Studies on the Population Biology of the Tropical Butterfly Mechanitis isthmia in Costa Rica

ALLEN M. YOUNG and MARK W. MOFFETT
Invertebrate Division, Milwaukee Public Museum, Milwaukee, Wisconsin 53233

ABSTRACT: The mortality of eggs and larvae of the tropical butterfly *Mechanitis isthmia* (Bates) (Lepidoptera:Nymphalidae:Ithomiinae) was studied in Costa Rica. This butterfly deposits large masses of eggs on species of *Solanum* (Solanaceae) possessing thick, fleshy leaves covered with defensive hairs (trichomes) and spines. The larvae from an egg mass stay together as one or more groups on silken mats, and feeding, resting, molting and movement are communal activities. Sometimes individual larvae on the periphery of a group become isolated and are quickly taken by wasps and spiders. Such mortality is high for first- and second-instar larvae. Older larvae survive well. Furthermore, more than 80% of the egg masses in an area are destroyed primarily by crickets, parasitic wasps and pathogenic microorganisms, with considerable plant-to-plant patchiness. The communal feeding allows young larvae to collectively clear away trichomes, but there is no apparent communal defense against predators. Older larvae, within a group, interlock their lateral tubercles, providing some form of communication among individuals. Most species of Ithomiinae are forest dwellers and deposit eggs singly on food plants; these solanums generally have smooth papery nonhairy leaves. Trichome-covered solanums are abundant in secondary habitats, and *Mechanitis,* in utilizing these plants as larval food, has evolved cluster egg-laying and gregarious forms of larval behavior.

INTRODUCTION

There is a growing body of evidence indicating that, for some tropical butterflies that have coevolved with certain larval food plant families (Ehrlich and Raven, 1965), substantial mortality of eggs and larvae occurs in local populations (*e.g.,* Ehrlich and Gilbert, 1973). Some families of tropical plants attract predators of butterfly eggs and young larvae found on these plants. Using this assumption, we conducted an investigation of egg and larval mortality in a population of the butterfly *Mechanitis isthmia* (Bates) (Lepidoptera:Nymphalidae:Ithomiinae) at a tropical wet forest locality in northeastern Costa Rica. As *Mechanitis* deposits masses of eggs on food plants (various Solanaceae) (Fox, 1967; Ajmat and Teran, 1970), a premise of these studies was that entire egg masses would often be destroyed by predators, parasites and pathogens. It was also suggested that the larvae, which also stay together in tight groups (same reference as above, and Rathcke and Poole, 1975), exhibit specialized forms of communal behavior associated with feeding and defense against predators. These studies help to explain the local population dynamics of *M. isthmia,* a widespread species throughout much of Central and South America.

METHODS

The studies of *Mechanitis isthmia* included: (1) the examination of oviposition and larval behavior, especially hatching, feeding, resting and pupation, and (2) the estimation of egg mass and larval mortality and the factors involved. Most observations were conducted at "Finca La Tirimbina," near La Virgen de Sarapiqui (220 m elev.), Heredia Province, Costa Rica; other observations were made at the "Barranca Site" (*see* Orians, 1969, for full description), Puntarenas Province (35 m elev.) and "Finca La Taboga," near Canas (10 m elev.), Guanacaste Province. The former locality is in the Premontane Tropical Wet Forest life zone, while the others are in Tropical Dry Forest (Tosi, 1969). The "Tirimbina" studies were conducted during January 1976, January-February and August 1977. The basic approach was to tag individual food plants bearing egg masses or larvae, and then determine their survival with daily observations. A field where egg masses were very abundant was mapped over a 3-week period for the locations of each plant bearing egg masses. As earlier observations suggested that *Mechanitis isthmia* deposits egg masses primarily on food plants in areas exposed to direct sunlight, an attempt was made to measure this effect. This was done by noting the occurrence of egg masses in shaded and exposed areas of a field.

Occasional disturbances resulted in a loss of some tagged plants, mostly from being cut by farm workers. Selected groups of larvae were then observed for behavioral analysis. The incidence of adult *Mechanitis isthmia* in areas where eggs and larvae were found was also noted. Data on rainfall, temperature and the extent of daytime cloud cover were recorded in order to determine any correlations with changes in behavioral patterns of larvae.

