

THE ECOLOGY AND ETHOLOGY OF THE TROPICAL  
NYMPHALINE BUTTERFLY, *VICTORINA EPAPHUS*.  
I. LIFE CYCLE AND NATURAL HISTORY

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This paper is the first in a series on the neotropical butterfly, *Victorina* (*Amphirene*) *epaphus* Latreille in central Costa Rica. Despite its widespread occurrence throughout the montane and upper premontane tropical wet forests of Costa Rica, little is known about its biology. According to Seitz (1924) the life cycle of this Central American species is undescribed. This paper describes the life cycle of this species, and brings together various observations on its ecology and ethology, to be explored in depth in later papers. Data on larval host plant specificity, oviposition, and survival of immatures in natural populations also are given.

METHODS

*V. epaphus* was studied at Cuesta Angel de Sarapiquí (Heredia Province, 1000 m elev.) at various times from February 1969 through July 1970. Observations were made at the bottom of a steep ravine, in relatively undisturbed, primary-growth forest. The study of *V. epaphus* consisted of three approaches: larval host plant studies, field studies, and laboratory studies.

Larval Host Plant Studies

The study site is near an extensive strip of the larval host plant, *Ruellia tubiflora* H.B.K. var. *tetrastichantha* (Lindau) Leonard (*Acanthaceae*) which borders the Río Sarapiquí and a foot trail at the bottom of the ravine. This plant, (a first record for *V. epaphus*) is an understory form, usually between 15–40 inches in height, and confined to very wet soil. At Cuesta Angel, it grows in continuous patches along with *Gynandropsis pulcherrinia* Standl. (*Capparidaceae*), another understory plant of similar height and growth form, which is a major larval host plant of *Itaballia caesia* (Pierinae), whose life cycle will be summarized later. Unlike the spatial distribution of larval host plants of tropical butterflies belonging to the genera *Morpho* (Young, in prep.), *Parides* and *Battus* (Young, 1972a, b, c), the larval host plant of *V. epaphus* is characterized by rather extensive homogeneous patches, permitting a concentration of reproductive effort (Labine, 1968) over small portions of the habitat.

The larval host plant of *V. epaphus* was in active vegetative growth during the study period and floral structures were absent despite the low degree of seasonality known for montane tropical wet forests (Richards, 1952; Roth & Bifano, 1971). Extensive searching revealed that it is the only host plant of this butterfly at Cuesta Angel.

### Field Studies

Field studies consisted of (1) mark-recapture studies on adults, (2) analysis of diurnal peak activity periods of adults, (3) observations on oviposition behavior, (4) records on the distribution of eggs and larvae on individuals of the host plant, including observations on larval activities, and (5) occasional records of predation and parasitism on larvae.

Mark-recapture study employed a standard sampling procedure in which adults were netted on several traversions through the host plant patch, marked, and immediately released. This was done at irregular intervals throughout the study period, using a marking system modified from Ehrlich & Davidson (1960) and in which sexes were differentiated. Estimations of adult populations then were made for each day of observation, using the Lincoln Index. Eggs, larvae, and pupae also were sampled in a standardized manner by walking transects through the patch once daily. Individual host plants along the transect were examined frequently for eggs and larvae. This sampling technique was very suitable since the host plant grew in large homogeneous patches, allowing many individuals to be sampled quickly.

### Laboratory Studies

Broods of eggs were reared, both in the laboratory and out of doors. Life stages and developmental time were studied in this manner. Laboratory cultures were established in tightly closed 8 in by 12 in clear plastic bags, prior to each of these receiving several eggs on cuttings of *Ruella*. This method has proven successful with several species of tropical butterflies (Young, 1972a, b, c, d, e). Various aspects of larval behavior were also noted, such as diurnal pattern of peak feeding, gregariousness, and aggressiveness. Laboratory rearing was undertaken to explore also the feasibility of using this widespread species for estimation of physiological life tables (Istock, 1970; Young, 1972e) to be eventually compared with realized life tables of natural populations. Other interests focused upon the suitability of such a widespread tropical species for electrophoretic studies of enzyme variability as a function of geographic and topographic distributions of populations.

