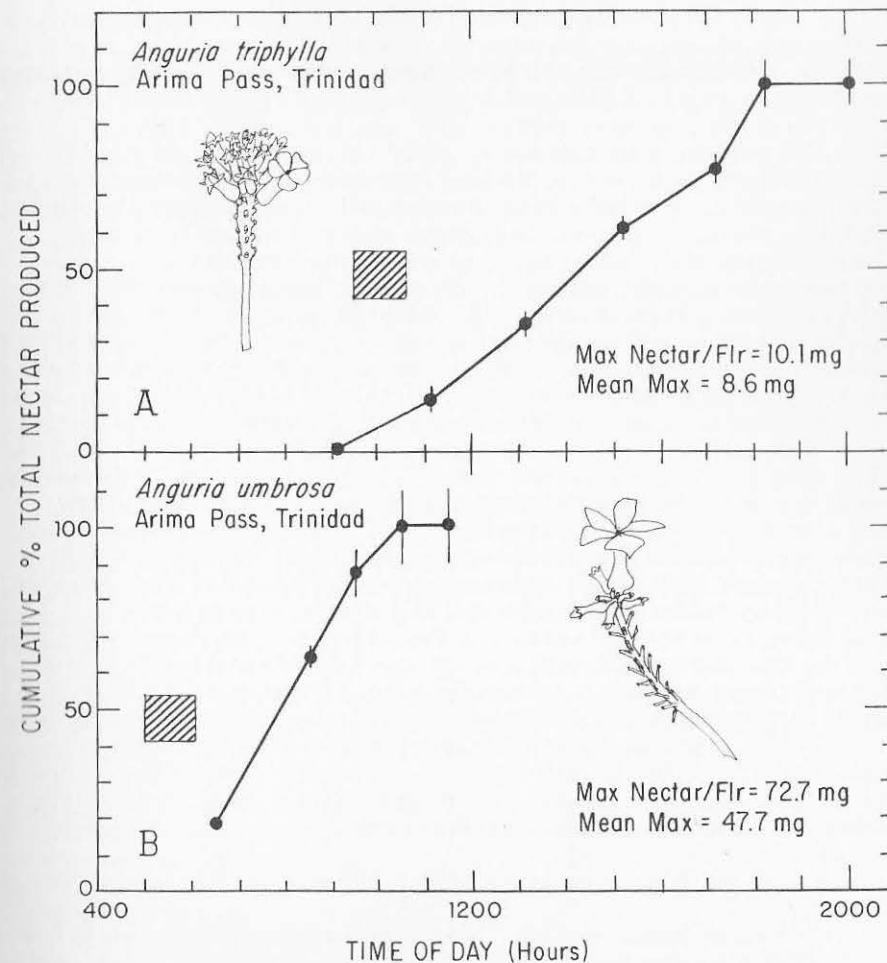


Figure 3. Temporal separation in pollen release (hatched box) and nectar flow patterns in two sympatric *Anguria* species from Arima pass Trinidad. (From Gilbert and Golding, in preparation.) Note that pollen is released before nectar flow is initiated.

is not certain, but the latter possibility is less likely under limited pollen supply. I know of no other clear example in which closely related plants with simultaneously opening flowers divide up a single group of pollinators by evolving different nectar flow and pollen release rhythms.¹⁸

The evolution of circadian isolation as is seen in *Anguria* is most feasible where the pollinator possesses an accurate circadian memory rhythm. The more finely tuned and sophisticated the memory rhythms, the more species of closely related sympatric plants could coexist while utilizing the same pollinator group. Koltermann's (1971) important work on bees demonstrated that bees entrained on different scents or colors through a day would, exactly 24 hours after each entrainment, respond in the appropriate way as long as different stimuli were originally presented at intervals of more than 20 minutes.

On the basis of the limited number of sympatric *Anguria* (no more than two) in all localities so far studied, my guess is that this interval is much larger for *Heliconius*; i.e., as an isolating agent to be divided among sympatric *Anguria* species, *Heliconius* (as a group) can only be divided two or three ways on a daily basis beyond which isolation would break down; and only future refinement of *Heliconius* circadian memory will allow more *Anguria* species to coexist. Reciprocally the plants have apparently evolved more effective circadian isolation by expanding into the crepuscular periods at each end of the day. This is indeed possible in the lowland tropics where high nighttime temperatures allow butterfly flight activity. Indeed, I would hypothesize that the diurnal shift in *Heliconius* ERG (Swihart, 1963, 1964), allowing early morning piloting, is ultimately the result of the butterflies coevolving with the cucurbits in a context of strong competition for limited pollen resources.

