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Behavioral Regulatory Mechanisms in Populations of the Butterfly Mechanitis isthmia in Costa Rica: Adaptations to Host Plants in Secondary and Agricultural Habitats

(Lepidoptera: Nymphalidae: Ithomiinae)

By

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With 10 figs. in the text and 8 plates

Abstract

The egg-mass oviposition and group behavioral patterns of larvae of the neotropical butterfly *Mechanitis isthmia* (Lepidoptera: Nymphalidae: Ithomiinae) were studied in northern Costa Rica. While most ithomiine butterflies of Central and South America are forest-dwelling forms with single ovipositions, solitary larvae, and larval host plants (Solanaceae) possessing smooth, papery, and non-pilose leaves, *Mechanitis* thrives in a broad range of secondary and agricultural habitats where the larval host plants are Solanum species with thick fleshy leaves covered with trichomes (defensive hairs) and spines. Along with a few other ithomiine genera, *Mechanitis* exhibits various forms of group behavior atypical for the subfamily as a whole; it differs from virtually all other ithomiines by its highly developed egg mass oviposition and synchronous habits (feeding, resting, molting) of the larvae. We suspected that this group behavior was related to its ability to exploit solanaceous host plants not used by other ithomiines, and to thrive in secondary habitats exposed to direct sun light. By observing oviposition and behavioral patterns of the larvae on host plants at various times over several years, we discovered that cooperative feeding and cooperative web-building were the two obvious advantages of group behavior. Young larvae collectively cut away trichomes to feed on leaf tissue and build silken webs apparently to protect themselves from being punctured. But mortality of eggs and young larvae is very high, from a variety of predators, and appears to be a trade-off for group behavior. Larvae do not exhibit cooperative defense against predators. The data are discussed in terms of the ability of this butterfly to exploit weedy Solanum species and its relatively high ineffectiveness as a defoliator of these plants in secondary and agricultural habitats.

Introduction

Herbivorous insects that successfully colonize secondary and agricultural habitats in the tropics have the potential to develop into pest species. When such shifts in habitat are made, and if the new habitat is abundant, such insects may escape in space from their predators and parasites that normally regulate their populations to a degree that usually precludes pest outbreak conditions. In the American tropics, there has been an accelerated rate of removal of the original vegetation cover in many regions, resulting in a proliferation of large-scale secondary and agricultural habitats. These habitats have been invaded to varying degrees by weedy plant species, presumably originating in forest marginal habitats where these plants are preadapted to colonizing episodes (sensu LEWONTIN 1965) as more vegetation cover is cleared away by man. Some herbivorous insects, including Lepidoptera, follow suit and exploit these plant species as they become weeds. A good example is the

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butterfly *Mechanitis isthmia* (Lepidoptera: Nymphalidae: Ithomiinae) and its larval host plants, various species of Solanum (Solanaceae). Most ithomiine butterflies are deep forest-dwelling forms, but a few, such as *Mechanitis* are adapted to living in secondary habitats. Two issues emerge from the interaction of *Mechanitis* and Solanum: (1) will this herbivore regulate these weed species through heavy defoliation of the plants in livestock pastures where farmers have been unsuccessful in eliminating them? (2) will *Mechanitis* become a pest insect of cultivated species of Solanum such as tobacco, tomato, potato, etc.?

This paper reports behavioral patterns of adults and immature stages of *Mechanitis isthmia* as related to the exploitation of larval host plants in secondary habitats (early successional stages) and abandoned pastures in both wet and dry lowland regions of northern Costa Rica. This topic has bearing on tropical agriculture since the larval host plants are stout, pilose, and spine-covered species of Solanum (Solanaceae) that thrive in livestock pastures and banana plantations. These Solanum possess numerous spines and trichomes that undoubtedly play a role in their interaction with *Mechanitis* (RATHCKE and POOLE, 1975). They are also close relatives of cultivated species of Solanum. The applied aspect of this research includes an exploration of why this insect has been successful in colonizing these host plants in secondary and agriculturally-important habitats. It is predicted that herbivorous insects colonizing secondary habitats in the tropics can easily become pests owing to the sudden increased availability of host plants and a lack of regulatory factors (predators, parasites) on their populations (JANZEN 1975). But we found that the survival of the eggs and young caterpillars on these plants is low (YOUNG and MOFFETT 1979), suggesting that although the butterfly is invading secondary habitats with considerable success, regulatory factors are still operative. Thus these plants must be removed by agronomic practices since the insect is not doing enough defoliation to control the plants; past conditions may still be developing in *Mechanitis*. Large-scale clearing away of the forest cover creates new habitats suitable for colonizations by herbivorous insects and these species may then become associated primarily with these and to a lesser degree with their original habitats. A long-term implication follows if cultivated plants (crops) are then planted in these areas and if they are close relatives of the wild host plant species, the herbivorous insect species may become a pest species if it leaves behind these regulatory factors.

Methods

The field studies were designed to examine the behavioral patterns of *Mechanitis* in secondary habitats where the larval host plants are abundant. Emphasis was placed on the construction of an ethogram, including the description of oviposition behavior, and behavior of caterpillars associated with activities such as hatching, feeding, molting, defense, and pupation. These behavioral patterns might be related to the potential ability of *Mechanitis* to develop outbreak or pest conditions on secondary growth Solanum species and cultivated Solanaceae. Most studies were conducted at "Finca La Tirimbina", a 4000-acre agricultural enterprise near La Virgen, Heredia Province, in northeastern Costa Rica. Here, about 60% of the area is cultivated in banana, cocoa, nutmeg, black pepper, rubber, Allspice, and another 15% is second growth ranging generally from one to twenty years old. This region is about 200 meters above sea level and part of the Premontane Tropical Wet Forest zone (TOSI 1969).

The Ithomiinae are very diverse in this region, although only a few such as *Mechanitis isthmia* and *Hypothyris euclea* occupy secondary habitats; most inhabit deep forest, forest light gaps, and other clearings (Plate 1, Fig. 1). The larval host plants of *Mechanitis*, Solanum hispidum PERS. and S. jamaicense MILL., are abundant in both fresh and abandoned pastures and secondary habitats less than ten years old. Both species are similar in size and general appearance (Plate 1 and 2, Figs. 2—3) although hispidum has a more serrated leaf. Both are characterized by thick coverings of extremely sharp spines on stems; both leaves and stems are very pilose, being covered with trichomes (small defensive hairs). These factors readily distinguish these species from most forest solanaceous plants, which tend to have non-pilose smooth, papery leaves and few or no spines. When brushed against, both species cause painful skin punctures and

farmers continually clear them away in order to protect themselves and livestock. These plants occur as isolated individuals or large clumps in a pasture or banana plantation. *Mechanitis* is the only ithomiine exploiting these species in this region, although a variety of other chewing and sucking insects (Orthoptera, Coleoptera, Hemiptera) also feed on them.

Mechanitis was also studied at the "Barranca Site", a patch of semideciduous mixed primary and old-secondary forest along the Pan American Highway in the Guanacaste Province. Another study locality in Guanacaste was "Finca La Taboga", a few km south of Canas (Plate 2, Fig. 4). At both localities, the host plants occur in secondary growth areas near streams and the most abundant species is Solanum ochraceo-ferrugineum (DUN.) FERN., strikingly similar to S. jamaicense (Plate 3, Fig. 5). These localities are within the Tropical Dry Forest zone (TOSI 1969) where a severe dry season lasts about six months each year. About 70% of the total field time, over a two-year period, was spent observing *Mechanitis* at the "Tirimbina" locality, with the remaining time in Guanacaste. The "Tirimbina" studies were conducted during January 1976, January—February 1977 and August 1977; Guanacaste observations were made intermittently during June—July 1974; 1975; and December 1975.

The basic field technique employed was to locate *Mechanitis* egg masses or groups of larvae, and then make frequent daily (and nocturnal) observations on behavior associated with hatching, resting, feeding, molting, defense, and pupation. The extent to which an individual host plant was defoliated by *Mechanitis* was also determined. Mating and oviposition behavior were also examined.

