Contributions in Biology and Geology

STUDIES ON THE EVOLUTIONARY BIOLOGY OF THE NEOTROPICAL NYMPHALID BUTTERFLY *ANARTIA FATIMA* IN COSTA RICA

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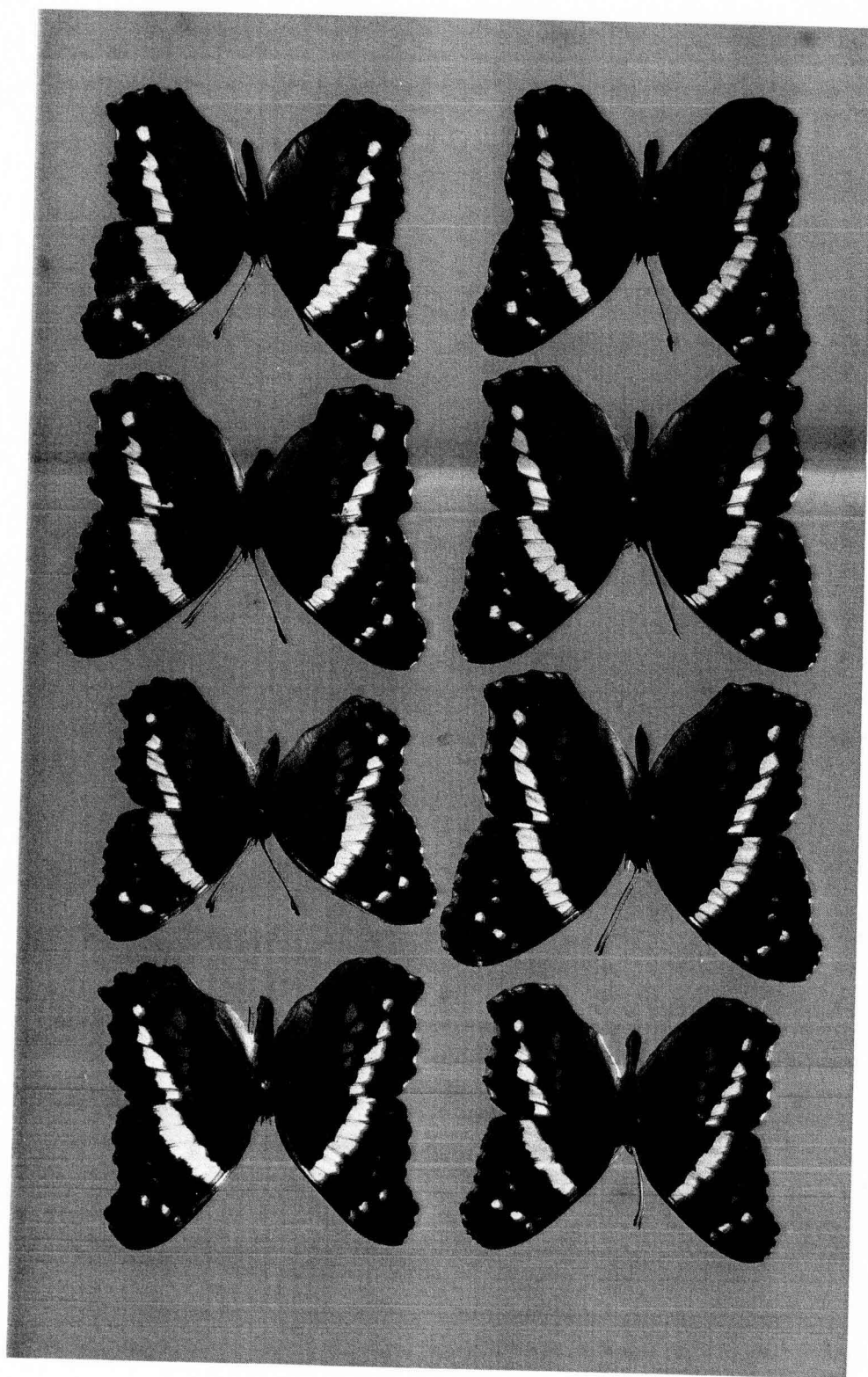
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A series of laboratory reared *A. fatima*. All of these butterflies were reared from
the egg stage, the left side gives a series of male and female "yellow" morphs,
while both sexes of "cream" morphs are shown on the right. All of these butter-
flies were killed within one hour after the wings hardened, and under shaded
conditions of the room.

STUDIES ON THE EVOLUTIONARY BIOLOGY
OF THE NEOTROPICAL NYMPHALID BUTTERFLY
ANARTIA FATIMA IN COSTA RICA

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ABSTRACT

Aspects of the biology of the familiar neotropical butterfly *Anartia fatima* (Nymphalidae: Nymphalinae) were studied both in the field and laboratory in Costa Rica. Life stages, behavior of immatures, and larval host plants are described. Oviposition was observed on two different species of Acanthaceae, although larvae are able to survive on only one of these in both the field and laboratory. Teneral adult butterflies of both sexes occur in one of two color morphs, "yellow" and "cream", with respect to the color of the prominent band on the dorsal surface of the wings. Previous field studies of this butterfly have centered upon the origin and possible adaptive role of a color polymorphism in natural populations. Emmel (1972) argued that the polymorphism is genetic, with adaptive value to climatic and other ecological factors. Taylor (1973) demonstrated that "cream" and "white" morphs in natural populations can result from the fading of "yellow" individuals, indicating that the polymorphism is partially nongenetic. Our data demonstrate that both genetic and environmental factors determine the polymorphism in this butterfly.

INTRODUCTION

During the past few years, the neotropical butterfly *Anartia fatima* (Lepidoptera: Nymphalidae, Nymphalinae) has become a focus of ecological and genetic research (Young, 1972a; Emmel, 1972, 1973; Taylor, 1973). The reasons for this interest are: (1) this butterfly is probably an extremely successful colonizing species of young secondary tropical habitats, and (2) more than one morph (dorsal wing band coloration) occurs in local populations. In fact, the origin and adaptive role of an apparent polymorphism in the color of the dorsal wing band (see Fig. 1 in Emmel, 1972) has become a controversy: Emmel originally argued (Emmel, 1972) that the two color morphs, "white" and "yellow", were genetic in origin, while Taylor (1973) demonstrated that yellow morphs can fade to white, thus attributing the polymorphism to environmental rather than genetic factors. Emmel (1973) subsequently reported additional data in support of a genetic origin of the polymorphism, which included some unpublished observations (Allen M. Young) of several morphs appearing from pupae.

In this paper, we continue to explore the nature of the dorsal band polymorphism, and provide new information related to the ability of this butterfly to be a colonizing species. On the

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latter topic, we deal primarily with interactions of this butterfly with its larval food plants at one locality in Costa Rica, the tropical region where the previous studies of this butterfly were conducted.

MATERIALS AND METHODS

Our studies cover four major categories: (1) laboratory studies on the description of the early stages, with estimation of developmental time under partially-controlled environmental conditions; (2) laboratory studies on the occurrence of wing-color morphs emerging from pupae when at least the morph color of one parent (the female) at oviposition is known in many instances; (3) field studies of oviposition as related to accuracy of egg-laying and the distribution of eggs in the habitat on correct and erroneous food substrates; (4) a capture-mark-recapture field study of one population designed to determine rates of fading in various morphs and the estimation of population dispersal. Under (3), these field studies included searches for eggs of *A. fatima* on potential food plants in San José (Los Yoses) study lots.