Heliconius learning, sexual selection and sex ration in *Anguria*:

In the previous section I described a way that sexual selection in plants might account for the great amounts of nectar and pollen given away by *Anguria* in the virtual absence of females. This hypothesis, which would apply equally well to the male parts of genetically incompatible or delayed monecious species, depends upon a pollinator which can discriminate different genotypes of male plant. In like manner it is possible to account for the male-biased sex ratio in *Anguria*.

One of the most fascinating population features of both *Anguria* and *Gurania* is the fact that sex ratios are heavily biased in favor of the males (usually $> 10:1$) in all species across all areas examined (Trinidad, Panama, Costa Rica; Gilbert, unpublished data). Indeed, only 20 out of 102 species are described from female flowers in the only major monograph on these genera

(Cogniaux, 1924). Recently Lloyd (1973) has described similar male excess in many of the sexually dimorphic perennial Umbelliferae of New Zealand. He accounts for this departure from the expected 50:50 ratio (Fisher, 1930) by hypothesizing that females have a shorter life expectancy than males due to greater energy expenditure in reproduction. Even if valid, this explanation will not hold for *Anguria* and *Gurania* since the yearly reproductive effort of a male can easily equal or exceed that of a female.¹⁵

Data from sterile plants collected in the field and grown to flowering and from the few plants that I have managed to grow from seed to flowering condition indicate either a large male excess in the primary sex ratio or extremely delayed monecious condition. To date no female plant has appeared among about 10-12 separate plants of the different species (grown from seed) which have flowered. While final proof on primary sex ratio is still pending, I am confident that to think about this sort of model may be highly useful in interpreting sex ratio data from tropical plants with intelligent pollinators.

The model is based upon sex-specific, frequency, and density dependent selection and requires that selection operate at the level of a sibling cluster. This is possible for plants if seeds drop near the parent or if dispersed in groups as is the case in *Anguria* where intact fruits, containing viable seed, are often dropped by rodents and parrots.

Anguria female flowers can be considered mimics of the male flowers. The important signal receiver to be deceived (Wickler, 1968) is the pollen-seeking female butterfly since they collect the majority of pollen. Deception might occur in several ways: 1) The female flowering branch in several *Anguria* species is telescoped in such a way as to look like a male inflorescence. 2) The stigmatic surface is covered with pollen-sized bumps, which may be more important than flower color mimicry since it is known that the butterflies confuse pollen and pollen-sized glass beads (Gilbert, 1972).

Male-biased sex ratio will occur 1) if *Heliconius* is able to discriminate and avoid mimics when they become too frequent relative to males in an area, and 2) if those high frequency clusters of females are the offspring of a female which produces (with high heritability) equal or female-biased sex ratios in her seedcrops.

Females in clusters are further disadvantaged by fruit and seed destruction caused by a moth species whose larvae attack female but not male reproductive parts. This is an additional sex specific, density dependent component which could be partly responsible for evolution of male-biased primary sex ratios in plants.

Egg-laying *Heliconius*, *Passiflora* leaf-shape diversity, and egg mimicry:

The apparent importance of vision and visual memory in larval host plant foraging by egg-laying *Heliconius* stimulated me to investigate the possibility that these females are agents of selection on *Passiflora* leaf shape. Under such visual selection *Passiflora* would be expected to evolve leaf shapes which would make them more difficult to locate. There should also be pressure to diverge from other *Passiflora* species since larval food niche breadth is considerably broader than that of ovipositing females and oviposition mistakes occur.¹⁹ The predicted high local diversity of *Passiflora* leaf shape in contrast to the often noted monotony of tropical leaves (Richards, 1951) is strikingly verified (Fig. 4). When leaves of two sympatric species are similar in shape, they usually differ in pubescence, reflectance, stipular structures or tendrils such that the gestalt of the plants are different (Gilbert, in preparation).

The literature on leaf shape is concerned almost entirely with shape as it relates to physical factors. Yet, just as the first recognition of mimicry in animals was by taxonomists who simply observed similarities and named species accordingly [e.g. various genera of moths named *Apiformis*, *Vespiformis*, etc. (Remington, 1963)], so *Passiflora* taxonomists have recognized the extensive convergence of *Passiflora* leaf shapes on those of common tropical plants which are essentially vast amounts of inedible substrate to *Heliconius*. The following species names are found in Killip (1938): *discoreaefolia*, *morifolia*, *bauhiaefolia*, *tiliaeefolia*, *capparidifolia*, *laurifolia*, *guazumaefolia* and *dalechampioides*. All of these are generic names of common tropical trees and vines.

