

**Notes on the Biology of *Phyciodes (Eresia) eutropia*
(Lepidoptera: Nymphalidae) in a Costa Rican Mountain Forest**

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Abstract: This paper discusses various aspects of life cycle and natural history for the neotropical butterfly, *Phyciodes (Eresia) eutropia* (Lepidoptera: Nymphalidae) as studied in the field at a mountain wet forest locality in central Costa Rica, and in the laboratory. Emphasis is placed on a description of life stages, larval food plant record, habitat selection by adults for egg laying, courtship, and mimetic interaction with other butterflies. The behavior of larvae associated with feeding and defense was also observed under field conditions. It was found that the early stages are very cryptic in coloration and this morphological crypsis is accompanied by various forms of cryptic behavior in the larvae (concealment, curling-up movement, etc.). The egg-adult developmental time in the laboratory is about 46 days when larvae are reared on cuttings of the natural food plant, *Pilea pittieri* (Urticaceae). Eggs are laid in large clusters on the ventral sides of leaves of this food plant, and although this plant occurs in both dark red and light green forms, females exhibit strong preference for laying eggs on dark plants. Oviposition is generally confined to heavily shaded river bottom forest where the food plant is abundant, but other aspects of reproductive behavior occur in sunlit alleys and corridors of secondary growth. There may also be mimetic association with *Ithomia heraldica* (Ithomiidae) here. If this is the case, then it is likely that *P. eutropia* is a Batesian mimic of *I. heraldica* since observations on the appearance and behavior of immatures in the former butterfly suggest palatability.

INTRODUCTION

This paper gives a description of the life cycle for the neotropical butterfly, *Phyciodes (Eresia) eutropia* Hewitson (Lepidoptera: Nymphalidae), and incorporates a variety of information regarding the natural history and behavior of adults and immature stages. Thus, this report comprises a preliminary and fresh survey of the general biology of this interesting, widespread, and geographically complex Central American species, as recorded for individuals studied from a single population in the central highlands of Costa Rica. The impetus

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for this sort of study takes its origin primarily from the need for more critical examinations of the local biology of many neotropical butterflies and places particular emphasis on accurate records of oviposition and larval food plants (Remington, 1952; Brower, 1958).

At the very outset, a word of caution is given concerning the species name of the butterfly used in this paper. The precise identity of this butterfly remains dubious until a complete revision of the genus in Central America is conducted, and the species designation used here must be regarded as provisional. Specimens reared in this study match up very well with individuals of *P. eutropia* collected elsewhere in Costa Rica (Turrialba) and from the Canal Zone (Gordon B. Small, Jr., pers. comm.). But males of presumably the same species from other Costa Rican localities and also from western Panama are very different, and these individuals may represent a sex-related polymorphic race. The problem here is essentially that of lumping together different morphs (apparently there are several in males) of a single highly polymorphic species (where different morphs displace one another geographically) under a single species name, and distinguishing these instances from other true species in the genus.

DESCRIPTION OF STUDIES

The following major studies were conducted at a single locality in Costa Rica at various times during the period 24 June through 5 September 1971. But the butterfly was not studied continuously during this period, but rather at intermittent times. These studies are: (1) adult habitat preference and larval food plant, (2) features of the life cycle, (3) behavior of adults and immatures, and (4) mimetic associations. The locality is Cuesta Angel, a mountain and ravine-studded region (900 to 1000 meters elev.) in the Heredia Province, and more specifically situated along the road connecting Puerto Viejo with the cities of Alajuela and Heredia. The site is about 9 km before the town of Cariblanco. The actual study area was eventually confined to a strip of relatively undisturbed forest understory bordering one side of the Rio Sarapiquí at the bottom of the 300-meter-deep ravine that constitutes Cuesta Angel. This study area is the same one used to study the biology of *Victorina epaphus* (Young, 1972a), *Itaballia caesia* (Young, 1972b), and *Hymenitis nero* (Young, 1972c). The butterfly is unusually abundant during the study period in this area of the forest, and this facilitated the initiation of the various studies stated above and described below.

The habitat preferences of adult butterflies were studied by walking through various types of vegetation associated with the river edge, and noting the general abundance of individuals, feeding spots, courtship interactions, and oviposition. A total of four days was spent doing this. The larval food plants were located by tracking ovipositing females through the understory and observing several different oviposition sequences; these observations were conducted for a total



FIG. 1. Overall view of the forest ravine, Cuesta Angel, in the central highlands (Heredia Province) of Costa Rica.

of five days. Both adult habitat preferences and larval food plants were usually examined between 8:30 A.M. and 3:00 P.M., but the actual number of hours spent doing this daily was very irregular.

