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SOME ASPECTS OF THE ECOLOGY AND COMMUNITY STRUCTURE OF ITHOMID BUTTERFLIES IN COSTA RICA

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INDIVIDUAL RESEARCH PROJECT

Some aspects of the ecology and community structure of Ithomid butterflies in C. R.

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I Introduction

TAXONOMY, DISTRIBUTION

The Ithomiinae is a sub-family of the Ithomiidae (Lepidoptera: Nymphaloidea) containing 35 genera, 24 of which are found in Costa Rica (Fox 1940, 1968). The group is restricted to the new world tropics where it ranges from South America (25°S Lat.) to Northern Mexico (23° N Lat.). Only two species occur in the Antilles, one on Cuba and one on Jamaica and Hispanola (Fox 1963). Sixty-two species occur in Costa Rica which represent 78% of the total Central American fauna (N=80). The biogeography of Central American ithomids has been summarized in Fox (1968). Apparently, the center of highest endemicity is from southern Nicaragua through Costa Rica into western Panama in mid to high montane wet forests. This region is known as "Chiriqui" in early writings on Central American butterflies

ECOLOGY

Little has been published on the ecology of the Ithomiidae. Their restriction to deep forest shade and moist ravines as adults has often been noted but perhaps over emphasized. The Solanaceae are well known food plants of this group but there are few published food plant records. (See Table 1) Fox (1968) generalizes that ithomid species have broad host ranges. However, he evidently combines food plant records for a given species over its entire range, which says little about food plant specificities within local community or population boundaries. Adult energy and moisture sources include bird droppings and the flowers of a few plant families. Most such plants frequented by ithomids produce inflorescences of white flowers. Table 2 summarizes some of the plants used by ithomids as nectar sources.

Ithomid butterflies are well known as the models for several of the common Central American mimicry complexes and there is a large descriptive literature on this topic.

PURPOSE

That which is described as community structure ultimately represents the summation and interaction of many component populations, each of which has a complex structure. One approach to understanding community structure would be to focus on these component populations and build upward. For example, community diversity is generated at the interface of genetics and ecology in local populations, and thus in dealing with the question of tropical species diversity one should ask questions not only at the level of species interaction, but at the level of genotype interaction within and between populations.

ITHOMID SPECIES	HOST PLANT(S)
Xanthocleis aedesia	*Cyphomandra betacea*
Mechanitis polymnia	*Solanum aculeatissimum*
Mechanitis lysimnia	*Solanum*: *conicum*, *hiroutum*, *arrebenta*, *arrebenta*, *auricutatum*, and *tuberosum* *Cyphomandra*: *betacea* and *velutina* *Lycopersicum esculetum* *Datura arborea*
Dircinna xantho	*Solanum* sp.
Ceratinia eupompe	*Witheringia* sp.
Ithomia negrlecta	*Solanum* sp.
Thyridia themisto	*Brunfelsia* sp
Tithorea harmonia	*Echites* spp: (Apocynaceae) (Doubtful record)
Mechanitis isthmia	*Solanum* sp.

Table 1. Larval food plants of some ithomid species. (Various sources) This list represents a substantial portion of the published food plant records for the Ithomiidae.

PLANT VISITED	FAMILY	REFERENCE
Tournefortia glabra	Boraginaceae	Ross 1967
Eupatorium macrophyllum	Compositae	
Eupatorium pittieri	Compositae	
Psychotria padifolia	Rubiaceae	
Genipa sp.	Rubiaceae	Gilbert 1966
Cilbadium sp.	Compositae	
Epidendrum panculatum	Orchidaceae	van der Pijl and Dodson 1966
Unidentified palm	Palmae	This study
Eupatorium sp.	Compositae	

Table 2. Nectar sources for adult ithomids, most of which attract large non-specific assemblages of these butterflies. Each of these plants produces inflorescences of small white flowers.

The purpose of this study is to examine the ithomid butterflies to assess the suitability of this group for answering certain questions about community ecology, particularly those questions which require knowledge about the component populations of a community. Ideally one would like to choose a group of species for which not only niche breadths and competition coefficients can be calculated, but for which one can know such parameters as population sizes, reproductive strategies, genotype frequencies, and selection coefficients, etc.

The reason that the ithomids were thought to be likely candidates for such a broad approach to community ecology are as follows:

1) Upwards of 30 species may occur in one small area, most of which are ecologically quite similar.

2) Ithomids as adults are large, day-flying and stay conveniently near the ground.

3) Ithomids are part of two distinct communities. As larvae, most ithomids are part of the herbivore community which feeds on second growth vegetation. As adults they are primarily scavengers in the understory and have a vast impact on other lepidopterans as distasteful models.

4) Ithomids are easy to rear in captivity and genetic studies should not be difficult.

5) Ithomids have a close association with the plant family Solanaceae, which might allow tests of the idea (Ehrlich and Raven 1964) that much of the high species diversity in the tropics is generated at the level of plant-herbivore interaction.

In the process of answering the general question of "whether ithomids are suitable...?" it was hoped that more specific questions could be answered. For example, why are wet localities more diverse in ithomids than dry, and within wet localities, why are mid to high elevations more diverse than wet lowlands?

II <u>Areas and Methods</u>

AREAS

Observations on ithomids were carried out in five Costa Rican sites. These were: (1) Finca La Pacífica, 5.5 km. NW Cañas Guanacaste, 10°28'N, 85°08'W, 150 feet elev. Study plot of 5.4 acres was 1686 yards NW of the station building in riparian forest along the Rio Corobicí, 12-17 July. (2) 2.5 km NE Tilarán, Guan. Small patch of woods on road to Arenal, 10°30'N, 84°57'W, 2000 feet elev., highly disturbed, cloud forest conditions, 19 km ENE of Pacífica study site, 11 July 69. (3) Finca La Selva, 5 km SE Puerto Viejo, Heredia Prov. 10°25'N, 84°01'W, 350 feet elev. Study plot was 5.4 acre patch of woods bordering Arboretum II, 700 meters SE of the field station, 1-8 August 69. (4) Finca Las Cruces, 7.8 km S San Vito, Puntarenas, 8°42'N, 83°00' W, 4000 ft. elev. Most observations were made along road through finca, 15-17 August 69. (5) Ciudad Universitaria near San José, 4000 ft. elev. Observations made along creek near Edificio de Microbiología, 29 June 69, 31 August 69. There is no natural forest near this location, but the Solanaceae is well represented in the creek-side vegetation.

Intensive observations were made only at La Pacífica, La Selva, and San Vito.

METHODS

The major study plots at Pacifica and La Selva were mapped using a pocket compass and graph paper. In each case an area of roughly 5.4 acres of forest bounded by second growth edge was laced with 1500 yards of well marked trails. Observations and captures of ithomids were made along these trails and positions of sittings, captures, etc. were plotted on the map. For each butterfly captured and marked, a yellow plastic tag was made and taped to a leaf at or near the positions of capture. On the tag was recorded the species, number, sex and time of observation. Typically the plot was covered on foot twice per day, once in the morning, once in the afternoon. The point of marking the individuals was first to prevent recounting of the same individual and second, to gain information on individual movements. No attempt was made to estimate absolute population sizes since this would take a massive effort by several persons.

Rapid field identifications of ithomids were carried out with the help of a determined set of wings of species taken previously in Costa Rica. These were mounted between plastic sheets ("Clear Seal, self-sealing plastic sheets", Dennison Manufacturing Co, Framingham, Mass., USA) prior to coming. As additional species were encountered during the course of the summer, new mounts were prepared.