## RESULTS

## Description of Life Cycle

The eggs are laid singly in small, loose clusters on apical, unfolding leafbuds of *Ruellia* (Fig. 1,A), and occasionally on older leaves. Anywhere from 1-6 of the dorso-ventrally flattened (diameter of 0.9 mm) ribbed eggs are laid by an individual female during one visit to a plant. When first deposited, each egg is pale green but rapidly (10-15 min.) becomes dark green between the yellowish ribs (Fig. 1,A). Eggs are placed carefully on leaves of *Ruellia* and "errors" in oviposition (Dethier, 1959a, b) have not been seen.

The first-instar larva devours its empty egg shell. The young larva then moves to the ventral side of an apical, unfolding leaf to begin feeding. The first-instar larva is jet black except for the first segment behind the head, and the two most posterior segments, which are a dull-orange color. The head is shiny jet black, bearing two long slightly barbed spines; shorter branched spines are present on all other body segments. With the exception of the single pair of head spines, all remaining spines are ringed with white at their bases. Each body segment, excluding the first behind the head, bears three pairs of these spines. The second-instar larva is about 7 mm long. The third instar is similar (Fig. 1,C) and about 16 mm long when molting to the fourth instar.

A drastic change in appearance occurs in the fourth instar. The larva is now between 29-35 mm long and the head is still shiny jet black, but the body is velvety maroon. The head spines are still long. All other spines are now bright yellow and more highly-branched (Fig. 1,D). The bases of all body spines are bright yellow. The final, fifth-instar larva (Fig. 1,E) is almost identical to the fourth instar except that the head spines and the most lateral pair of spines along the body axis are red. The expanded basal spots no longer are associated with each spine. Of the three pairs of spines on each body segment present in all five instars, only the most dorsal pair remains bright yellow; the next pair has the lower half a dull yellow and the upper half light orange; the third, most lateral pair of spines are entirely red. All spines remain very highly branched. The mature larva is between 45-55 mm in length.

Pupation typically occurs on the undersides of older leaves near the ground. The pupa (Fig. 1,F) is about 30 mm long, and pale, translucent green, although flecked with tiny black spots arranged in longitudinal rows on the thorax and abdomen. There are two prominent orange-based black spines originating dorsally from the first and second abdominal segments. The head region is slightly forked anteriorly, with projections being green below and black above.