Additional searches for adult activity were conducted from time to time at points higher up on one side of the ravine. A narrow winding gravel road connects the river bottom area with the ridge-top road which goes to Puerto Viejo, and it is easy to look for the butterfly at strategic points along the road. Other searches were made along the ridge-top which is accessible by the Puerto Viejo road and a small network of foot paths leading to more interior places.

Features of the life cycle examined included (1) description of the gross external morphology of immatures, (2) the sizes (body lengths) of immatures, and (3) the developmental time of several individuals from egg to adulthood. All of these were observed essentially simultaneously under laboratory conditions. The "laboratory" was an abandoned toolshed on the premises of the office of the Associated Colleges of the Midwest in San Jose. Here, cultures of the butterfly were maintained in 60×25 cm clear plastic bags kept very tightly closed and placed on a wooden table away from direct sunlight. A total of

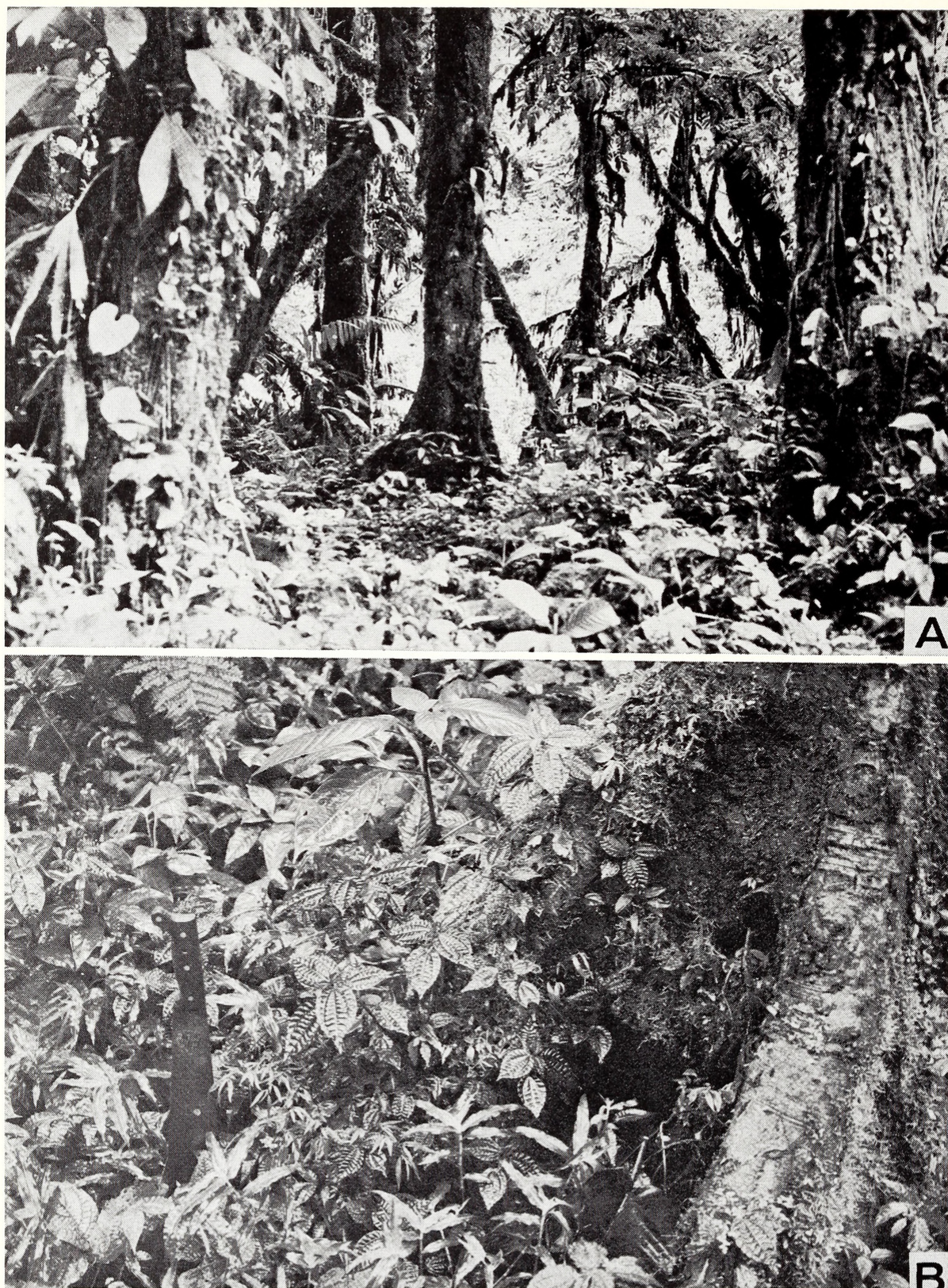


FIG. 2. Habitat selection for oviposition in *Phyciodes* (*Eresia*) *eutropia* at Cuesta Angel. (A) Herbaceous understory of the river-bottom forest where the larval food plant is found. (B) Vine growth form of the larval food plant, *Pilea pittieri* Killip (Urticaceae) at base of canopy tree (the dark red form of the plant is shown).

four different clusters (each containing several eggs—see below) was transported from Cuesta Angel to the San Jose laboratory within a few hours after being laid in the wild; two of the clusters were brought in very early in the study period (first week of July) and an additional two were retrieved from the wild during mid-August. Each cluster was placed in a separate clean plastic bag, along with additional cuttings of the food plant. The four bags were then examined intermittently, usually every two or three days, for egg hatching, differentiation of instars, etc. Bags were periodically wiped clean of larval frass and old food plant. The temperature in the toolshed was usually about 23°C during the midmorning hours; it is slightly cooler at Cuesta Angel at these hours (during the same months), being 19 to 21°C in the shaded understory where the eggs are typically found. For the first two groups of eggs studied, rearing continued successfully until the late fifth instar (for most of the larvae) when the cultures were neglected for several days and virtually every larva died. Thus the first two egg clusters provided life cycle data only through the first four instars. In the second group of two egg clusters studied later, all individuals successfully pupated but the pupae eclosed en route on a jet flight from Miami, Florida to Chicago, Illinois, with the result that many (virtually all) adults emerged with badly crumpled and damaged wings. Only five pupae (all females) were spared and emerged a few days later at the final destination (Appleton, Wisconsin).