There is some evidence from other plants that visual selection may be significant in determining leaf shape. For example, the striking similarities in both leaf shape and texture between numerous pairs of species in two south African plant genera, *Cliffortia* (Rosaceae) and *Aspalathus* (Fabaceae), (Dahlgren, 1971) probably reflect strong visual selection from herbivores. The convergence of Australian mistletoe leaf shapes on the leaf shapes of their host trees (mostly *Eucalyptus*) (B. A. Barlow and D. Wiens, personal communication of unpublished data) is in effect the same phenomenon as was described for *Passiflora* above: (i.e. small patches of edible plant blending in with a large amount of inedible foliage).

Further evidence that ovipositing females exert visual selection on *Passiflora* is the presence of butterfly egg mimics on several species. I first discovered these on *Passiflora cyanea* (Fig. 5), then on *P. auriculata* (both from Trinidad). Since most

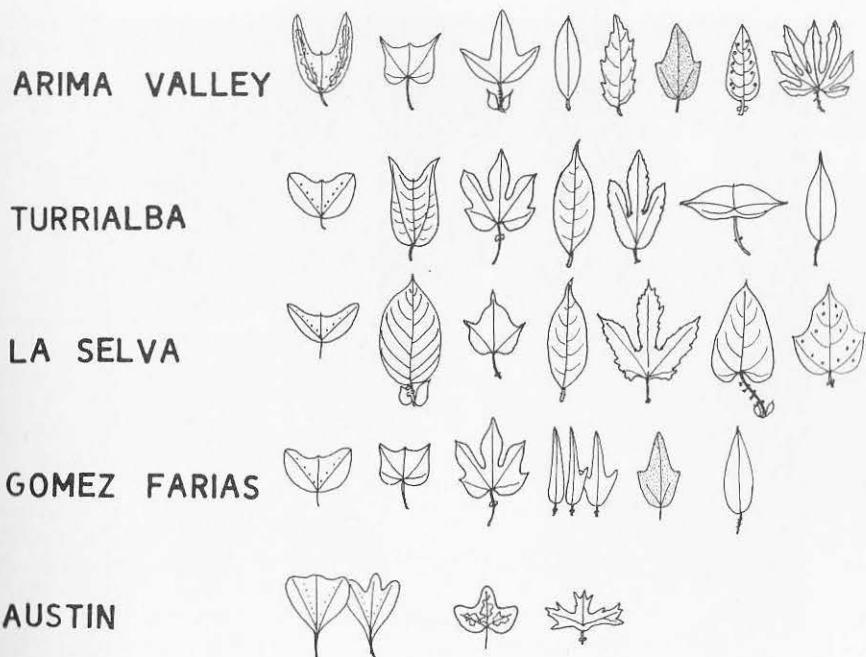


Figure 4. Leaf shape variation among sympatric species of *Passiflora*. The localities are from the top: Trinidad, Costa Rica, Costa Rica, Mexico and Texas. (From Gilbert, in preparation)