RESULTS

Habitat, oviposition and food plants.—Mechanitis isthmia occurs in secondary vegetation and other disturbed habitats of both wet and dry regions. The larval food plants are abundant in these habitats. At "Taboga," the larval food plant is *Solanum ochraceo-ferrugineum* (Dun.) Fern., and *S. hispidum* Pers., and *S. jamaicense* Mill. are food plants at "Tirimbina." Both *S. hispidum* and *S. jamaicense* occur as isolated individuals or small patches, with *S. jamaicense* being far more abundant. Both occur in the same habitats; we refer to them as Plants No. 1 and 2, respectively, in presentation of the data. In the tropical dry forest region, *S. ochraceo-ferrugineum* is a large bush.

Mating takes place in shaded spots within forest or dense secondary understory. Sometimes there are large flushes of fresh adults which mate in large numbers. These matings are followed by the appearance of many egg masses. It is seldom that larvae defoliate a food plant.

A female spends close to an hour depositing 30-60 eggs, as a single mass, on the upper side of a large leaf (Fig. 1). The eggs are arranged in generally neat rows and vary from less than 10 to ca. 60. Sometimes the same female lingers in an area over several days, laying multiple egg masses. From samples of dissected females taken from this locality over the past 4 years, it was found that fresh ones have 100±17 ($\overline{X}$±SE, N=48) eggs while older ones (moderately frayed wings) have 216±32 eggs (N=63). If a female is accidentally disturbed while ovipositing, she flies away and usually returns after several minutes and resumes egg-laying at the same spot. But field observations of egg masess having 10 or fewer fresh eggs suggest that sometimes a disturbed female may not return. Females presumably in search of host plants exhibit considerable selectivity before finally settling down to deposit eggs; this occurs even in an area where food plants are abundant.

Sometimes more than one egg mass is found at the same plant, but never, in our experience, are two or more eggs masses found on the same leaf. Of a total of 88 plants with eggs observed at this locality over four successive dry seasons, 71% (63) had a single egg mass while about 29% had two egg masses and another one had three. Another 16 plants had one or more egg masses and at least one group of larvae present at the same time on each plant. Thus some individual plants are used repeatedly for oviposition, even when other, unused plants are located in the same area. Although as many as 230 individuals of *Solanum jamaicense* occur in a "Tirimbina" field ca. 50 x 30 m, less than 10% of these will have eggs or larvae on them at any one time. If such a field is observed for a 4-6 hr period on a sunny day, less than 15 adults of *Mechanitis isthmia* are seen. This generalization excludes situations such as at the "Barranca Site" during the early dry season when large numbers of *M. isthmia* adults congregate in heavily shaded forest understory.

In a field with a high concentration of both *Solanum jamaicense* and *S. hispidum,* there were shaded areas (A, B—Fig. 2) where egg masses were never found. Both of these areas are depressions in the terrain with tall trees, and they are located near