Working out food plant relationships over a short time period is very difficult, particularly with low density populations, as is usually the case with most ithomids. Therefore, to supplement actual sittings of females laying on their host plants, each olanaceous plant encountered was searched for eggs and larvae. Eggs removed from females of different species were compared under the dissecting scope with eggs taken from plants. In most cases it was possible to match eggs with great certainty. Because of time limitations, it was possible to rear larvae to adulthood for identification in only five cases. Tentative identifications of the Solanaceae were made using Standley and Morton (19). Vouchers of each plant were taken and positive determination will be made later.

III *Community Structuring*

Time has not permitted full analysis of the dispersion data recorded on the maps. Interspecific associations, sex differences in temporal and spatial dispersion, and such information as mean female population distances from specific food plants are to be extracted later for statistical analysis. However, it is possible to pick out some general trends in these data by simple observation.

TEMPORAL STRUCTURING OF DAILY ACTIVITY

Gilbert (1966) working along the Rio Higuerón at Taboga near Cañas Guan. noted that *Mechanitis isthmia* flew in clearings as early as 0530 to visit the flowers of *Genipa* trees. Their activity in the open tailed off rapidly as the sun rose and all were in forest shade by 0830, the time most other butterflies were just becoming active. (Benson (1967) studied the time budgets for adults of *M. isthmia* at Taboga during the dry season) Later, in the afternoon when the conditions again became dark and cool, either because of the sun setting or because of rain clouds building up and covering the sun, *M. isthmia* would again leave the forest to fly out into the canopy and into clearings in search of nectar.

Nectar feeding

Early morning flower visitation in clearings and along edges is a characteristic of most ithomid species. However, dry forest *M. isthmia* are at the early extreme. In colder more humid localities such as la Selva these and other ithomids fly later for nectar, but still earlier than other butterfly groups. A possible explanation for early morning nectar seeking will be presented below.

Emergence

Emergence seems to occur from 0900 to 1000 hours based on times when soft winged individuals were taken. *Hypothyris euclea* and *Ithomia diasa* reared from larvae taken at La Selva both emerged at 0900. For the present we will assume that most ithomid species emerge during this interval.

Courtship activity

As the day warms and brightens (1030-1330), male ithomids assume perches along trails and in or near sunfleck and expose the long scent scales of the hindwing which are usually overlapped by the forewing (Figure 1). Presumably ithomid males are able to assemble females much the way female moths assemble males. Whether or not this is the case, and I have no conclusive proof that it is for all ithomids, one can readily see two strong reasons for such a system. First, because of the increased difficulty of visual navigation and learning of landmarks in the understory, it would be difficult for males to return daily to restricted areas where the probability of finding virgin females tended to be very high (virgin females would thus be a coarse-grained resource) as is the case in all territorial butterflies so far investigated (Gilbert 1968, Benson and Gilber, Ms. in prep.). Recapture data and observations on ithomid males do not reveal territorial behavior for any species.

As virgin females tend more toward being a fine grained resource, the optimum male strategy would tend toward a random search procedure. However, this would suggest a second reason for male ithomids to assemble females. For a clear-winged ithomid male to locate a virgin female by the "search and investigete" strategy, he would have to investigate as many as ten other clear-winged species in a small area. This is an outcome of the high degree of Mullerian mimicry in the Ithomiidae. Assembling of the proper females by pheromone would be much less energy consuming since it would allow a sieving out of most unwanted species. A male would need to investigate only suitable colored individuals approaching his position. From visual contact onward male ithomids react to potential females much like most other male butterflies do. Thus, regardless of the spatial pattern of virgin female recruitment into ithomid populations, the monotony of the visual environment in the forest understory and the disparity of ithomid species versus color pattern diversity make male assembly of females an optimum strategy.

Early morning flower visitation: Are Ithomids important pollinators

It is now possible to suggest a proximate cause for the extreme early morning nectar feeding of the Ithomiidae. Some territorial male butterflies such as *Papilio zelicaon* in California, feed early in the morning before virgin females would be likely to arrive at hill top territories and late in the evening after the probability of virgin female arrival has dropped to near zero. Such feeding activity away from territories during the period of day when male competition for females is strong would be selected against. Similar competitive pressures are likely to force males of non-territorial butterflies which have courting areas separated in space from nectar feeding areas, to feed before female emergence in the mornings (prior to 0900 for ithomids). More time spent in early morning feeding means less time spent feeding during the courtship period (1000-1300 for ithomids). Therefore, one would expect such male butterflies to fly as early as physiologically possible. Ithomids, being of the forest shade, are able to fly earlier than most other butterflies, and are therefore pushed by intraspecific competition to the limits of early morning flight activity for butterflies. It is interesting to recall that the flowers visited are white, a color typical of night and crepuscular pollination systems, but not of the generalized butterfly flowers which are vividly colored, often red. Although most ithomid populations may not be dense in an area, ithomids as a group are represented by many individuals on a year-around basis in all but the driest forests of Costa Rica. It is therefore quite possible that there are "ithomid flowers" just as there are "hawk-moth flowers".

Scavenging activity

During the warmer parts of the late mornings and early afternoons, 1000 to 1500 hours, ithomids search intermittantly and somewhat randomly in the forest for bird droppings and other moisture sources. This searching behavior is very similar to the behavior of ovipositing females searching for food plants. Both kinds of search involve flying weakly from leaf to leaf, landing briefly on each, and taking moisture from a bird dropping if one is found.

Oviposition

Oviposition occurs near mid-day, usually from 1030 to 1330 hours. This is the period of maximum solar energy input and the females may require such conditions for the vigorours activity of egg laying. At least for some species, like Hypothris euclea, egg laying may coincide with peak levels of foliage patrolling predator activity on the host plants. Judging from the long carful process H. euclea females go through in selecting an ovipositon site (almost each leaf of the plant is inspected over 15-20 minutes of hovering and landing) one gets the impression that these females are perhaps assessing the predator level before laying a cluster of eggs.

The graphs in figure 2 summarize approximately the temporal structure of the important daily activities of ithomids. The vertical axis represents the percentage of all ithomid individuals involved in a given activity at a given point in time, with time of day plotted along the horizontal axis. Three different Costa Rican localities are represented, each of which represents a different set of conditions. Although the relative sequence of daily activities remains constant, these activities are more or less compressed in time depending on how the various meterological factors vary in time at each site. Day to day variance in temporal structuring seems to be greatest at La Selva and least at San Vito.