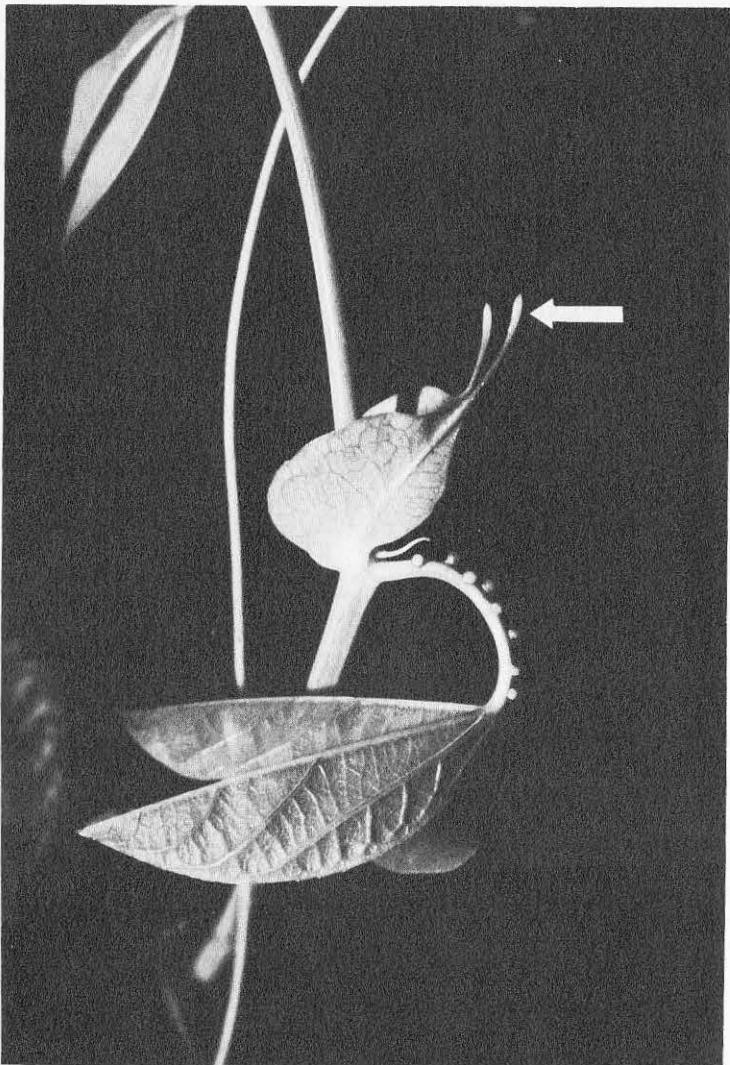


Figure 5. Mimetic egg (arrow) on stipule of *Passiflora cyanea*. Several days earlier, new growth point was sheltered within stipule so that fake eggs were presented in the area where eggs are usually deposited. Note extra-flora nectar glands on petiole.

larval *Heliconius* are cannibalistic to a certain degree it makes sense for the female to detect and reject growth tips of host which already possess eggs or young larvae. Interestingly the fake eggs are closer to the color of eggs near the point of hatching or young larvae (golden) than to the color of newly oviposited eggs (yellow).²⁰

Psychological limits to local *Passiflora* diversity:

The ability of ovipositing females to learn and discriminate shapes may greatly influence local *Passiflora* diversity. As was pointed out above, in spite of some 350 New World *Passiflora* species, the total number of species packed into a local habitat rarely exceeds 10. The hypothesis is that the number of *Passiflora* species should be approximately the number of shape categories discriminated by *Heliconius*. It can be easily seen that if an alien *Passiflora* "attempts" to colonize an area in which all possible leaf shapes are already represented it will be discovered by experienced females searching for its particular leaf category. Even if chemically different it will be severely damaged in its vulnerable seedling stage where loss of leaf area can mean death.

Only two *Passiflora* species known to me could possibly be added to an equilibrium community in spite of leaf shape. Interestingly these are two of the most wide-spread species in Central America. One, *Passiflora adenopoda* is unaffected by most *Heliconius* because of its cuticular trichomes which kill larvae (Gilbert, 1971). The second, *Passiflora serratifolia*, is, in the insectary, a favorite oviposition plant for many species in the genus. In fact, it is the "super-optimal" oviposition stimulus for all *Heliconius melpomene* races which do not overlap its range. *P. serratifolia* possess a chemical in the young leaves which, though not detected by ovipositing females, kills all young larvae (Gilbert, unpublished data).

Leaf shape and *Heliconius* diversity:

It was pointed out earlier that for reasons not adequately understood, the number of *Passiflora* species in an area predict reasonably well the number of *Heliconius*. If, as hypothesized, the degree of shape discrimination by the butterflies puts an upper limit on the number of species of *Passiflora* which can be packed into a community, then it follows that *Heliconius* can indirectly limit their own local diversity.

CONCLUSION

The study of animal-plant coevolution has generally focused upon the interaction between plant and herbivore in isolation from concomitant interactions with other relevant members of the community. In this paper I have developed a conceptual model of the ecological and evolutionary feedback occurring within a food-web of interacting species, which is greatly amplified and accelerated by a mutualistic interaction.

The *Heliconius-Passiflora-Anguria* system is in many ways a special case which I have greatly oversimplified. For instance, few insects outside of the Lepidoptera interact with plants as both mutualist and herbivore. Even within the Lepidoptera, *Heliconius* may represent the most elaborate instance of this life-history type. However, since so little is known of the adult nutrition of most lepidopterans, the uniqueness of these butterflies remains an open question.