Observations on adult behavior were limited to feeding site selection, oviposition, and courtship site selection. Again, the data here are essentially qualitative. Behavior of immatures refers to observations on the dispersal tendencies of larvae on the food plant in the wild. This was studied for eight days. Initially, the location of an egg cluster in the wild was noted and the number of larvae and their distribution on the plant was observed on later dates. This was done for a single egg cluster discovered on the morning of 30 July 1971. Larval dispersion associated with the onset of pupation was also observed. Finally, the defense behavior of individual larvae was studied both in the field and laboratory. This was done by suddenly prodding larvae with blunt forceps and observing their responses on the food plant.

Mimetic association was observed only in a very preliminary way. Attempts were made to observe other butterflies that resembled adult *P. eutropia* males and/or females both in appearance and habitat selection. These observations were done simultaneously with the observations of adult habitat preference outlined earlier.

RESULTS

HABITAT PREFERENCES AND FOOD PLANT

Both young males and females are most frequently seen on the borders of early secondary growth vegetation where there is a large amount of unobstructed

sunlight and very low (0.5 to 1.5 m) herbaceous canopy cover. These individuals are judged to be "young" by the teneral or near-teneral condition of the wings; they are very fresh with very little or no loss of scales from the wings and minimal tattering. It is interesting to note that adults of any age category are only seen at the bottom of the Cuesta Angel ravine (Fig. 1) and virtually no individuals are seen flying at intermediate levels or ridge-top area of this pronounced local topographic gradient. Adult activity is thus very much confined to the "river-bottom" area of the ravine, and typically within a few meters of the river edge. Here, in sunlit patches of low secondary growth, there is much play activity between young adults of both sexes; males frequently chase after females and this may be a form of courtship activity (although copulation and the immediate sequence of behavioral acts leading to it have not yet been observed in *P. eutropia*).