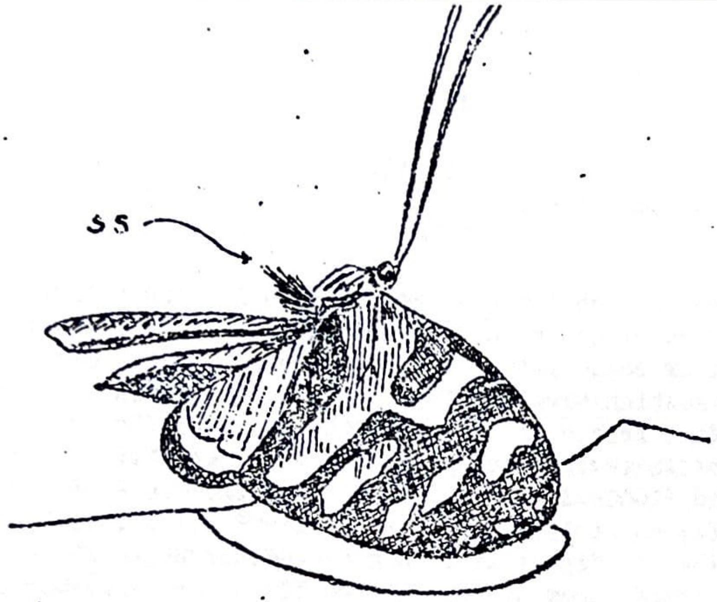

Figure 1. Male *Ithomia* *heraldica* with long
nt scales (ss) exp

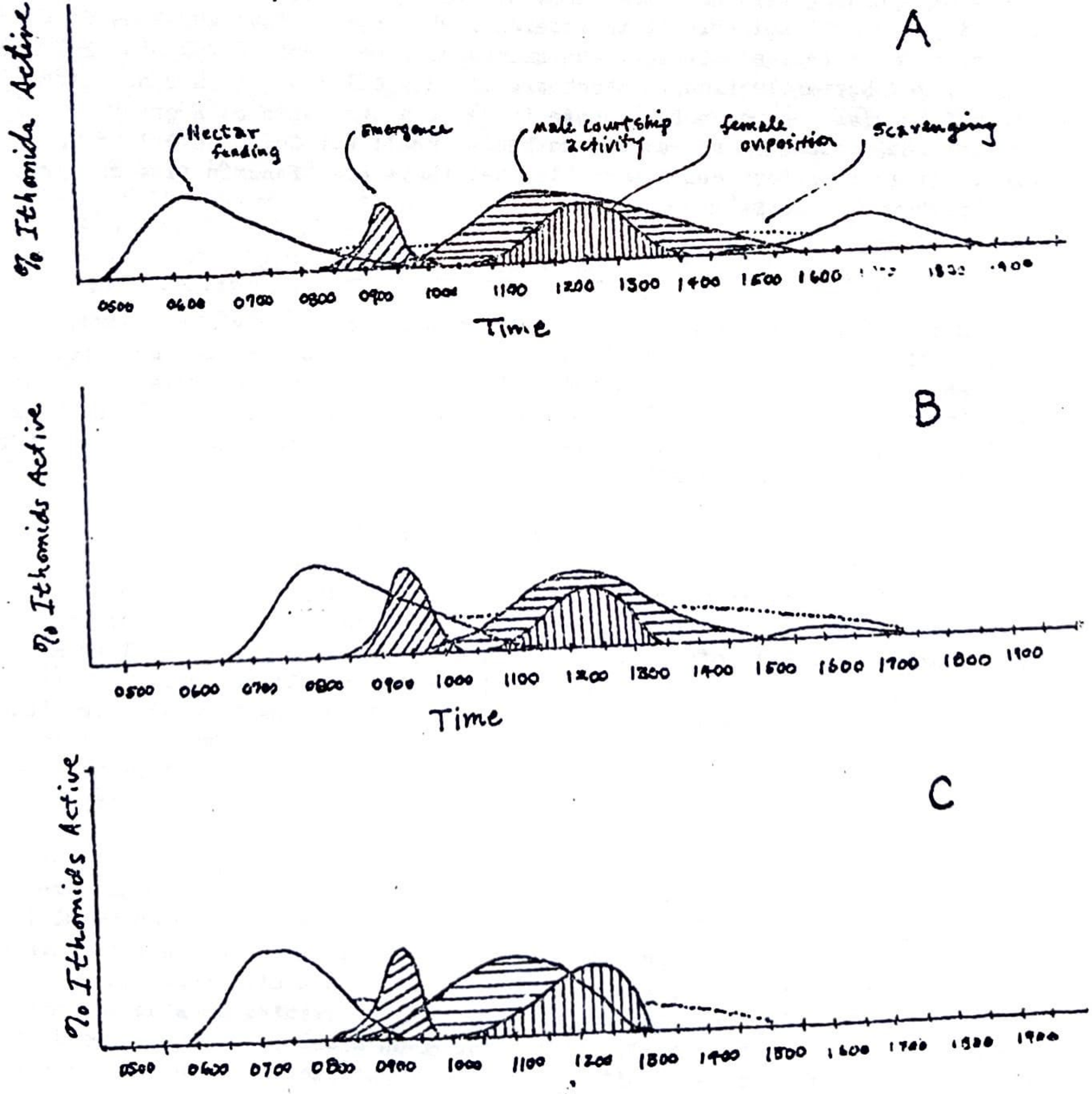

Figure 2. Temporal structuring of ithomid activity in three Costa Rican site (all wet season). A. Pacific lowland dry forest (Taboga, La Pacifica); B. Atlantic lowland wet forest (La Selva); C. Pacific slope mid-elevation forest (San Vito). At best these graphs are crude approximation to the average pattern at each site.

SPATIAL STRUCTURING

Lowland dry forest

Only one species of ithomid Mechanitis isthmia was present in most of the dry forest around La Pacífica in early July. However, in certain parts of the riparian forests moist pockets could be found in which several other ithomid species were flying. One such pocket was found on the north part of the same study area. It was bounded on the north by a 30 foot bluff, on the west by the Río Corobicí and by forest to the south and east. The river at that point makes a sharp bend. Spray and mist produced by the resulting turbulence are blown by prevailing breezes eastward and trapped by the bluff. As a result, high relative humidity and low temperatures perpetuate there. The dispersion over four days of two clearwing species, Hymenites oto and Pteronymia parva is compared with that of Mechanitis isthmia is figure 3. Note that although M. isthmia is clumped in the moist pocket, individuals occur over the entire areas and even in open areas (early morning primarily). In contrast, the two clearwing species were strongly clumped in the moist area and only occasionally were seen more then 50 yards from the center of density. The tightness of the clumping varied with the conditions. Outlying points of the dispersion pattern occurred on damp cool days while on hot sunny days clumping was at a maximum, all clearings occurring in an area 20 x 30 yards square or .13 acre. During the period of observation at least, these small clearwing populations had little or no contact with other nearby populations (if in fact there were others nearby. No other centers of clearwing density were found in the immediate area). Recapture rates were much higher for the clearwinged species (16 marked, 5 recaptured) than for M. isthmia (76 marked, 2 recaptured). The similarity between these results for M. isthmia at La Pacífica and those obtained at Taboga in the dry season by Benson (1967) (74 marked 2 recaptured) is striking.

Islands are bigger in the wet season

It would be interesting to follow the La Pacífica clearwing populations into the latter parts of the wet season, since in dry tropical areas the only contact between populations isolated on islands of high humidity might come at the height of the rainy season, at which point the area of moist refugia is likely to be much greater than in the dry or even early wet season. (The population sizes of ithomids should be greatest at that point as well.) Interestingly a similar situation is occurring in northern Mexico with the same two genera of clear-winged ithomids, Hymenitis oto and Pteronymia coytto populations occur in southwestern Tamaulipas on island of semi-evergreen tropical forest (Gilbert, Ms. in prep.) which is separated by some 20 miles of dry deciduous forest from the next patch of evergreen vegetation (see Martin 1958). Thus populations separated thorugh the dry season and early wet season have at least the potential for contact at the height of the wet season.

