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Mimetic asociations in natural populations of tropical papilionid butterflies. I. Life history and structure of a tropical dry forest breeding population of Battus polydamus polydamus.

by

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This paper describes the life history and the ecological characteristics of a small breeding population of the tropical papilionid butterfly, *Battus polydamus polydamus* Linnaeus (Fig. 1), at a tropical dry forest (HOLDRIDGE, 33) site in northwestern Costa Rica. Biological studies of tropical papilionids are virtually non-existent, with the notable exceptions of numerous detailed descriptions of life stages for various Mexican species (DYAR, 21; HOFFMANN, 32; COMSTOCK and GARCÍA, 12; ROSS, 50). However, even detailed data on Central American species south of Mexico have been lacking (SEITZ, 51). Despite the apparent paucity of ecological studies on the natural populations of tropical papilionid butterflies, considerable theoretical and experimental interest has centered around this group of insects with regard to their supposed functional roles in mimicry complexes. The studies of BROWER and BROWER (7) have shown that some species of papilionids, particularly those belonging to the tribe Troidini, *(Parides, Battus)* are unpalatable as food morsels to birds, thus implying that these butterflies may act as models in mimicry complexes in nature. Although there exists apparent taxonomic confusion on the generic labelling of various species, it is believed that many species of the genera *Battus* and *Parides* (in addition to a third genus, *Troides*, EHRLICH, 22) exploit various species of vines belonging to the family Aristolochiaceae (genus *Aristolochia*) —a family of alkaloid-rich plants (vines and a few shrubs) that have their greatest distribution within the New World Tropics (GOOD, 30). The Aristolochiaceae are typically the lianas

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of tropical forests, and there are an estimated 450 species known to occur in the "world tropics" and "subtropics" (PFEIFER, 46). The tribe Troidini, a member of the subfamily Papilioninae, are often referred to as the "pharmacophagous" or "Aristolochia" swallowtails, as the larvae of many species in this group feed on Aristolochiaceae, and it is believed that these foodplants render larvae and adults unpalatable to vertebrate predators. This subject has received a rather exhaustive treatment in the ecological literature and although the precise mechanism of unpalatability is not known, there exists a sizable body of literature showing neat correlations between palatabilities of various butterfly groups and their larval foodplants (REMINGTON, 48; RETTENMEYER, 49; BROWER, 5). The results of laboratory studies on the relative palatabilities of various butterflies to selected bird species seem clear and unquestionable in their implications for mimicry theory. However, such studies need to be complemented by studies on the population structure of models and mimics under natural conditions, in addition to studies estimating the relative abundance of models and mimics in various mimicry complexes. When such studies are performed, the functional role of mimicry in the ecological adaptation of butterfly species in their habitats may be elucidated more clearly. Several ecologists interested in the adaptive significance of mimicry have concentrated the bulk of their efforts on tropical heliconiine butterflies (ELTRINGHAM, 27; MOULTON, 42; DARLINGTON, 16; SHEPPARD, 53; TURNER and CRANE, 60; BROWER, BROWER and COLLINS, 8; TURNER, 58, 59). There have, however, been few comparable studies on papilionid mimicry complexes, with the notable exception of a study on the *Battus philenor* mimicry complex in the United States (BROWER and BROWER, 6).

Since mimicry complexes are more abundant in the tropics, ecological studies of these are necessary to understand their structure at low population densities over long periods of time within an area. The problem, to me, is twofold: on the one hand, we need to know the relative abundance of models and mimics within a given mimicry complex (so as to elucidate how mimicry contributes to local survivorship of species), and on the other hand, we need data on the population structure of models and mimics in these complexes so as to assess the role of local dispersal behavior and poplation cohesiveness in maintaining the *effective* association among models (Müllerian mimicry complex) or among models and mimics (Batesian mimicry complexes). Two papers, this and a second one, approach both aspects for a mimicry complex involving two papilionids, *Battus polydamus* and *Battus bellus* in Costa Rica. Both species appear morphologically and behaviorally similar in the adult stage, and their co-occurrence on a regular daily basis at a large stand of flowers *(Stachytarpheta jamaicensis)* in northeastern Costa Rica indicates that they comprise a mimicry complex. A second paper (YOUNG, in preparation) summarizes the mimetic association between these two species at adult feeding sites; the present paper discusses in depth the adult population structure of *Battus polydamus* at one breeding site, emphasizing the various factors responsible for successful maintenance of a low density adult breeding population which is apparently isolated from other populations of this tropical species. Data are included here on life history and description of life stages for *Battus polydamus,* since very little is known about the natural history of this species; a later paper will summarize similar data for *Battus bellus.*

THE HABITAT AND RATIONALE OF STUDIES

During early March, 1970, the concentrated, flying activity of several adults of *Battus polydamus* (i.e., several "black butterflies" flying very low over a small area) was noticed along one side of the Pan-American Highway, just south (about 3 miles) of Cañas (10°28'N; 85°09'W; 45 m elev.), in the Province of Guanacaste, Costa Rica. This region is tropical dry forest, characterized by a pronounced dry season ("verano") between December and April, and by a shorter, more variable (in terms of rainfall per month) dry period ("veranillo") occuring between July and August, however, during other months, the rainfall can be considerable (Fig. 2). It is known that many species of adult trees and vines synchronize their flowering or fruiting times with the dry season in this region of Costa Rica (JANZEN, 35) and probably only very few plants respond in this way to the "veranillo," since its occurrence is less predictable than the dry season.

All of the individuals seen in early March (a total of 11 were spotted within one hour on one day) were *Battus polydamus,* and their activity was restricted over a small rectangular patch (about 25 by 15 feet) of *Aristolochia veraguensis* (Aristolochiaceae) growing as a sprawling vine over the ground and on large boulders, along a small creek about 40 feet from the road. This species of *Aristolochia* has been reported from Panamá and southward into South America (46); it is seen to occur in Costa Rica also.

Although there were no shrubs present within or near the *Aristolochia* patch (to provide support for the climbing vines), the patch was interlaced with many young *Heliconia* plants and varios herbs; the vines did not grow over these plants, but rather, formed a thick mat of vegetation along the ground. The species of *Aristolochia* was tentatively recognizable by the diagnostic large, variegated leaves (46) which are bordered in whitish-yellow along major veins; at first there seemed to be three species of *Aristolochia* growing together; but *A. veraguensis* proved to vary considerably with age as to leaf shape and coloration. This discovery was facilitated by witnessing the oviposition by *Battus polydamus* on the vines: females oviposited only on the stems of very young leaves which were very hairy, uniformly light-green, and spear-shaped (Fig. 3). Stems used for oviposition were usually within the diameter range of 3 to 4 mm; occasionally, however, the spherical, honey-colored eggs were laid on the stems of older parts of the vine. In a total of 83 egg clusters actually witnessed being laid during this study, 75 were on stems 3 to 4 mm in diameter; eggs were never laid on leaves. The failure to lay eggs directly on the leaves may be the result of the manner in which they are affixed to the foodplant: eggs are laid in small, tight clusters (Fig. 3), usually 6 to 9 per cluster, that often partially engirle the young stems of *A. veraguensis.* The abdominal and body movements involved in achieving this type of oviposition would seem difficult for the butterfly to accomplish on flat surfaces. However, when the butterflies and the vines were first discovered (March 1970), it was apparent that this *Aristolochia* was in an active period of vegetative growth: young vines were seen everywhere, and these were easily distinguished from the older, darker vines by the leaves; the patch of *A. veraguensis* was probably of reproductive age, as indicated by the larger, woody vines present; but, curiously, flowers were completely absent and remained so for the entire period of study (March through June). Vegetative growth, on the other hand, was evident throughout this period. At present, very little is known about the seasonal patterns of flowering, fruiting, and vegetative growth in vines such as the Aristolochiaceae, and it would be interesting to quantify the monthly availability of young suckers for potential oviposition sites of *Battus polydamus.* Is there a seasonal contraction in vegetative growth that in turn reduces the number of available oviposition sites for this butterfly? Does the actual oviposition behavior of the butterfly change with season so that oviposition could take place on leaves rather than stems? Does a decrease in numbers of oviposition sites result in severe competition (intraspecific) among females for a very limited number of sites? All of these questions bear heavily upon the seasonal biology of *Aristolochia veraguensis,* which is, at present, unknown.