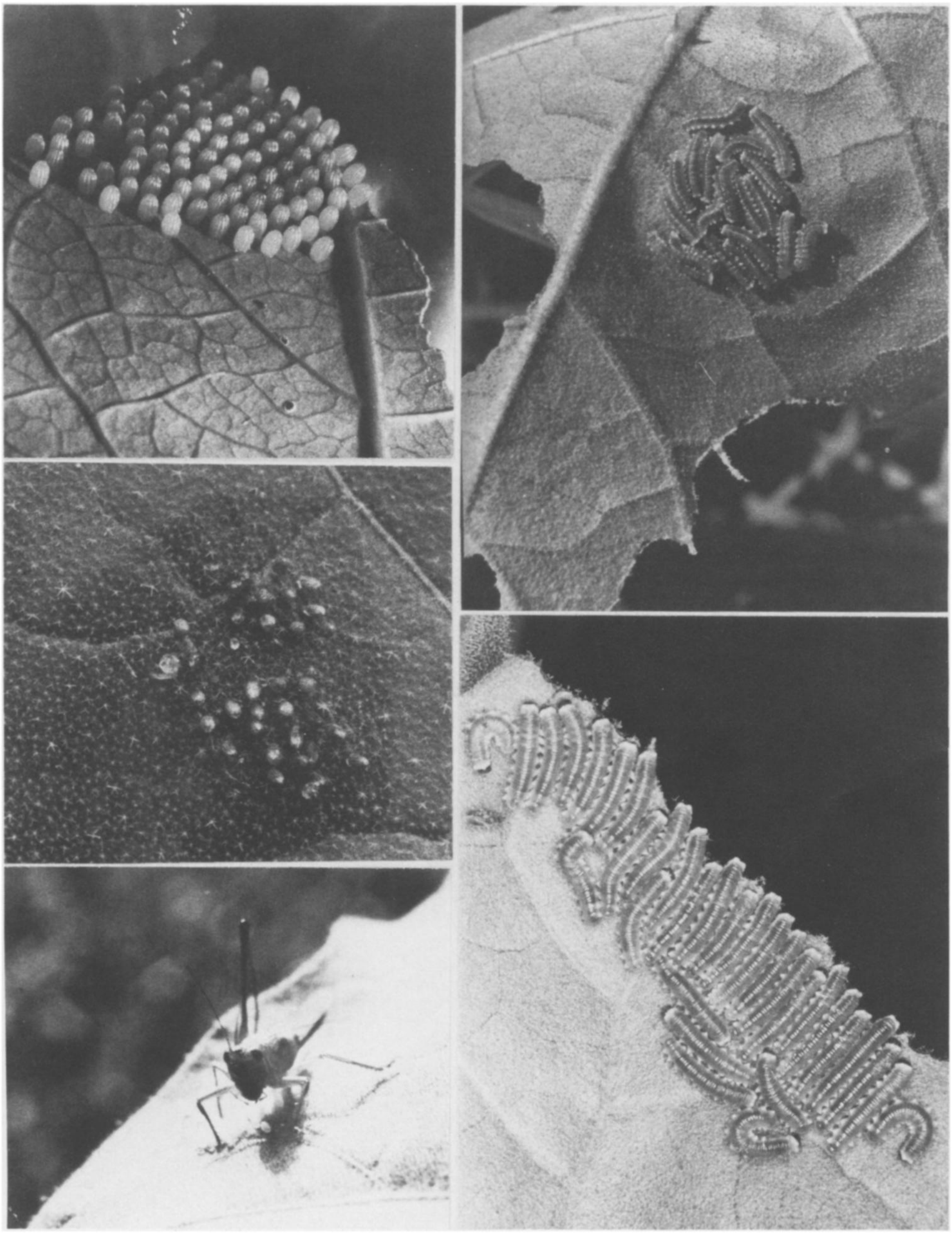

Fig. 1.—Upper left: healthy egg mass; middle left: eggs destroyed by pathogenic micro-organism; lower left: unidentified tettigonid feeding on eggs. Upper right: second-instar larvae in typical resting position on ventral side of a leaf, near feeding areas; lower right: second instars feeding

two houses (Fig. 2). Within each of these heavily shaded areas there are comparable numbers of food plants but not egg masses. Of 26 plants in Area A and 30 in Area B none had egg masses during 1977. But in two exposed areas of similar size and plant number (22 and 28 plants, respectively), 13 and 18 plants, respective-