Results

Habitats and Mating: *Mechanitis* is frequently encountered in young secondary habitats less than ten years old; these are areas where the larval host plants, Solanum spp. (Solanaceae), are abundant as weed species. Few or no adults are seen inside forests and small forest light gaps. In northeastern Costa Rica, it is unusual to discover more then ten adults in a field of 100 to 300 sq. meters in a 30-minute walk at 10:00 A.M. on a sunny day (N = 14 days; range of adults is 1—10). Densities of adults are generally low and adults spend considerable amounts of time passing through an area. In the wet lowlands, mating pairs are seldom seen, but during the severe Guanacaste dry season, dense aggregations of mating adults are found in heavily shaded forests near streams and near larval host plants (Plate 4, Fig. 6). During the early Guanacaste dry season, considerable reproductive activity takes place in heavily-shaded forests broken with secondary growth with Solanum. Adults are not as aggregated in the wet lowlands. The larval host plants in both regions often occur as large clumps in pastures, even ones currently used by grazing livestock.

Oviposition: Large, eliptical white eggs are deposited in masses upon the upper side of an older leaf of the host plant (Plate 5, Fig. 7). The general procedure is: the female flutters about the plant for several minutes, presumably inspecting its suitability for oviposition; she lands and immediately begins to deposit eggs; oviposition continues from about 14 minutes (about 12 eggs) to two hours (about 45 eggs), depending upon the numbers of eggs deposited and other factors such as disturbance. When a female is disturbed, she flies away but usually returns within several minutes and resumes oviposition. Egg masses discovered in the field and without any typical signs of egg destruction contain anywhere from less than ten to sixty eggs in a single mass. Multiple masses are often found on the same plant but only one egg mass to a leaf. Sometimes larvae and egg masses are found on a single plant. The eggs within a mass are arranged in neat rows and the female spends considerable time with oviposition. Egg masses are deposited well within the leaf or near the edge.

Oviposition is most prevalent in open habitats with a great degree of direct exposure to the sun most of the day. Solanum individuals overgrown with vines and other plants, otherwise healthy, are avoided. Large, dense clumps of Solanum are also avoided but scattered single plants are highly favored. This pattern is especially noticeable at "Tirimbina"; in Guanacaste, S. ochraceo-ferrugineum almost always grows in large clumps and egg masses of *Mechanitis* are often found in the peripheral plants of a clump. Of a total of more than

80 egg masses located at "Tirimbina" over two years, about 90% of these were found within 0.3 to 1.0 meters from the ground, and generally higher positions on tall plants are avoided. Medium-height plants with well developed lateral growth of large leaves are the ones with most egg masses. These are often plants with leaves already riddled with holes from herbivore activity (mostly Orthoptera); *Mechanitis* larvae are often found on the large leaves about half-way down the plant (Plate 6, Fig. 8).

In open pastures with considerable livestock activity as well as human activity, *Mechanitis* can be found frequently depositing egg masses on solanums next to paths and well-trodden areas. The butterfly exploits these habitats to a greater extent than less disturbed secondary habitats since the larval host plants in the former tend to be more exposed to the butterflies. This species displays considerable site-selection in the oviposition process, expressed in terms of selection of a plant of certain height range and exposure within the host plant population, and selection of certain leaves on a plant. Areas within a pasture or field habitat where the vegetation cover is thick are avoided by *Mechanitis*; these are areas where few if any Solanum occur.

Hatching: A consequence of laying eggs in large masses by *Mechanitis* is the synchronous behavioral patterns exhibited by the larvae, beginning at the time of hatching and lasting until an exodus from the host plant at the time of pupation. When deposited, the egg is uniformly white, but on the day before hatching, it turns light gray and develops an apical cap and medial-apical ring of darker gray. During the night before hatching, the egg also develops a ring of reddish flecks around the base of the apical cap. These color changes are reliable indicators of eggs hatching the following morning and these changes occur synchronously in all eggs in a mass. Hatching takes place en masse usually between 6:00 and 8:00 A.M. and the egg shells are consumed almost immediately. After consuming its own egg shell, a young larva will move on to another shell, or to an egg that hasn't hatched yet, suggesting cannibalism. Entire egg shells are eaten, save for a small gelatinous disc marking where an egg was attached to the leaf; these egg "scars" can be used to determine the number of eggs originally in a mass. Unhealthy eggs within a mass are not eaten during the hatching period, which usually lasts about 30—40 minutes for an average size egg mass of 25 eggs. Generally by 9:00 A.M. on the day of hatching, the larvae have completed eating egg shells or unhatched eggs and begin to move to the ventral side of the same leaf.

Initial Orientation on the Leaf: As more larvae hatch in a mass, there is a greater amount of wandering by individuals through the area of the egg mass, gradually resulting in some individuals straying away from the site; the leaf area encompassed by these wanderings expands in size, perhaps the result of a silken webbing being deposited on the surface. Evidence for silken trails is the observation of larvae repeatedly going over the same routes on the leaf. The general direction of the expansion of the area of wandering is towards the nearest edge of the leaf; larvae begin to orient towards the edge; when one larva reaches the edge, others follow it and the group eventually moves to the ventral side of the leaf. Not all larvae cross to the lower side at the same point and perhaps odor or vibrational cue is involved, rather than strictly being the adhering to a silken webwork. Occasionally a larva will become isolated from the group for as long as 40 minutes, but usually finds its way back. Once on the lower side of the leaf, the larva aggregate in tight formation and rest for awhile (Plate 7, Fig. 9). They remain this way until late afternoon and begin feeding. As they begin to feed on the leaf, their bodies change from a dull translucent yellow to dark green. The day following hatching is characterized by irregular group activities such as wandering, feeding, and resting; often times single larvae become isolated from the group but eventually wander back to it. By the end of this day, the group seems well-oriented to the leaf and activities become highly synchronized. Individual larvae that become isolated from the group do not feed but rather eventually wander back to it; very overcast weather and rains slow down the return of an isolated larva to a group.

When resting, the group usually stays within the leaf, rather than near the very edge. The initiation of feeding usually involves the group moving to an edge, although sometimes feeding begins within the leaf, generally with scraping away of tissue rather than biting completely through it.

Feeding Behavior: Most feeding takes place at night. General patterns of feeding, along with other activities, are illustrated for two different egg masses from "Tirimbina" in Fig. 1. First instar larvae initiate feeding either at the edge or within leaf; considerable time is spent probing among trichomes presumably in search of a spot where penetration of the leaf tissue is possible. When a larva finds a suitable feeding spot, it is quickly joined by the others and eventually a "feeding edge" orientation of the group is formed: heads are lined up as larvae feed synchronously next to one another (Plate 4, Fig. 6). As feeding progresses, a noticeable accumulation of trichomes building up as fluffy masses appears, indicating that the larvae bypass these defensive hairs and feeding on the primary leaf tissue. Feeding periods are separated by periods of resting and wandering. First and second instars do not ingest trichomes, but older larvae do. Resting periods are spent by either the whole group or a portion of it; usually resting sites are less than 20 mm from the feeding edge site. While egg shells and dead larvae are consumed, the molted cuticles are not; molting takes place synchronously. Movements of the larvae in a group are generally limited by a silken mat communally spun by the group; sometimes a larva wanders away but eventually returns. Additional larvae may follow, presumably guided by silken strands spun by the first larva.

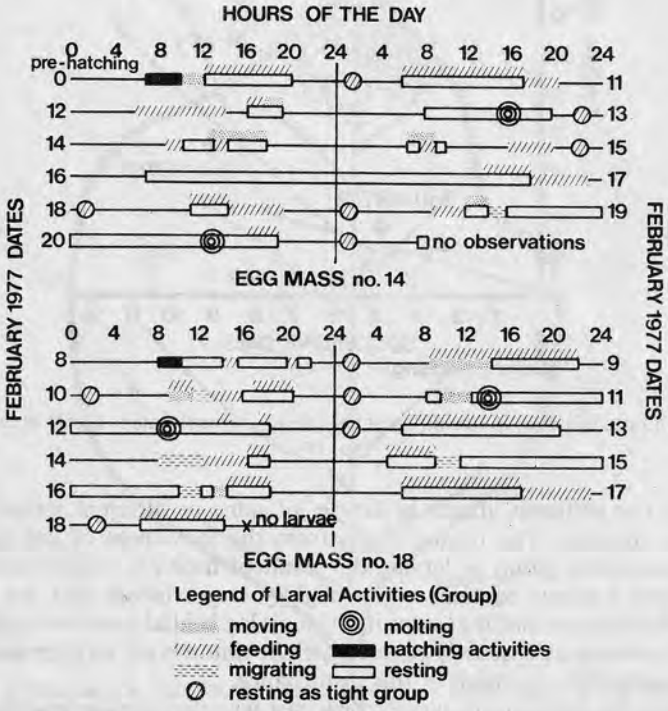


Fig. 1. The daily activity patterns of *Mechanitis* larvae as recorded for two different egg masses during February 1977 at Tirimbina

The group remains on a leaf until it is almost completely defoliated. The growth of larva proceeds rapidly over a two-week period (Fig. 2) and during this time the group may consume more than one large leaf. There is generally a definite pattern to the defoliation of a leaf (Figs. 3—8); most of the defoliation takes place in the last three instars (Fig. 2). Depending upon the size of the group, as much as 48 mm^2 of leaf tissue is consumed in the first instar and 400 mm^2 in the second instar. During these instars, the larvae from a single egg mass stay together as one group while resting and feeding; however, larger larvae (last three instars) may subdivide into two or more smaller groups on the same leaf or different leaves. When more than one egg mass was present on the same plant, different groups of larvae stay on different leaves while resting and feeding. Movements of larvae to different leaves most often begins in the third instar and the movements is either lateral or upwards to a higher leaf (Fig. 8). The larvae always remain on the lower side of a leaf. One larva leaves a leaf first, and it is followed by the others; presumably a silken trail guides the movement to a different leaf.