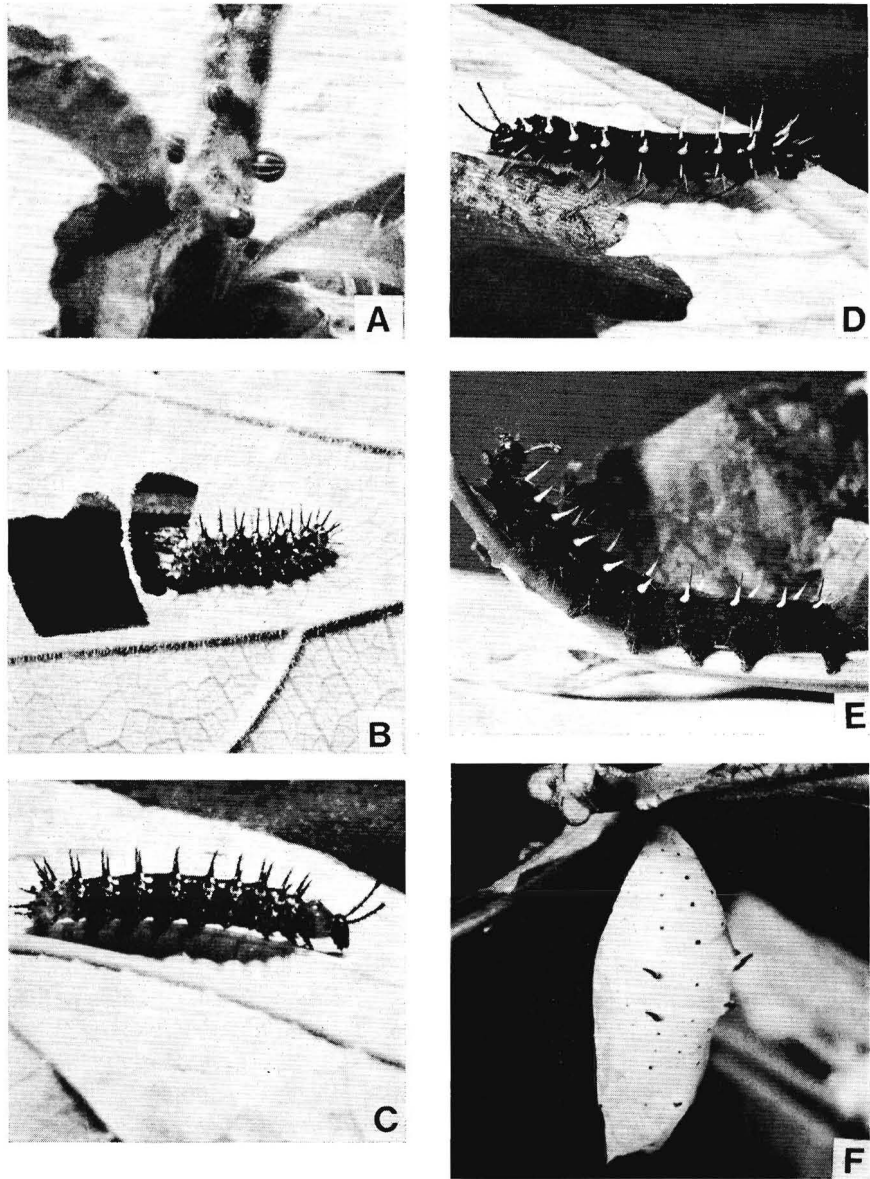


Fig. 1. Life cycle of *Victorina epaphus*: (A) eggs, (B) second instar, (C) third instar, (D) fourth instar, (E) fifth instar, and (F) pupa.

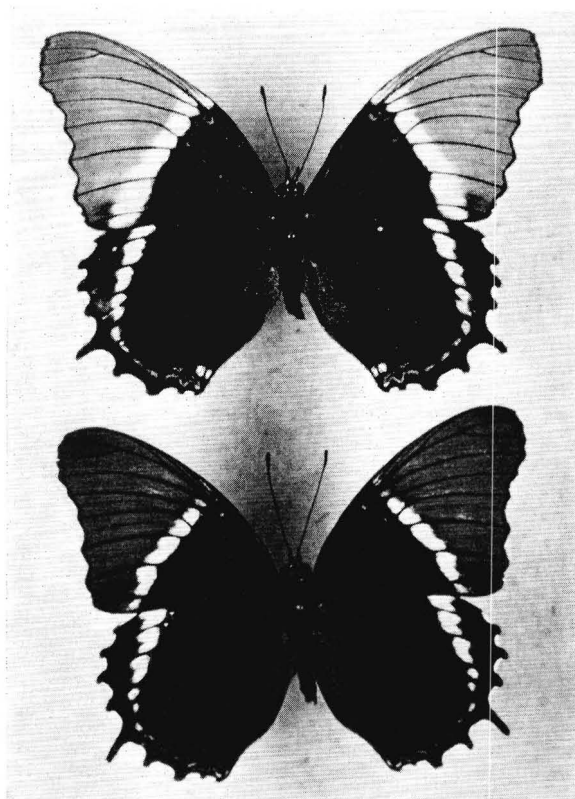


Fig. 2. Adult *Victorina epaphus*. Dorsal views of female (above) and male (below). Mean wingspan length is  $7.0 \pm 3.8$  cm ( $N = 34$ ) with females slightly larger than males.

A lack of sexual dimorphism characterizes the adults of *V. epaphus* (Fig. 2). However, the female generally is larger than the male (by 3–6 mm) and the cream-colored band separating distal orange areas and proximal brown areas of both wings is broader. It is very difficult to distinguish sexes in the field.

The developmental time for *V. epaphus* (summarized in Table 1), is slightly more than one month. Data on survivorship of larvae and pupae in the laboratory indicate that this insect can be reared successfully under artificial conditions (Table 1).

Development within egg clusters is highly synchronous, in the field and laboratory, with virtually no individuals completing postembryonic development markedly later than other individuals. Breeding is continuous throughout the year.