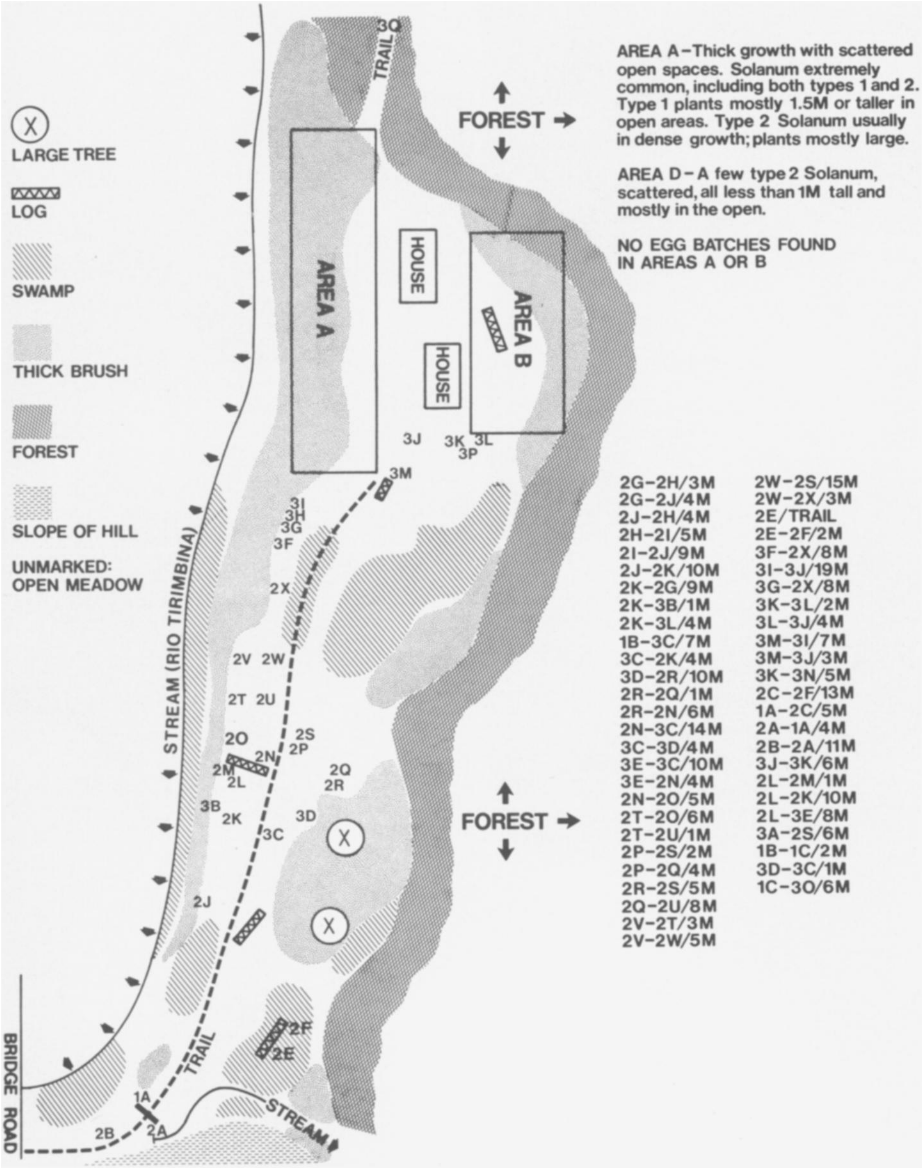

Fig. 2.—The field habitat showing positions of larval food plants having egg masses or larvae of *M. isthmia,* February 1977. Note that most infested individual plants occur along the trail. Codes to the right give the nearest neighbor distances between plants. Although many food plants occur in areas A and B, few of these had eggs or larvae

ly, had one or more during this period. Egg masses of *Mechanitis isthmia* are found in areas where food plants are exposed to direct sunlight for most of the day. Individual food plants overgrown with other plants are also avoided; large dense patches of *Solanum* are also avoided. About 90% of all egg masses found were less than a meter above the ground; tall plants are avoided but very small plants are commonly used. *Mechanitis isthmia* exercises considerable habitat and microhabitat selectively in choosing where to deposit eggs.

Behavior of larvae as related to feeding and survival.—Larvae eat egg shells upon emergence, and an individual larva may eat more than its own shell. As documented elsewhere (*e.g.,* Fox, 1967; Ajmat and Teran, 1970), larvae rest and feed gregariously (Fig. 1). Larvae feed in tight groups along a feeding edge of a leaf, and rest together in tight groups. Usually some feed while others rest, there being an exchange of individuals between the feeding and resting group. Sometimes all feed or rest together. A communal silk network is used for movement over a leaf and between leaves. The silk network is spun over the hairs (trichomes) on the ventral side of the leaf. As larvae grow, they move to different leaves, after partially or entirely devouring a leaf (Fig. 3).

Although they stay in groups, there is considerable exchange of individuals between the center and periphery of a group; in older larvae, the lateral tubercles of different individuals may interlock loosely in the group formation (Fig. 1). Many times one or more larvae fed, rested or explored in an area away from the majority of individuals, but usually they either soon returned or were joined by the rest of the group. Molting is synchronous and survival through molt periods is usually 100%. Almost 90% of the time larvae are split between feeding and resting groups, and some feed on their own away from other members of the group. When young larvae are feeding at the edge of a leaf (Fig. 1), they deposit a zone of sloughed-off hairs, indicating they do not devour these structures; larger larvae devour trichomes along with other tissue. In large groups, larvae almost invariably remain on the silk network. Larvae disperse individually at the time of pupation, which takes place away from the host plant.