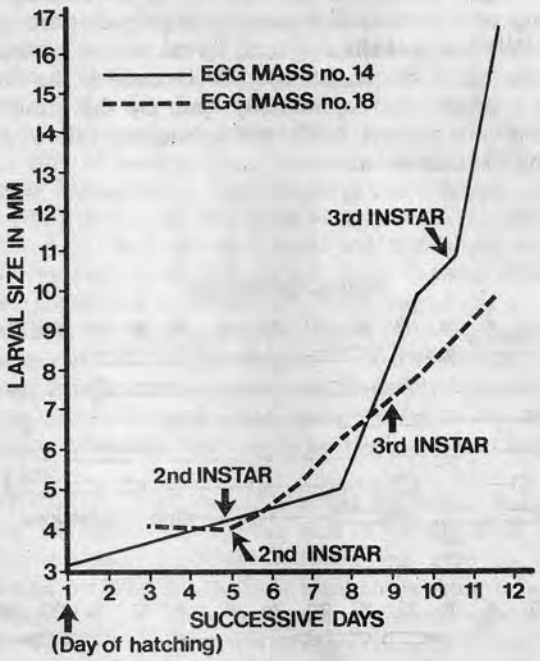


Fig. 2. The growth rates of larvae in two different egg masses. Growth rate is higher in the larger egg mass (no. 14)

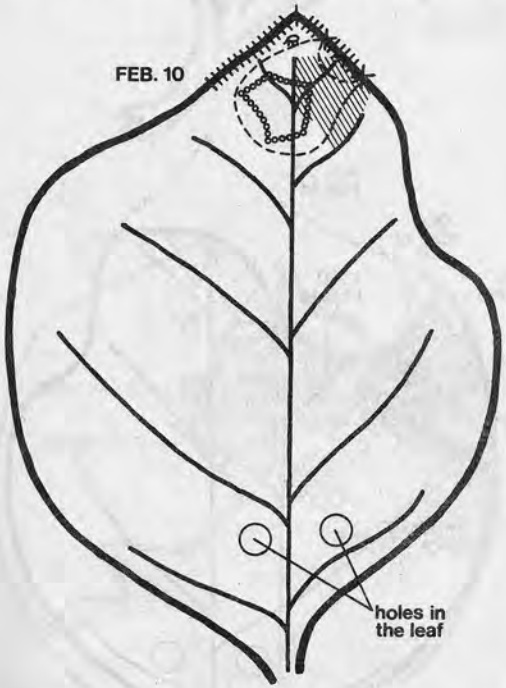
Occasionally two different groups of larvae, of same or different instars, on the same plant; will fuse together. The fusion results from the movement of one group to a leaf already having another group of larvae, the result of multiple ovipositions on the same plant. Sometimes a group contains a few slightly larger larvae and this is a result of asynchrony in hatching or molting; some individuals lag behind most members of the group. Very frequently when a field densely covered with Solanum is cut by farm workers, a group will become subdivided as a result of this disturbance.

Beginning with the third instar, larvae chew part way through the midrib vein of a leaf, causing it to droop over in a tent-like fashion (Plate 7, Fig. 10). The group generally rests in tight formation on the lower side of the leaf, near the point of vein-weakening. From

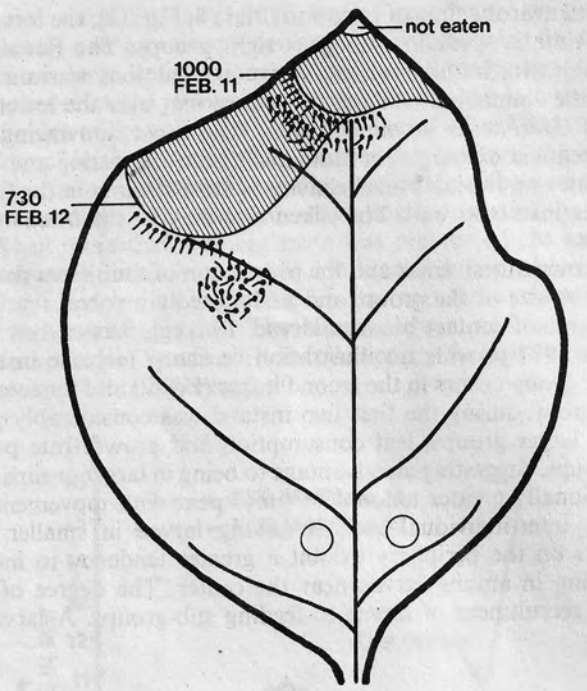
the third instar until near the time of pupation (Plate 8, Fig. 11), the larvae feed in loose formations and less time is spent in resting as tight groups. The function of the tent-like arrangement is unknown, but several alternative explanations warrant further study.

It is very likely the communal building of a silken mat over the lower surface of the leaf keeps a group of *Mechanitis* larvae together. The most convincing evidence for this prediction is the frequent exchanges of individuals between resting and feeding sub-groups along the same routes on the leaf; this behavior is most striking in the first two instars, but continues into later instars as well. The silken mat may be the mechanism that promotes group cohesiveness.

The degree of group cohesiveness and the proportion of time spent daily in feeding varies consistently with the size of the group, and undoubtedly involves reinforcement from the silken mat and degree of contact between larvae. Two egg masses, nos. 14 and 18, studied at "Tirimbina" in 1977 provide an illustration: a sharp increase in the growth rate of larvae in the larger group occurs in the second instar (Fig. 2) and the total leaf consumption per larva of this group during the first two instars, was considerably greater than in the smaller group. In larger groups, leaf consumption and growth rate per larva are higher than in smaller groups, suggesting an advantage to being in larger groups. In smaller groups, there is a proportionally greater amount of time spent with movements than in feeding. There is also less inter-individual contact among larvae in smaller groups. In larger groups, individuals on the periphery exhibit a greater tendency to move about, and to attempt at squeezing in among larvae near the center. The degree of contact may also play a role in the recruitment of larvae to feeding sub-groups. A larva leaving a resting