Although Fox (1963) says that Hymenutis and other clearwings are "frail" and implies that they are less fit for suboptimal conditions, nevertheless, Hymenitis and Pternonymia leave Mechanitis behind in reaching the extreme northern limits of latitudinal range for the group. Hymenitis is also the only ithomid genus which has made the hop to Antillean islands. Evidently Mechanitis isthmia are successful in areas with a strong dry season for one because they are able to enter reproductive diapause as adults (Taylor 1967). This would allow M. isthmia to build up to a vast population size rather rapidly after the beginning of the rains. This is in contrast to non-diapausing species which make it through the dry season by retreating into a few refugia of suitable conditions and in the process suffer great reductions in population size. It is quite possible that *Hymenitis oto* is a species of this latter type.

Lowland wet forest

Ithomid dispersion in the lowland wet forests at La Selva was in sharp contrast to that at Pacífica. The lack of strong clumping by any of the species reflects the uniformly humid and cold conditions of the wet forest. Five species of clearwings occurred in the study plot (*Ithomia patilla*, *I. diasa*, *I. terra*, *Hypoleria cassotis*, and *Oleria vacinia*) along with *Mechanitis isthmia*. Figure 4 shows that the strong contrast in dispersion between clearwings and *Mechanitis* seen in dry forests breaks down in wet forest situations. Data on individual movements, not yet fully analyzed, supports what is apparent from the dispersion data: individuals of clearwing species move more, and further in wet forest situations than in dry, while for *M. isthmia* the difference is less pronounced if there is a difference.

Dry vs. wet forest

An important contrast between dry and wet forests regarding ithomine dispersion is related to the first point discussed in this section. At Pacífica dispersion was based on gradients of physical conditions primarily. At La Selva dispersion patterns were based to some extent upon larval food plant distribution around the study plot. The main forest plot at La Selva was divided into two smaller plots A and B, each of which had a different set of food plants in adjacent second growth and clearings. The distribution of abundance of 17 species of ithomids (Table 3) in the two plots was compared using the Spearman rank correlation test and show to be significantly different (r-32). Those species contributing most to the difference were those for which food plants were abundant in one plot and not in the other. At Pacífica physical constraints restricted such population structural response to food plant dispersion.

At both dry and wet localities, most ithomids preferred areas of the forest floor which had relatively open shrub layers while retaining heavy shade from the canopy. Males, in particular during hours of courtship, tend to gather in semi-openings which have one half to one meter high herbaceous growth, with free air space 15 to 30 feet above. In such areas visibility is high (and air currents optimum for pheromone dissemination?). One often finds several males in or near sunflecks caused by the falling of a tree or along trails cut through the forest.

PATTERNS OF FOOD PLANT UTILIZATION

Broad patterns

Ehrlich and Raven (1964) have outlined the broad patterns of butterfly-plant relationship which are evident at the level of higher categories. The observed reciprocal relations led them to conclude that much of the observed organic diversity is generated by coevolutionary interaction at the plant-insect herbivore interface. With this generality in mind the food plant relations of the ithomid community seemed an obvious place to look for such plant-herbivore reciprocity at finer levels of resolution. Ultimately the level required for observation of the dynamics of coevolution will be populations of insects versus populations of food plant. Downey (1964) has made a significant step in this direction with butterflies. His observations on Lycaenids and Lupines are discussed below.

	Sub-plot A	Sub-plot B
Milinaea lilis	4	2
Mechanitis isthmia	15*	7
Mechanitis polymnia	2	6*
Scada zibia	4	8
Napeogenes tolosa	1	0
Hypothyris euclea	4	13*
Ithomia patilla	14*	4
Ithomia diasa	8*	4
Aeria eurimedea	2	2
Hyposcada virginiana	0	3
Dircenna euchytma	10*	3
Godyris zavaleta	3	2
Hypoleria cassotis	1	1
Hypothyris lycaste	1	3
Oleria vicinia	1	0
Ithomia heraldica	0	1
Ithomia terra	5	5
Total	75	74

Table 3. Distribution of individuals of 17 ithomid species in two sub-plots of the La Selva study area (see figure 4). The subdivision of the larger area was made in such a way so as to maximize differences in Solanaceae distribution between the two resulting sub-plots. Those species for which food plants were known, and whose food plant was common in one sub-plot but rare or absent in other are designated by * under the sub-plot where their food plant was most abundant.

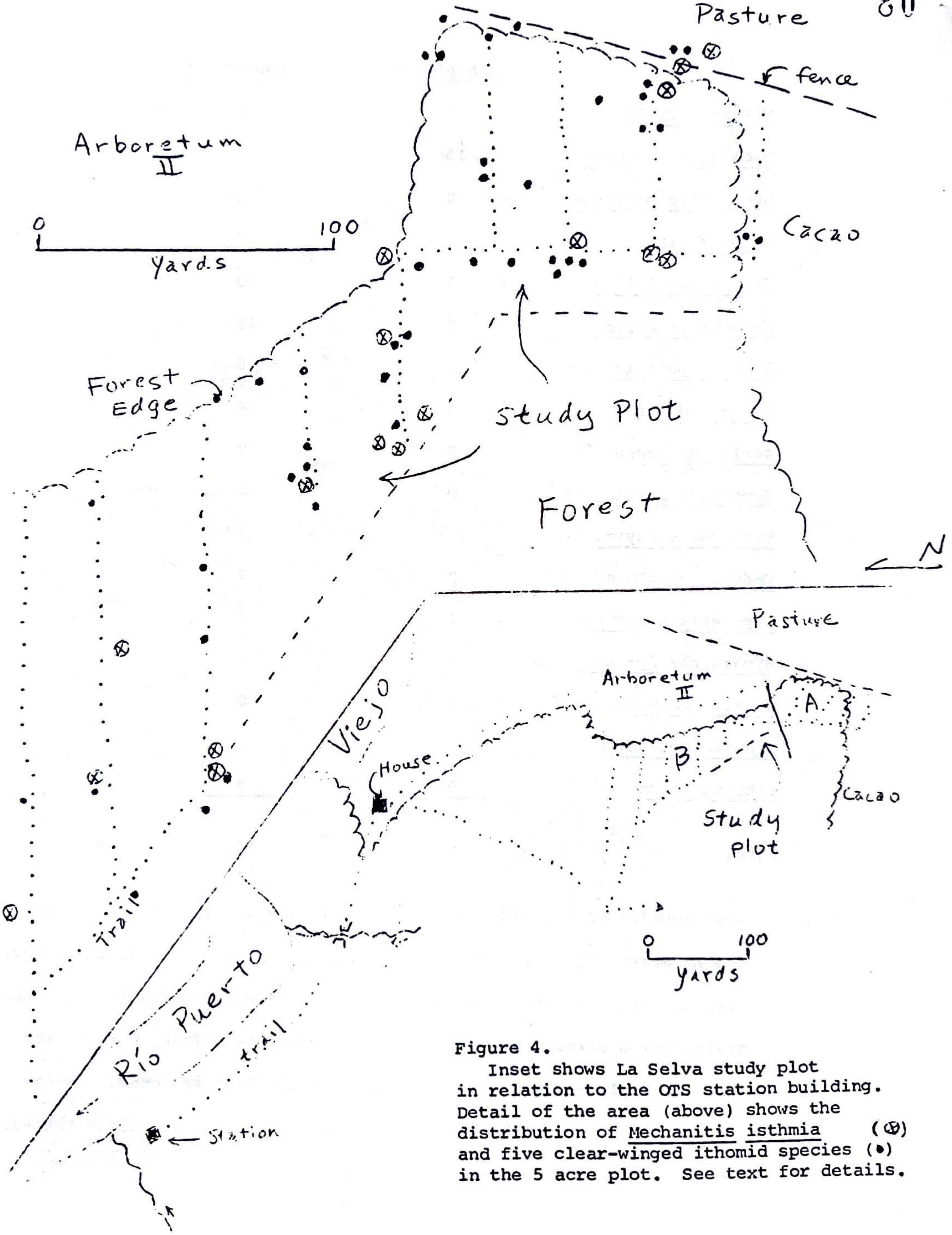

Figure 4.