At this locality, there is considerable daily variation in both temperature and rainfall; days of high rainfall (> 10 mm) were times of reduced feeding by larvae. For a group of 20 second-instar larvae observed feeding on both sunny and rainy mornings in August 1977, the average amount of leaf consumed per larva was 13 ± 2 mm^2 ($N = 15$) in six hr on a sunny morning, while for rainy mornings leaf consumption for the same larvae was 4 ± 2 mm^2. During a clear, dry night, the same larvae consumed 18 ± 3 mm^2 of leaf tissue (same leaf) while feeding was almost nothing on rainy nights. These patterns were observed for 4 days and nights. The greatest amounts of leaf surface area are consumed at night, especially after midnight. During the night larvae often spend several hours feeding, while during the day they feed more sporadically. On cool, cloudy days larvae feed for longer periods, much like they do at night.

Mortality of egg masses and larvae.—Egg masses of *Mechanitis isthmia* are killed in very high frequency at this locality (Table 1). Of 11 groups of surviving first-instar larvae observed during February 1977, all but one were killed. An additional five groups of third- to fifth-instar larvae survived. Of another 15 groups of first- to second-instar larvae (range in groups size from 5-31) observed during August 1977, only one survived to reach the third instar. Survivorship in an additional eight groups of fourth and fifth instars was 100%. The pattern which emerges from these observations is that egg masses and first- and second-instar larvae are extremely vulnerable to being killed.

The most frequent type of egg mass mortality is a darkening of eggs, suggesting a microorganism infection. At first one or two eggs would darken, showing signs of infection, but within a few days most would be darkened (Fig. 1). This is not infertility: infertile eggs fail to develop diagnostic color marks soon after deposition and all of the attacked eggs had these markings. Other egg masses were eaten by insects, such as a tettigonid (Fig. 1) and hemipterans. When a tettigonid is placed near an egg mass, it eats eggs. Some egg masses were killed by parasitic wasps. For example, egg mass no. 23 had several wasps on 12 February and by 19 February seven of the 36 eggs were destroyed; by 27 February all were destroyed.

Tettigonids devour the eggs entirely and will return repeatedly to an egg mass until all are eaten. Sometimes a few eggs survived such predation and many egg masses with less than 10 each are examples of ones not entirely depleted. Tettigonids