The early stages of *A. fatima* were observed but not described in a previous laboratory study (Young, 1972a), studied but not published by Alberto Muyshondt in San Salvador, and studied anew here. We employed two techniques to study the life cycle: eggs, after being retrieved in the field by observing females ovipositing were confined to either a tightly-closed clear plastic bag together with clippings of the food plant, or placed in small ice cream cups loosely sealed along with fresh pieces of the food plant. The eggs used in these studies came from three localities in Costa Rica: (1) twelve were obtained by A. Young in a pasture adjacent to the "Barranca site" (Orians, 1969) in lowland Guanacaste Province on February 4, 1975; (2) approximately 400 eggs were collected in an abandoned pasture on Finca El Uno near La Virgen de Sarapiqui (lowland Heredia Province) by Janice Iverson and Nancy Maxwell during March, 1975; (3) about 60 eggs were collected from a vacant lot in the San José suburb Los Yoses by D. Stein during March 1975. Thus, eggs were taken from three different populations of this butterfly during the dry season. The eggs collected by Stein, Maxwell, and Iverson were reared in ice cream cups in San José, while those of Young were reared in tightly sealed plastic bags. Due to problems with rearing immature stages in the laboratory, substantial mortality occurred so that the developmental time data was estimated from less than forty individuals. Rearing conditions included a room temperature of about 70°C. Air temperature and humidity within the sealed bags

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were less controllable. In general, the cups and bags were kept free of feces and old plant material. Containers were marked when the color morph of at least one parent was known, to detect any correlation in morphs among the progeny upon their ecolosion from pupae. Freshly-eclosed adults obtained in the laboratory were scored for sex and color of the dorsal wing band, as "yellow", "cream", or "white". These categories were based on our recognition in the field of these three color morphs.

The field studies of oviposition as related to food plant cover were conducted primarily in two "study lots" (here termed "A" and "B") in Los Yoses within San José (Figs. 1 and 2). These small lots were on opposite sides of a street about 200 meters from the offices of both The Organization for Tropical Studies, Inc., and The Associated Colleges of the Midwest. A search was initially made for all plants that A. fatima used for oviposition in both lots; subsequently, the density and spatial distribution of these plants were established, followed by censuses on February 25 and April 7, 1975 for eggs on these plants. Searches for eggs included scoring of egg shells left behind by first instar larvae. Measurements were made on the heights of plants where eggs were found. Additional notes were made on the morphological features of the plants, and pressed specimens were eventually identified with the assistance of the Museo Nacional de Costa Rica. Locations of individual eggs on these plants were noted in the field.
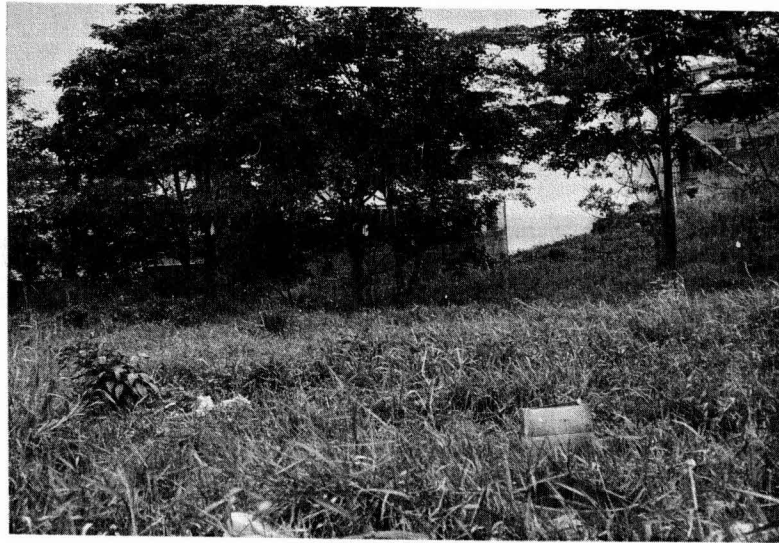

Figure 1. The "Site A" study area for *Anartia fatima* in the Los Yoses section of San José, Costa Rica. This is the larger of the two adjacent vacant lots where the butterfly was studied (March 1975).
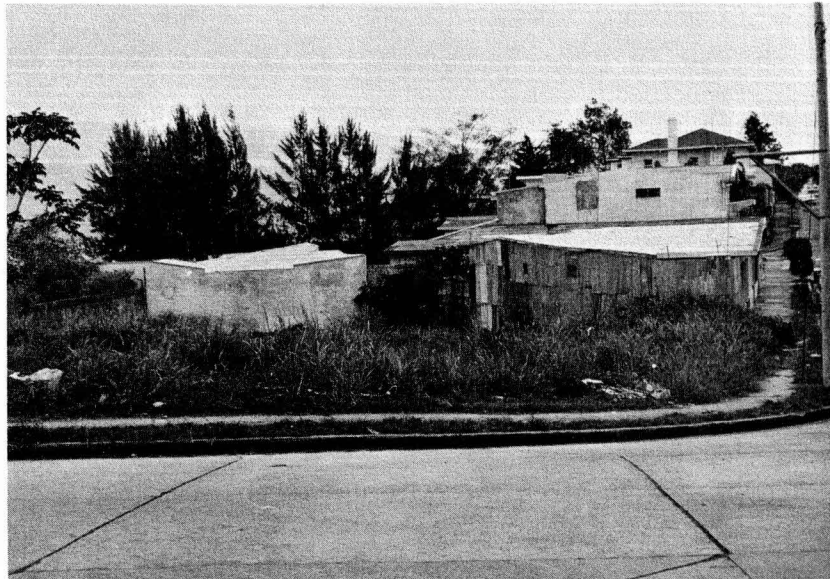
Figure 2. The "Site B" study area in Los Yoses. This site is just across the street (to the right) from "Site A", and considerably smaller.

A capture-mark-recapture analysis of wing color fading was conducted by D. Stein in study lot A at Los Yoses from February 24 through March 25, 1975. About every other day, usually in the morning, several hours were spent capturing butterflies, painting a code symbol on the wing, and followed by releasing them immediately. On these same days, recaptures of previously-marked butterflies were made. For each butterfly initially marked, the color morph (yellow, cream, or white) and wing condition (fresh, worn, or questionable) were recorded. The states of the same characteristics were scored for all recaptures.

A second capture-mark-recapture study was conducted at La Virgen by Janice Iverson between February 18 and March 8, 1975. This study was conducted in an abandoned pasture divided into four quadrants (each 20 x 20m) for estimation of individual movement over several days. On each day butterflies from one of the four quadrants were captured and marked. Each butterfly was scored for color morph, wing condition, and sex; butterflies from different quadrants were marked with a different color of enamel-base paint. Unlike Stein's study, this experiment attempted to assess movement of the butterflies in addition to changes in wing coloration with age.

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During February, 1975, members of the Organization for Tropical Studies, Inc. (O.T.S.) course, "Fundamentals of Tropical Biology", conducted a capture-mark-release study of *A. fatima* in a four-hectare area at Finca La Selva, another premontane tropical wet forest locality situated about ten km from the Tirimbina study site. This study involved the census of the adult population four times at about two-day intervals within the period February 5-12, 1975. As in our studies, it examined individual dispersal, and the existence of a positive correlation between individual age and wing band color (yellow, cream, white). The results of the O.T.S. study are used in this report for comparison with our data on similar studies.

RESULTS

Habitat, Oviposition Plants, and Larval Food Plant

In the study lots at Los Yoses, *A. fatima* lays its eggs on two different Acanthaceae (Fig. 3), *Blechum brownei* and *Dicliptera unquiculata*, both of which are weedy species of abandoned lots in the Meseta Central. At the time of the study, *B. brownei* was shorter, greener, less common, more delicate, and in flower. Study lot "A" contained far more *D. unquiculata* than *B. brownei*, with the reverse being true for study lot "B" (Table 1). In study lot "B" (Fig. 2) there was far less of either plant species, with about 5-10% of this field covered by both species; in contrast, study lot "A" (Fig. 1) was about 25% covered by both species.
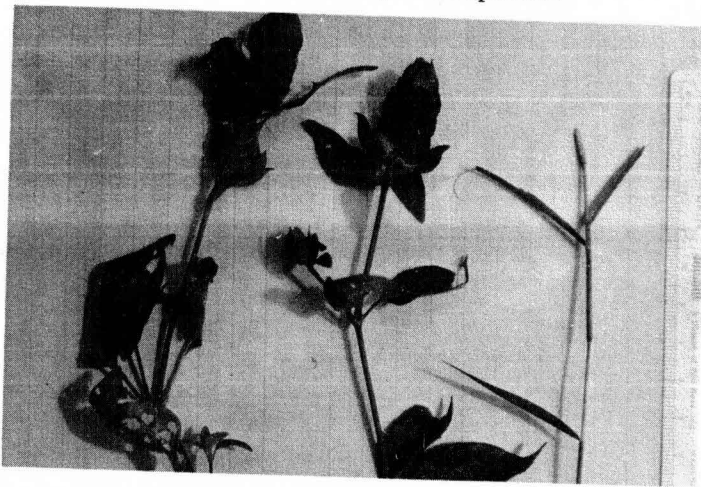

Figure 3. A larval host plant of *A. fatima*, *Blechum brownei* (Acanthaceae), shown here with a specimen of grass to contrast the life form of the plant.