It should also be made clear that the model is derived from experiments and observations on just a fraction of the many species of *Heliconius*, *Anguria*, and *Passiflora*. I have knowingly ignored potentially important organisms such as the pollinators of *Passiflora*, other pollen plants of *Heliconius*, other pollinators, and herbivores of *Anguria*, to name a few.

Further research will almost certainly modify the details of Figure 1. However, I believe this somewhat specialized model illustrates some general ideas about the significance of mutualism in communities which deserve further testing by students of community ecology:

1. Animal-plant mutualisms depend upon and help determine the behavioral sophistication of the animal involved.
2. The behavioral capabilities of animals in a food-web strongly influence the local diversity attained by various taxa in the web as well as other emergent properties such as phenologies and patterns of morphological diversity among the plants. (Visual search for plants by host-specific herbivores may help generate morphological divergence within, and convergence among, chemically distinct groups of plants in a community.)
3. The importance of mutualism in terrestrial communities is greatest: a) where the animals involved have strong trophic ties to several distinct groups of organisms, and b) in the humid tropics where seasonal restraints on extended reproductive longevity and life history variety are lacking.
4. Since mutualistic interactions between animals and plants affect a community primarily by indirect pathways, their

BUTTERFLIES AND PLANTS

consequences are less conspicuous and more difficult to quantify than are those of predator-prey and competitive interactions. In fact, in the case considered, the mutualism determines the rules for these latter interactions.

SUMMARY

Heliconius butterflies have coevolved with two groups of plants: *Passiflora* the larval hosts, and *Anguria/Gurania* which are the primary pollen and nectar sources for the adults. As a result of increased reproductive longevity, due to mutualistic interaction with the cucurbit vines, *Heliconius* have evolved highly sophisticated behavior patterns which include various forms of learning and memory. Many features of the individuals and populations as well as emergent properties of this coevolved sub-community are casually linked either by direct or indirect pathways to the mutualistic interaction. It is suggested that animal-plant mutualism can be a major factor in generating patterns of animal and plant diversity.

NOTES

1. Baker (1963) was one of the first to recognize the need to consider community level consequences of animal-plant mutualisms. Recently such interactions have been discussed in relation to plant spacing (Janzen, 1970, 1971; Heinrich and Raven, 1972), flowering phenology (Janzen, 1967; Heinrich and Raven, 1972) and to community diversity (Janzen, 1966, 1971). In one of the few theoretical considerations of the impact of mutualism on communities, May (1973) concludes that in small model ecosystems mutualistic interactions have a destabilizing influence. But mutualism as May treats it has neither time lag nor inequality between the benefits exchanged by species involved. It is consequently not representative of most plant-animal mutualism. In contrast to well studied predator-prey and competition interactions, mutualism has been almost totally ignored by the model-makers of ecology.
2. *Gurania*, a cucurbit genus very closely related to *Anguria*, contains several species which are primarily *Heliconius* pollinated in addition to its many strictly hummingbird pollinated species. For simplicity, I will occasionally lump all *Anguria* and *Gurania* visited by *Heliconius* under "Anguria".
3. In none of 10 neotropical wet-forest sites ranging from Trinidad to Mexico have I found more than 10 coexisting *Passiflora* species. W. W. Benson (personal communication) has obtained a similar impression in Central and South America.

4. *Heliconius*, in contrast to other tropical insect taxa, are better researched than most or all similar temperate zone groups. This fortunate state of affairs is due largely to two decades of heliconiine research supported or encouraged by the William Beebe Tropical Research Station near Arima, Trinidad. Much of the important literature on *Heliconius* biology has been reviewed elsewhere (Ehrlich and Gilbert, 1973).

5. Preliminary experiments (Gilbert, unpublished data) indicate that *Heliconius* can be conditioned to discriminate leaf models by shape when associated with a nectar reward, but further work is required to establish similar learning ability to be associated with oviposition rewards.

6. One of the *Heliconius* stocks at Austin has now persisted in captivity for 4-1/2 years. Several others are 2-3 years old. All attempts to maintain other groups of butterfly for long periods have failed. *Heliconius hecale* was maintained in a windowless laboratory for three months. Visits to artificial nectar, mating, roosting and oviposition on cuttings of host all proceeded quite normally. The tops of tall burets and ring stand supports were favored daytime perches!