While courtship and feeding in adult *P. eutropia* are confined primarily to sunlit corridors of young secondary growth, oviposition is clearly associated with very dark and damp forest understory in river-bottom forest. It is relatively easy to spot females searching for oviposition sites since (1) this is a sexually dimorphic species, and (2) these females are often frayed and tattered and thus easily distinguished from the young females which tend to remain in sunlit areas near the forest. Young (and presumably unmated) females are seldom seen in the forest interior, although occasionally teneral adults of both sexes are seen there early in the day. Presumably these individuals emerged from their pupae only a few hours before and have not yet moved out of the forest.

The plant used for oviposition and larval feeding is the herbaceous understory member, *Pilea pittieri* Killip (Urticaceae). At Cuesta Angel, this plant is most commonly encountered in the damp river-bottom forest (Fig. 2-A), where it thrives either as a small sprawling vine around the bases of large trees (Fig. 2-B) or as a small upright plant on the forest floor. Standley (1937) mentions that the genus *Pilea* is represented by more than 30 species in Central America, and that *P. pittieri* is found primarily at mountain elevations and generally in the central region of Costa Rica. While it has been noted that *Pilea microphylla* forms a major component of the herbaceous layer in the mountain valleys of St. Andrew in Jamaica (Robertson and Gooding, 1963), *P. pittieri* in the river-bottom forest at Cuesta Angel is distributed in a very patchy manner, and with considerable variation in patch sizes along the river edge. I have also found this species along stream beds near San Miguel (400-m elev.) and on the Caribbean slopes of the central highlands; the species in general appears to be endemic to the wet Caribbean slopes at elevations between 500 and 1500 meters (William C. Burger, pers. comm.). At Cuesta Angel, the plant is very frequently seen growing out of crevices between large boulders whose surfaces are continually wet from water dripping from places higher up

on the side of the ravine. The plant very conspicuously drops out as one walks up the ravine, and probably does not occur higher than 50 meters above the river bottom. While most individuals of this succulent plant are very dark red, there is a small fraction that are bright green; the origin and biological significance of this color dimorphism in *P. pittieri* is probably unknown. No other larval food plants were found at Cuesta Angel, and ovipositing females are very much confined to those areas of river-bottom forest where patches of *P. pittieri* occur.

Oviposition is very clearly limited to the dark red form of *Pilea pittieri* at Cuesta Angel. In addition to looking for oviposition acts in progress, searches of leaves of the green form revealed no eggs. I interpret this as indicative of strong selection for leaves of the dark red form for oviposition.

FEATURES OF THE LIFE CYCLE

Very soon after being laid, the egg of *P. eutropia* is uniformly creamy-yellow and pear-shaped (Fig. 3-A); there are no visible signs of grooves or ridges on the surface. The egg is about 1.0 mm tall, and just before hatching it turns light orange, which is the basic body color of the first instar larva prior to feeding. The first instar is yellow to light orange and covered with sparse hairs. Upon feeding on plant tissue, the larva immediately becomes dark reddish-green owing to the ingestion and presence of plant pigments in the digestive tract. The head remains light orange. By the end of the first instar, the larva measures about 4 mm in length.

The second instar (Fig. 3-B) is generally very dark green with the head becoming darker brown. The body is now adorned with three rows of highly branched yellow spines that are semi-translucent. The larva attains a body length of about 6 mm during this instar.

The third and fourth instars are essentially very similar in appearance to the second instar; the third instar is about 9 mm long by molting, and the fourth instar 16 mm long. The first four instars of this species are very difficult to photograph owing to their dark coloration and the almost perfect matching with the dark color of the food plant.

The body of the fifth instar is also dark green, but has become lightly speckled in white spots (Fig. 3-C). The head is orange but reflects a gold tinge in sunlight. As with earlier instars, the prolegs are also orange. The spines have become darker orange but with the same distributional pattern (three pairs per segment) as seen in earlier instars. The fifth instar possesses slight reflective properties owing to the cuticular nature of the spine, pigmentation of the head, and pattern of tiny white spots on the body surface. At the end of the active feeding period of the fifth instar, the larva is 29 mm long.