Figs. 3—8. The defoliation of a leaf of S. jamaicense by a group of *Mechanitis* larvae in an eight-day period at Tirimbina (February 1977). The hatched-line areas are ones devoured by the larvae and the numbers give hours of the day (with dates). The dotted line shows the original edge of the leaf. These larvae (young third instar) devour more than half of the leaf before moving to an adjacent leaf by the eighth day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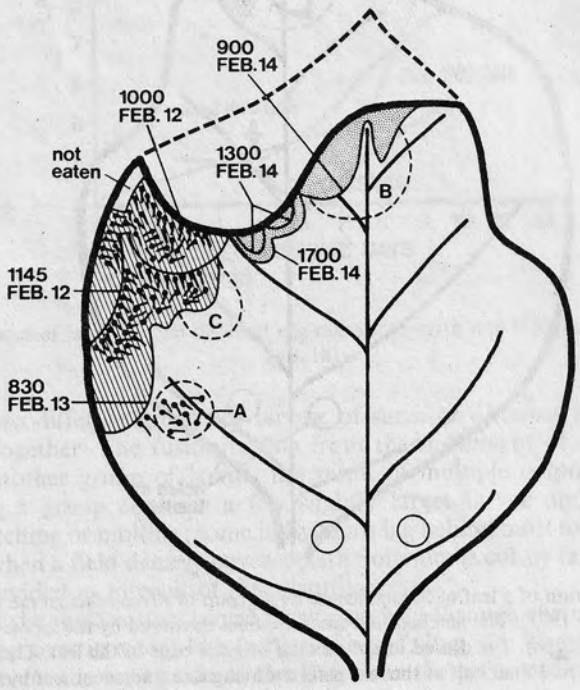
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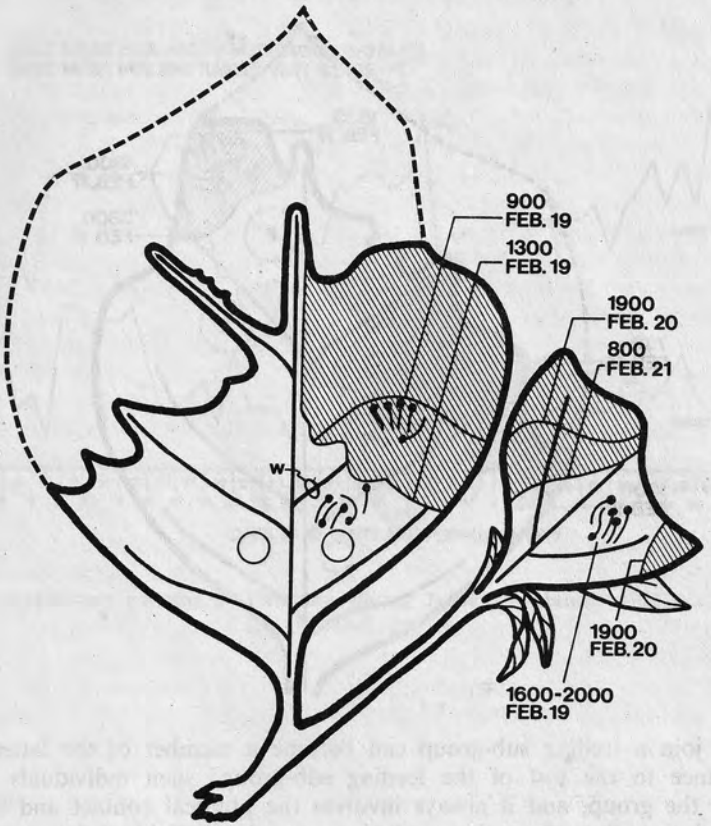
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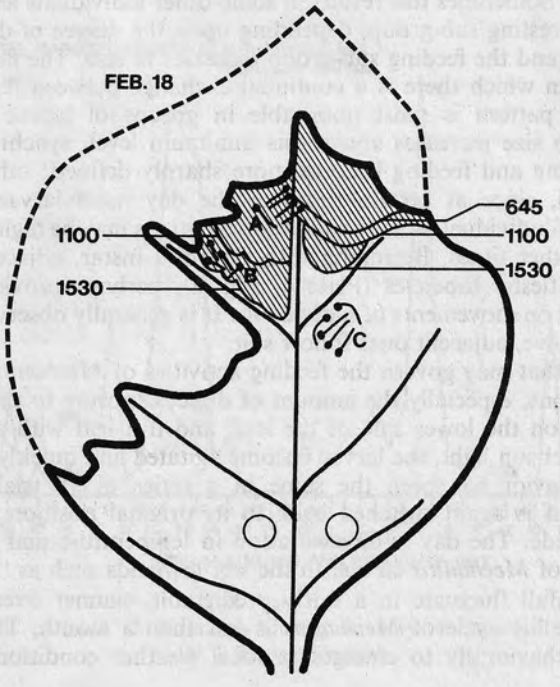
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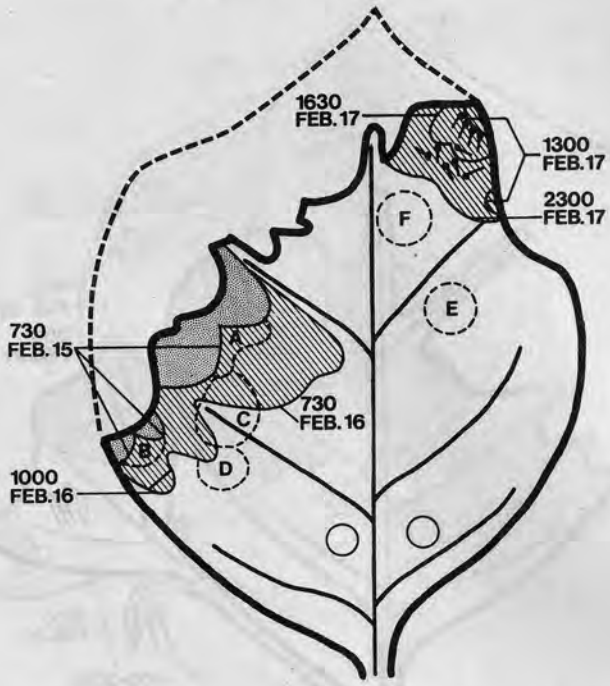

sub-group to join a feeding sub-group can become a member of the latter with very little disturbance to the rest of the feeding sub-group; such individuals are readily accepted into the group, and it always involves the physical contact and squeezing-in between other larvae. Sometimes this results in some other individuals leaving the feeding-subgroup to join the resting sub-group, depending upon the degree of disturbance. Other times no larvae leave and the feeding sub-group increases in size. The net result is usually a dynamic situation in which there is a continual exchange between feeding and resting individuals, and the pattern is most noticeable in groups of larvae greater than six individuals. As group size increases above this minimum level, synchronous behavioral patterns such as resting and feeding become more sharply defined; other factors clearly interact here as well, since at certain times of the day most larvae in a group are feeding. Thresholds of individual larvae to agitation by others may be higher at certain times of the day than at other times. Beginning with the third instar, adjacent larvae usually interlock the lateral fleshy tubercles (Plate 6, Fig. 8), perhaps providing a system of communication based on movements of individuals. It is generally observed that when one individual starts to move, adjacent ones follow suit.

Additional factors that may govern the feeding activities of *Mechanitis* larvae could be local weather conditions, especially the amount of direct exposure to the sun. *Mechanitis* larvae generally stay on the lower side of the leaf, and if a leaf with a group of larvae is flipped over in direct sun light, the larvae become agitated and quickly move to the new lower side. This behavior has been the same in a series of 18 trials using different groups. When the leaf is again switched back to its original position, the larvae again return to the lower side. The day-to-day variation in temperature and rainfall may also influence the activity of *Mechanitis* larvae. In the wet lowlands such as "Tirimbina", both temperature and rainfall fluctuate in a fairly predictable manner over a month's time (Figs. 9, 10), and the life cycle of *Mechanitis* is less than a month. Thus it is expected that larvae adjust behaviorally to changes in local weather conditions. Sudden heavy

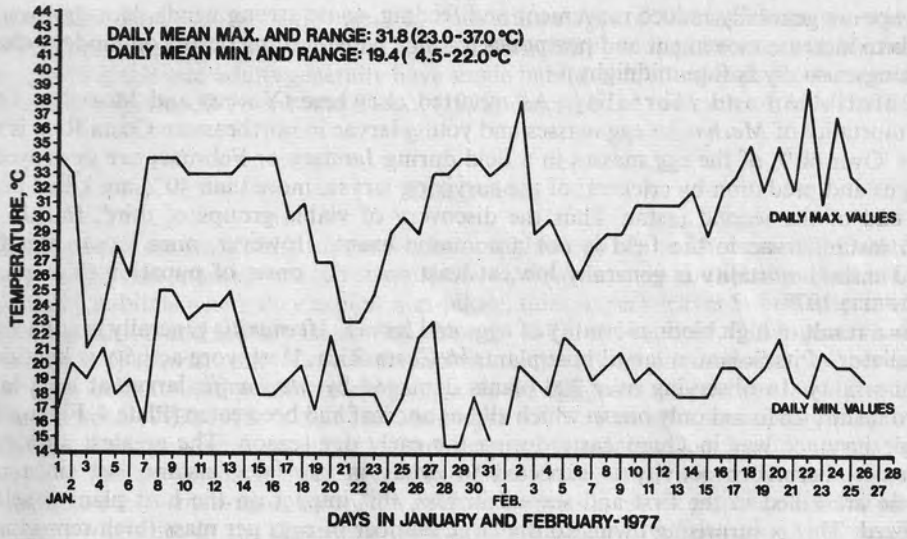

Fig. 9. Daily temperature patterns at Tirimbina during January—February 1977; data courtesy of Dr. J. ROBERT HUNTER