Unfortunately, the distribution of *A. veraguensis* with respect to climatic regions in Costa Rica is undetermined. Such data are needed in understanding the geographic availability of this vine as a potential larval foodplant of *Battus polydamus.* While collecting various species of *Aristolochia* for Dr. Howard W. Pfeifer during 1969-1970 in northeastern Costa Rica, I failed to locate this species. This tropical wet forest region of Costa Rica, is, however, rich in other species of *Aristolochia.* I have collected eggs and larvae of *Battus polydamus* from another species of *Aristolochia* near San Miguel (Province of Heredia) in the same region.

It is very unlikely that *Battus polydamus* is a polyphagous species, being able to undergo larval development on a variety of plant families; such behavior has been noted, however, for *Papilio glaucus* in the United States (BROWER, 3). *Battus polydamus* males are dimorphic for an odor (MÜLLER, 43), and one possible explanation for this could be different larval foodplants being exploited by this species within a region.

It thus appeared that a breeding population of *Battus polydamus* had been discovered; oviposition was observed, as well as "chases" between different individuals (male-female; male-male). Also, it was noted that the adults present tended to remain very close to the *Aristolochia* patch, occasionally wandering over to feed at blooming *Asclepias* sp. (Asclepiadaceae) which was very abundant on all sides of the foodplant patch. It was then decided that systematic observations would be initiated on adult activity, population size, and adult behavior at this site. The major part of this program consisted of marking all individuals sighted by giving each a different combination of colored dots painted on to the undersides of the forewings; care was taken to also distinguish between sexes by different markings on the hindwings. Females were more greenish in the spotting pattern on the upper surfaces of their hindwings (Fig. 1), while males were more yellowish. All individuals thus marked were released within 5 minutes after their capture. At the time of marking, each individual was scored according to condition of wings, with a description of any damage, fading etc. Special care was taken to detect evidence of bird predation; beak-mark impressions, and beak-mark rips in butterfly wings can be used to estimate frequency of attempted predatory attack (CARPENTER, 10). After this initial marking period, the site was visited several days each month from mid-March through early June 1970. On each visit, any unmarked individuals were netted, marked and released, as before. Adult activity was observed closely with binoculars usually from about 9:30 AM to 3:00 PM on a given day, although, on a few days, the study period was extended until 6:00 PM in order to record the diurnal activity pattern of adults at the breeding site.

In addition to observing adult numbers and adult behavior, samples of larvae were netted (with cheesecloth) on the vines in order to estimate developmental time in the field. Two clusters of eggs (6 and 8 eggs) were brought into the laboratory and reared to record life stages and note larval behavior. Other samples of larvae were brought into the laboratory in order to estimate levels of parasitism; any adults emerging in the laboratory were marked, and returned to the population. Detailed observations were occasionally made on larval behavior in the field, including locations of pupation sites.

Interactions among males, and among males and females were observed in an attempt to understand the spatial-structuring of the adult population over the *Aristolochia*. In connection with these observations on adult interactions, a small experiment was performed in which several virgin females were introduced into the population to estimate the age of first reproduction. Other aspects of these studies will be mentioned as the data are discussed below.

LIFE HISTORY AND PARASITISM

For the entire study period (March through June) *Battus polydamus* was active in the adult stage; adults of both sexes were found at *A. veraguensis* on every day of observation.

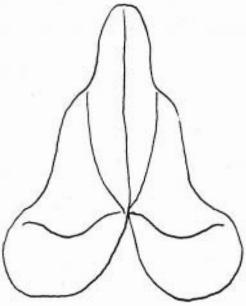
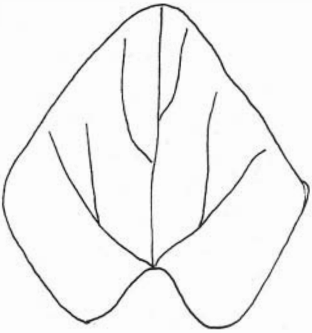
The honey-colored, spherical eggs measure 2.0 mm in diameter (Fig. 3) and they take 7 to 10 days to hatch in the laboratory. Upon hatching, the first-instar larvae (Fig. 4) immediately devour their emptied egg shells and begin to chew on the fine hairs of the stem. At this stage, they are uniformly orange-brown in color, with shiny black heads, and with the body covered with fine hairs. They move rapidly (within 8 to 17 hours) onto the very young leaves of *A. veraguensis* and feeding consists of chewing away the matted hairs of these young leaves, and also devouring apical leaf tissue. Between 1.5 and 2 days after hatching, the larvae are between 8 and 10 mm in length (at time of first molt), and dark brown, with the beginnings of short, fleshy white, and brown tubercles located dorsally along the body axis (Fig. 5). The head is still shiny black, although the larvae are now hairless. Larvae measure between 11 and 13 mm in length by the second molt. This instar lasts 4 to 5 days. During the third instar, larvae appear similar to the previous instar (Fig. 5) and by the end of this stadium, they measure 17 to 22 mm in length. This instar lasts between 3 and 4 days. During the fourth instar, the larvae change dramatically in appearance: the general body color is now grayish-brown with pronounced transverse black streaks (Fig. 6) and the head is dull black. On the first segment (I) behind the head, the first pair of fleshy tubercles has increased greatly in length and become whitish-orange at the base, with the terminal portions black; a white transverse band extends between these two tubercles, across the segment dorsally. On the second body segment (II), there are two pairs of tubercles —one lateral, and one dorsal pair (corresponding to the single pair on the first segment); on this segment and the one following it (III), the dorsal tubercles are much longer than the lateral pair. In the next body segment (IV), the dorsal pair is reduced in length while the lateral pair is now greatly elongated; for the next four segments, (V-VIII), only the dorsal pair is present, and there are now very tiny tubercles at the very base of each segment—near the false feet. On the next segment (IX), there are again two pairs of tubercles of equal length. On the next segment (X), there are again two pairs, but the dorsal pair is longer than lateral. On the next segment (XI), there is only dorsal pair. On the second segment (II) behind the head, there is a conspicuos shiny-black band that first appears during the first instar as a thin band. This band thickens with subsequent instars (Figs. 7, 8) and is restricted dorsally to the area between the dorsal tubercles. During the fourth instar, the prolegs are shiny black and the false feet are laterally-striped in brown and black bands. The fourth instar lasts between 3 and 4 days, and the fifth-instar larva appears very similar to it, although it is now lighter in general body color. During the fourth instar, larval length reaches between 32 and 38 mm. The fifth-instar larva is basically dull-gray in color, with black, transverse streaks on the body segments (Fig. 8). By the end of this instar, larvae measure between 41 and 45 mm in length and are 17 mm thick; this instar lasts between 4 and 5 days under laboratory conditions.