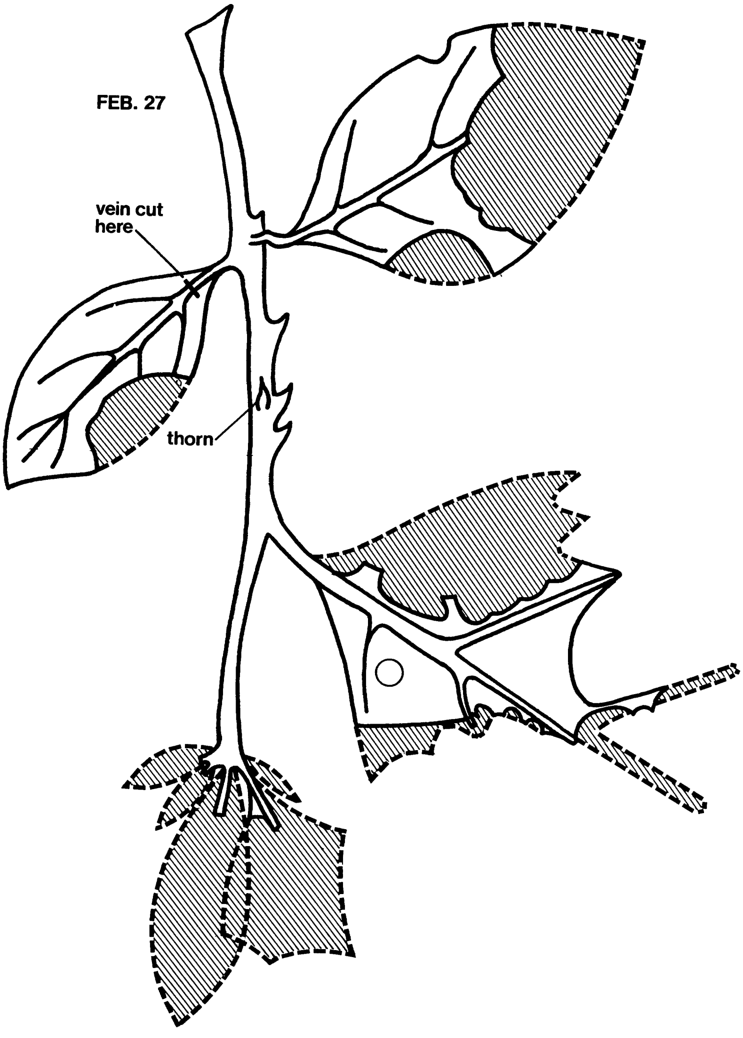

Fig. 3.—The generalized defoliation of a medium-sized plant of *S. jamaicense* by an average-sized group (28) of *Mechanitis* larvae by the fifth instar. The shaded areas represent destroyed leaf tissue

and hemipterans begin their attack on an egg mass by devouring the peripheral ones first; the last to be eaten or the ones that will survive are the innermost eggs.

Jumping spiders and polybine wasps were predators of young larvae. In several instances, a wasp returned repeatedly to take larvae, eventually removing all within a day. Once larvae reached the third instar, they were not attacked. Large *Polistes* rapidly take young larvae from a group, removing peripheral ones first. Isolated larvae were attacked more readily than grouped larvae and were devoured by jumping spiders and wasps. *Solanum* plants attract an unusually high density of orthopterans, hemipterans and chrysomelid beetles, and many of these may be predators of *Mechanitis isthmia* eggs and young larvae. When a larva is being attacked by a wasp or spider, there is no group behavior that discourages the attacker. The attack generally happens so fast that other larvae either remain resting or continue feeding. In instances where a predator left the remains of killed and partially eaten larvae, survivors usually devour these quickly. Typical patterns of larval group depletion by predators are shown in Figure 4. Interestingly, eggs and larvae were not attacked by ants. A captive *Anolis biporcatus* was successfully force-fed nine larvae with no ill effects on subsequent days. A captive *A. limifrons* ate two larvae without coaxing, and with no noticeable ill effects. Both anoles, especially *limifrons,* are abundant in field and forest-edge habitats where *Mechanitis* occurs.

DISCUSSION

Based primarily on recent studies of *Heliconius* butterflies (Ehrlich and Gilbert, 1973; Gilbert, 1975), it has been suggested that populations of butterfly species in the tropics are limited primarily by predation and other forms of biotic mortality. *Heliconius* larval host plants with extrafloral nectaries attract ants which in turn act as predators on eggs and young larvae. The association of ithomiines such as *Mechanitis isthmia* with the Solanaceae as larval host plants is another example of coevolved relationship, yet the sources of mortality operating in populations are very different from those of the *Heliconius.* Gilbert (1972) and Dunlap-Pianka *et al.* (1977) have shown that pollen feeding extends the adult life span of *Heliconius,* and such an effect buffers high egg and larval mortality in natural populations (Ehrlich and Gilbert, 1973). Owing to the lack of such mechanisms in *Mechanitis,* one might expect adult numbers to vary considerably with time in a local population, since egg and larval mortality can be high. The role of *Mechanitis* and other ithomiines feeding on fresh bird feces on adult life span should be explored (Drummond, 1976; Young, 1977a).

The apparent attractiveness of *Mechanitis isthmia* food plants to predatory and parasitic athropods provides selection pressure favoring cluster oviposition and communal larval behavior (*see also* Young and Moffett, 1979). L. M. Cook (pers. comm.) found that the gregarious larvae of *Heliconius doris* on Trinidad suffer high levels of mortality from ants during periods of synchronous molting. It is known that *Heliconius* food plants, Passifloraceae, attract many ants, owing to the presence

TABLE 1.—A summary of mortality of egg masses of the butterfly *Mechanitis isthmia* at one locality in northeastern Costa Rica, 1976-77

