

## **Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest**

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**Abstract.** 1) Paired traps showed that fruit-feeding nymphalid butterflies in the subfamilies Nymphalinae, Charaxinae, Morphinae and Satyrinae are stratified between the canopy and the understory by species composition, and abundance, size, and color pattern. 2) Short wing lengths and uniform underside patterns are found in the canopy, whereas long wing lengths and underside patterns bearing eyespots are found in the understory. 3) Wing length and color pattern cannot be separated from taxonomic affinity, and hence, these butterflies stratify by subfamily: Charaxinae and Nymphalinae in the canopy, Morphinae and Satyrinae in the understory. 4) A general model is presented to explain the apparent breakdown of stratification along forest edges and how light levels act as barriers to maintain insect stratification.

### **Introduction**

The tropical rainforest has been described in terms of component layers or strata (Richards, 1966), and stratification (i.e. vertical distribution) of rainforest organisms has been documented for mammals and birds (Allee, 1926; Dunn et al., 1968; Orians, 1969; Pearson, 1971), and for insects (Bates, 1944, 1947; Corbet, 1961a & b; Davis, 1944; Elton, 1973, 1975; Erwin, 1983; Erwin & Scott, 1980; Garnham et al., 1946; Galino et al., 1951; Haddow, 1945; Haddow & Corbet, 1961a; Jackson, 1961; Papageorgies, 1975; Pittendrigh, 1950a & b; Rees, 1984; Snow, 1955; Sutton, 1979, 1984; Sutton & Hudson, 1980; Wolda, 1979).

Studies on the stratification of insects other than mosquitos range from general overviews of all insect taxa taken in a sample (Elton, 1973; Sutton, 1984; Sutton & Hudson, 1980) to comments on a few taxa within a sample (Corbet, 1961b; Erwin, 1984; Erwin & Scott, 1980; Jackson, 1961; Papageorgis, 1975; Rees, 1984; Wolda, 1979). Of these studies, only two have attempted to quantify the stratification of butterflies. Jackson (1961) documented the presence of rare Lycaenidae and Nymphalidae in a Ugandan forest canopy, but his study ignored all species in the understory. In Peruvian lowland rainforest, Papageorgis (1975) found that some warningly colored butterflies and diurnal moths tend to fly at different levels in the forest according to mimetic pattern.

Excluding those species where males visit wet sand or plant material for non-nutritional resources (see Boppré, 1984; Collenette & Talbot, 1926; Norris, 1936), any tropical forest community of butterflies can be divided into two adult feeding guilds: those species that obtain the bulk of their nutritional requirements from flower nectar (all Papilionidae, Pieridae, Lycaenidae, Riodinidae and some Nymphalidae), and those species that feed upon the juices of rotting fruits, fermenting sap, or animal waste (several subfamilies of the Nymphalidae (*sensu* Ehrlich, 1958)). In the neotropics, only the members of the nymphalid subfamilies Satyrinae, Morphinae, Charaxinae, and some members of the Nymphalinae feed exclusively on rotting fruits or other non-floral liquid as adults. These latter subfamilies, hereafter referred to as "fruit-feeding nymphalids," may account for over 50% of the nymphalid species diversity in some Central American habitats and can, in general, only be collected by baiting them with rotting fruits (DeVries, 1987).

By virtue of their feeding habits, fruit-feeding nymphalids may be used to study stratification because individuals can be selectively sampled with traps. In this paper I present quantitative evidence for several patterns of stratification among these butterflies from a Costa Rican rainforest, and discuss how forest structure may effect stratification.

## Methods

The study was conducted from 20 October 1979 through 2 January 1980 at Finca La Selva, Heredia Province, Costa Rica, within the area known locally as the 'Washington Plots.' Five trapping sites (see trap design in DeVries, 1987) within closed canopy forest, each of which had an emergent canopy tree with a small lightgap at its base, were chosen on the basis of their receiving at least one hour of direct sunlight each day. The entire study was done during the rainy season, a time when butterfly abundance is low.