Table 1. A comparison of the relative abundances and heights of *Blechum brownei* and *Dicliptera unquiculata* (Acanthaceae) in study lots "A" and "B" in San Jose' (Los Yoses).

	Study Lot "A"		Study Lot "B"	
	Blechum brownei	*Dicliptera unq.*	*Blechum brownei*	*Dicliptera unq.*
Height (cm.)	9.8 cm.	22.5 cm.	8.0 cm.	15.0 cm.
Relat. Abundance (%)	31-36%	64-69%	73%	26%

Eggs are laid singly on the upright flower heads of either species (i.e., Fig. 4), but later in the Guanacaste dry season, the flower heads of *B. brownei* (*D. unquiculata* was not observed) turn brown (Fig. 5), probably excluding egg laying activity by *A. fatima* then. An egg is generally attached to the ventral side of the small leaflet within the flower head (Fig. 4), although if such a leaflet is bent down, the egg can be found on the dorsal side. Eggs have not been found on older leaves or stems lower down on either plant. Oviposition sites are virtually identical for both plant species. Females ready to lay eggs cruise low over the vegetation and apparently locate the oviposition plants by seeing the upright flower bracts. Unlike many butterfly species, the first instars of *A. fatima* usually do not devout the egg shell; the egg shell is left behind as a record of oviposition in addition to the eggs themselves. Sometimes several eggs can be found within a single flower bract, with individual eggs on different leaflets. Possibly the occurrence of multiple eggs on a flower bract signifies several isolated incidents of oviposition by different female butterflies.

It is interesting that the majority of eggs in study lots "A" and "B" were found on the most abundant of the two plants used for oviposition: in study lot "A", most eggs were found on *D. unquiculata* while in "B" most were found on *B. brownei* during the February-March census (Table 2). However, this pattern of oviposition was essentially reversed later in the dry season (Table 2).

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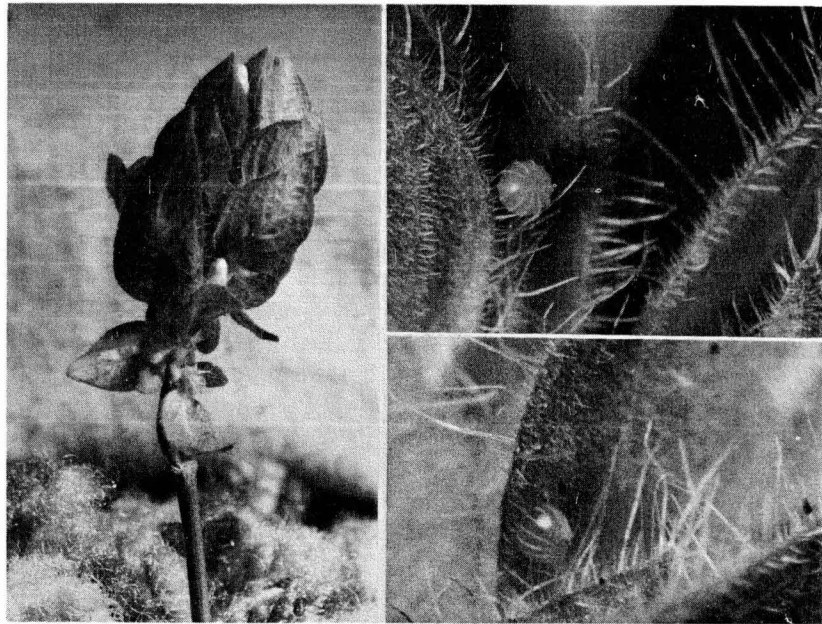
Figure 4. Left: Terminal bract of the larval host plant, *Blechum brownei* Acanthaceae), used by *Anartia fatima* in San José and at other localities in Costa Rica. Right: Two views of how the egg of *A. fatima* is positioned within the terminal leaflets of *B. brownei*. Note that an egg may rest within the fine hairs of the leaflet.

Figure 5. Dry, brown terminal bracts of *B. brownei* at Finca Taboga, Guanacaste Province, Costa Rica, near the end of the dry season (April 1975).

Table 2. Summaries of field searches for eggs of *Anartia fatima* on two Acanthaceae plants in San José (Los Yoses).

Date	Study Lot "A"		Study Lot "B"	
	Blechum brownei	*Dicliptera unq.*	*Blechum brownei*	*Dicliptera unq.*
Feb. 25 Mar. 3, 1975	3 eggs 1 egg shell (5.3%*)	55 eggs 7 egg shells (94.7%)	19 eggs 1 egg shell (66.6%)	8 eggs 2 egg shells (33.3%)
Apr. 7, 1975	54 eggs 45 egg shells (75.0%)	25 eggs 8 egg shells (25.0%)	9 eggs 19 egg shells (75.5%)	6 eggs 3 egg shells (24.5%)

*The percentage of total eggs discovered on both plants.

Although both of these acanthaceous plants are used for oviposition by *A. fatima*, first instar larvae die when they attempt to eat leaves of *D. unquiculata*. Ten first instar larvae were tested on *D. unquiculata* and an additional nine on *B. brownei*; all of the larvae on the former plant died within two days while all of the larvae on the latter plant survived through ecolosion. These results indicate that only *B. brownei* is a larval foodplant even though both this plant and *D. unquiculata* are oviposition plants for this butterfly in the same habitat. In field searches for larvae of any star, these insects have only been found on *B. brownei* and none have been seen on *D. unquiculata*. At both the Barranca site and La Virgen, the larval foodplant is *B. brownei* or a species very close to it (i.e., *B. pyramidatum*). A similar species of *Blechum* is a larval foodplant of this butterfly in several other regions of Costa Rica, i.e., Rosario de Grecia, Cañas, etc. In other parts of Central America, such as El Salvador, where there occur as many as 35 species of Acanthaceae, only five are used as larval food plants by *A. fatima* (A. Muyshondt, pers. comm). In Costa Rica, another nymphaline genus, *Victorina*, also exploits the same foodplants, and in El Salvador, *B. pyramidatum* is used not only by *A. fatima* but also several other butterflies, including *A. jatrophe*, *Victorina (Metamorpha; Siproeta) epaphus*, *V. (M.; S.) stelenes*, and *Precis (Junoia?) genovera* (A. Muyshondt, pers. comm.). As in Costa Rica, both *A. fatima* and *Victorina* (Young, 1972b; 1974) use *Justicia* (Acanthaceae) as larval foodplants (A. Muyshondt, pers. comm.).

A curious property of the oviposition behavior of *A. fatima* (Young, 1972a) is that the butterfly has the propensity of laying eggs on a wide variety of erroneous substrates, including dead twigs, moss, rocks, walls, dry leaves, logs, etc. Many times, the female butterfly acts as if she is going to lay an egg, but seldom does. We have seen eggs deposited on the erroneous substrates listed above, but often eggs are not laid although the female goes through virtually the entire behavioral sequence leading to deposition.

Life Cycle and Developmental Time

The green, spherical egg (Fig. 4) is small ($0.12mm^3$), ornamented with a series of whitish vertical grooves, and slightly flattened above. Females produce from a few hundred (200 — Young, 1972a) to several hundred (400) eggs during their lifetime. Probably, there is considerable variation in the total eggs produced by individual females within a population. An egg is usually attached to the tissue of a leaflet, but sometimes it sits loosely in hairs from a leaflet (Fig. 4).