The pupa (Fig. 3-D) is generally dark greenish-brown and, after a few days, the wing pads develop lighter patches of brown. There are very few noticeable

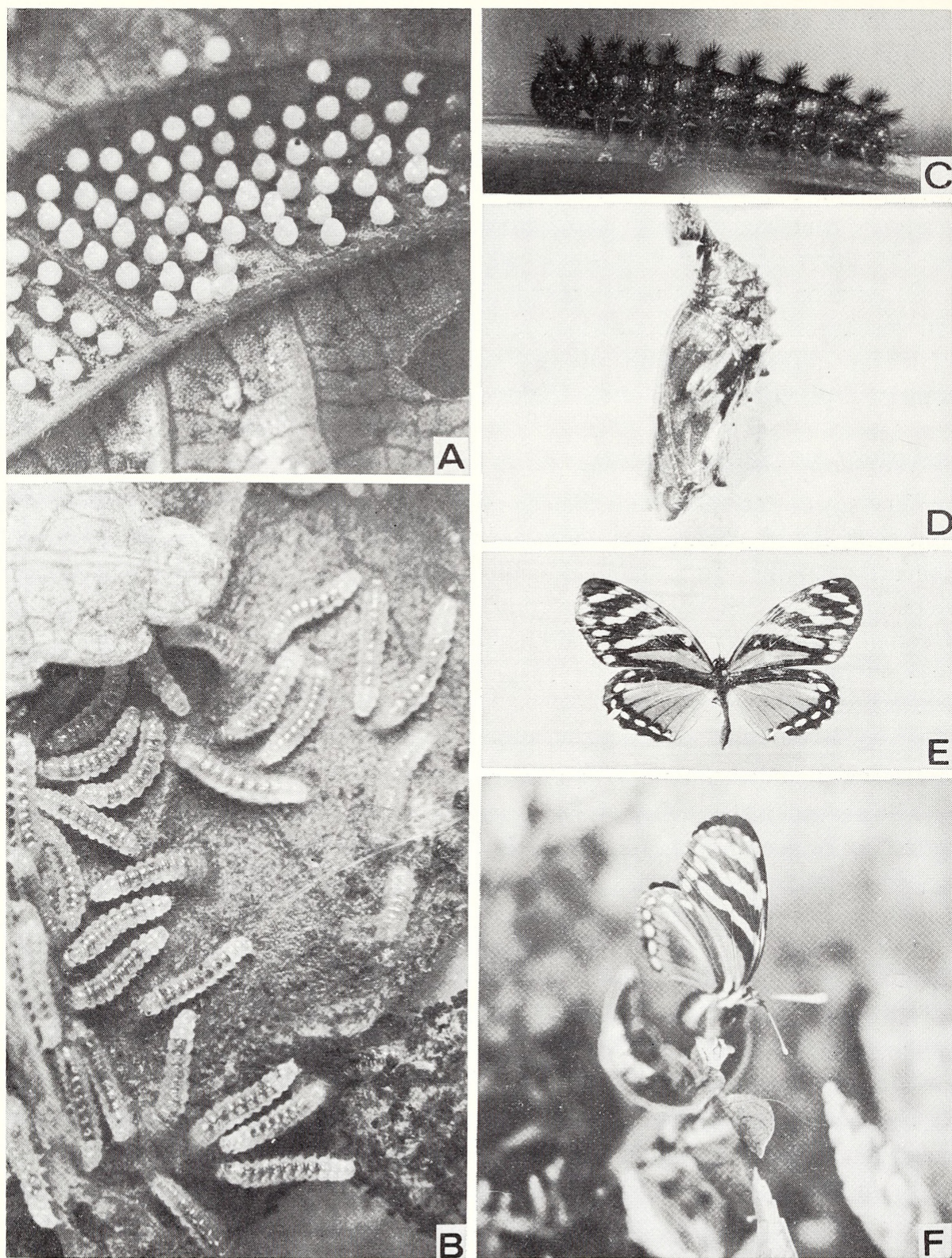


FIG. 3. Life cycle of *Phyciodes eutropia*. (A) Egg cluster, (B) second instar larvae, (C) fifth instar larvae, (D) pupa, (E) adult female, dorsal side, and (F) female ovipositing on *Pilea pittieri*.

TABLE 1. The developmental time* of *Phyciodes (Eresia) eutropia* on *Pilea pittieri* as determined in the laboratory**

Statistic	Egg	Instars					Pupa	Total, egg to adult
		1	2	3	4	5		
Duration (in days)	10	4	4	6	6	6	10	46
± S.E.	1.0	1.3	2.4	2.0	3.0	4.4	1.1	
N	228	225	225	225	220	114	108	

* As determined for individuals measured in four different egg clusters through the fourth instar, but for only two egg clusters through the pupa.
** Laboratory conditions, in San Jose, are 20 to 26°C and about 50 percent relative humidity.

markings and the pupa is generally shiny in a manner similar to the fifth instar. The pupa is about 15 mm long.