Larval behavior varies with different instars. Common to all instars are: (i) larvae do not devour cast exuviae; (ii) larvae invariably molt on the ventral surfaces of leaves; (iii) the time of molting is highly variable among individuals and there is no apparent diurnal pattern; and, (iv) larvae feed continuously throughout the day but not during the night. First- and second-instar larvae feed on the dorsal surfaces of very young leaves of *A. veraguensis,* but by the third instar, they move to the ventral sides of leaves. Feeding from the underside of leaves is retained throughout the remainder of larval life. Also, during the third instar, larvae move onto older (but still young) leaves on suckers of *A. veraguensis.* These leaves are of different shape and texture than those fed on by first- and second-instar larvae (Fig. 4), being elongated and devoid of hairs (see the leaf in Fig. 5 and contrast with the leaf shown in Figs.

3, 4). By the fourth instar, the larvae move onto the larger, and older leaves, these being the diagnostic yellow-white veined leaves known apparently only in this species of *Aristolochia.* These observations on larval preferences for different kinds of leaves of *Aristolochia* were initially witnessed in the laboratory, but the same trends were subsequently noticed in field samples, with only minor variations (Table 1). Fifth-instar larvae remain on the older leaves, and eventually the majority of them will pupate on the stems of the foodplant—as seen both in the laboratory and in the field. Pupae range in length from 32 to 35 mm, and are 13 to 17 mm thick at their widest point; they are generally light green in color but with the ventral area of the abdominal region yellow (Figs. 9, 10). Under laboratory conditions, the pupal stage lasts about 14 to 16 days. Out of a total of 15 larvae (fifth-instars) observed in the field, 12 pupated on the stem of the foodplant where they had been feeding. The developmental time is summarized in Table 2.

TABLE 1

Distribution of various age-classes (instars) of larval B. polydamus *among 3 different classes of leaf-shape (and size) of* Aristolochia veraguensis*, *near Cañas, Guanacaste, Costa Rica, March-June 1970*

Leaf shape			
Length range:	10-33 mm	40-95 mm	>100 mm
Properties:	Hairy, light green	Smooth, light green	Smooth, dark green with major veins yellow
	Numbers of larvae counted in the field:		
First-instar	45	1	0
Second-instar	43	4	3
Third-instar	5	37	1
Fourth-instar	0	0	36
Fifth-instar	0	0	35

* These data show numbers of larvae of different instars seen on *Aristolochia* vines that were marked (by tying a small band of orange tape around woody stems) for future observations on larval movements.

TABLE 2

Developmental time for Battus polydamus *under laboratory conditions*, estimated from a total of 20 eggs, representing 4 different clusters deposited on different vines by a single female, within a 35-minute period (11:15-11:50* AM *C.S.T.) on April 14, 1970, near Cañas, Guanacaste, Costa Rica*

	Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Pupa	Total
Mean (days)	8.55	1.74	4.46	3.42	3.55	4.37	15.23	41.32
S.E.	±1.82	±.06	±.53	±.28	±.61	±.31	±1.72	±2.64
Range	7-10	1-2	4-5	3-4	3-4	4-5	14-16	36-46
No. of individuals	20	20	20	20	20	20	6	6
Died**	0	0	0	0	0	0	14	14

* Cultures were kept at low density (one egg cluster per 8" x 12" clear plastis bag filled with *Aristolochia* vines) in San José, Costa Rica.

** Mortality due to parasitism by a tachinid, *Patelloa* sp.

The discrimination by the different instar larvae of *Battus polydamus* is very interesting, and is presumably the result of tactile and/or olfactory-chemical cues received from different kinds of leaves by the larvae as they pass through ontogeny. DETHIER (18) shows that immature stages of some insects prefer young leaves while others prefer older leaves of the same plant; some insects that feed on alkaloid-rich species of *Papaver* (Papaveraceae) prefer young leaves, which are relatively poor in alkaloid content. And as discussed by FLÜCK (29), the chemical composition of plants changes with age, sunlight, and other environmental factors. Such results have implications for associations between herbivorous insects and their host plants—especially plants rich in toxic secondary substances (WHITTAKER and FEENY, 62) such as the Aristolochiaceae. In the present study, it is seen that different instars of *B. polydamus* select different age-classes of *Aristolochia* leaves for consumption; the mechanism for such selection may be changes in the alkaloid (or other chemical) content of different age-classes of leaves, and/or the presence or absence of hairs (and the amount of hairs) on leaves of different ages. The problem offers fascinating opportunities to study subtle discriminations in lepidopterous larvae on their foodplants. Related to this is, of course, the site of oviposition: egg clusters are oviposited almost solely on the youngest stems of *A. veraguensis*, thus placing larvae very near the youngest leaves very early in life.

Mechanisms of oviposition-site selectivity in butterflies are not known, although it is suspected that a color stimulus is involved. VAIDYA (61) discusses various experiments on color preferences (various shades of green) of female

Papilio demoleus Linn. (the "Lemon Butterfly") for resting and oviposition behavior under laboratory conditions. In his studies, various shades of green are offered to the butterflies and the experiments are similar in rationale to those of ILSE (34) with *Pieris brassicae* (Pieridae, Cabbage White Butterfly). His study showed that under laboratory conditions, the female *Papilio demoleus* will select blue-green leaves for both resting and oviposition, surprisingly ignoring yellow-green.. This species is a *Citrus* feeder during the larval stage, as is *Papilio anchisiades,* a Costa Rican species. However, *Papilio anchisiades* oviposits only on the distinctly yellow-green young leaves, completely ignoring the usual dark-green ("blue-green") leaves. Also, in this study, *Battus polydamus* selects the lighter green young suckers of *A. veraguensis* for egg-laying—leaves and stems of these suckers are much lighter green in color than the darker older leaves in a patch of this vine. Furthermore, various species of papilionids in the *Parides* mimicry complex in northeastern Costa Rica (Finca La Selva) oviposit on very young (light green) vines of *Aristolochia* spp. Thus, all of these field observations indicate that in natural populations of these butterflies, egg-laying females do not rely on color alone. More likely, there are important and essential olfactory differences between young and old leaves of certain kinds of larval foodplants that induce oviposition-site discrimination in fecundated females. The mechanism, in light of DETHIER's study (18), may have important selective value for first-instar larvae of species that feed on plants rich in toxic and aromatic compounds: perhaps young larvae do not possess the proper metabolic machinery and/or physiological tolerance range to accomodate a build-up of toxic compounds, or other molecules that place a metabolic stress on the insects. Dethier's finding that younger leaves of *Papaver* contain less alkaloids than older leaves on the same plant suggests that such a mechanism would indeed be of supreme selective value. The matter is discussed by EHRLICH and RAVEN (25) and also by WHITTAKER and FEENY (62).