The first instar larva (Fig. 6) has a shiny black head capsule and black body covered with light brown bristles that signify the positions of the scoli on future instars. This instar and often the next hide inside the terminal flower bract (Fig. 6) and feed there. There is no evidence of nest construction, rather the configuration of the leaflets (Fig. 4) provides a natural resting and feeding place for these younger (smaller) larvae. By the first molt, the larva is about four mm long. The second instar (Fig. 6) closely resembles the previous one, although behaviorally, they are found outside of the bracts as well as inside. It is with this stage that another behavioral trait of *A. fatima* caterpillars becomes very evident: when disturbed outside of the bract, the larva always drops to the ground immediately. This trait persists during the subsequent three instars. After dropping from a leaf, the larva remains in a curled position for several minutes before crawling away. As the second instar matures, the body becomes light brown although the head capsule remains shiny black. The scoli are apparent with this instar. The distribution and morphology of the scoli are extremely similar to those described by Young (1972b, 1973) for the larvae of *Victorina* (both species). By the second molt, the caterpillar is about eight mm long.

With the third instar (Fig. 6), the body becomes noticeably different from previous instars: (1) the head capsule is more heart-shaped than round (although still shiny black and still bearing the recurved head scoli appearing in the second instar); (2) the body is
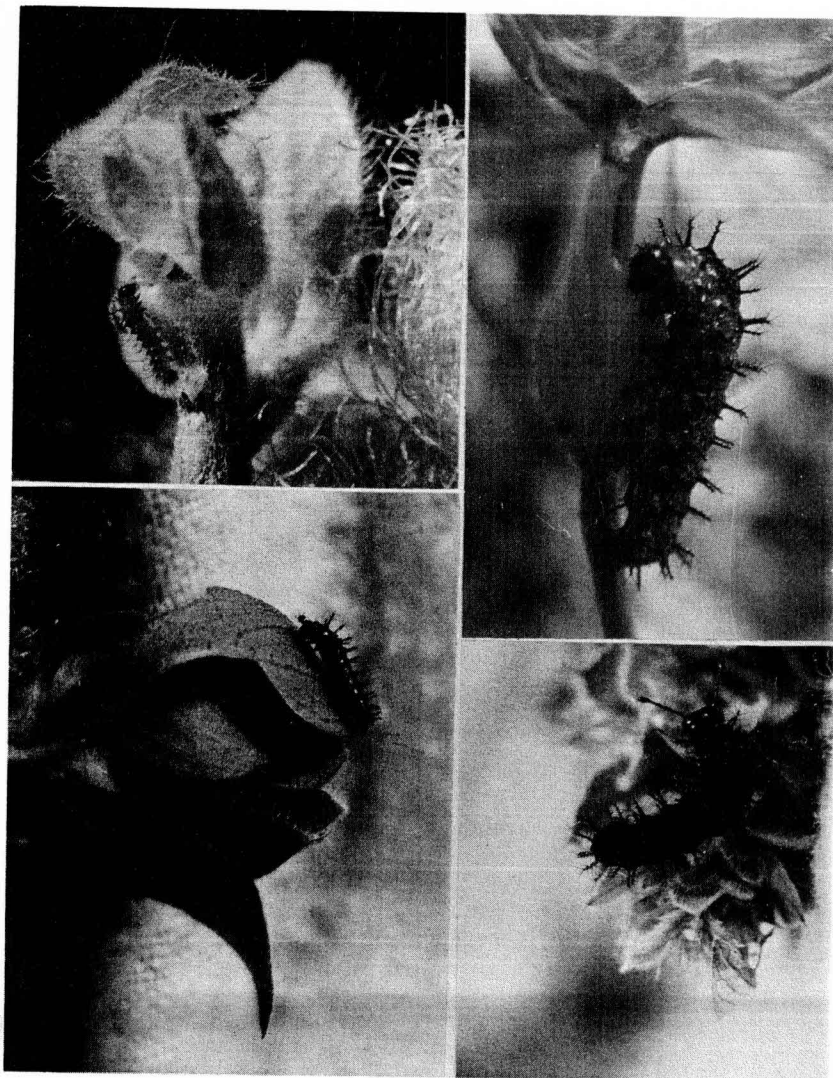
Figure 6. Life stages of *A. fatima.* Upper left: first instar; lower left: second instar, upper right: third instar; lower right: fourth instar.

orange-brown with the scoli remaining black or dark brown; (3) the body "glistens". The third instar rests on both dorsal and ventral sides of leaflets further down on the terminal bracts; they are wedged in between leaflets, presumably for hiding while not feeding. By the time of the third molt, the caterpillar is about 16 mm long.

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The fourth and fifth instars (Figs. 6-7) closely resemble each other. The branched, recurved, and clubbed conditions of the long head capsule scoli are very apparent with these instars, and there is a sizable reduction in the head capsule as compared to earlier instars. In the fourth instar, the general color hue of the body is dull greenish-brown; in the fifth, the body is velvety jet black with the scoli being dark blackish-brown. The head capsule, especially in the fifth instar, bears a vivid purplish reflection in bright light. The fourth instar is about 20 mm long by the fourth molt, and the fifth instar 24 mm long by the time of pupation.
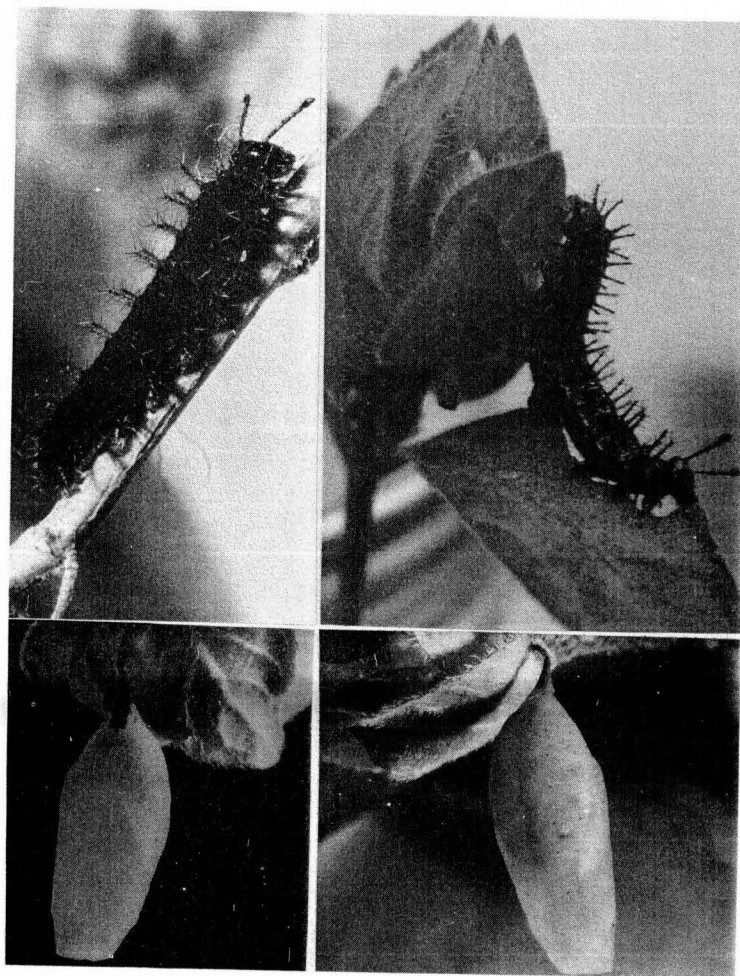

Figure 7. Life stages of *A. fatima*. Upper left: fifth instar resting; upper right: fifth instar feeding on the older leaf of *B. brownei*; lower left: pupa, ventral aspect; lower right: pupa, dorsal aspect.