The dorsal aspects of the adult female are shown in Fig. 3-E, and both sexes are shown together in Fig. 4. Good general accounts of the wing color patterns for this and other species of *Phyciodes (Eresia)* are given in Seitz (1924) as the adults have been known for some time. The sexual dimorphism (Fig. 4) is very pronounced, including the shape of the wings, and only one morph of each sex has been found in the population at Cuesta Angel. There is no evidence from rearing studies and wild-caught individuals that the population is polymorphic locally for either sex.

Female adults are larger than males and the egg-adult developmental time of the former is greater by about two days in the laboratory (Table 1). The discrepancy in developmental time between the sexes occurs in the duration of the fifth instar (Table 1). Under field conditions, the developmental time for both sexes may be extended slightly since air temperature there is slightly lower than in the laboratory.

In the laboratory, egg hatchability is very high and there is very low physiological death of eggs under these conditions. The sex ratio of adults which eventually arise from an egg cluster is very close to unity. This was determined from examination of genitalia of individuals emerging from the last two egg clusters studied.

BEHAVIOR OF ADULTS AND IMMATURES

It has already been mentioned that adults, especially young ones, feed and undergo courtship activity in exposed secondary growth vegetation near forests. Undoubtedly there is a limited amount of feeding that also occurs in the forest interior soon after adults eclose. Courtship may truly be limited to sunlit areas if aerial visual cues at distances between the sexes play a major role in mate encounter strategy in this butterfly.

By far the single most noticeable adult activity in the forest in oviposition

(Fig. 3-F). The eggs are laid in orderly clusters (Fig. 3-A) on the ventral surfaces of *Pilea pittieri* and the deposition of a single cluster of 60 to 70 eggs may take between twenty and thirty min. Cluster size apparently varies considerably in the wild. Of a total of six clusters found, the egg number per cluster was: 41, 55, 60, 64, 72, and 76 eggs. It is not known if a female will lay more than a single cluster. A cluster is typically laid only on a single leaf, and during the oviposition, the female remains exceedingly immobile, only shifting slightly the position of her curled abdomen (Fig. 3-F) from her position on the dorsal edge of the leaf. The time of day for oviposition is variable and the process has been witnessed between 11:00 A.M. and 1:45 P.M., usually under conditions of very heavy overcast. Females oviposit on both vines and upright herbs of the food plant and show no preference for either growth form. Owing to the manner in which the leaves droop slightly on either growth form, the eggs remain well hidden to the human eye and perhaps also to cruising predators and parasites. For the cluster observed closely in the wild for several days, there was no loss of eggs prior to hatching.

The larvae of *P. eutropia* must provide one of the best examples of crypsis among the larvae of neotropical butterflies in general. Because of their coloration and reflectance, both of which match beautifully the leaves of the food plant, the larvae are difficult to detect visually during all of their instars. The larvae during all instars remain highly gregarious (Fig. 3-B) both in the laboratory and wild, but this behavior, in the context of predator-avoidance activities, is counteracted by the highly cryptic appearance of these insects. There is relatively little dispersal of larvae from one another until the time of pupation. Feeding occurs both day and night in the laboratory. When prodded just slightly with forceps, a larva will drop off the leaf and curl up into a very tight ball and remain in this position motionless for a few minutes. In the wild, most larvae are found only within a few centimeters of the ground (since *Pilea* is a low herb) and when they drop off the plant, they invariably crawl back up within several minutes. The curling-up behavior results in the highly branched spines being directed in several directions and this may represent an effective deterrent to predator attack. It has not yet been determined if the larvae possess odoriferous defensive chemical secretions against their predators. However, this would appear to be an unnecessary precaution owing to the excellent crypsis and added curling-up and dropping escape behavior of these larvae.

MIMETIC ASSOCIATION

The very familiar "tiger stripe" dorsal wing pattern of orange, black (brown), and yellow, seen especially in the females of *P. eutropia* suggests mimetic association with a variety of other medium-sized sympatric butterflies. Where young adults are most active in sunlit areas near the forest, the most likely



FIG. 4. Probable Batesian mimicry complex involving *Phyciodes eutropia* at Cuesta Angel. From top to bottom: Female *P. eutropia*, male *P. eutropia*, and male *Ithomia heraldica* (*Ithomiidae*). Dorsal aspects of all individuals are shown.

candidate for mimetic interaction is *Ithomia heraldica heraldica* (Fig. 4) in the *Ithomiidae*. This species feeds at the same flowers as *P. eutropia* and generally flies at the same time of day. In the absence of detailed quantitative data on the relative abundances of both species where they occur together and also on the possibly greater interaction of *Ithomia* with male *P. eutropia*, it is difficult to conclude that mimicry is operating between them.