One trap of each pair was placed in the canopy, the other in a small lightgap immediately below it. Canopy traps were positioned by fastening a pulley to a tree limb growing over a lightgap and using a rope to raise and lower the trap from ground level. Traps were checked twice each day, and rotting banana bait replaced regularly. All butterflies caught in the traps were killed, measured (winglength), and determined to species and sex and the trap position of capture was noted. Winglength data (measured from base of forewing to the forewing apex) were supplemented for species with small sample sizes using Costa Rican specimens from the Museo Nacional or British Museum (Nat. Hist.) collections (Table 3); these data were log transformed for analysis. The nomenclature used here follows DeVries (1987), and for analyses the subfamily (Table 2) Brassolinae was collapsed into the Morphinae of Ehrlich (1958).

## Results: Patterns of Stratification

The wet season depression of butterfly abundance is reflected by the low numbers of individuals trapped: in 10 weeks the traps collected a total of

182 butterflies in 46 species (Table 1). As one might expect, some rare species (based on museum abundance) were common in the canopy, and in all categories (by subfamily and trap position) significantly more (DF = 4;  $G = 49.1$ ;  $p < .001$ , DF = 1;  $G = 42.3$ ;  $p < .001$  respectively) males were caught than females (Table 1). The trap samples also contained previously undescribed taxa (see Singer et al. 1983; DeVries 1987). Without addressing the problems of trap effect, heterogeneity of trap catch, or the possible effects of sampling without replacement, these overall patterns were noted:

1. Most species tended to be trapped only in the canopy or the understory, but a few species were found in both (Table 1).
2. Species richness was about the same in canopy and understory, with 24 taxa trapped only in the canopy, 15 only in the understory, and 7 taxa in both (Table 1).
3. Canopy traps collected significantly more individuals than did understory traps (Table 1).
4. Stratification occurred at the subfamily level, with members of the Charaxinae and Nymphalinae in the canopy, and members of the Morphinae and Satyrinae in the understory (Table 2).
5. Species trapped in the canopy had smaller mean winglengths than those species trapped in the understory (Table 3).
6. Mean winglengths differ between subfamilies, implying that winglength and position of capture cannot be separated from phylogenetic affinity (Table 3).
7. Canopy and understory butterflies differ in possession of eyespot patterns (Table 4), and these differences are linked to taxonomic affiliation: Morphinae and Satyrinae have eyespots while other groups generally do not.

## Discussion

This study showed that certain genera and species of fruit-feeding nymphalid butterflies were trapped consistently in the canopy, others in the understory, while a small fraction of the species were found in both canopy and understory. Overall, the data here indicate differences between canopy and understory butterflies in abundance, species composition, wing length, and color pattern (Tables 1-4). However, the stratification of butterfly species by wing length and color pattern cannot be separated from taxonomic relatedness. This is to say that position of capture, size, color pattern, and subfamily are correlated to some degree, and that similar patterns may be found in other arthropods.

The winglength data presented here are consonant with size data from other arthropod studies (Wolda 1979; Erwin & Scott 1980; Rees 1982; Erwin 1983), suggesting that smaller relative size may be a general characteristic of canopy insects. This trend, however, is reversed

for Costa Rican Papilionidae, where larger winged butterflies occur in the canopy (DeVries, unpublished data).

Stratification by color pattern in fruit-feeding nymphalids is not likely to be explained by the mimetic resemblance hypothesis of Papageorgis (1975) *per se*. In her system, predators maintain the stratification of butterflies by selecting for similar mimetic patterns within distinct strata. However, virtually all of the species in the present study are cryptically colored, palatable to predators, and non-mimetic (Chai 1986; DeVries 1987). Since predators are clearly important in selecting the appearance of cryptic insects (Kettlewell 1955, 1956; Chai 1986), the stratification of eyespots (or lack of them) found in this study may also be due to stratification patterns of the butterflies' predators. It is quite reasonable to assume that the species composition of vertebrate predators (i.e., lizards and birds) differs between the canopy and understory, and that these predators exert differing selection pressures on butterflies. Perhaps studies on a single subfamily that contains species found in both canopy and in the understory (e.g., Nymphalinae or Satyrinae) may prove fruitful for probing the effects of how predator communities in the canopy and understory act on eyespot pattern (and body size) of these cryptic butterflies.