7. For example: *Papilio zelicaon*, *Limenitis bredowii*, *Cethosia cyane*, *Euphydryas editha*, *Actinote* spp., *Eumenes debora*, *Battus philenor* (but some *Parides* do well).

8. This statement is based on my own visual comparisons of many butterflies and should be verified by actual measurements.

9. Recently, I have found that male *Heliconius charitonia* actually rape the female pupa (Gilbert, in preparation) as a routine mating procedure.

10. Two frequently observed behaviors of egg-laying female butterflies indicates the use of chemical cues in recognition of suitable larval host plant. The first, antennal tapping, presumably relates to olfactory recognition (Minnich, 1924); the second, drumming the leaf with fore legs (Vaidya, 1956) is more than likely a direct tasting of the leaf juices (Calvert, 1974).

11. *Heliconius charitonius* Linn., *H. cydno* Doubleday, *H. erato* Linn., *H. ethilla* Godart, *H. hecale* Fabr., *H. melpomene* Linn.

12. *Anguria triphylla* Miq., *A. umbrosa* Kunth., *A. limonense* Pittier, *A. warcewiczii* Hook., *Gurania spinulosa* Poepp. et Endl., *G. costaricense* Cogn., *G. levyana* Cogn.

13. Microkjeldahl analysis indicates that a large (no. 3) load of *Anguria* pollen (dry wt. 0.7 mg) contains .028 mg nitrogen. Since one .50 mg (wet wt.) *Heliconius* egg contains about .006 mg nitrogen, such a pollen load contains the nitrogen equivalent of about five eggs (Gilbert and Norris, unpublished data).

14. We now know from radioisotope labelling experiments that nitrogenous compounds in the spermatophore contribute directly to egg production and may be of greatest importance in the first few days of oviposition, before the female has located pollen sources (Gilbert and Summers, in preparation). In the insectary, males seem to collect pollen more vigorously and successfully on the day following a mating.

15. For instance, in one year (November 1971 - November 1972) under greenhouse conditions an *Anguria umbrosa* male produced 10,000 flowers, the equivalent of 145 gm of dry sucrose and 20 gm of pollen (Gilbert, unpublished data). As this paper is delivered (August, 1973), this plant is still in flower.

16. *Anguria* pollen measures about 80 microns in diameter. It is interesting that rubiaceous plants which attract *Heliconius*, such as *Palicourea* and *Cephaelis* have unusually large (80-100 micron) pollen for their family.

17. A female which lives for 4-6 months and routinely revisits the same passion vines will quite likely encounter several generations of her own offspring emerging within her home range. If, as limited evidence indicates, young individuals follow older butterflies, the chances of families roosting together would be high. Allozyme studies of roosting groups would be of singular interest.

18. Kleber (1935) long ago demonstrated daily rhythms in nectar flow (and nectar concentrations) among numerous European plants, and partitioning of pollinators on a seasonal basis is documented (Mosquin, 1971).

19. Ovipositing female butterflies occasionally deposit eggs on inappropriate host plants (e.g. Singer, 1971). Such behavior often results from a rarity of the primary or favored host, possibly due to defoliation. I have observed insectary *Heliconius* oviposit on cucurbit vines which resemble the appropriate host. Lesser mistakes, i.e. eggs-laid on the wrong *Passiflora*, are not unlikely and are indicated by eggs found in the field on incorrect *Passiflora* (Alexander, 1961a).

20. W. W. Benson (personal communication) has independently noticed the egg mimics on several other species of *Passiflora*.

ACKNOWLEDGEMENTS

I owe particular thanks to Paul R. Ehrlich who provided support (NSF-BG19686 and GB22853X) and collaboration with the first study in Trinidad and all other persons associated with that work. Equal thanks go to the Organization for Tropical Studies in Costa Rica, where, through use of facilities and interaction with colleagues, I have benefited immeasurably. Woody Benson, Keith Brown and John Turner have provided many helpful letters and discussions and will undoubtedly be able to provide other, perhaps better, insights into the biology of *Heliconius*. I hope I have accurately acknowledged their work in the text. Other persons providing helpful discussions, criticisms of the paper or general inspiration are Martha Condon, Dan Janzen, Gordon Orians, Mike Singer, John Smiley and Joan Strassman. To these and many others who have provided useful comments at seminars I am grateful. Much of the research discussed above is supported by NSF grant GB4074X-P.