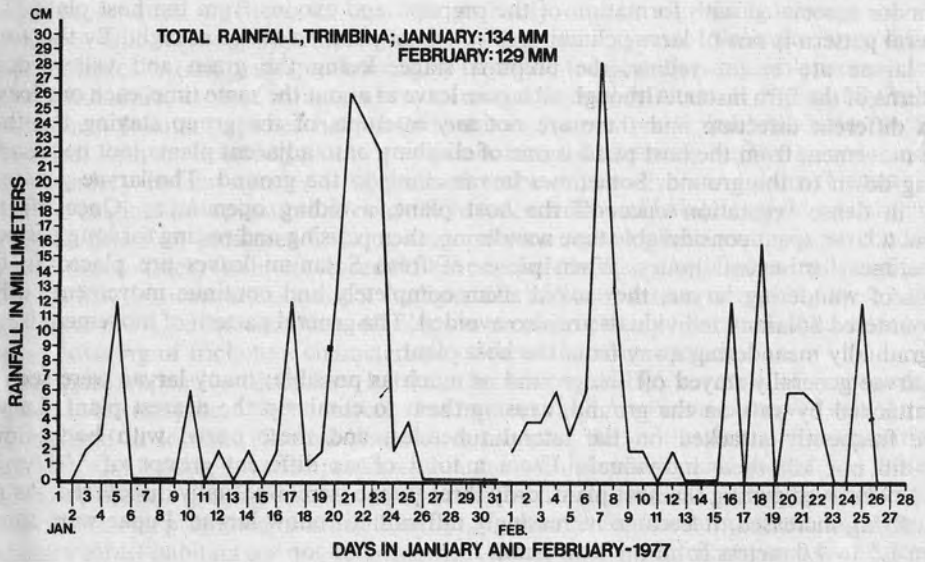

Fig. 10. Daily rainfall patterns at Tirimbina during January—February 1977; data courtesy of Dr. J. ROBERT HUNTER

downpours generally reduce movement and feeding, as do strong winds. Hot dry weather tends to increase movement and postpones feeding. Most feeding occurs on moderately dry evenings, usually before midnight.

Defoliation and Mortality: As reported elsewhere (YOUNG and MOFFETT, 1979), the mortality of *Mechanitis* egg masses and young larvae in northeastern Costa Rica is very high. Over 60% of the egg masses in a field during January or February are destroyed by fungus and predation by crickets; of the surviving larvae, more than 40% are killed before the end of the second instar. Thus the discovery of viable groups of third, fourth, and fifth instar larvae in the field is not a common event. However, once larvae reach the third instar, mortality is generally low, at least until the onset of pupation (YOUNG and MOFFETT, 1979).

As a result of high biotic mortality of eggs and larvae, *Mechanitis* generally is not a major defoliator of its Solanum larval host plants in Costa Rica. Herbivore activity is kept down by mortality. In observing over 200 plants damaged by *Mechanitis* larvae at least in the third instar, we found only one in which all but one leaf had been eaten (Plate 4, Fig. 6). This single instance was in Guanacaste during the early dry season. The greatest amount of potential herbivore activity is expected to occur in the later instars, but since most larvae are killed in the first and second instars, this impact on the host plant is seldom realized. This is surprising owing to the large number of eggs per mass (high reproductive output) and the often assumed role of group behavior in non-social insects in defense against predators and parasites. The data are particularly convincing for the wet lowlands of Costa Rica since most observations were made here. Less clear is the impact of biotic mortality factors on populations in highly seasonal regions such as Guanacaste. But generalizing from the wet locality data, it appears that weedy species of Solanum thriving in secondary habitats such as pastures, roadsides, and even some crops (bananas) are not regulated to any degree by *Mechanitis* as a herbivore.

Prepupation Behavior: From an earlier study of *Mechanitis* in Brazil (AJMAT and TERAN 1970), we had assumed that larvae in our studies would pupate on the host plants. We found that this was not the case, and that there is a definite form of behavior associated with formation of the prepupa and exodus from the host plant. The general pattern is one of larvae climbing off the host plant en masse at night. By this time, the larvae are bright yellow, the prepupa stage, losing the green and yellow color patterns of the fifth instar. Although all larvae leave at about the same time, each one leaves in a different direction and there are not any attempts of the group staying together. The movement from the host plant is one of climbing onto adjacent plants, not necessarily going down to the ground. Sometimes larvae climb to the ground. The larvae generally stay in dense vegetation once off the host plant, avoiding open areas. Once off the plant, a larva spent considerable time wandering, then pausing and resting for long periods, sometimes for several hours. When pieces of fresh Solanum leaves are placed in the paths of wandering larvae, they avoid them completely and continue movement; other encountered Solanum individuals are also avoided. The general pattern of movement is one of gradually meandering away from the host plant.

Larvae generally stayed off the ground as much as possible; many larvae were seen to be attacked by ants on the ground, causing them to climb up the nearest plant. Larvae were frequently attacked on the lateral tubercles, and these oozed with body fluids but did not kill these individuals. From a total of six different groups of *Mechanitis* larvae observed exiting the host plant, only three pupae were eventually discovered. As the wandering increased, it became increasingly difficult to follow larvae. Pupae were found from 1.5 to 4.0 meters from the host plant.

Pupation occurs singly and no pupae have been found on the host plant in more than two years of study. In the laboratory, larvae sometimes pupate near one another (Fig. 5). AJMAT and TERAN (1970) give a photograph of several *Mechanitis* pupae on the same leaf.

Additional illustrations of single pupae and other life stages of *Mechanitis* are given in FOX (1967). Thus, although oviposition and larval existence are group phenomena in *Mechanitis*, pupation is single and adults generally have single habits, exhibiting little or no gregariousness in our experience. AJMAT and TERAN (1970) describe the life cycle of *Mechanitis*.

Discussion

Other studies on the life histories and behavioral biology of the Ithomiinae in Costa Rica have revealed that most genera (*Hymenitis*, *Oleria*, *Godyris*, etc.) and species dwell in forest understory habitats where they exploit non-pilose, thin, papery-leaves Solanaceae and have single oviposition and solitary larvae (e.g., YOUNG 1972; 1974a, b, c). Other genera such as *Dircenna*, *Hypothyris*, and *Mechanitis* exploit thick, pilose and spinose Solanaceae of secondary habitats and exhibit varying degrees of egg-mass oviposition and gregarious larvae (YOUNG 1973; 1976; YOUNG and MOFFETT 1979). It is also noteworthy that forest-dwelling ithomiines tend to have transparent to translucent or hyaline wings while secondary habitat forms such as *Mechanitis* have fully-scaled wings. The transition for some ithomiines to man-made secondary habitats such as livestock pastures, banana plantations and roadsides in the American tropics may have involved selection pressures very different from those operating in primary forest understories. At least one genus, *Mechanitis*, is well on its way to inhabiting these secondary habitats and perhaps at one time it was preadapted for such a transition by occupying naturally-occurring marginal habitats such as forest light-gaps (created by tree-falls) and mudslides. The data gathered in this report reveal some of the ways in which *Mechanitis* is adapting to both marginal and large-scale secondary and agricultural habitats. Other genera such as *Dircenna* and *Hypothyris* may be starting such transitions.

We believe that the evolution of egg-mass oviposition and communal behavioral patterns of *Mechanitis* larvae is closely related to the ability of this insect to occupy secondary habitats and exploit pilose-spinose species of Solanum. The general strategy of larval host plant exploitation on a broad scale is probably one of colonizing weedy species of Solanum. Our working hypothesis maintains that these types of Solanum, very different morphologically (and perhaps chemically) from the forest understory Solanaceae used by most ithomiines, evolved in naturally-occurring marginal habitats. It is generally believed that some Solanum species have been cultivated since pre-Colombian times in South America, with artificial selection for spineless forms (HEISER 1968). The spined condition of secondary habitat species is considered to be a primitive conditions (HEISER 1968), and the original host plants of *Mechanitis* in forest marginal habitats might have been very spinose. Selection pressures favoring the evolution of the pilose and spinose conditions, in addition to thick, fleshy leaves, could have included grazing by large animals and protection against dessication from direct sunlight. Herbivorous insects occupying these habitats may have provided another form of selection pressure placing added selective value on the dense covering of trichomes characteristic of these Solanum species.