TABLE 1. The developmental time (days) for *Victorina epaphus* under laboratory conditions.\*

	Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Pupa	Total
Mean	6.85	4.97	5.05	4.14	2.20	2.15	10.35	35.71
S.E.	±.10	±.11	±.08	±0.9	±.10	±.04	±.25	±1.24
Range	6-9	4-6	4-7	3-6	2-5	2-4	9-11	32-38
No. of Individuals	57	54	54	54	51	48	48	48
No. which Died	0	3	0	0	3	3	0	9

\* Times estimated from a total of 57 eggs, representing 10 clusters deposited on 10 individual foodplants by a single female within an 18 minute period (1440-1458, CST) on 29 Jan. 1970 near Cuesta Angel, Heredia Province. All cultures were kept in large (8 × 12 in.) clear plastic bags in one large room in San Jose, Costa Rica. Eggs were collected at Cuesta Angel immediately following oviposition and brought directly to San Jose for culture.

### Population Size and Mortality

Estimations of adult population sizes are summarized in Table 2 along with frequencies of immature stages. A striking result of this survey is that both egg and adult numbers remain constant throughout the year despite fluctuations in numbers of larvae and pupae.

Survivorship from egg through pupa in the field high (Table 3). Predation and parasitism on eggs and larvae are probably low. However, the large fluctuations in larval numbers and the diminished numbers of pupae (Table 2) suggest operation of undetected mortality factors. I have consistently failed to rear tachinid or braconid parasites from larvae collected in the field.

TABLE 2. Weekly frequencies of adults and immature stages of *Victorina epaphus* at Cuesta Angel, Heredia Province, Costa Rica from early February through early April, 1969.

Stages	Number of Individuals Seen Per Week								
	Feb. 3	Feb. 10	Feb. 17	Feb. 24	Mar. 10	Mar. 17	Mar. 24	Mar. 31	Apr. 7
Adults	44	40	43	26	38	59	63	44	49
Eggs	134	168	159	103	97	107	115	78	133
Larvae	109	115	123	73	68	89	100	52	102
Pupae	22	18	20	7	20	31	18	9	23
Total	309	341	345	209	223	286	296	183	307

Adult figures are based on capture-mark-recapture estimates. No observations were made during the week of March 3.

TABLE 3. A summary of some measurements of population parameters of the tropical nymphalid, *Victorina epaphus*.\*

Egg Cluster No.	No. of eggs per cluster	No. eggs killed by predation	No. eggs failing to hatch	Larval mortality	Pupal mortality	Overall % survivorship
1	7	5	0	1	0	13.8%
2	5	3	0	0	0	40.0%
3	8	4	0	1	1	25.0%
4	6	0	0	3	0	50.0%
5	6	0	0	2	0	20.0%
6	5	2	0	2	0	20.0%
7	7	2	0	3	0	29.0%
8	8	0	1	5	1	12.5%
9	10	1	0	6	0	30.0%
10	4	4	—	—	0	0.0%
11	6	0	1	3	0	33.4%
12	5	0	0	2	0	60.0%
13	7	3	0	3	1	0.0%
14	6	2	0	2	0	33.4%
15	6	2	0	1	1	33.4%
16	5	2	0	1	0	40.0%
17	5	2	0	2	0	20.0%
18	8	1	0	3	1	37.5%
19	6	0	1	2	0	50.0%
20	5	0	0	2	1	40.0%
21	7	3	0	3	1	0.0%
22	7	0	0	2	0	71.4%
23	5	2	0	1	0	40.0%
24	8	2	0	2	0	50.0%
25	6	1	0	2	0	50.0%
26	6	0	0	2	0	66.7%

\* These measurements were made in the field on immatures staked out on various individual foodplants within a large rectangular area of forest understory.