As with both the egg and caterpillar stages of this butterfly, the pupa also bears an incredibly similar resemblance to the pupa of *Victorina* (compare Fig. 1-F in Young 1972 or Fig. 3-A in Young 1973 with Fig. 7 in this report). The similarities in the pupa between these two nymphaline genera concern color and profile, with the greatest difference being that the pupa of *Anartia* is smaller than that of *Victorina* (as with the other early stages). The pupa of *A. fatima* (Fig. 7) is about 15 mm long, six mm across the dorsal-ventral axis, and six mm across the left-right sides axis. The basic color is light green while the cremaster is pink ventrally but dull black dorsally. There is a complex system of tiny black dots distributed as follows: (1) supra- and sub-spiracular rows, with the latter being smaller; (2) medial doublet row dorsally on abdomen and the same size as the supra spiracular dots; (3) a tight quartet dorsally on the thorax; (4) one raised dot at the base of each forewing pad; (5) two or three faint reddish dots on each forewing pad. The head region is forked bluntly and the silk of the attachment "button" is reddish. The day prior to eclosion, the wing pads darken so that the dorsal wing band is clearly recognizable; this darkening is preceded by a general darkening of the body, beginning at the head. Mating behavior, including copulation (Figs. 8-9) has been observed in fresh adults.
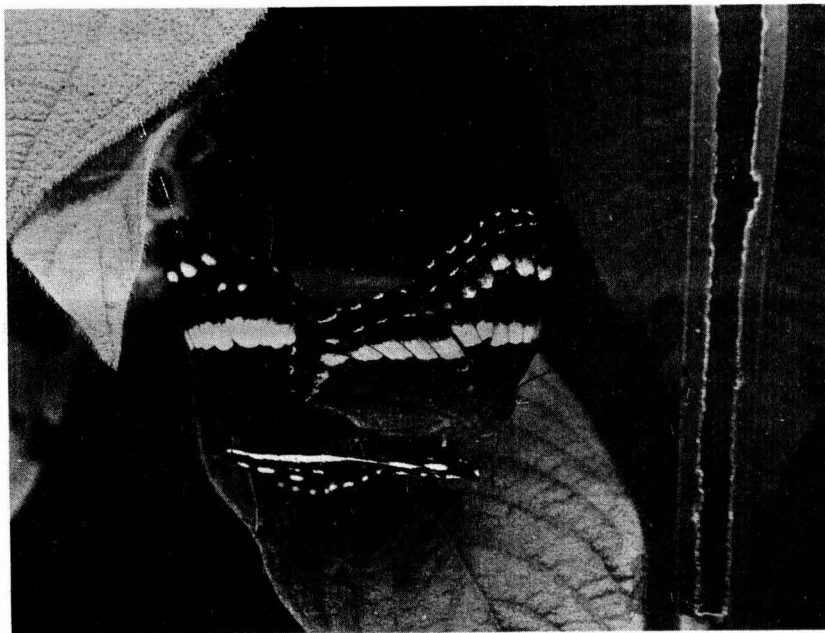

Figure 8. A copulating pair of *A. fatima* in the field at Finca La Tirimba, Heredia Province, Costa Rica (January 1975). The female ("white" morph) is on the left; the male is a "cream" morph.
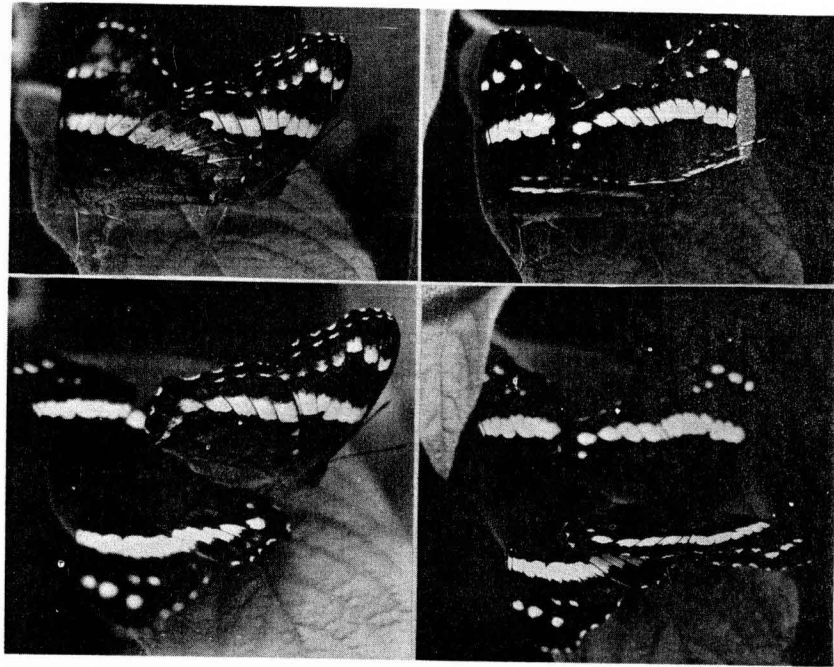
Figure 9. Wing movements during stationary copulation in *A. fatima* (the same pair as shown in Fig. 8). Although the pair remains perched in one spot for several minutes, there are periodic bursts of wing movement in both partners.

From a sample of less than 40 individuals, the developmental time can be summarized as follows under the laboratory conditions employed: (1) egg — 6 days; (2) caterpillar — 33-35 days; (3) pupa — 7-8 days. Thus, the total developmental time is about 46-49 days in the laboratory. No significant differences were found between individuals reared in ice cream cups and those reared in the plastic bags. Developmental time data under field conditions is not available, although we suspect that its accuracy or biological value would be no different than laboratory data since natural populations probably have different development times due to varying environmental conditions.

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Wing Band Color Morphs at Eclosion in the Laboratory

Upon eclosion, all adults obtained from pupae in the laboratory were examined for color of the dorsal wing band; some of these individuals were then killed and pinned immediately. They were then photographed in color. Two discrete color morphs exist at the moment of eclosion, regardless of whether the eggs initially came from Guanacaste, San José, or La Virgen; we call these two morphes "yellow" and "cream" (frontispiece). We also noted that on several "cream" butterflies, there were small, scattered patches of yellow, especially near the front border of the forewings. Also, "cream" butterflies were generally lighter brown than "yellow" butterflies. Both males and females may occur as either color morph. Both "cream" and "yellow" butterflies can be obtained from eggs deposited by either "yellow" or "white parents. As we did not discover any "white" butterflies in our admittedly small sample of freshly-eclosed adults, we conclude that the "white" phenotype does not occur at eclosion, but probably results from the fading of primarily "cream" individuals (see below). But it should be mentioned that even "cream" teneral butterflies often appear white in the field. Ourselves and others (O. R. Taylor, Jr.) have seen very fresh white butterflies that are probably cream individuals. Of course, it is always possible that truly white butterflies occur in very low frequency at the time of emergence. Table 3 summarizes the color morphs of parents (when at least one is known) and progeny. Multiple eggs obtained from a single "white" female produce both "cream" and "yellow" progeny, although sometimes one or the other morph was obtained from single females and not both. A "white" female seen mating with a "cream" male (Fig. 9) produced both "yellow" and "cream progeny (Table 3). It is not known if female A. fatima successfully mate more than once during their lifetime, but spermatophore counts by A. Young indicate single mating. Young (1972b) observed (as cited in Emmel, 1973) that three phenotypes occurred at eclosion with the third being called "white". Since these specimens were checked for color at various times after they were killed and pinned, the "white" butterflies possibly were really faded cream or yellows. As demonstrated below, "white" females (Table 3) are really only faded "yellow" or "cream" butterflies.

No careful examination of color morphs was made immediately at the time of eclosion in the previous study, thus shedding some doubt on the former impression (quotation from Young in Emmel, 1973) that there exists a "white" phenotype for freshly-eclosed adults. But Young's sample was small and if white butterflies occur in very low frequency, a small sample would not necessarily include them.

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those originally marked) fade to either "cream" or "white" within a few days. By comparing part ii of Table 5 with Table 4, it is clear that the ratio of "yellow" to "white" morphs in the population strongly shifted from predominantly "yellow" to predominantly "white" by the time of recaptures. This shift was not due to biased collecting (i.e., where "white" morphs were easier to recapture than "yellow" morphs), but to the fact that many yellow-banded butterflies became white-banded individuals through time due to fading. Field observations during the experiment revealed that butterflies faded from yellow to white, from yellow to cream, and from cream to white; butterflies did not change from white to cream or white to yellow. These results are similar to those obtained by Taylor (1973).