Both in the laboratory and in the field the larvae, upon hatching, disperse to different young leaves, but they usually do so in small groups of 2 to 4. Thus, while there is some dispersion of larvae, small aggregates remain throughout all instars (see the pairs of larvae in Figs. 4-8). The association is intimate when larvae are resting, although they feed separately on different parts of the same leaf. No silken webs ("trails") are laid down on the foodplant by larvae, and the small aggregations are formed each evening and larvae remain quiet throughout the night, with feeding resumed the following morning. The significance of this gregarious behavior is not clear; it is probable that such behavior could evolve in these insects since they are unpalatable, although very little is known about levels of predation by vertebrate and invertebrate predators on the larvae. Such gregariousness, in the absence of other effective predator-deterring defensive behavior, would be of high selective disadvantage in larval populations of palatable butterflies. Further studies, under laboratory conditions, are planned regarding the function of gregarious habits in larval populations of *Battus polydamus.*

Out of 14 larvae hatched in the laboratory and reared on *A. veraguensis* leaves, only 3 gave rise to adults. The remaining 11 larvae pupated, but from these there emerged tachinid flies about half-way through the pupal stage. All of these pupae died before eclosion. Since rearing was done in large, tightly closed plastic bags, it seemed very improbable that larvae were attacked by adult flies (for egg-laying). It was suspected that the larvae had ingested eggs of the parasites present on the foodplant. According to Dr. Curtis W. Sabrosky (personal communication), the tachinid parasite of *Battus polydamus* is a new species of *Patelloa*—a group in which many species deposit eggs on the foodplants of their lepidopterous hosts; the hosts then ingest the eggs along with plant tissue during normal feeding activity, and the parasite completes development within the hosts' body. On several days each month during the study period, samples of fourth- and fifth-instar larvae were collected from *A. veraguensis* and brought into the laboratory to estimate levels of parasitism (Table 3) in the population of *Battus polydamus.* Usually, a parasitized pupa gave rise to 3 to 5 *Patelloa* flies, the only parasite seen during the study period; emergence of adult parasites always took place after pupation of the infested *Battus polydamus* larvae. Larvae of the parasites drop from the host through the abdominal segments of the pupae and then pupate in the soil. Adult flies emerge 10 to 13 days later. While it has been noted that several species of tachinids attacking lepidopterous larvae infest their hosts by depositing eggs on larval foodplants (SIMMONDS, 54), little is known about the synchronization of these host and parasite populations. More is known about tachinid species that attack larvae for oviposition (KLOMP, 36) and can be synchronized with their host populations Although we do not know precise levels of parasitism in *Battus polydamus* larval populations, it is apparent that they are high, as seen on various sampling dates (Table 3) and that they account for most of the larval mortality. I found high levels of parasitism due to two species of tachinids in larval populations of Monarchs *(Danaus plexippus)* and Queens *(Danaus gilippus)* in northeastern Costa Rica over several months time and studied the possible role of this mortality in governing adult population size. In the next section, data is summarized on adult population size in *Battus polydamus,* illustrating the low numbers of "recruits" to the breeding population; low recruitment is believed to be due primarily to high mortality resulting from parasitic attacks by *Patelloa* flies on the larvae. *Battus polydamus* larvae may be a major host ("primary host") for this species of *Patelloa* in Guanacste, since successful parasitism occurs over several months' time (Table 3) in one breeding population. If this is true, it would be interesting to study the host-searching behavior of this tachinid, and the possible role of the odorous properties of *A. veraguensis* in this behavior. READ, FEENY and ROOT (47) discuss how braconid parasites of aphids on crucifer plants (which contain large amounts of mustard oils), exploit plant odors to locate hosts. Earlier, MONTEITH (40, 41) found that the tachinids *Drino bohemica* and *Bessa harveyi* are attracted, in part, to their sawfly hosts by the odors of the foodplant. Perhaps *Patelloa* successfuly locates larvae on *A. veraguensis* through odors emitted by the plant. The results of such studies would be of importance to our understanding of the biotic control of populations of *Battus polydamus* on different species of *Aristolochia* and in different habitats

TABLE 3

Pupal mortality due to parasitic attack by Patelloa *sp., a tropical tachinid, in a larval population* of* Battus polydamus, *near Cañas, Guanacaste, Costa Rica, March-June 1970.*

Monthly Samples	Total No. pupations observed	No. pupae yielding flies	% Mortality
March	32	27	84.4%
April	27	20	74.1%
May	28	19	67.9%
June	40	34	85.0%

* Fifth-instar larvae collected from the field and allowed to pupate in the laboratory; also included are data of larvae pupating in cheesecloth bags in the field.

No other major sources of larval mortality were noted in this breeding population of *Battus polydamus* during the study period. Eggs appear to have close to 100% survivorship, not being detected by ants or other predators. however, egg clusters can sometimes be easily dislodged when the vine is knocked gently, the entire cluster falling to the ground. Here, the eggs could be subject to predation, although no data are available on this at present Apart from parasitism by *Patelloa,* predation on larvae is apparently low. EMMEL (28) reports a very high incidence of a viral disease in a sample of larvae of the North American papilionid, *Papilio polyxenes asterius* on the foodplant *Heracleum lanatum* (Umbelliferae) in which over 90% of fifth-instar larvae died from this infection. Such infections have not been observed in larval populations of *Battus polydamus* in Guanacaste. Pupae of *Battus polydamus* enjoy high survivorship in the field: I staked out 10 pupae on vines of *A. veraguensis* (in their original locations) and all of these successfully eclosed. In the laboratory, pupae that survive parasitism enjoy 100% survivorship.

ADULT POPULATION STRUCTURE

Analysis of adult population structure in *Battus polydamus* entailed observations on recaptures ("resightings") of marked adults, sex ratio of adults, individual movements relative to location of the larval foodplant patch, and changes in age-structure of the adult population. Virtually every individual marked during the study period was resighted on several different days. Population turn-over (replacement of adult deaths with recruits) was generally low, although consistent each month (Table 4). The very high percentages of resighting of marked individuals (greater than 90% for the entire study period) revealed that adult population is small at this patch of *A. veraguensis* (Table 4) and very

TABLE 4

Monthly numbers of adults in a breeding population of* Battus polydamus, *near Cañas, Guanacaste, Costa Rica. Population size was estimated from a capture-mark-resight program*

		Adult butterflies:						
		Males			Females			
Month	N**	Marked	Unmarked ***	Total	Marked	Unmarked ***	Total	Total population size
March	10	5	2	7	4	1	5	12
April	15	7	1	8	5	1	6	14
May	12	6	2	8	6	2	8	15
June	8	7	2	9	7	0	7	16

* All adults captured at one isolated patch of a larval foodplant, *Aristolochia veraguensis.*

** N is the number of days of observation in each month; usually days of observation were scattered throughout the month.

*** "Unmarked" adults were always very young and fresh, interpreted as new "recruits" to this population, having eclosed at this breeding site.

cohesive in structure. Adults do not forage far from this breeding site, since there is usually an array of various flowers in abundance (especially *Asclepias* sp.) within the immediate vicinity; feeding consists of occasional movements of individuals from the foodplant patch to flowers, but with these adults always returning to the breeding site. Similar types of individual movement in *Battus polydamus* were observer in another breeding population in northeastern ("tropical wet") Costa Rica (YOUNG, in preparation) and it was concluded that this species possesses low vagility. The individual male *Battus polydamus* will leave the breeding site for feeding an average of 55 times (55 ± 9.3; N = 13) daily while a typical female makes an average of 84 foraging excursions (84 ± 14.5; N = 10). Males appear to be more residential than females at the breeding site, and as will be discussed in the next section, this is probably related to the reproductive behavior of this species. It was also noticed that fresh males become very tattered within a few days after eclosion. This was noted in fresh males that were marked, and also, in a few instances, in newly-eclosed males (less than 20 hours old) released into the population after emerging from pupae in the laboratory. Males become tattered and frayed due to intraspecific aerial clashes with other males over the foodplant; this behavior is part of a functional system of territoriality that will be described in the next section and is mentioned here since it confounded attempts to estimate changes in age-structure (since wing condition is used to do this). However, females do not participate in such aerial combat and their wing condition was a helpful and realible means of studying age-structure. It was found that adults are very long-lived and that adults eclosing at the foodplant patch remain there for at least four months, and probably longer. For example, of the 9 fresh-appearing females that were marked on March 14, 1970, 7 were still active at this site on June 3, 1970. By June, these adults were very tattered and frayed, although none bore evidence of attempted bird predation (beakmarks). YOUNG (in preparation) summarizes the data on the lack of beak-marks on wings of male and female *Battus polydamus* in this breeding population and maintains that adults are afforded protection through avian recognition of their unpalability. Although wing condition as an indicator of age could not easily be studied for males, it was found that out of a total of 14 males (9 of which appeared fresh) marked during an 8-day period in March, 1970 at the site, 11 were seen on a regular basis until June, when the observations were terminated. In addition, new recruits of both sexes were seen regularly at the site (e.g., individuals marked during April and May). At the time of marking, all of these latter were fresh adults, providing strong evidence that they eclosed at the breeding site, and were not immigrants from another population.