### Larval Behavior

Larvae, although diurnal feeders, are difficult to detect in heavily shaded forest understory. These observations suggest that *V. epaphus* is a palatable species which employs a protective strategy of crypsis while going through ontogeny. Some genera of Acanthaceae contain alkaloids and may be toxic (Irvine, 1961), but it remains unknown whether species of the genus *Ruellia* are toxic. While predation on adults by birds and lizards in the field has not been observed, laboratory feeding studies of a related species, *V. steneles*, indicate non-toxicity (Brower & Brower, 1964). But in Costa Rica, larvae of this latter butterfly feed on *Justicia* in the Acanthaceae (Young, 1972e). They invariably feed from the ventral leaf surface and are therefore usually concealed from potential predators foraging from above. Presumably in the dark forest understory, the larvae would be difficult to detect by predators on the ground. Such larval

behavior may also lower parasitic attack by hymenopterans and tachinids which lay their eggs directly upon the host.

Larvae are capable of violent jerking movements of the anterior region of the body, presumably as a means of defense against predators. However, they do not exhibit these movements collectively, as noted for larval sawflies (Prop, 1959). The pupae of *V. epaphus* are also capable of similar movements, possibly a means of deterring parasitic wasps and flies (Cole, 1959). The numerous spines on all instars and to a lesser extent on pupae, coupled with violent jerking movements, may provide an effective predator-parasite deterring mechanism.

Larvae are never gregarious, despite eggs being laid in loose clusters. Immediately following devouring of empty egg shells, larvae disperse and never reassociate during ontogeny. Crowded larvae in the laboratory are aggressive towards one another. Such behavior may permit effective dispersion on host plants. However, larvae never leave an individual plant to feed on another one nearby. This is true despite the fact that *Ruella* grows in large patches of high density on the forest floor. Apparently larval densities per individual host plant never reach levels at which overcrowding and aggressiveness result in dispersion from the plant.

#### Adult Behavior

Adults of *V. epaphus* restrict their flying activities to *Ruella* patches. Here the sex ratio remains close to unity, although adult numbers are low (Table 2).

Presumably courtship occurs near host plant patches and females are mated within 5 days after eclosion. Of 38 young females examined, only 3 contained more than one spermatophore.

Oviposition generally takes place throughout the day and each female performs several oviposition sequences on any given day. Observations on young marked females indicate that each individual conducts up to 11 oviposition sequences within a single *Ruella* patch before resting. Resting periods between groups of oviposition sequences are brief. Each female deposits a mean number of  $5 \pm 1.4$  eggs per plant.

Adults sometimes feed collectively in small numbers at moldy leaf litter on the forest floor, although they probably also forage at flowers. At Bajo la Hondura, this species has been observed to feed at odorous small growths of fungi on tree trunks. Collective feeding in this species is not structured and individual feeding also prevails. Feeding appears to be most frequent during the morning hours.

Adults are not commonly encountered in second-growth plant communities, but appear restricted to primary-growth montane forests. Adults



fly low, seldom higher than 10 feet off the ground. It therefore is a montane forest species concentrating reproductive and feeding activities, as well as general flight activity, to understory habitats.

#### DISCUSSION

The above notes on the biology of *V. epaphus* may best be integrated through consideration of an adaptive strategy for inhabiting understory regions of primary-growth forests. Several discussions (Pires, Dobzhansky, & Black, 1953; Slobodkin, 1970) have emphasized the structural complexity and stability of primary-growth tropical rain forests. Component species of such habitats are predicted to have a long evolutionary history integrating them into communities (e.g. MacArthur, 1969). The adaptations of *V. epaphus* to the forest understory environment will therefore be emphasized in this discussion.

The strategy of ecological adaptation in a butterfly is molded by the spatial distribution and numerical abundance of the host plant (Singer, 1971). Given the patchy distribution of *Ruellia* in montane wet forest understory and the relatively large size (high and numerical abundance) of individual host plant patches, some predictions about the ecological traits of *V. epaphus* (and other herbivores of *Ruellia*) can be formulated.

*V. epaphus* can be described as a non-seasonal breeder with reproduction occurring throughout the year. Ecological studies of tropical butterflies should focus upon the major adaptations of life cycle to seasonal contractions or expansions in the amount of larval host plant (i.e., by seasonal differences in vegetative growth rates) in a given type of plant community, and at different altitudes. For example, *V. epaphus* is predicted to be a non-seasonal breeder since it is an understory species. It has been stressed by botanists (e.g. Webb et al., 1967) that the understory component(s) of primary-growth tropical forests provides a buffered environment for many organisms, protecting them from the major local vagaries of climate experienced by the canopy.