Table 4. Wing condition, color and changes with time in the San José (Los Yoses) population of *Anartia fatima.**

	Wing Condition:	Fresh	Worn	?	Σ
Wing Color (Y, C, W)		(i) No. captured butterflies including recaptures			
	Y	98	5	6	109
	C	13	3	6	22
	W	19	71	5	95
	?	0	0	2	2
	Σ	130	79	19	
		(ii) No. captured butterflies not including recaptures			
	Y	88	5	1	94
	C	11	0	1	12
	W	14	24	1	39
	?	0	0	0	0
	Σ	113	29	3	
		(iii) No. captured marked butterflies			
	Y	7	1	4	12
	C	1	3	4	8
	W	3	50	2	55
	?	0	0	2	2
	Σ	11	54	12	
		(iv) No. recaptured butterflies			
	Y	6	5	0	11
	C	1	6	0	7
	W	2	27	0	29
	?	0	0	0	
	Σ	9	38	0	

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Table 5. Corrected morph ratios* of recaptured butterflies by "unfading" the faded individuals to the morph they were originally scored as when they were first captured.

(i)   11 Yellow   +   12 Yellow   +   5 Yellow   =   28 "true"
      Recaptured   Faded to White   Faded to Cream   Yellow
      Butterflies   Butterflies   Butterflies   Recaptures

(ii) 7 Cream   −   5 Yellow   +   1 Cream   =   3 "true"
      Recaptured   Faded to Cream   Faded to White   Cream
      Butterflies   Butterflies   Butterfly   Recaptures

(iii) 29 White   −   12 Yellow   −   1 Cream   =   16 "true"
      Recaptured   Faded to White   Faded to White   White
      Butterflies   Butterflies   Butterfly   Recaptures

*See text

Table 5 corrects the color morph ratios of recaptured butter-flies by "unfading" the faded individuals to the morph they were originally scored as when they were first captured. Thus the 18 individuals in Table 6 that were recaptured as "cream" or "white" butterflies, are "unfaded" to the yellow and cream morphs that they were scored as when originally marked before fading took place. This "unfading" is performed so that all butterflies can be referred to by the color morph they were originally scored as. But these data (Table 5) do not note individuals that possibly faded before they were originally captured and scored. This prevents accurate assessment of the polymorphism unless even further mani-pulations are made. In summary, 17 out of 38 marked recaptured yellow butterflies faded while one out of three recaptured cream butterflies faded (results of Tables 5 and 6). The fastest recorded fading from yellow to cream took two days; the fastest fading from yellow to cream took two days; the fastest fading from yel-low to white took three days. These are the fastest recorded fadings. Taylor (1973) found that it took four days for butterflies to fade from yellow to white in direct sunlight.

Eleven of the 28 recaptures did not fade. Probably, this is because the less than 5 day interval before recapture was not long enough for fading to occur. Probably, all yellow butterflies, given enough time, at least five or more days, will fade to white.

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Table 6. Fading (of wing band) tendencies in the marked population of *Anartia fatima* in San José (Los Yoses)*.

From the data in cases ii and iv in Table 3. We have:

(a) 12 butterflies faded from yellow to white

(b) 5 butterflies faded from yellow to cream

(c) 1 butterfly faded from cream to white

*See text for details

Our findings on the fading of yellow butterflies to white as they age agree with the data obtained by the O.T.S. group at La Selva. The results of their survey, given in Table 7, show that 77% of young individuals captured (fresh) had yellow wing-band coloration. Furthermore, about 70% of the intermediate age individuals had cream wing-bands (creme), and 76% of old individuals had white wing-bands (Table 7). There is a strong positive correlation between age of the individual and wing-band coloration, as indicated also by our findings. The La Selva group also found that 32 individuals changed wing-band color during the seven-day study period: seven changed from "yellow-fresh" to "creme-intermediate" and another seven changed from "creme-intermediate" to "white old". The remaining individuals changed age, class and color in different combinations, but there were no cases of individuals changing from white to another color, or creme individuals becoming yellow. These findings support our results.

Color Morphs and Dispersal in the La Virgen Population

Of the 226 butterflies originally marked from the four quadrants, there were 44 or about 13% recaptures. Out of these, 17 butterflies exhibited some color change from fading from yellow or cream to lighter shades and white. The shortest time for a yellow butterfly to become white was three days. There was considerable movement of marked butterflies among the quadrants: twenty of the 41 recaptures were recaptured in a quadrant different than the one in which they were marked. Furthermore, only 75 butterflies were marked outside of the quadrants. Of

Table 7. Population census results for wing-band color and age in *Anartia fatima* at Finca La Selva, Heredia Province, Costa Rica.*

Age Class	Census Dates	"Yellow"			"Cream"			"White"		
		Recaptures	New	Total	Recaptures	New	Total	Recaptures	New	Total
Fresh	Feb. 5	—	19	19	—	9	9	—	1	1
	7	1	18	19	0	1	1	0	0	0
	10	1	12	13	0	3	3	0	0	0
	12	0	16	16	1	5	6	0	0	0
Total		2	65	67	1	18	19	0	1	1
Intermediate	5	—	3	3	—	23	23	—	8	8
	7	0	3	3	8	5	13	1	3	4
	10	4	1	5	6	8	14	0	2	2
	12	2	0	2	15	3	18	1	1	2
Total		6	7	13	29	39	68	2	14	16
Old	5	—	0	0	—	6	6	—	20	20
	7	0	0	0	7	1	8	11	3	14
	10	0	0	0	4	1	5	10	3	13
	12	0	0	0	3	0	3	20	3	23
Total		0	0	0	14	8	22	41	29	70

*Data gathered by students in Organization for Tropical Studies, Inc. course, "Fundamentals of Tropical Biology (January-February 1975 section).

these, two were recaptured within the quadrants. We postulate, therefore, that *A. fatima* is a highly mobile species; future studies over larger areas of tropical habitats are needed to prove this. Also, individual movement in different populations can be very different. For example, some studies (unpublished) have shown that there is little movement of *A. fatima*, and that yellow butterflies tend to move about more than white butterflies (O. R. Taylor, Jr., pers. comm).

In support of this is the finding by the O.T.S. La Selva study group that, out of a total of 276 male butterflies captured during the study period, 95 were captured at least twice. This result of about 38% recapture for male *A. fatima* is higher than our findings, even though the O.T.S. group sampled a larger area of habitat. Our data lumps sexes together, and since females are probably more mobile than males, combining the sexes would tend to lower the recapture estimate figure, even though females might be less abundant than males in a population. The O.T.S. group found that females comprised only 17% of the total adult population. If females were more abundant in our Tirimbina population, this would lower the recapture figure considerably. It was also found that as the recapture population aged, there were fewer recaptures of yellow butterflies even though new captures included a high percentage of these individuals (Table 7). This suggests that yellow individuals tend to move about more than older butterflies, with new captures of yellow butterflies resulting from immigration into the study area and births (eclosions) within the study area.

DISCUSSION

All butterflies species must: (1) locate suitable larval food plants in the habitat, (2) have suitable adult food sources, and (3) escape predators, parasites, and other sources of mortality.

Oviposition and Larval Food Plant Exploitation Patterns

Anartia fatima is a mobile species found primarily in secondary tropical habitats. It appears to be well adjusted to such a habitat by having high fecundities. However, local populations probably have high mortality due to eggs being deposited on a food plant that the caterpillars do not eat. Since our observations were made during one part of the dry season, we need similar field observations for the wet season to see if this pattern is generally

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true throughout the year at this locality. Possibly, seasonal changes in the two oviposition plants lead to changes in the oviposition pattern. The butterfly early in the dry season lays most of its eggs on the more abundant plant species, but the shift later in the dry season may be due to a physiological response of the plants so that the preference is switched.