Inset shows La Selva study plot in relation to the OTS station building. Detail of the area (above) shows the distribution of *Mechanitis isthmia* (⊗) and five clear-winged ithomid species (•) in the 5 acre plot. See text for details.

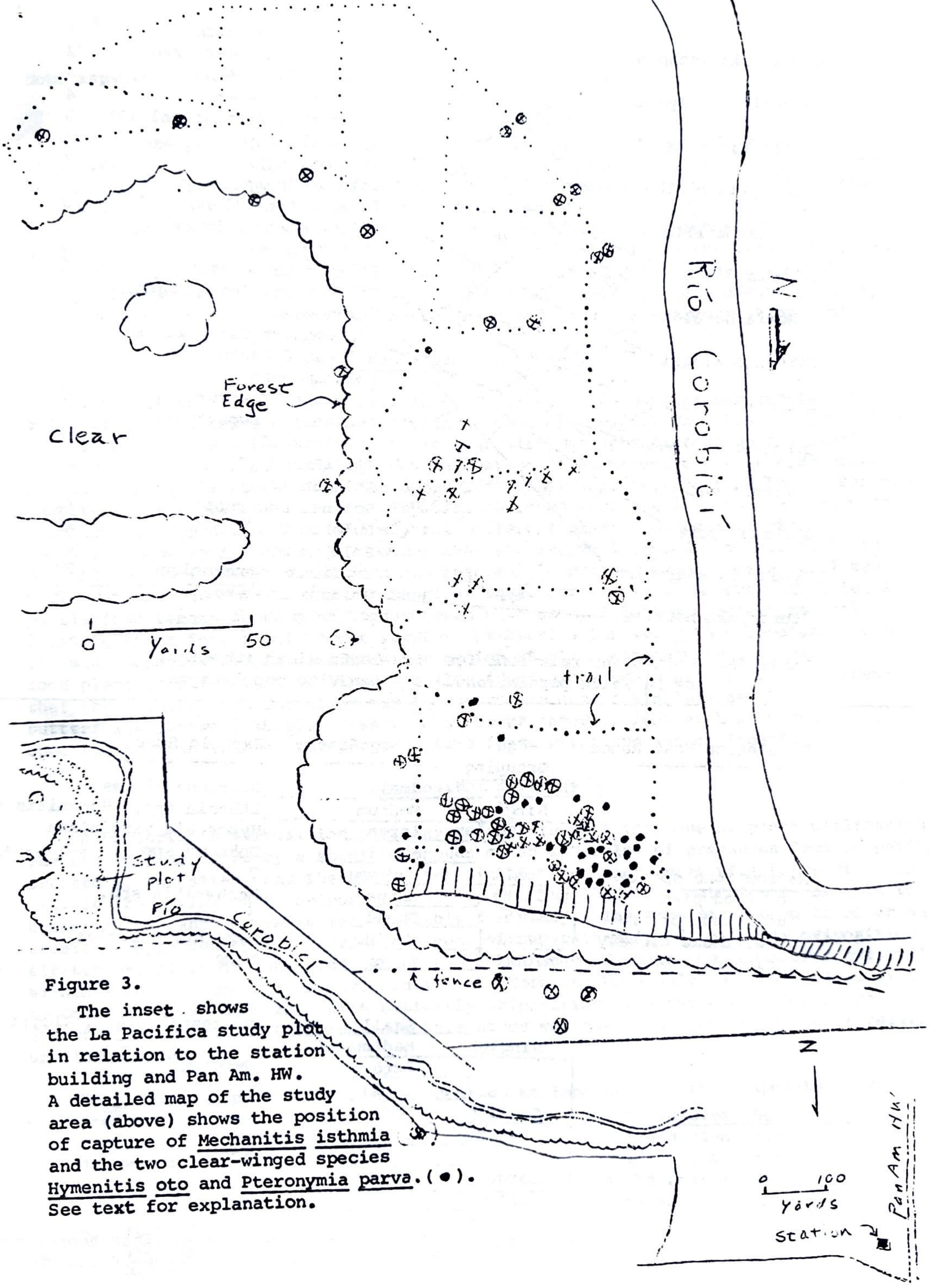

Figure 3.

The inset shows the La Pacifica study plot in relation to the station building and Pan Am. HW. A detailed map of the study area (above) shows the position of capture of Mechanitis isthmia (⊗) and the two clear-winged species Hymenitis oto and Pteronymia parva. (●). See text for explanation.