The lack of vagility in adult *Battus polydamus* is strikingly clear; during the study period, over 90% of the individuals marked remained in this population and there was virtually no dispersal into other breeding populations. YOUNG (in preparation) discusses the apparent very patchy distribution of *Aristolochia* in second-growth habitats in northeastern Costa Rica as severely restricting both the size and spatial contact between different populations of *Battus polydamus* and also, *Battus bellus*. It was pointed out that such small adult breeding populations of these butterflies could be maintained by an effective system of mimicry that would ensure adult survivorship from predation and would help to counteract the devastating effects of rampant parasitism in larval populations. MACARTHUR and WILSON (37) showed that small populations are frequently subject to random extinction. Breeding populations of *Battus polydamus* are very small and the single population studied did not go to extinction during the study period. However, it is not clear whether such a small population could maintain itself over longer time intervals—through the vagary of parasitism, there could be a point at which such mortality would destroy enough potential recruits to the breeding population, resulting in extinction. If this "patch" was so small that this actually occurred, extinction would take place faster than recolonization (due to low vagility of adults) and the population would disappear. High death rate (from parasitism) and low vagility would almost ensure local extinctions in such a species. If this is true, then we should be able to find some foodplant patches vacant of *Battus polydamus;* it is mainly for this reason that it is important to map out the distribution of foodplant patches in the habitat, and note whether or not various isolated patches are populated with *Battus polydamus.* Given the generally low birth rate of *Battus polydamus* the major factors contributing to local extinction would be parasitism and low vagility.

In the present study, there was no evidence of mimetic association of *Battus polydamus* at either breeding or feeding sites and presumably this small population was not involved in a regular mimicry complex (at least during the 4 months of study). However, recent laboratory studies (COPPINGER 13, 14) suggest that birds, considered major predators of adult butterflies, are frightened upon visual contact with warningly-colored butterflies, regardless of effective mimetic associations. This indicates that in nature, would-be avian predators can learn immediately to avoid warningly-colored butterflies and these insects will enjoy high survivorship. The lack of beak-marks on the wings of *Battus polydamus* in this population, and the failure to discover mimics, suggests that birds avoid this species due to recognition of its unpalatable condition as advertised by wing coloration and pattern. During the study period, several species of birds were active in the vicinity. In another population of *Battus polydamus,* studied at a concentrated feeding site, a mimetic association of this species (presumably Müllerian) with *Battus bellus varus* was very evident, and under these conditions, the operation of an effective system of mimicry was interpreted as reducing avian predation on both species. However, from the present study, it is clear that there probably exist local populations of at least *Battus polydamus* which are not in mimetic association, and observed high adult survivorship is presumably a result of either (i) a previous evolutionary history in which both species occurred together, thus reinforcing their distastefulness to avian predators, or (ii) the ability of avian predators to recognize rapidly the distastefulness of either species in the absence of an evolutionary history of mimetic association.

Another intersting point emerging from observations on the adult population concerns the unity sex ratio seen at the breeding site (Table 5). When

TABLE 5

Sex ratios in the small breeding population of Battus polydamus, *near Cañas, Guanacaste, Costa Rica, as seen on several different days* each month*

Date	Males	Females	Proportion female
March 15	7	5	0.42
March 20	7	3	0.30
March 28	6	5	0.46
April 3	7	5	0.42
April 10	8	6	0.43
April 18	8	6	0.43
April 26	6	4	0.40
May 6	7	7	0.50
May 13	7	7	0.50
May 22	7	8	0.53
June 5	9	8	0.47
June 11	9	7	0.44
June 19	8	7	0.47
June 28	9	7	0.44

* These are not the total number of days on which observations were made, but representative dates illustrating sex ratio trends in this population.

observations on a given day were extended over several hours, it was found that there were usually equal numbers of males and females active at the breeding site; males, however, were more residential per unit time of observation. SHAPIRO (52) maintains that in low population densities of the pierid *Pieris protodice* Boisduval and Le Conte the observed close to unity sex ratio does not induce female dispersal, since sexual interactions are relatively less frequent than at higher population densities; at higher adult densities, SHAPIRO (52) found a paucity of females in these populations. In *Pieris protodice,* it wes found that the increased frequency of attempted matings at high population densities resulted in an exodus of fertilized females ("colonizers"). Such a mechanism does not operate in the small populations of *Battus polydamus,* since apparently sexual interactions are not frequent enough (since population density is low) to induce dispersal of fertilized females from the breeding site. On the other hand, in a study of an African butterfly, *Acraea encedon* L. (Acraeinae), it was found that small, highly polymorphic and predominantly female populations exist as genetically-isolated units (OWEN 45). This species is involved in various Batesian and Müllerian mimicry complexes. The aberrant sex ratio in some of these populations, favoring females, is thought to be an adaptive mechanism for preventing the spread of young males to other populations, thus maintaining close, genetic adjustment of each population to local environmental conditions (as suggested by the large differences in the relative frequency of the polymorphism among populations). Neither preponderance of females nor of males is seen in populations of *Battus polydamus;* small populations are maintained without polymorphism and without dispersal of either sex to other populations. Examinations of adult specimens from this population and also from a second population in northeastern Costa Rica revealed no seasonal changes in appearance (wing-markings) of the butterflies. In an unpalatable species of butterfly, there should be strong selection against polymorphism since the existence of various morphs within a population would tend to prolong the learning process by would-be predators that the species is unpalatable. Also, density-related dispersal in butterflies would be expected to exist in species genetically programmed for colonizing vagility (ABBOTT, 1; DETHIER and MACARTHUR, 19). *Battus polydamus* in Guanacaste and in northeastern Costa Rica exist in small, rather sedentary breeding populations. Such local population structure has been noted in other species (DOWDESWELL, 20; EHRLICH, 23, 24), while in at least one other species, *Erebia epipsodea* (Satyrinae), populations are very large and there is a great deal of individual movement over large areas of the habitat (BRUSSARD and EHRLICH 9). In *Battus polydamus,* low reproductive rate, high larval mortality, high adult survivorship, and low adult vagility all interact to permit this species to exist as a very patchy distribution that corresponds, to some extent, to the patchy distribution of *Aristolochia* foodplants in suitable habitats. For a given region, it would be interesting to document how much of the available larval foodplant (i.e., how many of the available patches) is actually exploited by breeding populations of the butterfly and to what extent mimicry complexes involving *Battus polydamus* would be found at different patches.

ADULT BEHAVIOR AT THE BREEDING SITE

Adult behavior at the breeding site is best discussed as two components: male-male interactions, and male-female interactions, since both types of activity exist at the patch of *A. veraguensis* on a regular basis. Also, oviposition behavior will be described.