	Initial No. of egg masses (N)	Mean No. Eggs per Mass (N ± SE)	Range	No. egg masses destroyed, N	% Mortality of egg masses
6-28 Jan.-1976	10	31 ± 11	9-43	10	100%
12 Jan.-19 Feb. 1977	25	31 ± 16	2-60	20	80%
12-22 Aug. 1977	40	27 ± 12	7-2	33	83%

of extrafloral nectaries on many species (Gilbert, 1975). The apparent lack of extrafloral nectaries and ants from *Solanum* permits high survival of *Mechanitis* larvae during synchronous molting periods. Although ants are not a source of mortality in *Mechanitis* populations at the present time, workers of *Ectatomma* stroke the heads of communally feeding first- and second-instar larvae but do not provide protection from attacks by wasps (Young, 1977b).

To compensate for high mortality of eggs and larvae, butterflies disperse eggs over large areas. The low density of adult *Mechanitis isthmia* in an area, in part the result of low adult recruitment, is also the result of dispersal. Gilbert (1969) summarized mark-recapture data for *M. isthmia* at "Taboga" and nearby "La Pacifica" which showed a very low recapture level, suggesting a high dispersal tendency of individual butterflies in the dry season. He also states that the butterfly is confined to moist pockets during the dry season. In a wet forest habitat, the adult population disperses over even larger areas. Brown (1977) mentions that *M. lysimnia* (Fabricius) is a highly mobile species in Brazil.

An additional factor contributing to the pattern of food plant exploitation by *Mechanitis isthmia* is oviposition site selection; many plants have no eggs and larvae, and both selectivity in oviposition and mortality result in the patchy distribution. An

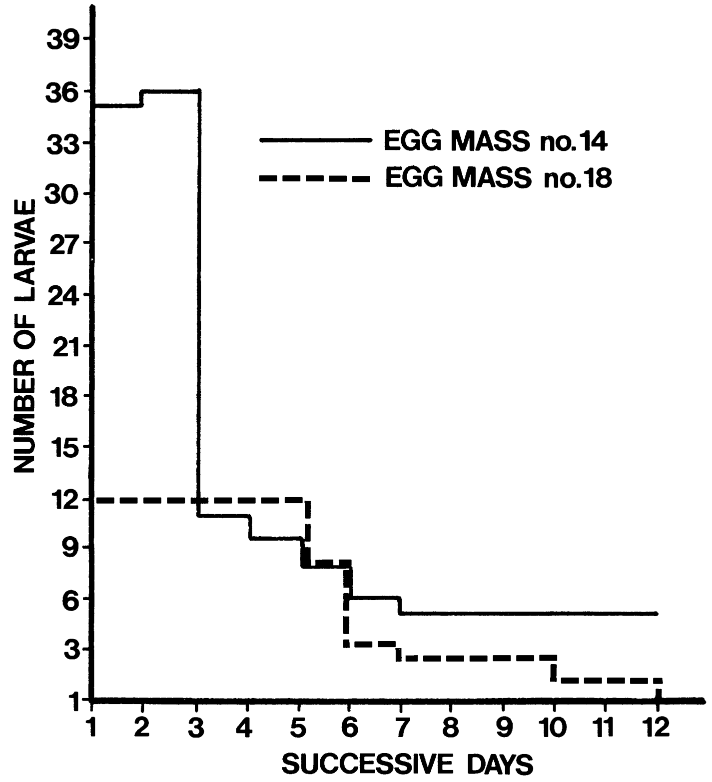

Fig. 4.—Survivorship curves for larvae of *M. isthmia* in nature. The greatest reduction in numbers takes place during the 1st few days of larval life, the result of predation and parasitism by wasps and spiders

important evolutionary implication of this patchiness is that it can increase the variation in the number of eggs laid per parent and thereby decreases the effective population number and increases inbreeding.

If the survival of larvae is related to their gregariousness, group survival mechanisms may depend on a critical minimum number of eggs. Gilbert (1969) suggested that the return to an incomplete egg mass by the female butterfly, to deposit more eggs, signifies the need for a minimal number of eggs in a mass. There may exist a minimal larval group size that allows cooperative feeding and thereby ensures a certain number will survive. Otherwise, it is difficult to envision the significance of laying large egg masses that are so easily destroyed.