The understory represents a non-seasonal environment, and species of butterflies which breed there may possess non-seasonal patterns of reproduction. The strategy is in part a function of host plant selection in the understory community, and discrimination of young vegetative growth zones (unfolding leaf buds or apical meristems) for oviposition. Also, first-instar larvae may be physiologically and morphologically adjusted for feeding only on the youngest leaf tissues, in response to both physical (leaf shape, thickness, toughness) and chemical (quantitative and/or qualitative differences in secondary compounds involved in gustatory cues) properties of the leaves. Tropical butterflies may therefore fall

into three major classes of breeders: wet season breeders, dry season breeders, or non-seasonal breeders. The more seasonal breeders are predicted for typically second-growth species, although understory habitats cannot be excluded entirely, especially for tropical dry forests.

Oviposition should be very precise in *V. epaphus*, if selection pressures are favoring the evolution of very specialized behavior patterns (Margalef, 1968). Errors in oviposition are predicted in species having high fecundities and colonizing episodes, a good example being the second-growth butterfly, *Anartia fatima* (Nymphalinae) (Young, 1972e). Understory species such as *V. epaphus* concentrate the bulk of their reproductive effort (Labine, 1968) over a relatively small portion of the available habitat containing substantial numbers of the larval host plant. Adult vagility, under such conditions, would be low. At least one temperate zone species of pierid associated with second-growth plant communities experiences density-related dispersal of gravid females, presumably in response to increase in local adult population density (Shapiro, 1970). High adult vagility has also been measured in a second-growth satyrid (Brussard & Ehrlich, 1970).

On the other hand, studies of *Euphydryas editha* (Ehrlich, 1961) indicate low vagility. In tropical forest understory, butterflies may be less prone to dispersal due to reduced visibility resulting from shading and dense foliage. But comparisons of adult numbers with numbers of pupae (Table 2) suggest some adult dispersal, assuming negligible mortality. Nevertheless, a high proportion of individuals remain residential at the host plant. Such behavior gives breeding a patchy distribution, corresponding to the distribution of host plant patches (although not all host plant patches need be colonized by *V. epaphus*). Both factors, in conjunction with either low fecundity or high mortality of immatures, prevents over-exploitation and local extinctions of populations of *V. epaphus*.

Oviposition on tiny unfolding leaf buds may lower rates of predation or parasitism upon eggs. Eggs are partially concealed from wandering predators such as ants and aerial forms such as predatory Hemiptera. The unfolding leaves of *Ruella* appear much lighter in color than older leaves to the human observer. It has been demonstrated under laboratory conditions for various butterflies, that ovipositing females are capable of discriminating shades of green, corresponding roughly to age differences in coloration of leaves seen in host plants (Ilse, 1941; Vaidya, 1969). A similar discriminatory mechanism presumably occurs in *V. epaphus*, since the majority of eggs are deposited on the very young leaves of *Ruella*. A major selective force favoring such discrimination may be site selec-

tion for oviposition where eggs are least likely to be detected. Certainly increased ease of feeding for first-instar larvae on tender leaf tissue may also be an important factor (Thorsteinson, 1960).

The marked variability in time of oviposition is attributed to persistent cloud cover over these regions for a substantial portion of each day. Persistent cloud cover is a major feature of montane tropical forests (Myers, 1969; Roth & Bifano, 1971) and plays an important role in the adaptation of various organisms to these habitats. Oviposition in understory butterflies occurs over a wide range of hours since light remains at low intensity throughout the day. Thus, potential predators of ovipositing females such as understory birds would experience equal difficulty all day long in detecting their prey. There would be no hindrance to the ovipositing butterflies since they rely mainly upon olfactory and not visual cues in locating host plants.

In lowland tropical forests, oviposition is predicted to occur during moments of prolonged cloud cover (which usually takes place during the afternoon) since potential predators would be less of a threat during periods of reduced and diffused light. Oviposition in such species that have experienced a long evolutionary history involving adaptation to living in understory, should be lowest during the morning hours, when bright sunlight can filter down through the canopy. Such an oviposition pattern has been observed in *Victorina steneles*, a butterfly which is very common in tropical wet lowlands (Young, 1972e).