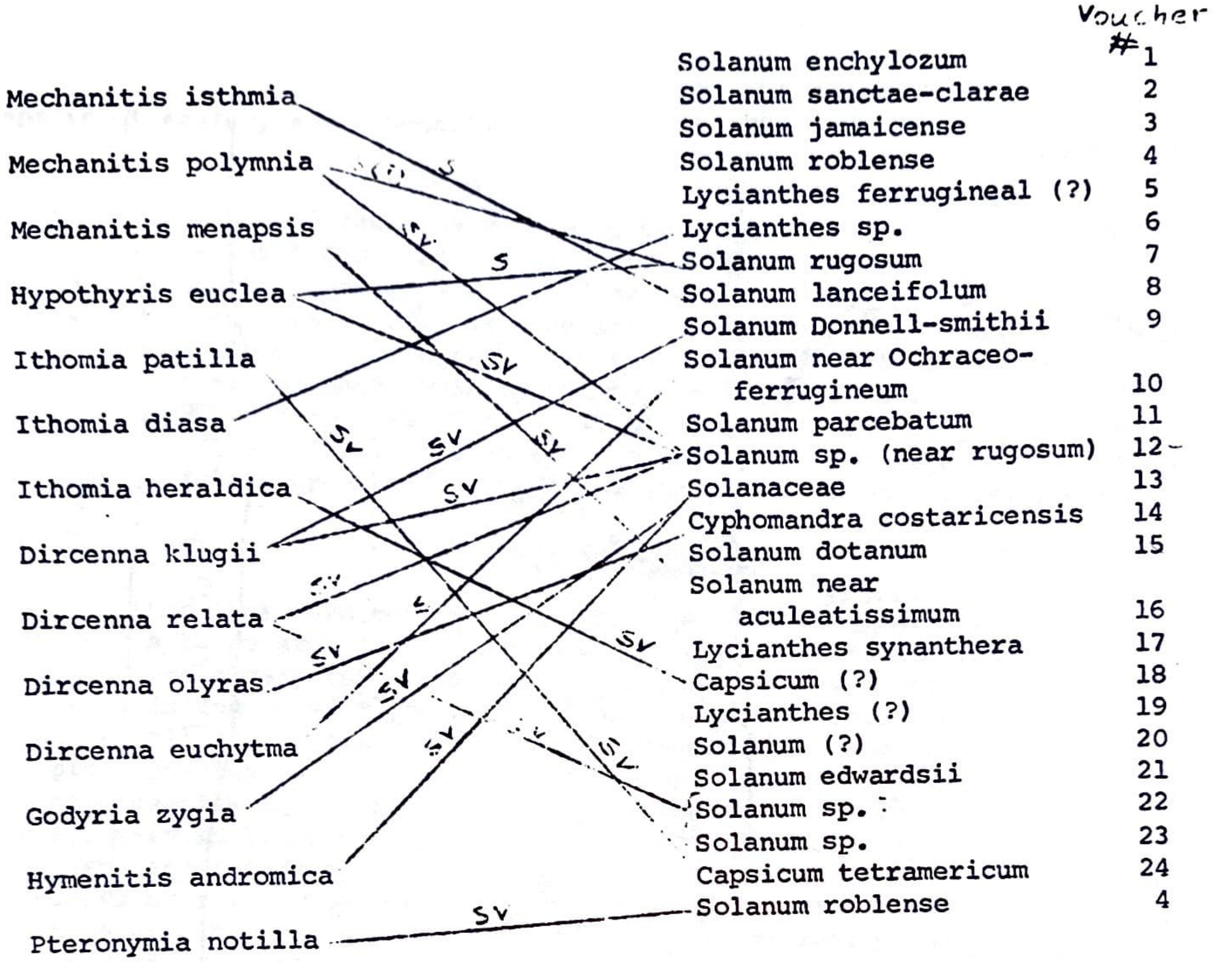

Table 4A. Host plant relations for some Costa Rican ithomids.
s= La Selva populations. sv= San Vito populations.

Population Host Range	Egg Grouping	Egg Size	Example Species
Narrow (one species of food plant utilized, or if two, these closely related.)	Single	Small	Dircenna olyras
		Medium	Ithomia spp.; Hymenitis sp
		Large	Hyposcada virginiana
	Small cluster <75	Small	Unknown spp. (only eggs found)
		Medium	?
		Large	Mechanitis spp.
	Large cluster >75	Small	?
		Medium	Hypothyris euclea
		Large	None
Broad (several to many host plant species used by population, often different genera.)	Single	Small	Dircenna relata, klugii
		Medium	
		Large	~~[illegible]~~ None
	Small cluster	Small	
		Medium	
		Large	
	Large cluster	Small	
		Medium	
		Large	

Table 4B. Oviposition strategies of the Ithomiidae. (Rough first approximatic
Egg Sizes: small≦.15 mm^3, medium=.15-.50 mm^3, large=.5-1.5 mm^3.

Twenty one genera of Solanaceae native to Costa Rica support 24 genera of Ithomiidae. Of the total Costa Rican solanaceous flora 103 species are of genera known to be utilized by ithomids and therefore were considered at least potential food plants. This amounts to $\frac{103}{62}$ or 1.66 plants per ithomid species in Costa Rica. Interestingly the only other subfamily of butterflies for which similar data is available to me at present, the Heliconidae (Nymphaloidea) has the same relationship: 34 species of passiflora in Costa Rica to 21 species of Heliconids or 1.67 plant species per butterfly species. The reason for such close correspondence in this ratio between different groups of butterflies and plants is obscure at present.

Population specificity

The fact that there are more than one species of food plant per species of butterfly over a large area is a trivial outcome of the fact that the butterfly species range more widely (at least altitude wise) as species than do the plant species. This is undoubtedly why Fox 1963 states that Ithomids have a wide host range. But at all study sites the number of ithomid species exceeded the number of observed plant species. And most ithomids observed were specific to one host plant, although some species do utilize several different plant species in a given locality (summary in Table 4). Downey 1964 studied 78 isolated populations of the blue Plebejens icarioides and found 28 species, 10 subspecies of Lupines utilized as food plants over the extensive range of these butterflies. However, individual populations tended to be monophagous (even with several lupine species present), limiting their food plant to one species, or hybrids involving this species. Among ithomids, competitive interactions may be important in determining the degree of food plant specificity in a given locality (food niche breadth). There is evidence that the results of competition may be observable over a single season in some butterflies (Brower, 1962). Thus we must be prepared to look at host plant specificity with respect to space and time for a given species of ithomid.

Oviposition strategy

A butterfly's oviposition strategy defines in part its mode of plant utilization. The strategy employed by a species depends on an interplay of pressures from competitors, predators, parasites, and the host plant itself. Much more work will be required to explain the variation in oviposition strategy among ithomids, but it was possible to describe the range of variation available for study. The Ithomiidae seem to offer an excellent opportunity for providing a general understanding of butterfly oviposition strategies, since one can find almost the full range of variation known from butterflies within a local ithomid commuity. Until now there has been only one solid discussion in the literature concerned with butterfly oviposition strategy and reproductive effort (Labine 1968). Unfortunately this study was based on a small sample of relatively unrelated species.

The following parameters were recognized as important in the ovipositon strategy of ithomids:

1. egg size
2. cluster size
3. total egg production
4. temporal aspects of egg depositon (includes reproductive diapause)
5. location of egg(s) on plant
6. degree of host plant specificity

Table 4B summarizes those species for which it was possible to define oviposition strategies in terms of several of the parameters listed above. Although it is not possible to explain fully the variation seen for each parameter, observations made during the study allow discussion of egg clustering by Hypothyris euclea and oviposition on the upper side of leaves by Mechanitis isthmia.

Egg clustering and larval behavior in Hypothyris euclea

A population of eggs and larvae of Hypothyris euclea was discovered on Solanum rugosum in Arboretum II at La Selva. Thirty-one plants examined in the study area were found to have a total of 912 individual butterflies ranging from egg to last instar larvae (eggs + instar one = 598; instar two = 189; instars three and four = 87; instar five = 38, adults in adjacent forest = 11 males, 10 females).

H. euclea lays large clusters of small eggs on the undersides of mature leaves. Larval gregariousness resulting from such egg clustering has at least two major functions. First, it allows small caterpillars to gang up on a tough leaf such that each caterpillar obtains more food per unit energy expended than it would alone. Second, gregariousness is one kind of predator defense strategy, involving either the production of a composite "super warning signal" to vertebrate predators, or the construction of communal silk tents which keep out parasitic wasps and flies, or both.

As with Heliconius (Benson 1967), ants are a major mortality factor for H. euclea and other ithomid larvae. In additon, Polistes wasps and to a lesser extent mutillid wasps were observed to be frequent predators. Ithomids, unlike heliconids, are unarmed, and as individuals have little defense other than spitting up large putrid drops of gut juices when attacked by predators. Gregariousness in early H. euclea larvae is therefore directed to still a different variation of the predator defense theme. Groups of larvae on the underside of a leaf react explosively to ants walking directly overhead on the topside of the leaf by dropping off and suspending themselves on about one inch of silk. Other insects and crude models will not elicit this reaction. Ants and wasps approaching these larvæ on the leaf underside cause "ejection" of larvae on the perimeter of the group while the central larvae continues to feed unhampered. Often a larva is taken from the perimeter if the predator is quick enough. During ecdysis when the caterpillars must be quiescent for a long period, predators undoubtedly take many larvae, but mostly those on the outer edges of the group, again giving those in the center a better chance for survival than those which happen to be near the perimeter. Even last instar larvea, which are no longer gregarious, will drop down on a length of silk when approached by a large Ectatoma, an ant seen predating large fourth and fifth instar H. euclea but not earlier instars.