The communal behavior and high survivorship in the last three instars also suggest the operation of a group survival mechanism. Larvae spin communal silk networks (Rathcke and Poole, 1975) and the lateral tubercles interlock perhaps to form a group tactile communication system. The function of the communally spun silk network used by larvae may vary on different species of *Solanum.* Rathcke and Poole (1975) found that *Mechanitis isthmia* larvae on *S. hirsutum* (tentative identification) use the silk lines to walk over numerous spines on the leaves. The paucity of such spines on *S. jamaicense* ond *S. hispidum* enabled larvae in the present study to avoid them altogether. The networks keep the larvae together by confining their movements and ensuring group feeding and other communal activities.

Stamp (1977), in a study of communal behavior in the larvae of the butterfly *Chlosyne lacinia crocale* (Edwards), found that young larvae spin and feed communally, and that larger larvae subdivide into smaller groups. The subdivision results in fewer larvae per group and reduces competition for food and the possibility of disease. Larger larvae eat faster and exhibit less movements than younger ones. As in the present study, larvae disperse individually at the time of pupation, perhaps to avoid severe pupal parasitism. The growth rate of *Mechanitis larvae* is higher in larger groups than in smaller ones (pers. observ.), suggesting a very different mechanism than found by Stamp (1977).

While in butterfly species with single oviposition and nongregarious larvae mortality may take very heavy tolls (*e.g.,* Dempster, 1967), the reproductive biology of *Mechanitis isthmia* may be geared toward ensuring a minimal number of individuals belonging to a particular egg mass. The mechanisms by which larval group cohesion in *M. isthmia* is maintained are not determined, although silk (Rathcke and Poole, 1975) and perhaps odors (Fitzgerald, 1976) very likely play major roles. As many Solanaceae have various means of defense against herbivores (Webster, 1975), communal behavior may function to reduce such deterrents. Invertebrate species that exhibit group behavior usually do so for protection, feeding and escape (*e.g.,* Allee and Rosenthal, 1949; Fraser Rowell, 1967; Ghent, 1960; Wellington, 1957). Thus egg mass-oviposition and communal behavior of larvae in *M. isthmia* may have evolved to ensure a minimal number of larvae to exercise cooperative feeding on an otherwise impenetrable food source.

At the same locality, another ithomiine, *Hypothryis euclea,* lays huge masses of eggs on *Solanum rugosum,* and the larvae form tight clusters on the leaves (Young, 1977c). The ventral sides of the leaves of this plant are extremely rough to the touch, being covered with trichomes. Another ithomiine, *Dircenna relata,* scatters several eggs on the same leaf, and the larvae form a loose group (Young, 1973). This may be a primitive form of cluster egg laying, and the food plant possesses large leaves with spines and dense trichomes. Most, if not all, ithomiines with single oviposition and nongregarious larvae feed on solanaceous species with thin, nonhairy leaves. That first- and second-instar *Mechanitis isthmia* larvae avoid eating trichomes suggests that either these structures are toxic or else mechanically difficult for handling as food. In addition to counteracting predation, communal behavior in *M. isthmia* evolved to cope with defensive hairs; the trichomes may be too repelling for an individual larva to chew through to the nutritive tissue, especially the younger instars, but several larvae may cooperate by spinning silk over them or removing them rapidly. Ghent (1960) documented cooperative feeding in the jack pine sawfly.

The present-day widespread abundance of *Mechanitis* species in secondary habitats over much of Central and South America may be a pattern very different from that of most forest ithomiines. While it is generally held that Ithomiinae are distasteful butterflies to visually hunting predators (Brower and Brower, 1964) owing to the coevolutionary relationship with Solanaceae (Ehrlich and Raven, 1965), the observed mortality of *Mechanitis* larvae from both arthropod and vertebrate predators suggests that this species is not very toxic. Rehr *et al.* (1973) found that non-ant acacias had toxic substances in their leaves whereas ant acacias lacked them. Thus while some *Solanum* may have evolved fleshy leaves and dense trichomes as deterrents to most herbivorous insects, thin-leaved, nonhairy species may have toxic substances that make other ithomiines toxic. Cluster oviposition and communal larvae may be important behavioral traits allowing *Mechanitis* to exploit solanums impenetrable to ithomiines with single oviposition and solitary larvae. These particular solanums are the most abundant members of this family in secondary habitats, and *Mechanitis* is the genus most frequently encountered in these places.

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