The forest understory also provides a suitable habitat for the exploitation of crypsis as an adaptive strategy for larvae. Not only does shade reduce the hunting success of visual predators, but the feeding positions of larvae on the host plant also contribute to protection. Older larvae generally feed ventrally along the edges of leaves; they adopt feeding positions that apparently optimize food intake per unit time as their positions fit very well recent predictions concerning such behavior (Heinrich, 1971). This results from progressive movement of larvae down the plant as they grow larger; older larvae invariably feed on the lowest (generally oldest) leaves. The adaptive significance of this behavior is clear: larvae, as they get bigger, are able to take in more plant tissue per unit time and are less exposed to potential predators while feeding. Selection may favor the evolution of such behavior in a palatable species since it helps to maximize escape from predators which forage from above. This hypothesis, however, remains to be confirmed.

If further study reveals that the realized life table ("realized fitness"—Istock, 1970) approaches the physiological life table ("physiological fitness") for *V. epaphus* (Young, 1972e), then the idea that species well-

integrated into stable tropical communities possess very specialized and efficient defense mechanisms against predators, pathogens, and parasites would be confirmed (Margalef, 1968; Pianka, 1966). Adult survivorship in natural populations of *V. epaphus* is generally high (Young, 1972e), although the reasons for this are not known. A related species, *V. steneles*, enjoys high adult survivorship both in Batesian mimetic association with the heliconiine, *Philaethria dido* (Brower & Brower, 1964) and even when not in mimetic association (Young, 1972d). Recent studies of second-growth species of Costa Rican butterflies (Young, 1972a; Young & Muysshondt, in prep.) reveal high rates of parasitism on eggs and larvae during selected times of the year. High levels of biotic mortality, if persistent, suggest lack of integration of herbivorous species into second-growth communities.

The depression in adult numbers during February–April (Table 2) may indicate decreased availability of adult food sources associated with diminished rainfall during this period. Cuesta Angel experiences a short and erratic dry season (“veranillo”). Reduction in monthly precipitation may destroy some food sources, such as fermenting patches of fungi on trees, or even flowers. During the wetter months, some adults may be killed off by heavy rains, although this is apparently constant (Table 2), and not highest at the beginning of the wet season, as observed for *Parides* (Papilionidae) on Trinidad (Cook, Frank & Brower, 1971). Such an adult mortality factor would be very sensitive to local topographical and climatological features, varying greatly at different localities, especially along altitudinal gradients (Holdridge, 1967).

The narrow local host plant specificity of larval *V. epaphus* is interesting. Although there have been discussions of mutualistic effects among plants and their lepidopterous herbivores (Ehrlich & Raven, 1965), relatively few studies have dealt with local host plant specificities at the species and generic levels, with the notable exception of some temperate zone lycaenids (e.g., Downey & Fuller, 1961; Downey & Dunn, 1964), *Papilio glaucus* (Brower, 1958), and *Euphydryas editha* (Singer, 1971). The single host plant of *V. epaphus* at Cuesta Angel is probably the only one that this butterfly exploits in this region of Costa Rica. At Bajo la Hondura, a montane region located on the Pacific slopes of the Cordillera, but of the same forest type and elevation as Cuesta Angel on the Atlantic slopes, *V. epaphus* exploits a different host plant, *Hygrophila guianensis* Nees (Acanthaceae). Like *Ruella tubiflora* at Cuesta Angel, this plant is characteristic of river edges at a wide range of elevations throughout Central America (D. C. Wasshausen, pers. comms.). But *Ruella* is not found at Bajo la Hondura nor is *Hygrophila* found at Cuesta Angel. It

would be interesting to determine whether two distinct strains (or sibling species) of *V. epaphus* have evolved in Costa Rica, in response to differences in levels of host plant toxicity between the two localities (Cuesta Angel and Bajo la Hondura). Clearly experimental feeding studies are needed to demonstrate differences in palatability between the two populations. Brower & Brower (1964) found that adults of *V. steneles* are palatable although various members of the Acanthaceae are known to contain alkaloids (Arthur, 1954; Irvine, 1961). Levels of toxicity for either *Ruella* or *Hygrophila* are not known.