As more expansive secondary habitats became available, a result of increased agricultural activities, these plants increased in numbers and *Mechanitis* followed suit. As much of the land in lowland Central America is used for the cultivation and propagation of livestock and fodder, selection pressures maintained high pilosity and spinosity as protective measures against grazing and increased insect herbivore pressure. Precisely what environmental factors promoted a transition by *Mechanitis* to forest marginal habitats from primary forest habitats are not determined. It is known that different genera and species of ithomiines in wet regions of northern Costa Rica utilize different species of Solanaceae as larval host plants, suggesting specialization. It is generally maintained that ecological specialization in the tropics results from interspecific competition for scarce resources

(e.g., PIANKA 1966); selection pressure is created favoring a switching to new resources as they appear. An assumed switch of *Mechanitis* from primary forest to marginal and secondary habitats may have been a result of such competition with other ithomiines. Indirect evidence in support of the prediction comes from the observation that survival of eggs and larvae of solitary forest ithomiines is high, thus placing a greater demand on host plants (YOUNG 1972; 1974a, b, c).

Other studies have indicated that group behavior in immature non-social insects is a mechanism of protection against predators (e.g., GHENT 1966; FRASER ROWELL 1967; ALLEE and ROSENTHAL 1949). But STAMP (1977) found that the adaptive value of group formation in young larvae of the butterfly *Chlosyne lacinia* (Nymphalidae) has increased ease of feeding per larva in the group; groups were reduced in size in later instars and Stamp attributed this change in behavior to the avoidance of disease and parasitism. The data on *Mechanitis* (this report and YOUNG and MOFFETT 1979) indicate high mortality of both egg masses and young larvae, suggesting that group behavior in this insect has little or nothing to do with defense against predators and parasites. Rather the advantage to group existence has more to do with feeding. First and second instar individuals cooperate in tearing away trichome layer in order to reach the primary leaf tissue (epidermis and mesophyllic layers) for feeding; the discarded trichomes accumulate as fluff along the feeding edge of the leaf. Several larvae often cooperate in breaking off individual trichomes.

The additional cooperative behavior of constructing a silken mat over the leaf for communal living is another mechanism for keeping the group together and protecting against punctures of the cuticle. RATHCKE and POOLE (1975) have emphasized the role of the silken mat of *Mechanitis* in Venezuela as a means of protecting larvae against punctures from trichomes and spines of the host plant. They found that larvae spun silking coverings over spines in addition to over the leaf surface. We have not observed this behavior in our studies, probably because these particular Solanum species do not have many spines on the leaves. But, in general, there are at least two functions of group behavior in *Mechanitis* larvae, namely cooperative feeding and cooperative web-building; both activities are aimed at overcoming physical defense systems of the host plants.

Although it is known that some adult Ithomiinae are highly unpalatable to vertebrate predators in laboratory studies (BROWER and BROWER 1964), less is known about palatability in natural populations. BROWN and NETO (1976) found that a tanager *Pipraeidea melanonota*, successfully captures and eats large quantities of *M. polymnia* in Brazil. Internal organs are ingested but body wall tissues are generally avoided. If *Mechanitis* is generally unpalatable, then the larvae are also capable of handling chemical defense systems of the host plants, assuming that unpalatability is the result of the incorporation of toxins from the host plant during the larval stage. The cutting of a major leaf vein by older larvae may act as a means of changing the composition of fluids in leaf tissue. BREWER (1977) reported that similar behavior in larvae of the Monarch Butterfly *Danaus plexippus* may function to reduce the flow of toxins to areas of the leaf to be devoured. Such behavior regulated the intake of toxins by the insect. A similar form of behavior was discovered in the ithomiine *Aeria eurimedea*, which uses Apocynaceae as larval host plants (YOUNG 1977).

Some insects with group behavior such as aphids have developed mutualistic associations with ants; the aphids provide a food source (secretion) for the ants and the ants in turn protect the aphids from predators. There is one instance of an ant species (*Ectatomma* sp.) taking droplets of plant sap from the feeding edge of a leaf created by *Mechanitis* larvae, although wasps still take large number; of larvae (YOUNG 1978). The ants do not protect the larvae. Although a mutualistic association is not evident, the early stages of one could be present.

High mortality of eggs and young larvae is a consequence of group behavior in

Mechanitis, and presumably this behavior is maintained as a result of intense selection pressures associated with feeding on particular Solanum species. In addition to the role of communal web-building, an additional integrative mechanism might be pheromonal, as known for tent caterpillars in North America (FITZGERALD 1976). Such a mechanism might be especially operative in young larvae since web-building is just beginning and a major problem is orientation on the leaf.

Although the life cycle (egg-to-adult) requires less than 30 days in *Mechanitis* (AJMAT and TERAN 1970; YOUNG and MOFFETT 1978), this is ample time for mortality factors to take heavy tolls of eggs and young larvae. Older larvae and probably pupae appear less affected by mortality factors. The usual subdivision of a larval group into smaller groups in the last two instars, followed with the dispersal of larvae off the host plant at the time of pupation, may act as behavioral adaptations increasing survivorship. Group behavior seems to be most important in the first two instars, the result of the type of host plant and its defense systems against herbivores. The result is that adults are seldom numerous at a locality since few are recruited to the breeding population each generation. This pattern is most evident in the wet lowlands of Costa Rica; more seasonal regions such as Guanacaste may have populations with greater fluctuations in adult numbers, the result of seasonality upon predators and parasites of immature stages. Fluctuations are expected to occur in wet region populations as well since some types of predators, such as crickets, may have patchy distributions. Whether or not biotic mortality and its regulatory effects on *Mechanitis* populations is high in other regions is not determined. The species of *Mechanitis* such as *isthmia* and *polymnia* are very widespread and sometimes locally adults are very abundant in certain seasons (BROWN 1977).

The severe dry season of Guanacaste may impose population cycles on *Mechanitis* not predicted for populations in wet lowland areas such as "Tirimbina". GILBERT (1969) reported that *Mechanitis* adults clump in moist forest pockets during the Guanacaste dry season and adults may enter into a reproductive diapause; presumably breeding is resumed in the early wet season as a response to Solanum undergoing new vegetative growth. We found considerable clumping and mating of *Mechanitis* in the moist Barranca Site forest early in the dry season. This observation suggests that mated females enter into a reproductive diapause to pass the dry season; such an effect, coupled with some mortality of adults resulting from the dry season, results in population cycles. Dispersal of adults into moist forest pockets in Guanacaste in the dry season is high (GILBERT 1969), creating highly clumped or patchy distributions. In the wet lowlands, dispersal is predicted to be less owing to the more uniform temperature and humidity conditions present there throughout the year (GILBERT 1969). Nevertheless, some dispersal in these regions may also be adaptive in allowing the species to escape from pockets of high mortality and to locate new populations of host plants. Under such conditions, the effective population size might be large for *Mechanitis*. Increased dispersal ability might be one means of adapting to selection pressures created by intense predation and parasitism on immature stages, and it is an evolutionary tradeoff for exploiting larval host plants that require group feeding behavior by *Mechanitis*.

The striking degree of group behavior of *Mechanitis* larvae and the lateral tubercles are two major departures from most ithomiines; to this we add the general type of host plant. We believe that the well developed lateral tubercles of *Mechanitis* larvae function to communicate movements of adjacent individuals in a tight group of feeding or resting individuals. These structures are lacking from other ithomiine genera. Thus the necessity for *Mechanitis* to exploit very spinose and pilose Solanum species involves both behavioral and morphological changes from the more typical ithomiines of tropical forests. The larvae of another secondary habitat ithomiine, *Hypothyris euclea*, are very gregarious but lack the lateral tubercles of *Mechanitis* (YOUNG 1976). The larval host plant, Solanum rugosum, is more similar in general appearance to most host plants of forest ithomiines with

single oviposition and single larvae. Yet the ventral sides of the leaves of S. rugosum are pilose but not nearly as much as *Mechanitis* host plants such as S. hispidum and others. The leaves are also more papery than those of *Mechanitis* host plants. *Hypothyris* spins a communal mat over the leaf and larvae feed synchronously. Mortality in all instars is high (YOUNG 1976). *Dircenna relata* is another secondary habitat ithomiine in Costa Rica that scatters eggs in a loose formation on the ventral side of the leaf; this species places the eggs loosely in the dense layer of stellate trichomes and the larvae stay in loose groups but do not exhibit well-structured group behavior (YOUNG 1974a). By the fifth instar, the larvae exhibit almost solitary behavior. These examples of *Hypothyris* and *Dircenna* may represent less developed forms of group behavior that are adapting these ithomiines to spinose or pilose host plants in secondary habitats. It is interesting to note that the larval host plants of both genera have very patchy distributions in secondary growth on the margins of primary forest; individual patches or clumps are often quite large. Neither host plant has the broad and very abundant local distribution of the *Mechanitis* host plants of pastures, roadsides, and banana plantations.