First, it appears that the function of population cohesiveness at the larval foodplant is indeed the bringing about of effective reproductive activities, as illustrated by the frequencies of mating pairs and ovipositing females observed during the study period (Table 6). Ovipositing females show the same behavior

TABLE 6

Occurrence of mating pairs and ovipositing females in the small breeding population of Battus polydamus, *near Cañas, Guanacaste, Costa Rica, March-June, 1970*

Dates		Mating pairs*	Ovipositing females*
March	13	0	2
	14	0	1
	15	1	0
	27	0	0
	28	2	1
	30	1	0
April	9	0	0
	10	0	0
	11	0	2
	15	2	0
	16	0	1
	17	1	1
	18	1	0
	26	0	1
	27	0	1
May	6	1	2
	7	1	1
	8	0	0
	12	1	0
	13	0	0
	14	0	1
	22	0	1
	23	0	0
June	10	0	0
	11	1	0
	12	0	0
	17	1	1
	18	1	1
	19	0	0
	27	0	1
	28	1	1

* Numbers seen in 4-7 hour observation periods, on a given day.

pattern over and over on different days: from observations on marked individuals, it was seen that an ovipositing female will flutter around and above the *Aristolochia* patch for several minutes, occasionally resting on a plant between flutters. She will oviposit only a few times on a given day during such activity and one act of oviposition consists of the female grasping onto a young vine with the legs, keeping the wings fluttering, and then depositing a small rosette of eggs on the stem. This is usually accomplished within 30 seconds and on a given day, a female will oviposit, between 5 and 12 times. Eggs are not laid singly but always as clusters (Fig. 3). It was often noticed that a female was not always successful at ovipositing on a stem; on several occasions, the female appeared to have difficulty grasping the stem before depositing the cluster of eggs; on such occasions, the female attempted to grasp the stem 3 or 4 times at the same spot on the vine, finally resulting in successful oviposition or in flying away to find another site. Usually, however, such trials ended in successful oviposition. Oviposition usually occurs between 9:00 AM and 2:00 PM on sunny days and deposition of egg clusters is interspersed with long periods of resting, feeding, and fluttering over the foodplant. Oviposition does not occur on very cloudy days, when adult activity is generally restricted.

A small experiment was conducted in which 4 virgin females (less than 20 hours old) were released into this population on a single morning. These individuals remained at the site and all were ovipositing within 2 days. By following these and other individual females marked at the study site, it was found that females can oviposit over several months. Mating of newly-eclosed virgin females can occur within one day after appearance of the female. Although actual copulating pairs have been observed, the courtship ritual leading to their formation was not witnessed. Copulating pairs rest quietly on vegetation (usually on *A. veraguensis*) and they are seen between 11:00 AM and 4:00 PM. Age of the female may be an important factor in determining the rate of mating. CRANE (15), in discussing the courtship patterns of several species of *Heliconius* butterflies on Trinidad, observes that these rituals change with age of the females; BROWER (4) observed that *Papilio multicaudatus* females copulate faster when they are young virgins. Females typically mate only once, although in a series of females examined from another locality, out for a total of 11 that had spermatophores in the bursa copulatrix, 3 had two spermatophores. At the study site, females were not examined for spermatophores and data on frequency of mating consisted solely of observations on copulating pairs. Copulating pairs remain together (in tandem) anywhere from 25 minutes to more than 2 hours, although this range may even be greater since initial stages were not observed.

Courtship in *Battus polydamus* is undoubtedly facilitated by male behavior. Males at the breeding site appear to be territorial; i.e., individual marked males return repeatedly to the same perches in the foodplant patch and defend the immediate vicinity of these perches against other males. Also, it was discovered, both in the laboratory and in the field, that males eclose before females within an egg cluster; adult males emerge almost 2 full days earlier than females. In the laboratory, males are ready to mate within 24 hours after eclosion. Such a strategy ensures that when the females appear there will always be several sexually-competent males in the population for breeding purposes. This, in addition to the fact that females can mate almost immediately after eclosion, ensures that sufficient numbers of sexual encounters will occur at low population density in *Battus polydamus*. Similar observations have been made in various species of pierid butterflies (SMITH, BRYAN, and ALLEN, 55; STERN and SMITH, 56; SHAPIRO, 52). Frequently, there are inter-male aerial clashes in which physical contact is made; this repeated behavior is probably the major factor causing the wings of males to become very tattered while females of comparable age ramain fresh in appearance. Individual marked males maintain the same perches on different days, usually leaves of the foodplant that are higher than most of the surrounding vegetation. Distances between perches of different males are usually several feet apart and never closer than 3 feet; these perches are distributed over the foodplant patch and on vegetation immediately adjacent to it. Ovipositing females will be approached by a perched male when they flutter near the perch of the latter, but once a female has begun oviposition, the curious male will take leave of her and return to his perch. Observations were not detailed enough to account for "signs" given by ovipositing females that tell males when they are unreceptive to their advances. Unreceptive postures in female butterflies have been described in various pierids (CLENCH, 11; STERN and SMITH, 56; DAVID and GARDINER, 17; SHAPIRO, 52) and female flight-avoidance behavior has been described in other groups (STRIDE, 57). Further detailed behavioral studies of *Battus polydamus* should reveal the courtship patterns and unreceptive postures of females.

The functional existence of territorial behavior in tropical butterflies is of considerable interest to ecological theory since it represents a very specialized form of behavior associated with the survivorship of populations at very low densities (MARGALEF, 38). In the present study, it was difficult to objectively define the size and shape of individual territories of male *Battus polydamus* since the actual "territory" of an individual consisted of its perch and some unknown portion of the aerial space surrounding it. Estimations of sizes and shapes of an array of territories within a population of an animal are very valuable data for characterizing the "area pattern of distribution" (ALLEE *et al.*, 2; ELTON, 26) of the species in its suitable environment. However, it has been suggested (GRANT, 31) that at low population densities, the size and shape of a territory bears little or no relation to adult numbers, and under such conditions, these attributes are probably determined mainly by characteristics of the habitat itself. It has also been suggested for bird species that are territorial (ORIANS, 44), that differences in sizes and shapes of territories within a species-population may have important evolutionary significance to the species: females may select certain males for mating based on the "quality" of the territory (among other factors). Under such conditions, the more fit males would mate with most of the females in such polygynous species. From the marking studies conducted here, it was observed that every male in this breeding population mated more than once during the study period. Such data may provide indirect evidence that the qualities of different territories were similar, and that polygyny is not a strategy of mating in breeding populations of *Battus polydamus.* Rather, territorial behavior has evolved in this papilionid butterfly to ensure an adequate level (frequency) of matings at low population density, in which all territorial males partake of reproductive activity. Non-territorial males (defined here as individuals that did not possess perches), while few in number (4 to 7), were not observed to copulate at the breeding site. At low population density, it is undesirable for females to leave the breeding area, an event which could result from severe competitive interactions among several males for a single female. A possible strategy to retain females at the foodplant, while restricting male activities to individual areas, would be an "interference" mechanism of competition (MILLER, 39) that would permit an adequate mating frequency due to the reduction of multiple male interference in courtship interactions. Individual males "defend" their territories throughout the day, leaving only for foraging purposes at nearby flowers. By observing the assaults of perched males on passing males, it was seen that they will defend the area around their perches from all sides, and that the actual distances of flight from perches during such skirmishes are very variable and inconsistent. On one day of observation, a single male left his perch in aerial assaults a total of 107 times between 11:00 AM and 3:00 PM, under conditions of sunny skies; the straight-line distances of his flight from the perch ranged from about 2 to 15 feet, with these distances being determined, in part, by the aftermath of the assault (i.e., sometimes clashing males flew off together in one direction before separating, although their actual point of aerial encounter would be much closer to the perch).