A case of allopatry between *V. epaphus* and *V. steneles* may exist in Costa Rica. *V. steneles* is common throughout the Caribbean and Pacific lowlands (10–100 m elev.) of Costa Rica, where its major larval host plants, various species of *Justicia* in the Acanthaceae (Young, 1972e), are located. Here *V. epaphus* is generally absent, with the lowest elevations of its distribution being the Meseta Central (San Jose Province) between 200–500 m. However both species successfully complete development on the other's host plants in the laboratory. Therefore, other environmental factors, such as physiological adjustments to temperature and ecological barriers associated with topography may be important in determining altitudinal ranges of both species (Janzen, 1967). In the lowlands, *V. steneles* enjoys high adult survival as an understory species of primary-growth forest (Young, 1972d, e), where it represents a major zoogeographical expansion of the genus *Victorina* at low elevations. At higher elevations, a similar major adaptive radiation is portrayed by *V. epaphus*. The distribution of these species along altitudinal gradients varies greatly in different regions of Central America. In El Salvador, *V. steneles* occurs at elevations up to about 600 m, and *V. epaphus* is found at higher elevations (Young & Muysshondt, in prep.).

#### SUMMARY AND CONCLUSIONS

(1) The life cycle of *V. epaphus* is described for the first time, and data on developmental time are given.

(2) *V. epaphus* is an understory species of montane tropical wet forests, where it exploits localized patches of its larval host plant.

(3) Larval host plant specificity in *V. epaphus* is very high on a local basis, although different host plants are exploited in different parts of its extensive geographical range along the Cordillera in Costa Rica. At Cuesta Angel, a locality along the Atlantic (Caribbean) slopes, the host plant is *Ruella tubiflora*, while at Bajo la Hondura, a locality of similar elevation and forest-type on the Pacific slopes, the host plant is *Hygrophila guianensis*. Both plants are in the Acanthaceae.

(4) Immatures and adults of *V. epaphus* have high survival rates. Predation and parasitism are low. Such life table characteristics are correlated with low fecundity, low adult vagility, and cryptic behavior patterns of larvae.

(5) The genus *Victorina* in Central America seems to have undergone allopatric speciation, splitting into two species, *V. epaphus* and *V. steneles*, along altitudinal gradients. The former species is characteristic of montane forests and plateaus, while the latter species is more characteristic of the lowlands. However, larvae of both species can complete development successfully on the other's host plants.

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## PIERIS NAPI L. (PIERIDAE) AND THE SUPERSPECIES CONCEPT

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This is a subject to be treated at greater length on some future occasion: the present note is intended to draw attention to unresolved taxonomic questions, which particularly affect the North American populations.

When the European collector enquires, "Is *bryoniae* Ochseneimer a separate species?" he may mean either of two different things. He may be asking whether ssp. *bryoniae* is reproductively separate from the other *Pieris napi* L. flying in the same country, or he may want to know whether *bryoniae* + *flavescens* Wagner + *neobryoniae* Sheljuzhko and perhaps *adalwinda* Fruhstorfer + *hulda* Edwards + . . . . . are reproductively isolated, severally, from *napi* + *britannica* Verity + *meridionalis* Heyne + *oleracea* Harris + *venosa* Scudder + . . . . . The answers are likely to be different, and only that to the simpler question can be unequivocal.

Dobzhansky (1970), quoting Mayr and also Amadon, defines a superspecies as a monophyletic group of closely related and largely or entirely allopatric species, or as a group of . . . . essentially allopatric taxa that were once races of a single species but which have now achieved specific status. The components of the superspecies are semispecies or allospecies; gene-exchange is still possible among semispecies but not as freely as among conspecific populations. Thus the Holarctic *Pieris napi-bryoniae* complex is a perfect example of a superspecies.

The definition involves "species," which can itself be defined in many different ways. For butterflies, a formally new, though quite theoretical, criterion of species status has been given (Bowden, 1972):

Where the taxa have come into contact, if sympatry is leading to increased genetic and sexual barriers between them, the populations are to be taken as already belonging to distinct species; if not, not. This fixes speciation at a rather earlier stage than the "full speciation" of many systematists, and transfers a number of supposed semispecies to the