Singer (1971) noted that the butterfly *Euphydryas editha* in one population lays most of its eggs on one plant, but the caterpillars feed on a second plant species of a different family. Singer referred to the second larval food plant as a "cryptic resource". This could be an example of how a plant in a special ecological niche can be protected from predation (by larvae) through the co-occurrence of another food plant in the same habitat. In such cases, a female butterfly may be confused by plant distribution with which she is unfamiliar, and mistakenly lay her eggs on this wrong plant. This might be the case with *A. fatima* in the Los Yoses area where the confusion is apparently between two similar-appearing species of Acanthaceae. In most other Costa Rican localities, the correct food plant occurs by itself so that the situation in Los Yoses might be an unusual case of co-occurrence.

An alternative explanation for abundant oviposition on the wrong plant could be that this plant is evolving faster than its predators in a "coevolutionary race". A plant under severe predation pressures may have developed a secondary compound defense system that the butterfly has not been able to detoxify. Thus, there could continue to be oviposition on this plant without the butterfly realizing that its progeny will die. Probably, this alternative is weak since: (1) predation pressures in the field seemed to be very low, and (2) oviposition on *D. unquiculata* is probably rate so that it is unlikely that this plant would develop a secondary compound.

Still another explanation concerns the ability of *A. fatima* to colonize new secondary tropical habitats. Certain population characteristics of this butterfly in Costa Rica (see Young, 1972a) suggest that it is a colonizing species. Part of the colonizing "strategy" for this butterfly might involve attempts to enter new larval food plant niches; i.e., instances where the butterfly lays eggs on a different plant than the one usually used for oviposition and larval development. Especially for a plant in the same family, these are attempts for the species to take over a new niche for caterpillars. Until further field studies are conducted, we cannot distinguish whether or not *A. fatima* is a careless (passive) or gambling (active) colonizer, attempting to use *D. unquiculata* as a new larval resource, in addition to the usual *B. brownei.* Depending upon gene-

tic and physiological flexibility among different phenotypes, the butterfly might eventually enter into this new niche, despite the apparently high cost of selection operating at the present time.

The oviposition strategy of *A. fatima* involves the behavioral responses of females to the "attractive" features of potential plants used for oviposition. Several environmental factors might influence how *A. fatima* select their oviposition plants in Los Yoses. For example, the female prefers a patch of food plant rather than an isolated plant; most eggs were found on one or several plants located in a clump of Acanthaecae. This suggests as Singer (1972) observed with *E. editha* that the first cue an egg-laying female looks for is a sizable patch of green. Furthermore, the female prefers a more accessible food plant. Where tall and short food plants were intermingled in the Los Yoses study lots, the egg would often be found on the lowest accessible part of the taller food plant. When tall *D. unquiculata* was mingled with short *B. brownei*, the eggs were more commonly found on the former plants. Though the butterfly might detect that *B. brownei* was the right food plant for the caterpillars, because it was often harder to get to, eggs were laid on *D. unquiculata* anyway. Finally, females preferred fresher, moister individual plants. This may explain the apparent shift in egg distribution from *D. unquiculata* to *B. brownei;* i.e., a shift to the plant on which caterpillars would survive. At the time of the second field census of eggs, the dry season had advanced considerably and many individuals of *D. unquiculata* had become very dry and tough. But *B. brownei*, if anything, had gotten much taller with leaves remaining fresh. This was curious since *D. unquiculata* appeared to be the hardier plant — the plant better adapted to survive the dry season. It was not a physiological weakness that accounted for *D. unquiculata* drying up, but its location, for the most part, in sunnier (exposed) areas of the lots. Thus there probably is a seasonal trading off between the two plants in terms of their relative attractiveness for oviposition by *A. fatima.*

In tropical regions with a very pronounced and long dry season, such as lowland Guanacaste Province, the adaptive strategy of *A. fatima* in terms of both oviposition and larval development appears to be that of "holding on" as long as possible. For example, early in the Guanacaste dry season (February 1975), *B. brownei* was observed to be still lush; there was considerable activity by *A. fatima*, with many eggs being oviposited. But by May, the food plant had turned brown and no butterflies were seen in the area. It seems that the butterfly continues to breed here until the food plant dries up. At this time, there might exist a reduced "refugium" adult population that survives until the next

wet season, or else, larger caterpillars and pupae might go into a diapause until the rains begin. There is also evidence that adults go into a reproductive diapause during the Guanacaste dry season, and some adults presumably migrate to other areas (O. R. Taylor, Jr., pers. comm.). It seems that this environment is harsh on the butterfly in the sense that adult lifespan and reproduction might be greatly reduced. On the other hand, it may be argued that the severe initial rains of both this region and that of the tropical wet lowlands provide a different form of environmental stress by causing outright mortality of many adult butterflies.

General Biology

One of the most outstanding discoveries of the early stages of *A. fatima* is the remarkable morphological resemblance of egg, caterpillar, and pupa stages to those of another neotropical nymphaline genus, *Victorina (Metamorpha*, Siproeta). Owing to these striking similarities, at least at the gross morphological level (see Young, 1972a, 1973), we suggest that there might exist a close phylogenetic relationship between *Anartia* and *Victorina*; we base this idea from our knowledge of the early stages, and also from the fact that members of both genera are strictly feeders of Acanthaceae during the larval stage. Other similarities are oviposition site-preference for the apical tissues of Acanthaceae, and similar behavioral traits of the caterpillars. Seitz (1913) lists both genera together and gives some information on the early stages. But phylogenetic relationships have not been adequately assessed. Members of both genera occur together in the same secondary habitats in various regions of Central America. Therefore, on morphological, behavioral, and ecological levels of adaptation, the genera are quite similar. We have yet to determine the ecological relationship of *A. fatima* with *A. jatrophe* in Costa Rica, although we know that both species often co-occur in the same habitats. One of us, A. Young, is planning a field study of the geographical distributions and comparative ecology of these two species in Costa Rica.

Assuming there exists a close evolutionary relationship between the two genera (in the sense that they diverged from a common ancestor), it is further interesting that species of both genera are highly palatable in the adult stage to avian predators in the laboratory (Brower and Brower, 1964). Also note that the larval and pupal stages of *Anartia*, like those of *Victorina*, are very likely cryptically colored to potential predators that hunt with color vision; either the food plants are low in chemical defense systems or the caterpillars lack the detoxification mechanisms to handle the secondary compounds that could render them unpalatable otherwise.

Wing Color Band Variation in Natural Populations

What can be stated definitely regarding the occurrence of yellow, cream, and white-banded butterflies in natural populations? Our data on ecolosion of morphs in the laboratory shows that the cream and yellow forms have a genetic basis. As suggested by Taylor (1973), we qualify this by adding that the discrete nature of the two morphs is questionable since we have seen freshly eclosed adults that appeared cream but with flecks of deep yellow within the band. Other than a usual case of genetic polymorphism (Emmel, 1972), we cannot rule out the possibility that this is a case of gene penetrance with variation that may be continuous in nature; our present sample is too small to bracket the extent of this variation. A closer look at the genetics of the band color is needed.

We have also noted that conditions, such as time of day, degree of cloudiness, whether the butterfly was in direct sunlight, shade, or indoors, change the perceived color of the morph. Accurately scoring butterflies in the field is always a problem. In Emmel's study, we suggest that his scoring of white morphs were really either faded yellow or cream morphs, as our data show that white is not a phenotype present at eclosion, but rather a result of fading — something implicit in Taylor (1973). Thus, the existence of two general morph patterns (with some variation yet to be quantified) at eclosion and the fading of these during subsequent days of life for adult butterflies, results in a complex spectrum of color morphs in natural populations. Unlike the clarity of the adaptive significance of the color morphs implied by Emmel (1972; 1973), it now appears that the question of adaptive role of morph variation must be approached very differently. Given the apparent spectrum of morph variation at birth and subsequently, we suspect that there is likely very little significance attached to the existence of this variation. For example, it is difficult to attach significance to an argument of preferential male-approach behavior in natural populations. Emmel (1972) discusses the preference of both yellow and white males for white females. The argument implies selection against yellow females. From our findings, the argument can no longer be applied since both white males and females are either yellow or cream individuals, genetically or developmentally! We wish, therefore, to advance the suggestion, for future study, that the existence of color band morphs in *A. fatima*, rather than representing a polymorphism that is balanced (Emmel, 1972), is a complex interaction of genetic or developmental effects coupled with environmental factors affecting caterpillars (e.g. humidity, host plants, etc.). Further field study of the courtship behavior of *A. fatima*

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should focus on the issue of mate selection rather than on approaches of mates to females: females of this species might select their mates, as is the case for most butterflies (e.g., Taylor 1972).