Although the data here show that fruit-feeding nymphalid species are stratified between canopy and understory when feeding, they do not necessarily indicate where these butterflies spend their time when not feeding. For instance, the males of some species trapped only in the understory (*Archaeoprepona camilla*, *Morpho cypris*) spend much of their time patrolling in the canopy (presumably searching for females), and conversely, females of some rarer canopy species (*Cissia pseudoconfusa*, *Megeuptychia antonoe*, *Catonephele orites*) are known to oviposit on hostplants occurring near ground level in gaps and along forest edges (DeVries 1986; 1987). Clearly, the location of mate seeking areas or larval hostplants can be entirely different from where non-ovipositing adults are found. Furthermore, these data here do not indicate whether or not further stratification would be revealed if traps had been placed at intermediate levels between the canopy and understory. The data do, however, raise the question of why these butterflies show pronounced stratification: if Newton was correct about apples, rotting fruits fall to the ground and canopy butterflies should feed on them there. This suggests that fruit-feeding nymphalids may eventually be shown to have feeding specializations with respect to rainforest fruit species.

Most tropical collectors are aware that canopy flying nymphalids can be trapped close to ground level along a forest edge. Such knowledge implies an intuitive appreciation that stratification breaks down in some situations. A testable, general model is offered here to explain how different light levels maintain the stratification observed in fruit-feeding nymphalids, and why stratification is less pronounced in certain habitats. The model assumes that for diurnal insects such as butterflies,

Table 1. Summary of taxa trapped during the study. See DeVries (1987) for nomenclatural details.

Species	Canopy	Understory	Total
<b>CHARAXINAE</b>			
Prepona			
omphale	6	1	7
Agrias			
amydon	1	0	1
Archaeoprepona			
demophon	2	1	3
camilla	1	4	5
meander	0	1	1
Zaretis			
itys	1	0	1
Memphis			
morvus	5	0	5
cleomestra	3	0	3
laura	1	0	1
aureola	1	0	1
xenocles	3	0	3
<b>NYMPHALINAE</b>			
Hamadryas			
laodamia	21	0	21
arinome	16	2	18
amphinome	3	0	3
Catonephele			
numilia	4	0	4
orites	11	0	11
Nessaea			
aglaura	1	4	5
Myscelia			
leucocyana	5	3	8
cyaniris	1	0	1
Eunica			
monima	1	0	1
Callicore			
lyca	1	0	1
patelina	2	0	2
Historis			
odius	3	0	3
acheronta	3	0	3
Smyrna			
blomfildia	3	0	3
Colobura			
dirce	8	0	8
Tigridia			
acesta	2	2	4

Table 1. (cont'd)

Species	Canopy	Understory	Total
MORPHINAE			
Morpho			
peleides	0	1	1
amathonte	0	1	1
cypris	0	1	1
Antirrhea			
miltiades	0	1	1
Caligo			
eurilochus	0	4	4
atreus	0	9	9
illioneus	0	2	2
Catoblepia			
orgetorix	0	1	1
Opsiphanes			
tamarindi	0	1	1
invirae	2	0	2
cassinae	2	0	2
SATYRINAE			
Cithaerias			
menander	0	2	2
Dulcedo			
polita	0	1	1
Cissia			
pseudoconfusa	3	0	3
joycae	1	0	1
hesione	0	3	3
Megeuptychia			
antonoe	11	0	11
Taygetis			
Andromeda	0	5	5
xenana	1	3	4
Total	129	53	182
	male-female	male-female	
Subfamily	canopy	understory	Total
Charaxinae	19:5	5:2	31
Nymphalinae	59:26	7:4	96
Morphinae	2:2	15:6	25
Satyrinae	13:3	14:0	30
Total	129	53	182

Table 2. Abundance of individuals by subfamily and position of traps. Expected values are in parentheses. Significantly more butterflies were trapped in the canopy than the understory [DF = 3; G = 54.67; p. < .0001].