While it is known that predaceous ants take heavy tolls of eggs and young larvae of some species of *Heliconius* butterflies (Nymphalidae: Heliconiinae) resulting in populations being free of resource (host plant)-limitation (GILBERT 1975), we did not find evidence of ant predation on *Mechanitis*. GILBERT (1969) predicted predaceous ants to be regulatory factors of *Mechanitis* populations and noted that larvae seldom defoliated host plants. From our data, we wish to modify this statement by saying that eggs and larvae of *Mechanitis* are predator-regulated, as predicted by GILBERT, but that the major factors in the populations we studied were parasitoids, crickets, and pathogens.

The interaction of *Mechanitis* and its Solanum larval host plants in Costa Rica, and perhaps elsewhere in Central and South America, provides a generalized picture of how a tropical insect is following its resources as the latter become more abundant and assume the characteristics of weed species in secondary habitats and agricultural regions. In this particular case, the host plants also attract a complex of biotic mortality agents which keep *Mechanitis* populations well below pest-outbreak conditions. Group forms of behavior associated with feeding on these host plants also result in considerable mass mortality of eggs and young larvae; nevertheless, selection pressures favoring group behavior must be considerably stronger than opposing pressures since the group behavioral traits examined here are highly synchronous and clearly illustrative of inter-individual dependence in young larvae. We believe that this selection pressure is primarily in the form of *Mechanitis* adapting to unusually pilose and spinose host plants; it has little to do with defense against predators and parasites. The substantial mortality of immatures postpones the intensification of a coevolutionary race between *Mechanitis* and Solanum, since this interaction does not usually result in severe defoliation. If, however, future environmental changes reduce the effectiveness of these biotic mortality factors, we expect the race to intensity. If this was to happen, it would be one means of controlling weed species that injure livestock and farm workers. Crickets, as herbivores of these Solanum species, may play a major role in regulating *Mechanitis* defoliation and these crickets might have been coevolving with these plants along with this butterfly.

A gross departure from the usual picture of niche expansion is the apparent inability of *Mechanitis* to lose the various biotic mortality operative on egg masses and larvae. The usual result when an insect has the opportunity to expand in distribution owing to an increased availability of the most plant, is a large increase in abundance. This is apparently not happening in the case of *Mechanitis* since it experiences high biotic mortality in secondary habitats. It is generally predicted that herbivorous insect populations in early successional stages may experience outbreaks, i.e., attain pest conditions, as a result of leaving predators and parasites behind (JANZEN 1975). But for the *Mechanitis*-Solanum interaction, considerable population regulation by extrinsic factors is still evident, perhaps

the result of either the close proximity (spatial) of naturally-occurring marginal habitats (where biotic mortality factors could have been evolving with the herbivore), or the very rapid adaptation of new predators and parasites to *Mechanitis* as prey or host. The end result is that the plant species becomes a weedy or pest species because at least one herbivore is kept well below population size characteristic of an outbreak. But as tropical secondary and agricultural habitats are continuously altered further in various ways, these regulatory factors may be reduced or disappear, and *Mechanitis* may become very aboundant. With egg mass oviposition and group behavior of larvae, it is an insect species potentially well adapted to do so. The widespread occurrence of *Mechanitis* through much of Central and South America indicates that it is a highly flexible species capable of existing in a broad range of habitats.

At the present stage in the interaction between *Mechanitis* and Solanum species in secondary habitats, the herbivore is continuing to exploit a complex of strikingly similar wild host plants, some of which, or all, evolved in naturally-occurring marginal habitats in forests. If selection pressures in secondary habitats were to change in such a way as to relax the intense mortality on eggs and larvae of *Mechanitis* resulting in a removal of population regulatory mechanism, *Mechanitis* could become a major defoliator of these plants, perhaps to the point of becoming resource (food)-limited in some areas. At this point, alternative hostplants, including cultivated species if available, could be exploited. Some cultivated solanaceous species such as tomato (Lycopersicon esculentum), tobacco (Nicotiana tabacum), and egg plant (Solanum integrifolium) posses varying degrees of pilosity (e.g., WEBSTER 1975), and this could allow *Mechanitis* to exploit these as host plants. A major feature of many cultivated plants is a loss of defense systems, and if chemical defenses of tomato and others are lower than closely related wild species. As a group, the Solanaceae are considered to be of great economic importance, especially in Central and South America and many genera and species have been cultivated for food, spices, and ornamentals, including many species of Solanum (HEISER 1968). Should *Mechanitis* make a transition to cultivated solanaceous plants it may become a major pest if its predators and parasites are left behind.

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Fig. 1. Young secondary growth habitat at "Tirimbina" where *Mechanitis* larval host plants, Solanum spp. (Solanaceae) are abundant. This field has been converted into a livestock pasture.

Fig. 2. A major larval host plant of *Mechanitis* at "Tirimbina" is Solanum jamaicense shown here.

Fig. 3. An individual of Solanum hispidum at "Tirimbina", showing areas of leaves defoliated by *Mechanitis* larvae.

Fig. 4. A secondary growth habitat at Finca La Taboga in Guanacaste Province, where a *Mechanitis* larval host plant, Solanum ochraceo-ferrugineum is very abundant.

Fig. 5. At Finca La Taboga, S. ochraceo-ferrugineum grows in larga clumps in secondary growth habitats. *Mechanitis* adults deposit large masses of eggs on older and peripheral leaves of a plant. The larval host plants in wet lowlands regions such as Tirimbina are considerably shorter in height.

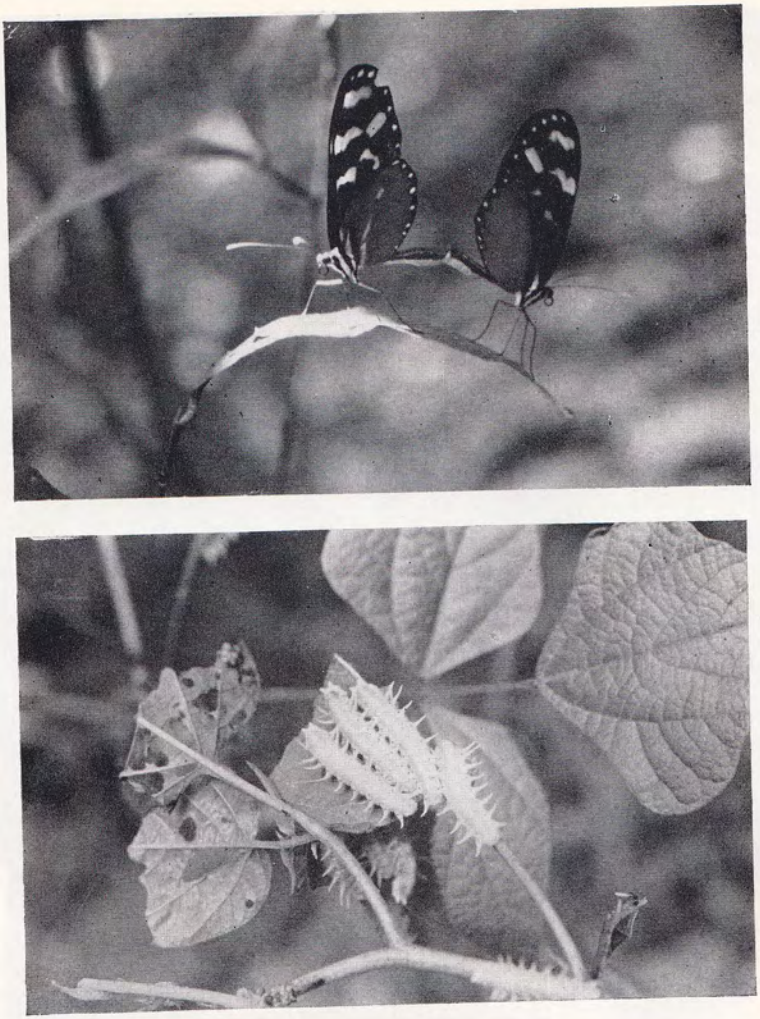

Fig. 6. Above: mating pair of *Mechanitis isthmia* in the understory of a pocket of moist forest, the "Barranca Site", in the early dry season (December 1975). Below: several fourth instar larvae of *Mechanitis* defoliating the host plant at the Barranca Site in the early dry season. Note interlocking lateral tubercles of different larvae.

Fig. 7. Above: *Mechanitis* female beginning to deposit eggs on S. ochraceo-ferrugineum at Finca La Taboga. Egg masses are deposited on the upper surface of an older leaf. Below: Oviposition. Note egg mass.