LITERATURE CITED

- Alexander, A. J. 1961a. A study of the biology and behavior of the caterpillars and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. Part I. Some aspects of larval behavior. *Zoologica* 46:1-24.
- Alexander, A. J. 1961b. A study of the biology and behavior of the caterpillars and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. Part II. Molting, and the behavior of pupae and emerging adults. *Zoologica* 46: 105-124.
- Baker, H. G. 1963. Evolutionary mechanisms in pollination biology. *Science* 139:877-883.
- Benson, W. W. 1971. Evidence for the evolution of unpalatability through kin selection in Heliconiinae. *Amer. Natur.* 105:213-226.
- Benson, W. W. 1972. Natural selection for mullerian mimicry in *Heliconius erato* in Costa Rica. *Science* 176:936-939.
- Bernstein, S. and Bernstein, R. A. 1969. Relationships between foraging efficiency and the size of the head and component brain and sensory structures in the red wood ant. *Brain Research* 16:85-104.
- Brower, L. P., Brower, J. V. Z. and Collins, C. T. 1963. Experimental studies of mimicry. 7. Relative palatability and mullerian mimicry among neotropical butterflies of the subfamily Heliconiinae. *Zoologica* 48:65-84.
- Brower, L. P. and Brower, J. V. Z. 1964. Birds, butterflies and plant poisons: a study in ecological chemistry. *Zoologica* 49:137-158.
- Brown, K. S. and Mielke, O. H. H. 1972. The Heliconians of Brazil (Lepidoptera: Nymphalidae). Part II. Introduction and general comments, with a supplementary revision of the tribe. *Zoologica* 57:1-40.
- Calvert, W. H. 1974. The external morphology of foretarsal receptors involved with host discrimination by the nymphalid butterfly, *Chlosyne lacinia*. *Ann. Ent. Soc. Amer.* (in press).
- Cheesman, E. E. 1940. Cucurbitaceae (Passiflorales). In *Flora of Trinidad and Tobago*, Vol. I. pp. 436-448.
- Cogniaux, A. 1924. Cucurbitaceae - Fevilleae et Melothrieae. In Engler Ed. *Pflanzenreich* IV 275:178-230.
- Crane, J. 1957. Imaginal behavior in butterflies of the family Heliconiidae: changing social patterns and irrevelant actions. *Zoologica* 42:135-145.
- Dahlgren, R. 1971. Multiple similarity of leaf between two general of Cape plants, *Cliffortia* L. (Rosaceae) and *Aspalathus* L. (Tabaceae). *Botaniska Notiser* 124:292-304.
- Edwards, W. H. 1881. On certain habits of *Heliconia charitonia* Linn., a species of butterfly found in Florida. *Papilio* 1: 209-215.
- Ehrlich, P. R. and Raven, P. H. 1965. Butterflies and plants: A study in coevolution. *Evolution* 8:586-608.
- Ehrlich, P. R. and Gilbert, L. E. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. *Biotropica* 5:69-82.
- Emsley, M. G. 1965. Speciation in *Heliconius* (Lep. Nymphalidae): morphology and geographic distribution. *Zoologica* 50:191-254.

- Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Oxford University Press.
- Futuyma, D. J. 1973. Community structure and stability in constant environments. Amer. Natur. 107:443-446.
- Gilbert, L. E. 1971a. Butterfly-plant coevolution: has *Passiflora adenopoda* won the selectional race with heliconiine butterflies? Science 172:585-586.
- Gilbert, L. E. 1971b. Distribution and abundance of resources of factors which determine population structure in butterflies. Ph.D. Thesis, Stanford University.
- Gilbert, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. Proc. Nat. Acad. Sci. 69:1403-1407.
- Gilbert, L. E. and Singer, M. C. 1973. Dispersal and gene flow in a butterfly species. Amer. Natur. 107:58-72.
- Heinrich, B. and Raven, P. 1972. Energetics and pollination ecology. Science 176:597-602.
- Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20:249-275.
- Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21:620-637.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Natur. 104:501-528.
- Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. Science 171:203-205.
- Killip, E. P. 1938. The american species of Passifloraceae. Publ. Field. Mus. Nat. Hist. (Bot) 19:2-613.
- Kleber, E. 1935. Hat das Zeitgedächtnis der Bienen Biologische Bedeutung? Z. vergl. Physiol. 22:221-262.
- Koltermann, R. 1971. 24-Std-Periodik in der Langzeiterinnerung an Duft-und Farbsignale bei der Honigbiene. Z. vergl. Physiol. 75:49-68.