DISCUSSION

The habitat distribution of the adult breeding population of *P. eutropia* at Cuesta Angel is essentially limited to the moist and shady river-bottom areas

of the ravine where the larval food plant, *Pilea pittieri*, is found. This plant species apparently has low water intolerance and is restricted to very wet microhabitats. The butterfly moves only very little distances from places where the plant is abundant, and even courtship and feeding sites in sunlit patches of young secondary growth vegetation are in close proximity to places of intense oviposition activity. The general lack of *Pilea* farther up the sides of the ravine may be a major contributing factor to the noticeable absence of the butterfly at high places. The butterfly is thus a forest understory species and its populations are limited in spatial distribution to a large degree by the distribution of the food plant. Further studies are needed to define the dispersal abilities of adults, and if it were found that there is low vagility in either or both sexes, gene flow may be restricted and microevolutionary processes in different populations could lead to evolutionary divergence in a variety of phenotypic traits (Ehrlich and Birch, 1967).

Another major aspect of the adaptive strategy of this species concerns predation pressures on adults and immatures. Populations of animals are confronted with the problem of maintaining one or a variety (seasonal) levels of numerical abundance in order to avoid local extinction. At the morphological and behavioral levels of animal organization, selection often favors the evolution of defense mechanisms that reduce the risk of predation or parasitism to reproductively (or pre-reproductively) competent individuals in the population. The intensity and array of predator threats will vary greatly from one population of the species to the other. In butterflies, one major ecological interface that provides an evolutionary matrix for the development and perfection of defense mechanisms is the food-plant-larva (herbivore) association in different populations of the species. There is a substantial body of information that suggests lepidopterous larvae incorporate into their digestive tracts and perhaps body tissues toxic compounds derived from their food plants (see the review in Brower and Brower, 1964), therefore rendering themselves unpalatable to at least some of their predators. This sort of adaptive pattern is dependent upon the coevolutionary interactions between the butterfly species and its larval food plants (Ehrlich and Raven, 1965). An alternative and very different adaptive pattern to similar selection pressures is the apparently *de novo* synthesis of highly volatile compounds that are discharged (upon appropriate stimulus being received) usually from specialized cuticular glands (Eisner, 1970). Not only is the biochemical origin of these two strategies of predator defense very different but unpalatability necessitates the advertisement of the distasteful properties to the attacker, and chemical defense secretions infer that crypsis is the best strategy. In some instances, a single organism may possess both mechanisms of defense (Eisner et al., 1971), where each one is functional against a different array (vertebrate versus invertebrate) of predators.

Clearly the adaptive pattern of the larvae of *P. eutropia* against at least

vertebrate predators is one of crypsis. Here, the morphological and behavioral components of the crypsis have been perfected to the extent that further defense mechanisms would appear to be unnecessary energy expenditures. There is the strong suggestion that the larvae and adults are palatable, receiving little or no defensive compounds from *Pilea*. It is not determined if the larvae or adults give off odoriferous secretions; there is no evidence of this to the human observer when larvae or adults are handled. The presence of highly branched and numerous spines, cryptic coloration, and curling-up defense movements, suggest that the strategy is one of predator avoidance and not advertisement. The gregarious habit of the larvae may be the result of strong selection pressures for cluster oviposition on a food plant with a very patchy distribution and may bear no relation to predation pressures. While cluster oviposition is generally unusual among many species of butterflies studied (Labine, 1968), instances of it and resulting larval gregariousness may be adaptations to a locally scarce food plant (especially if many females are ovipositing in the area, and the interpretation of "many" will vary tremendously with different species and food plants). Under such conditions, it is better to release most of the eggs as soon as possible. An alternative explanation would be that gregariousness imparts some advantage against predators, especially leaf-roaming forms like small amphibians and a variety of arthropods. If each egg cluster is viewed as a kin group, some individuals in the group will be eaten as larvae if they distract predators from the rest of the group. The larvae remain together until pupation and this may be evidence for the existence of some cooperative mechanism by members of the group against predators.