This predator-prey system is of interest because it may involve a predator effect on the prey population quite apart from the direct taking of prey for food. This effect is that of prey starvation resulting from high predator density and/or high patrolling rates on the leaf surfaces. Obviously, larvae hanging on silk threads are not able to feed. Such disruption of insect herbivore feeding is a component of plant protection which may be of importance in cases where plants attract ants and other predaceous insects by using extra-floral nectaries.

Factors which tend to increase the time spent avoiding predators would tend to prevent caterpillars from surviving to pupation. This is because butterfly larvae can slow down their development only to a point; beyond that point they must either diapause or die. Slowed development also means more time spent per instar, which increases the probability of direct predation.

Plants with many small ants would have a higher patrolling rate per unit leaf area than plants with a few large ants. It would be expected then that plants with the small ants would have less larvae on the average than those with big ants. In the study plot at La Selva the predominant ants on Solanum rugosum were a small black species of Solanopsis which was often associated with membracid bugs on the plants, and a large red Ectatoma which occurred on Solanum plants contacted by vines patrolled by these ants for nectar. Apparently these two species of ant do not co-exist on the same plant and the consequences for H. euclea larvae are very different, depending on which ant is present.

Three plants patrolled by Ectatoma averaged 18 fourth and fifth instar larvae per plant, while eleven plants patrolled by Solanopsis averaged less than 0.3 larvae per plant.

Egg clustering is assumed to be a response to heavy predator patrolling of the food plant since this would decrease the average time spent avoiding predators per larva (averaging in central larvae which are rarely disturbed). Increasing the cluster size would increase the number of larvae protected relative to those eaten or disturbed on the perimeter of the cluster. This follows since the number of larvae on the perimeter is a linear function of the cluster radius while the total number in the cluster increases as the square of the radious. There are good reasons however, for not putting all the eggs in one or just a few clusters, and thus there is counter pressure for more, but smaller clusters. Cluster size (as distinct from total egg production) in butterflies is more a function of female behavior than of physiological capacity. Therefore it might be expected to be much more responsive to selection than is clutch size in birds.

The average cluster size for Hypothyris euclea at La Selva was in excess of 120 eggs per cluster (N=7, this includes counts of early larval groups). At San Vito, on the other hand, where the number of species and number of individuals of foliage patrolling ants is much reduced relative to La Selva, two clusters averaged less than 75 eggs per cluster. Such a small sample is not conclusive, but further work on this system is warranted.

Egg cluster relocation by Mechanitis isthmia ✓

Butterflies in the ithomid genus Mechanitis typically lay clusters of 40 to 60 medium to large white eggs. Of three species observed, two, Mechnitis polymnia and Mechanitis isthmia, oviposit eggs on the tops of leaves, while a third, M. menapsis, oviposits on the undersides of leaves. In all cases, the resulting larvae stay on the underside of the leaves.

An observation made at Finca Pacifica is relevant to the discussion of egg cluster size and egg position on leaves. Walking along the edge of the forest in the Pacifica study plot, I disturbed a female M. isthmia in the process of laying a cluster of eggs. She flew away rapidly but turned after about 50 yards and began a slow weaving flight back toward the samplespot. Within two minutes she had relocated the eggs and resumed oviposition in the same cluster. I then purposely disturbed the same female a second time and the relocation behavior was repeated. This observatio reinforces the notion that a certain minimum number of eggs is a critical parameter in the reproductive biology of cluster-laying ithomids, and that female behavior is an important factor in determining the number of eggs per cluster. The price of increased egg vulnerability (eggs more visible on surface of leaf) is evidently counterbalanced by the advantage of females being able to visually relocate incomplete clutches.

DIVERSITY

Dry vs. wet lowland forests

Tables 5 and 6 summarize for each locality the species present, number of individuals of each species, values of H', h" max, and H'/H' max (equitability). Calculations of H' follow Lloyd et al. 1968. Table 6 also includes data from Collenette and Talbot (1928) based on collections of ithomids made in the Matto Grosso areas of Brazil in 1927.

A sharp difference in ithomid diversity is seen between the lowland dry riparian forest at Pacifica (6 species, H' =.38) the lowland wet forest at La Selva (17 species, H'=1.26). This is partly the result of many more species of the Solanaceae at La Selva (10 species observed in the study area) than at La Pacifica (3 species observed in the study area). The low equitability (.50) La Pacifica compared to La Selva (.81) results largely from the predominance of one species, M. isthmia, at Pacifica. As the wet season progresses and moist refugia expand (see section on spatial distribution) one might expect an increase in both H' and in equitability at Pacífica, as the less abundant species spread into areas of food plant previously not available due to physical constraints previously considered.

The diversity gradient between La Pacifica and the study site near Tilarán, only 19 km away, is remarkable. In a sample of 50 individuals taken in three hours at the Tilarán site, there were 20 species of ithomids present (H'=1.13, H'/H' max.=.88).

Both Matto Grosso sites, Serragem and Tombardor, were at 1500 feet in dry forest riparian situations (14°S latitude). The general conditions described for that region (Collenette and Talbot, 1928) are similar to those found in the Cañas region of Guanacaste. If we compare the ithomid diversity in these two sites with the two Guanacaste sites (Pacífica and Tilarán) we find that the number of species, H', and equitability values all fall between the values found for Pacífica at 250 ft. and those for Tilarán at 2000 ft. (serragem: 13 species, H'=.87, H'/H' max = 77; Tombardor: 9 species, H'=.82, H'/H' max. =.86. Since the Brazilian sites are intermediate in elevation between Pacífica and Tilarán, it could be suggested that elevation is an important parameter to consider in attempting to explain ithomid diversity gradients. Unfortunately, the Tilarán site is a much moister location than the others, in addition to being higher in elevation.

Low vs. high wet forests

Therefore, three Costa Rican localities, all with wet forest conditions but at different elevation, were compared with respect to the number of species, diversity and equitability of their ithomid communities. The areas compared were: La Selva (250 ft.) Tilarán (2000 ft.) and San Vito (4000 ft.). Absolute numbers of species known from each locality including wet season and dry season observations increases from 18 at la Selva to 25 at San Vito. Calculated H' values do not increase, but this is likely the result of more limited samples at Tilarán and San Vito. However

voucher #	Species	A	B	C	D	E	F	G
6	Tithorea tarricina			2	1			
7	Tithorea harmonia	5						
8	Melinaea lilis		7	1				
11	Xanthocleis aedesia						1	1
12	Mechanitis isthmia	120	24	14	3	4	5	9
13	Mechanitis polymnia	4	8	2	1			
14	Mechanitis menapsis			1	4	1	2	3
16	Scada zibia		13					
18	Napeogenes tolosa		1	2	1			
19	Napeogenes paedaretus						2	2
21	Hypothyris euclea		21		7			
22	Hypothyris lycaste		4	3				
23	Hyalyris excelsa					2		2
24	Ithomia patilla		18	5	6	8	5	13
25	Ithomia bolivari		?	?				
26	Ithomia diasa		15					
28	Ithomia heraldica	1	1	5	10	12	16	28
29	Ithomia celemia				1			
31	Ithomia terra		8					
32	Aeria eurimedea		4	1				
33	Hyposcada virgiana		4	3	2			
32	Oleria vicina		1					
38	Oleria rubescens				10			
39	Oleria paula			1	3			
41	Ceratinia tutia			1	2			
42	Callithomia hezia			1				
46	Dircenna klugii			1	1	8	16	24
48	Dircenna relata			1	11			
49	Dircenna olyras				2			
50	Dircenna euchytma		15				2	2
52	Godyris zavaleta		5					
53	Godyris zygia				16			
55	Hymenitis oto	23		1		1	6	7
56	Hymenitis nero			1				
57	Hymenitis andromica				6			
62	Hypoleria cassotis		3					
65	Pseudoscada utilla				2			
66	Epi/cada salvinia							
68	Pteronymia donata (?)					2	1	3
73	Pteronymia notilla			4	5			
78	Pteronymia parva	8		1				
	Total	161	152	50	94	38	56	94

Table 5. Ithomid species and numbers of each, occurring at five Costa Rican localities. July-August, 1969.