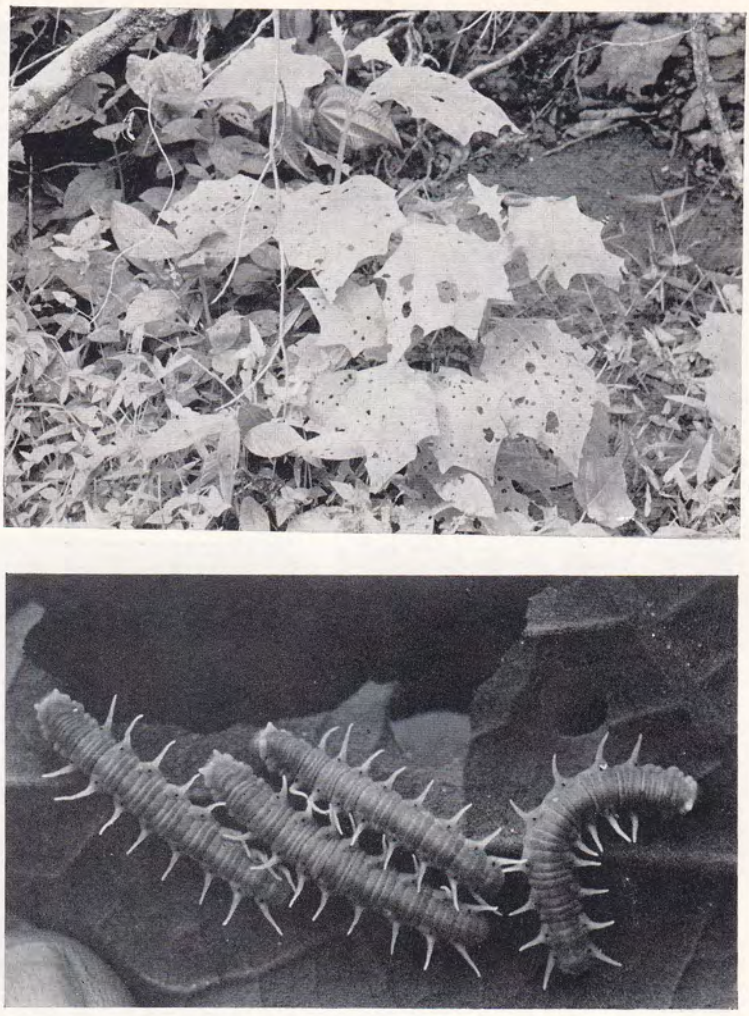

Fig. 8. Above: Solanum jamaicense showing heavy defoliation from a variety of insects such as Orthoptera and selected Coleoptera; some of these insects are predators of eggs and young larvae of *Mechanitis*. Below: fifth instar larvae; note interlocking of lateral tubercles.

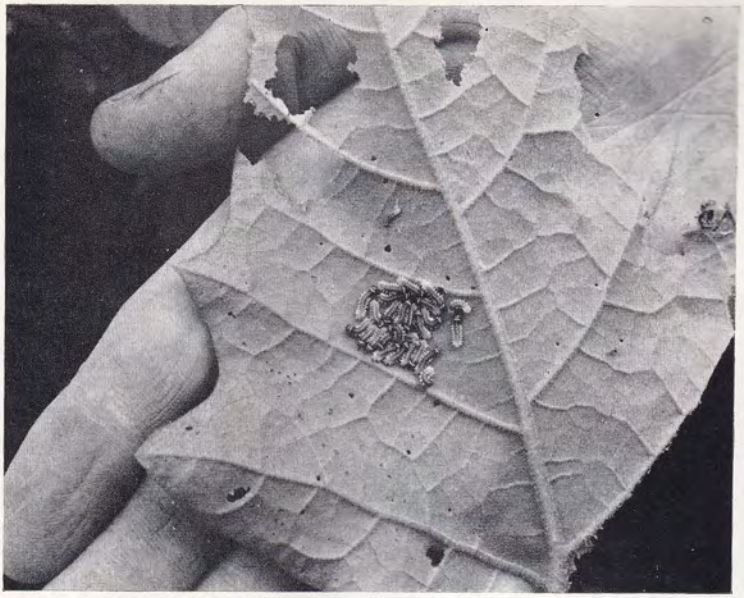

Fig. 9. Group resting behavior of second instar larvae of *Mechanitis* on S. hispidum. Note feeding edges (areas) on the leaf; larvae generally form resting groups away from feeding edges.

Fig. 10. Tent-like arrangement of host plant leaf resulting from the weakening of the midrib ventrally by communal biting by *Mechanitis* larvae (third instar).

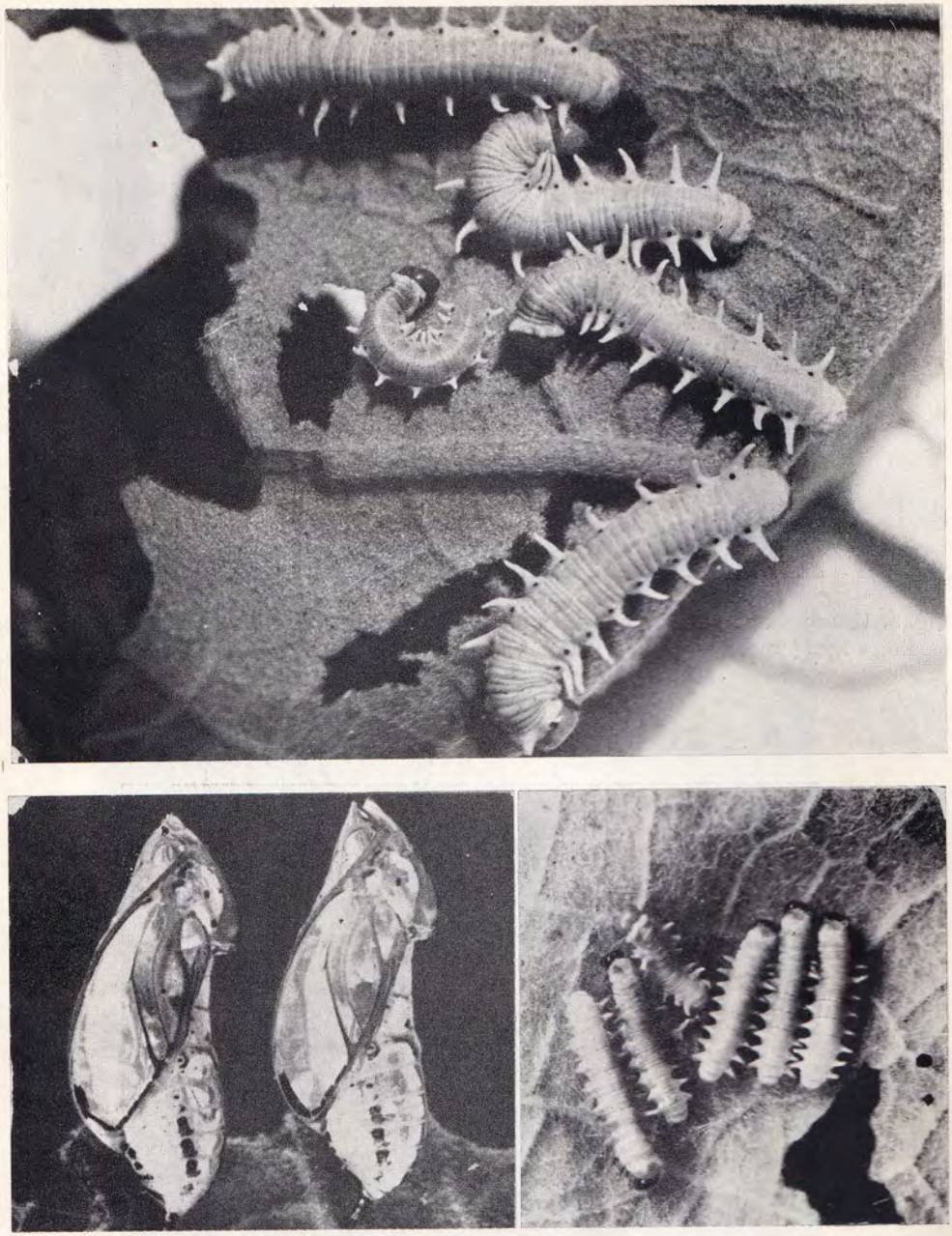

Fig. 11. Above: fifth instar *Mechanitis* larvae; below, left: communal resting on silken mat; right: pupae of *Mechanitis* in the laboratory.