The adults of both sexes may enter into a Batesian mimicry complex with *Ithomia heraldica*, with the latter being the model since the Ithomiidae are reputed to be unpalatable butterflies which results from their larvae feeding on Solanaceae (Brower and Brower, 1964). It is the female *P. eutropia* that appears to resemble *Ithomia heraldica* far more so than the male. Instances of essentially non-mimetic males and mimetic females are very numerous among species acting as Batesian mimics in the New World tropics. The occurrence of sexual dimorphism in *P. eutropia* and the stronger resemblance of the female to an unpalatable species is indirect evidence that Batesian mimicry may be operating at Cuesta Angel. Both species are seen flying and feeding in close proximity at the river bottom and the preference for *P. eutropia* to feed and court in sunny places may be a form of habitat selection enhancing its Batesian association with *Ithomia heraldica*. Vertebrate predators are more likely to associate the two species in sunnier places than in shady places, but ovipositing females in shady forest understory, since they are more mimetic than males, may still stand a better chance of not being attacked, especially during the morning hours.

The strong preference exhibited by ovipositing females for the dark red

form of *Pilea pittieri* and general avoidance of the lighter green form suggests further that crypsis and palatability characterize the adaptive strategy of the larvae against their predators. The larvae would appear more conspicuous against the leaves of the green form owing primarily to the (1) lack of reflectance luster on the leaves of the green form but still present on the larvae, (2) the shadow effects produced by the intricate body spines and reinforced with larval movements, and (3) the gregarious habit of the larvae forming conspicuous large clumps on the small leaves.

Literature Cited

- BROWER, L. P. 1958. Larval food plant specificity in butterflies of the *Papilio glaucus* group. *Lepid. News*, **12**: 103-114.
- BROWER, L. P. AND BROWER, J. V. Z. 1964. Birds, butterflies, and plant poisons: A study in ecological chemistry. *Zoologica*, **49**: 137-159.
- EHRLICH, P. R. AND BIRCH, L. C. 1967. Evolutionary history and population biology. *Nature* (London).
- AND RAVEN, P. H. 1965. Butterflies and plants: A study in coevolution. *Evolution*, **18**: 586-608.
- EISNER, T. 1970. "Chemical Defense Against Predation in Arthropods." *In* Chemical Ecology (ed. by Sondheimer, E., and Simeone, J. B.), pp. 157-218. New York: Academic Press.
- , KLUGE, A. F., IKEDA, M. I., MEINWALD, Y. C., AND MEINWALD, J. 1971. Sesquiterpenes in the osmeterial secretion of a papilionid butterfly, *Battus polydamus*. *J. Insect Physiol.*, **17**: 245-250.
- LABINE, P. A. 1968. The population biology of the butterfly *Euphydryas editha*. VIII. Oviposition and its relation to patterns of oviposition in other butterflies. *Evolution*, **22**: 799-805.
- REMGINGTON, C. L. 1952. The biology of nearctic Lepidoptera. I. Food plants and life-histories of Colorado Papilionioidea. *Psyche*, **59**: 61-70.
- ROBERTSON, E. T. AND GOODING, E. G. B. 1963. "Botany for the Caribbean." London: Collins Clear-Type Press.
- SEITZ, A. (ed.). 1924. "Macrolepidoptera of the World." Vol. 5. *The American Rhopalocera*. Stuttgart: Alfred Kernan Verlag.
- STANDLEY, P. C. 1937. Flora of Costa Rica. Part I. Field Museum Nat. Hist. 18, 396 pp.
- YOUNG, A. M. 1972a. The ecology and ethology of the tropical nymphaline butterfly, *Victorina epaphus*. I, Life cycle and natural history. *J. Lepid. Soc.*, **26**: 155-170.
- YOUNG, A. M. 1972b. A contribution to the biology of *Itaballia caesia* (Lepidoptera: Pieridae) in a Costa Rican mountain ravine. *Wasmann J. Biol.*, **30**: 43-70.
- YOUNG, A. M. 1972c. Notes on the biology of *Hymenitis nero* (Lepidoptera: Ithomiidae) in Costa Rica. *Psyche*, **79**: 284-294.



Young, Allen M. 1973. "Notes on the Biology of *Phyciodes (Eresia) eutropia* (Lepidoptera: Nymphalidae) in a Costa Rican Mountain Forest." *Journal of the New York Entomological Society* 81, 87–100.

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