Letters across top refer to the following localities:

A= La Pacifica
B= La Selva
C= Tilaran
D= San Vito
E= Cd. Univ. 29/6/69
F= Cd. Univ. 31/8/69
G= Cd. Univ. Total

Locality Habitat	Elev. ft.	Dates	# Sp	N	H'	H' max.	H'/H' max.	Notes
La Pacifica Dry forest riparian	250	12/7/69- 17/7/69	6	161	.38	.76	.50	Expect increase in no. of sp. and H' later in wet season.
Serragem Dry forest riparian	1500	12/8/27- 27/8/27	13	1216	.87	1.13	.77	Sample taken near beginning of a wet season, over a short time span.
Tombardor Dry forest riparian	1500	24/7/27- 28/8/27	9	378	.82	.95	.86	Sample taken over 5 wk. period, less comparable to Costa Rican data than is Serragem sample.
Tilarân Wet forest	2000	11/7/69	20	50	1.13	1.28	.88	
La Selva Wet forest.	250	1/8/69- 8/8/69	17	152	1.26	1.55	.81	Dry season sampling (II-68) adds one species to wet season total. Total=18 sp.
San Vito Wet forest	4000	15/8/69 -17/8/69	18	94	1.22	1.25	.97	Dry season sampling (II-68) adds 7 sp. to wet season total. Total=25 sp.
Cd. Univ. No forest	4000	29/6/69 + 31/8/69	11	94	.83	1.04	.80	Species composition and diversity in the 2 samples almost same.
Gomez Farias Semi-evergreen moist forest	1500	7-8/65 9/1/69 11/9/67	2	20	-	.30	-	At 23°N lat., this is the northern-most forest which supports the Ithomiidae.

Table 6. Diversity and equitability of Ithomid samples in various localities.

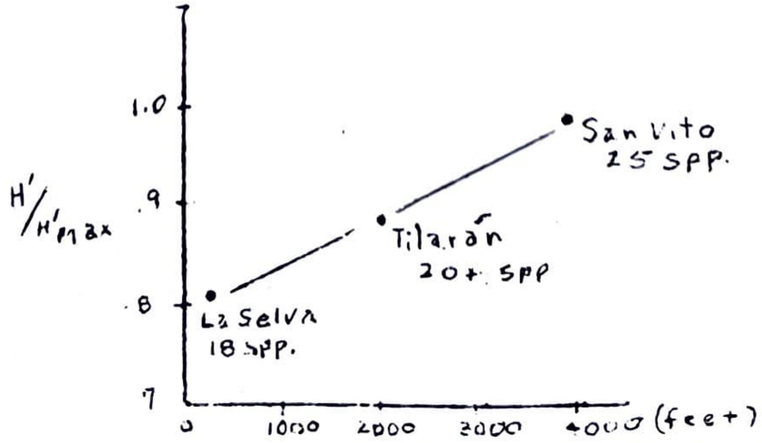

Figure 5. Increase in Ithomid H'/H/max. from low to mid-elevation wet forest localities.

equitability within these wet forest localities increases with elevation (figure 5) and presumably, more intensive sampling would reveal a similar trend in H' values. For small samples, of regular species, the total number of species may be a good measure of diversity (Pianka 1966).

In searching for an explanation for increasing ithomid equitability (and diversity) at higher elevations, I took another look at the food plants of these butterflies. Of 119 native species of solanaceae, 71% of the species (N=85) occur above 1000 meters while only 36% (N=43) occur below 600 meters. In comparing the Solanaceae in the study areas at La Selva and San Vito it was apparent that not only the absolute numbers of species observed was greater at San V ito, (18 species at San Vito to 10 species at La Selva) but that relative frequencies of each species tended to be much more evenly distributed at San Vito than at La Selva. That is, H' for ithomid food plants increases with altitude within a general moisture regime. This gradient in Solanaceae species diversity I suggest to be largely an outcome of topography. That is, as one goes from lowlands into mountains, the frequency of small streams dissecting the landscape increases with increasing steepness of the countryside. In addition, areas of natural clearings due to land slides increase substantialy with increasingly steep terrain. This all means that the total area of second growth vegetation relative to the area of mature forest increases with altitude. Since most Solanaceae are second growth species it is reasonable to expect that the increased area available for early succession at mid elevations would support a higher diversity of that similar plant families. Evidence that plant diversity can be regulated by the amount of area available is provided by Johnson et. al. (1968).

Ithomid diversity and the indirect food limitation hypothesis

Thus, it seems probable that for ithomid butterflies, species diversity is determined to a great extent by the diversity of their larval food plants. This would predict that at the population level, the number of each ithomid species in an area is geared to the amount of food plant available.

However, no evidence for food limitation could be found which might parallel the situation in the oak feeding wintermoth (Feeney 1967) or the *Heliconia* feeding Hispid beetles (Janzen et al. 1969) both of which are probably limited to a large extent by the availability of suitable young leaf material. Ithomid larvae generally feed on the older leaves (as would be expected of distasteful herbivores) and rarely damage more than parts of a few leave per plant. What happens to *Hypothyris euclea* and probably most other ithomids is that predaceous ants and wasps, rather than direct starvation, limit the sizes of ithomid populations by responding to the prey populations in a density dependent fashion*. However, since in this case the density of prey is

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* The major predators for ithomids and perhaps most other tropical butterfly larvae are social insects which are present year around and which are able to respond to areas of high larval density with instantaneous recruitment of individuals from the colonies or nests. There will not therefore be the sort of lag in predator response to increasing prey density which generates cyclic fluctuation in prey abundance so typical in temperate areas. Braconid wasps and tachinid flies, the parasitic insects most responsible for predator induced perturbations in temperate butterfly populations, although a factor to tropical groups like ithomids, do not cause cyclic fluctuations because ants and wasps consume a high percentage of parasitized as well as non-parasitized larvae. (This would prevent build up in parasite populations as a response to prey density.) One might hypothesize that this distinction between tropical and temperate predation systems is responsible in large part for the apparent stability of butterfly population size in the tropics relative to the temperate zones. The same reasoning should apply to other insect groups as well.

measured in terms of the leaf area of food plant, the density of each ithomid species reflects indirectly the amount of food plant available. This would explain how the diversity (H') of the ithomid community might be determined by the diversity (H') of their food plant community. However, the reciprocal response of food plant diversity to ithomids is not occuring in this case. Low density populations of leaf eaters would not be expected to have as strong a coevolutionary impact on plants as would low density populations of fruit, seed, and flower eaters (relevant here: Janzen 1969, Ehrilich and Breedlove 1968).

At present it is not possible for me to predict the magnitude or direction of differences in overall butterfly diversity between lowland and mid-elevation wet forests. The apparent increase in overall butterfly diversity along this transect is most likely due to the increase in butterflies like the ithomids whose larvae are part of the second growth community. Canopy species would not be expected to follow this trend and may infact drop off with increasing elevation.

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