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SUMMARY

A small breeding population of the butterfly *Battus polydamus polydamus* Linnaeus was studied at a tropical dry forest site in northwestern (Guanacaste Province), Costa Rica, from March through June, 1970. Life history, adult population size, adult turnover, adult dispersal, breeding behavior, territorial behavior and biotic mortality in larval populations were studied. It was concluded that the apparent patchy distribution of the larval foodplant *(Aristolochia* vines) results in a very patchy distribution of breeding populations of this butterfly; low vagility, high adult survivorship and localized breeding interactions at the larval foodplant account for the apparent high population cohesiveness in this species, despite high levels of parasitism during the larval stage. Males eclose before females and establish "territories" at the breeding site and adult numbers remain consistent over long periods of time. The latter is believed to be a result of high adult survivorship (from predation by birds), with low mortality associated with old age being counterbalanced with low recruitment of new adults to the population. The relation of such a population structure to mimicry theory is also discussed.

RESUMEN

En un ambiente de bosque seco tropical en el noroeste de Costa Rica (Provincia de Guanacaste) se estudió, durante los meses de marzo a junio de 1970, el ciclo de vida, el tamaño de la población, reposición, dispersión, comportamiento sexual y territorial en adultos de la mariposa *Battus polydamus polydamus*, así como la mortalidad biótica de sus larvas. El patrón de población en grupos diseminados tiene relación con la distribución de las plantas de *Aristolochia* que constituyen la fuente de alimento de las larvas. A pesar de los altos niveles de parasitismo, existe un alto grado de cohesión de la población al rededor de su habitat, debido probablemente al bajo grado de dispersión, a la longevidad de los adultos y a las interrelaciones larvales estrechas. Los machos eclosionan antes que las hembras y establecen "territorios". El número de adultos permanece constante durante largos períodos de tiempo. Se cree que esto último se deba a la alta sobrevivencia de los adultos (defensa contra predación por aves) y a la baja mortalidad, que se contrarrestan con el bajo reclutamiento de individuos nuevos a la población original. Tales estructuras de población aparentemente están relacionadas con la teoría de mimetismo.

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Fig. 1. Adult *Battus polydamus polydamus* Linnaeus; above: female, below: male . The scale on the left is in cm.