Natural populations, as shown from our mark-recapture data and other studies, contain many fresh yellow butterflies and many worn white butterflies, but few of anything else. We first attributed this to possible behavioral differences between the two morphs, i.e., freshly eclosed yellows were more active fliers and tended to emigrate more, and that whites were less active and tended to stray in a given field (lot) to become worn. Yellows do seem to be more active fliers; this is probably not due to an evolutionarily selected advantage of the yellow morph, but to being younger butterflies and whites, the older ones. And while it is clear that white morphs result from the environmentally induced fading of yellow and cream morphs, it may seem puzzling at first as to why behavioral differences should exist between yellow and white morphs, if the latter are only faded yellows or creams. Both Emmel (1972) and Taylor (1973) found that the white female is preferred by almost two to one by males in approach flights. White morphs came out earlier in the morning, yellows came out later and remained active longer. We have found that yellows are faster fliers and more difficult to catch. How can these behavioral differences be explained if the white morph is only a faded yellow or cream individual? The answer very likely lies in the strong correlation between yellow and young individuals, and white and older individuals. The terms "white" and "old" or "worn" are essentially interchangeable. Thus behavioral differences that may casually be explained as differences associated with different morphs of the same butterfly species, may also, and we propose more correctly, be explained as to differences associated with different age classes of the butterflies. Extending this reasoning to Emmel's suggestion that the yellow morph is the more hardier morph, we suggest that he is really saying that younger butterflies are hardier than older ones.

Both Emmel and Taylor reported that the yellow band of *A. fatima* absorbs ultraviolet (UV) light while the white band reflects it (Taylor also found that cream reflects UV light but less so than white — suggesting a continuum). Since the butterfly's eye is sensitive to UV images, the different ways the yellow and white bands react to UV light probably acts as an important mechanism for the butterflies to distinguish between the two morphs, especially in approaches of males to females. This may be important in explaining why white was found to be the preferred morph in approaches to females. At first it seems a wasteful mechanism for the older white females to be preferred in approaches over the

younger yellows because since females probably only mate once (Emmel, 1972), a male would have a better chance of successfully mating with a younger yellow than an older white. This assumes, however, that approaches by males to females result in mating; this may not be the case if, in fact, females are mated even before they fly (Emmel,1972). But males attempt to approach most butterflies they see (including males), and since most females in a population have already been mated and males constitute at least half the population (our pers. data), there is no shortage of interested males to approach any female in the population. What is important is not that every male gets an opportunity to make approaches, but that every female is able to be mated if approaches result in mating. It is unlikely that any *A. fatima* females of either color morph goes unmated. The preference of white females is probably just an unintentional consequence of the fading process. Emmel (1973), in his response to Taylor (1973) said he did not see how it could be possible that a negative absorptive UV image (associated with yellow) could fade to a positive reflective UV image (associated with white). He was implying that Taylor's fading data was weak, and this was another reason why fading could not take place (due to the face that no mechanism was known for UV fading). But as we now see that the fading does occur, it does not seem unlikely that the UV images could fade as well. Thus the reason why faded white females are preferred in mating is because they have the attractive UV band on their wings. In other words, it is not that males are showing preference for older (white) butterflies, but that they are cueing in on the reflective UV band that exists only on faded white (older) butterflies. All of this suggests that it is likely unadaptive for males to pursue males or females that are UV positive when neither are likely to be receptive. Thus a reasonable argument, given the data at hand, is that males maximize their mating fitness if they pursue any object which bears a resemblance to a UV negative female, and this includes males and thus lots of "homocourtships".

In light of these findings, the question of what makes a given population of *A. fatima* predominantly yellow or white must be re-examined. Rather than approaching this question in terms of the genetics of color morphs as Emmel (1972) did, the question has to be approached in terms of age-structure of the adult population (since color morphs correlate with age). Butterflies remain for five days or less before fading in nature. The average butterfly in nature lives for about three or four weeks (Gard Otis pers. comm.), despite higher longevity observed in captivity (Young, 1972a). Thus an *Anartia* butterfly lives about five days as a yellow, and about two or three weeks as a white butterfly, if it lives that long. Therefore, the younger the adult population, the greater

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the number of yellows; the older the population, the greater the number of whites. We suggest the following list of factors that could affect the morph ratio of an *A. fatima* population in Costa Rica:

YELLOW POPULATION (young)	WHITE POPULATION (older)
low survivorship	high survivorship
high fecundity (larger clutch)	low fecundity (smaller clutch)
wet, fairly non-seasonal envt.	dry season severe
exposed habitats	sheltered habitats
high predation rates	low predation rates
newly colonized habitat	population in stable habitat

Under the above scheme, we have an alternative explanation as to why Emmel (1972) found predominantly yellow *A. fatima* adult populations in tropical lowland environments and predominantly white adult population of the butterfly in highland regions of Costa Rica. The tropical wet lowland environment is harsh to species in the sense of heavy rains (known to kill *Parides* butterflies in Trinidad — Cook, Frank, and Brower, 1972), higher daily temperatures with greater fluctuation in the diurnal cycle, and perhaps a greater density of predators on immatures and adult butterflies. The greater insularity of highland tropical regions, less temperature fluctuations, and reduced seasonality might promote greater longevity. The lowland tropical dry environment (Guanacaste) might also be harsh due to strong seasonality and a greater paucity of suitable habitats owing to intense agriculture and ranching. Although such a generalization appears attractive, it must be considered that in any region, there exists many habitats and micro-habitats that superimpose tremendous complexity upon our synthesis.

ACKNOWLEDGEMENTS

LITERATURE CITED

Brower, L. P., and J. V. Z. Brower. 1964. Birds, butterflies, and plant poisons: a study in ecological chemistry. Zoologica 49: 137-159.

Cook, L. M. K. Frank, and L. P. Brower. 1971. Experiments on the demography of tropical butterflies. I. Survival rate and density in two species of *Parides*. Biotropica 3: 17-20.

Emmel, T. C. 1972. Mate selection and balanced polymorphism in the tropical nympahlid butterfly, *Anartia fatima*. Evolution 26: 96-107.

Emmel, T. C. 1973. Reply to Taylor on *Anartia fatima*. Evolution 27: 164-165.

Orians, G. H. 1969. The number of bird species in some tropical forests. Ecology 50: 783-801.

Seitz, A. (ed.) 1913. Macrolepidoptera of the world. Vol. 5. The American Rhopalocera. Stuttgart: A. Kernan Verlag, 1143 pp.

Singer, M. C. 1971. Evolution of food-plant preference in the butterfly *Euphydryas editha*. Evolution 25: 383-389.

Singer, M. C. 1972. Complex components of habitat suitability within a butterfly colony. Science 173: 75-77.

Taylor, O. R., Jr. 1972. Random vs. non-random mating in the sulfer butterflies, *Colias eurytheme* and *Colias philodice* (Lepidoptera: Pieridae). Evolution 26: 344-356.

Taylor, O. R., Jr. 1973. A non-genetic "polymorphism" in *Anartia fatima* (Lepidoptera: Nymphalidae). Evolution 27: 161-174.

Young, A. M. 1972a. Breeding success and survivorship in some tropical butterflies. Oikos 23: 318-326.

Young, A. M. 1972b. The ecology and ethology of the tropical nymphaline butterfly, *Victorina epaphus*. I. Life cycle and natural history. J. Lep. Soc. 26: 155-170.

Young, A. M. 1973. Ecological studies of the butterfly *Victorina stelenes* (Lepidoptera: Nymphalidae) in Costa Rica and El Salvador. Stud. Neotrop. Fauna 8: 155-176.