- Levins, R. 1975. Evolution in communities near equilibrium. In Ecology and Evolution of Communities. Belknap Press, Harvard University. (in press).
- Lloyd, D. G. 1973. Sex ratios in sexually dimorphic umbelliferae. Heredity 31:239-249.
- May, R. M. 1973. Qualitative stability in model ecosystems. Ecology 54:638-641.
- Minnich, D. E. 1924. The olfactory sense of the cabbage butterfly, *Pieris rapae* Linn., an experimental study. J. exp. Zool. 39:339-359.
- Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. Oikos 22:398-402.
- Poulton, E. B. 1931. The gregarious sleeping habits of *Heliconius charitonius* L. Proc. Roy. Entomol. Soc. London 6:4-10.
- Remington, C. L. 1963. Historical backgrounds of mimicry. Proc. XVI International Congress of Zoology, Vol. 4:145-149.
- Richards, P. W. 1964. The Tropical Rain Forest. Cambridge University Press.
- Singer, M. C. 1971. Evolution of food-plant preference in the butterfly *Euphydryas editha*. Evolution 25:283-389.
- Swihart, C. A. 1971. Colour discrimination by the butterfly *Heliconius charitonius* Linn. Anim. Behav. 19:156-164.
- Swihart, S. L. 1963. The electroretinogram of *Heliconius erato* (lepidoptera) and its possible relation to established behavior patterns. Zoologica 48:155-165.
- Swihart, S. L. 1964. The nature of the electroretinogram of a tropical butterfly. J. Ins. Physiol. 10:547-562.
- Swihart, S. L. 1967. Hearing in butterflies (Nymphalidae: *Heliconius*, *Ageronia*). J. Ins. Physiol. 13:469-476.
- Turner, J. R. G. 1971. Experiments on the demography of tropical butterflies II. Longevity and home-range behavior in *Heliconius erato*. Biotropica 3:21-31.
- Vaidya, V. G. 1956. On the phenomenon of drumming in egg-laying female butterflies. J. Bombay Nat. Hist. Soc. 54:216-217.

- Vaidya, V. G. 1969b. Form perception in *Papilio democleus* L. (Papilionidae, Lepidoptera). Behavior 33:212-221.
- Williamson, M. 1972. The analysis of biological populations. Edward Arnold, London.
- Wickler, W. 1968. Mimicry in plants and animals. McGraw-Hill, New York.

AUTHOR INDEX

- A
- Adey, W. R., 129
Agthe, C., 100
Alexander, A. J., 211, 213
 214, 234
Andrewartha, H. G., 54
Arvey, M. D., 167
Auclair, J. L., 116
- B
- Bailey, L., 109
Baker, H. G., 54, 55, 101, 104,
 105, 109, 111, 113, 114, 116,
 117, 121, 124, 192, 193, 199,
 203, 233
Baker, I., 101, 104, 105, 109,
 111, 113, 116, 117, 121, 124
Baker, R. R., 21
Bang, B. G., 26
Bänziger, H., 101
Barbier, M., 28
Bardach, J. E., 35
Barlow, B. A., 228
Bawa, K. S., 196, 204
Baxter, C. F., 129
Baylor, D. A., 23, 31
Becker, J., 127
Bell, C. R., 127
Benson, W. W., 212, 214, 224, 233
Bequart, J., 81
Bernard, G., 212
Bernstein, S., 213
Beutler, R., 102, 103, 117
Bilz, R., 21
Birch, L. C., 54
Boaler, S. B., 194
Boch, R., 28
Bonnier, G., 100
Boothroyd, A., 31, 32
Borenstein, B., 40
Bowman, R. I., 164, 165
Bradford, D. F., 66
Braekman, J. C., 47
- C
- Cain, A. J., 121
Calvert, W. H., 233
Cheesman, E. E., 215
Chen, L., 181, 183, 185
Chun, M. W., 37
Clarke, C. A., 37
Clinch, P. G., 127
Cogniaux, A., 215, 227
Corner, E. J. H., 183
Corvino, J. M., 6
Cotti, R. H., 117
Crane, J., 212
Critchfield, W. B., 60
Croat, T. B., 194
Cross, R. M., 200
Crouch, J. E., 167
Croze, H., 72
- D
- Dadd, R. H., 25, 26, 41, 116
Dahlgren, R., 228
Daloze, D., 47
Darwin, C., 92
Darwin, F., 80
Davey, P. M., 61
Daw, N. W., 24, 31, 41
Derae, C., 47