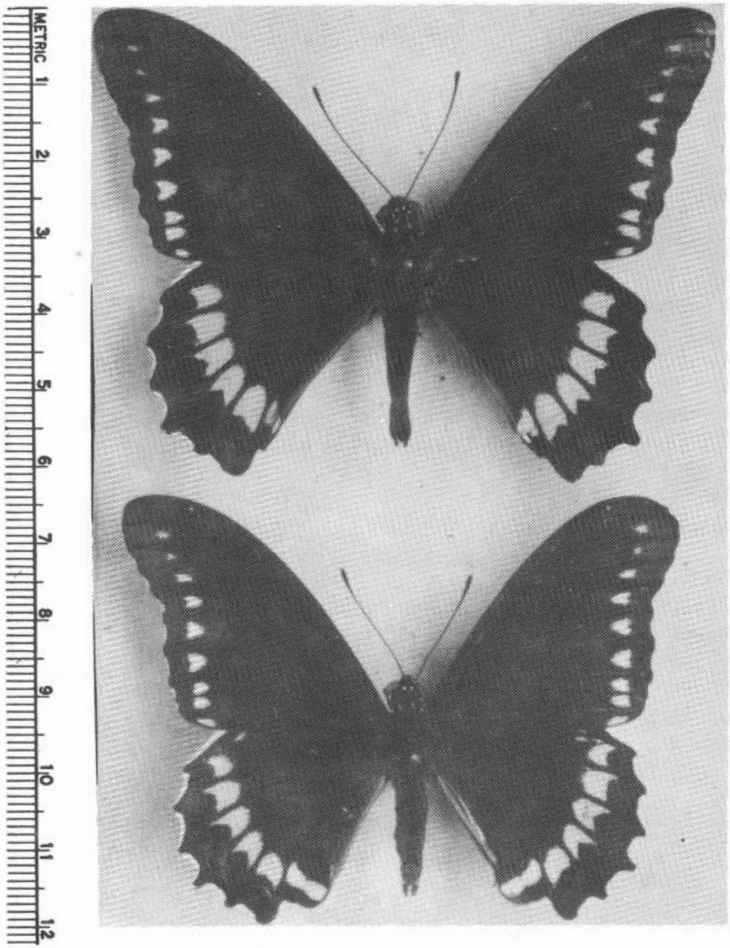

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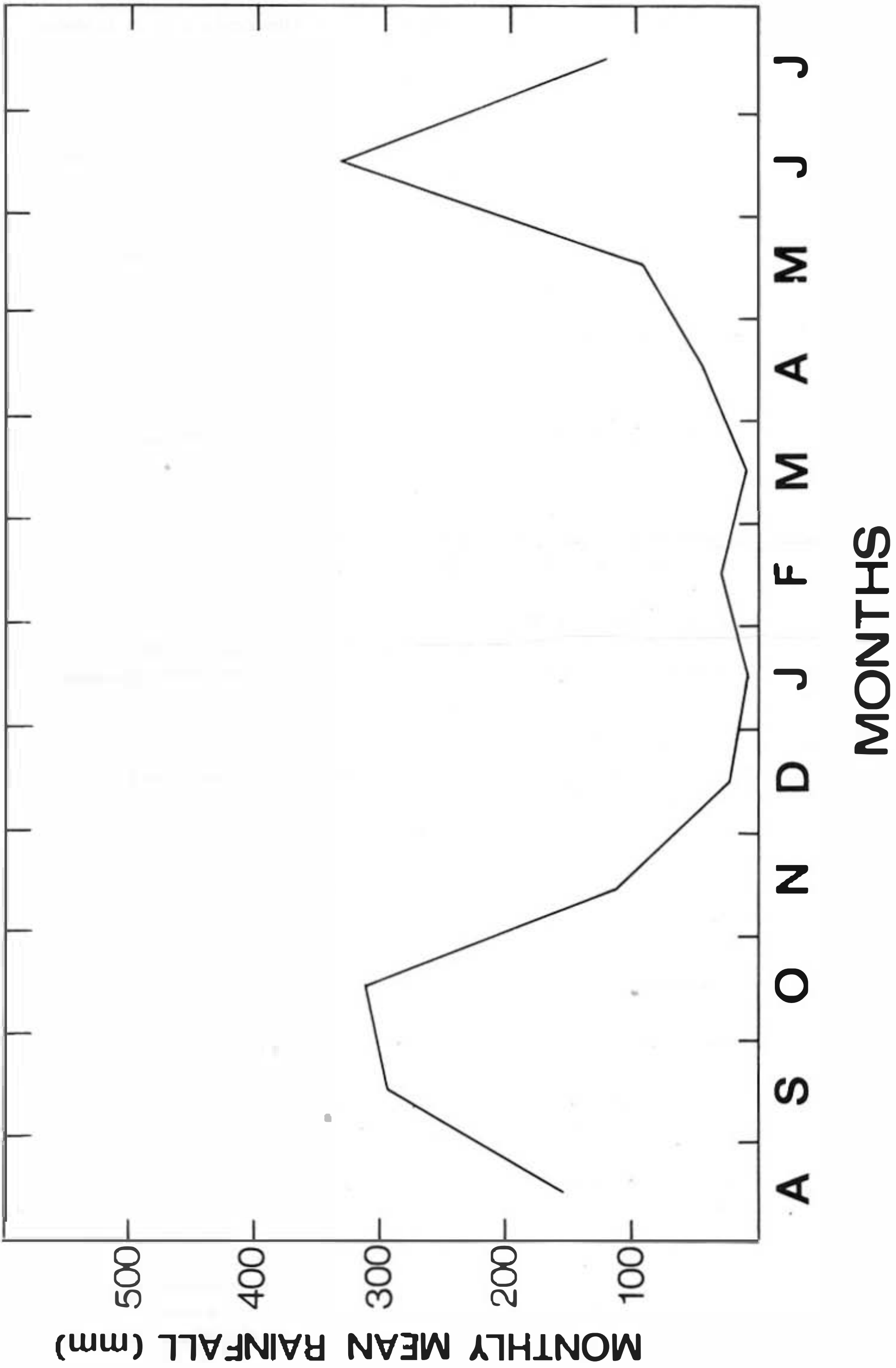
Fig. 2. Monthly mean rainfall at Cañas, Guanacaste Province, Costa Rica. Plotted are monthly averages for the ten-year period, 1960-1969, using data obtained from the Servicio Meteorológico de Costa Rica. A pronounced dry season ("verano") occurs between December and March in this region of northwestern Costa Rica.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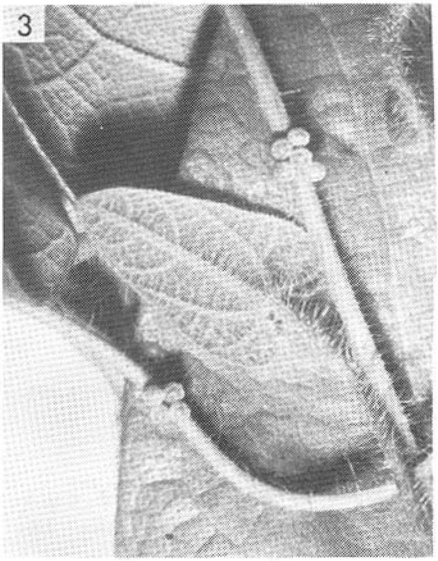
Figs. 3-6 Some life stages of *Battus polydamus*, illustrating the gregarious habit in their distribution on a larval foodplant, *Aristolochia veraguensis* (Aristolochiaceae). Eggs are usually laid in small clusters attached to young stems (Fig 3), and upon hatching, the larvae remain together in smaller groups (usually 2's or 3's) throughout all instars until pupation. First- and second-instar larvae (Fig. 4) feed on the dorsal surface of the youngest leaves, third-instar larvae (Fig. 5) feed on the dorsal surfaces of older leaves, and fourth-instar larvae (Fig. 6) feed on the ventral surface of the oldest leaves.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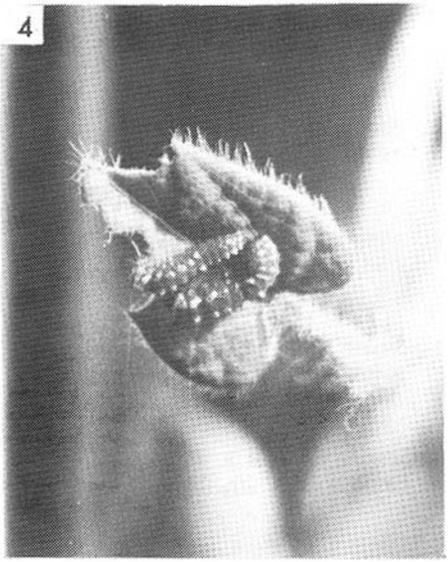
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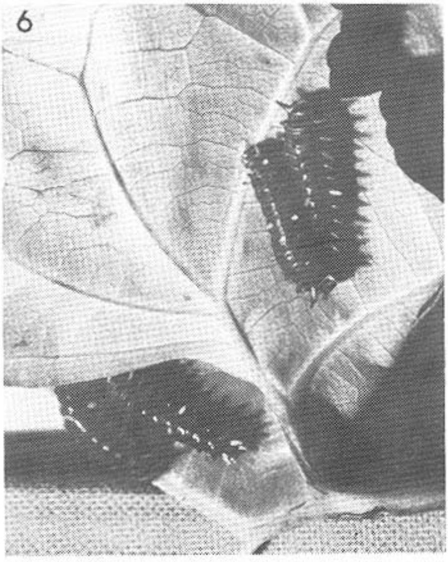
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Figs. 7-10. Other life stages of *Battus polydamus.* Fifth-instar larvae (Figs. 7-8) continue the gregarious habit seen in earlier instars, and feed and rest on the ventral surface of the oldest leaves. Resting larvae are best seen in Fig. 8 — note the hidden position of the head region of these larvae. Pupation takes place on the larval foodplant and pupae (Figs. 9-10) are shaded in light green and yellow that blend very well with the colors of the vines.

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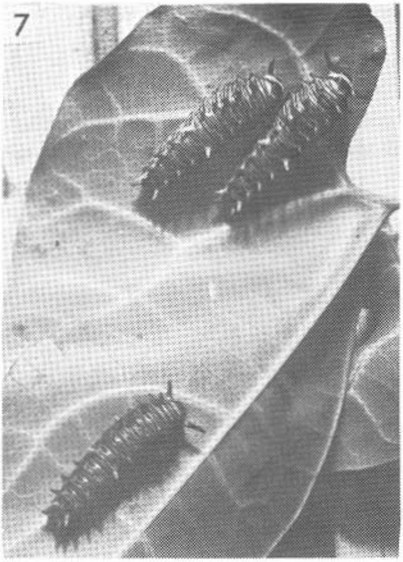

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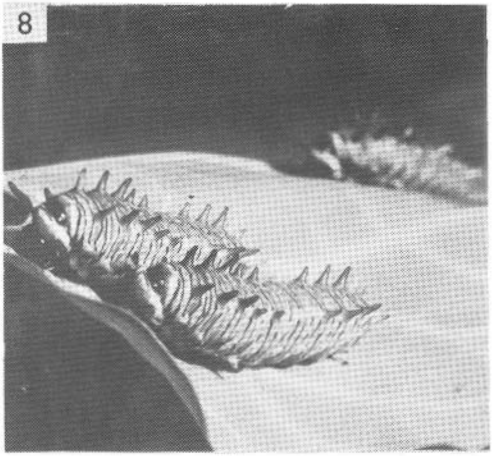

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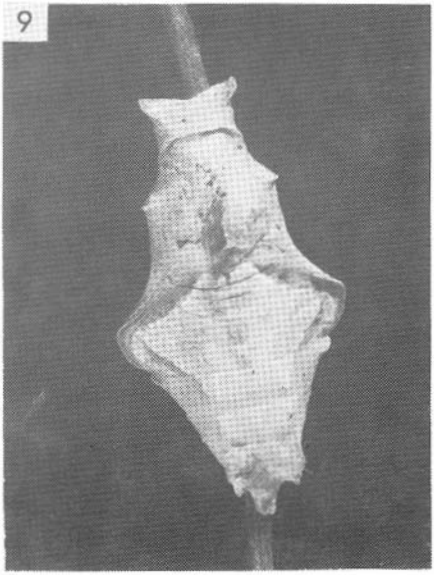

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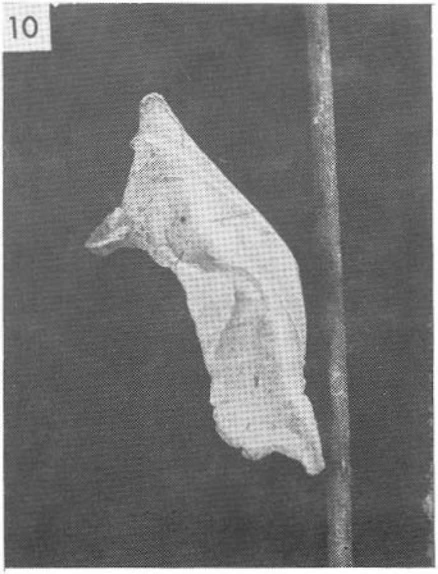

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