Subfamily	Canopy	Understory	Total
Charaxinae	24 (21.97)	7 (9.03)	31
Nymphalinae	85 (68.04)	11 (27.96)	96
Morphinae	4 (17.72)	21 (7.28)	25
Satyrinae	16 (21.26)	14 (8.74)	30
Total	129	53	182

Table 3. Mean Winglengths based on Costa Rican Specimens

Species	N =	Winglength	Subfamily	Position
omphale	7	48.4	charax	both
demophon	9	55.5	charax	both
camilla	6	59.5	charax	both
meander	8	53.7	charax	under
itys	7	35.1	charax	canopy
morvus	8	32.4	charax	canopy
cleomestra	12	32.8	charax	canopy
aureola	7	35.4	charax	canopy
xenocles	7	29.5	charax	canopy
laodamia	8	35.0	nymph	canopy
arinome	8	37.0	nymph	both
amphinome	9	37.7	nymph	canopy
numilia	7	36.2	nymph	canopy
orites	8	34.1	nymph	canopy
aglaura	8	35.9	nymph	both
leucocyana	9	29.3	nymph	both
cyaniris	10	34.1	nymph	canopy
monima	10	21.8	nymph	canopy
lyca	10	25.7	nymph	canopy
patelina	8	28.7	nymph	canopy
odius	8	56.0	nymph	canopy
acheronta	5	44.0	nymph	canopy
blomfildia	8	41.2	nymph	canopy
dirce	7	32.5	nymph	canopy
acesta	10	25.7	nymph	both
peleides	12	71.3	morph	under
amathonte	10	78.1	morph	under
cypris	8	70.0	morph	under
miltiades	9	47.3	morph	under
eurilochus	9	81.6	morph	under
atreus	8	77.7	morph	under

Table 3. (cont'd)

Species	N =	Winglength	Subfamily	Position
illioneus	6	69.9	morph	under
orgetorix	10	51.8	morph	under
tamarindi	13	48.9	morph	under
invirae	8	43.0	morph	canopy
cassinae	11	42.0	morph	canopy
menander	10	30.3	satyr	under
polita	6	34.4	satyr	under
pseudoconfusa	8	20.9	satyr	canopy
hesione	7	20.8	satyr	under
antonoe	7	31.9	satyr	canopy
andromeda	8	37.0	satyr	under
xenana	9	36.4	satyr	under

One Factor ANOVA on Winglength across trap position and subfamily.

Source	S.S.	DF	Mean sq.	F-test
between traps	1.343	2	0.672	6.716
within traps	4.000	40	0.100	
Total	5.344	42		p < .005
between subfams	2.935	3	0.978	15.84
within subfams	2.409	39	0.062	
Total	5.344	42		p < .0001

Table 4. Stratification of species by presence or absence of eyespot pattern. Expected values are in parentheses. Eyespot patterns are found with a significantly greater frequency in the understory than in the canopy (DF = 1; G = 25.23; p = .0001). Note that this cannot be separated from taxonomic affinity: Morphinae and Satyrinae have eyespots.

Eyespots	Canopy	Understory	Both	Total
Present	5 (9.39)	13 (5.87)	0 (2.74)	18
Absent	19 (14.61)	2 (9.13)	7 (4.26)	28
Total	24	15	7	46

light is more important than the related factors of temperature and humidity for explaining patterns of stratification. The model therefore predicts that: 1) butterfly taxa usually fly in certain light levels within any habitat, and that 2) drastic changes in light intensity act as barriers between habitats.



The flower-feeding butterflies *Anartia fatima* (Nymphalidae), *Phoebis philea* (Pieridae), *Battus polydamas* (Papilionidae) that usually fly in bright sun, at ground level, provide an illustration of the effects of a light barrier. I commonly see these butterflies fly across a pasture towards the forest edge, ascend at the forest edge, fly across the canopy, and descend once again to ground level when the next pasture is encountered. They do not move through the shade of the forest, but rather they treat the canopy as an elevated pasture, despite the 40 meter difference in height between canopy and ground levels. In this example, a butterfly changes vertical distance from the ground without experiencing an appreciable change in light intensity. I strongly suspect that butterfly species that inhabit the vegetational interface between sunny and shaded areas (i.e., canopy/edge) treat the forest canopy and forest edge without regard to vertical position, since light levels within the interface should remain roughly the same regardless of height.

Stratification then, in both canopy and pasture species is probably maintained by their preference for certain light levels. From field observations I further reason that there are three major distribution zones for butterflies within a closed canopy forest: open areas above and around the canopy (high light levels), the combination of within canopy and forest edge (medium light levels), and the shade of the forest interior (low light levels). Canopy species can be trapped at ground level at the forest edge because they normally inhabit the light level interface between bright sunlight and deep shade, and like vining plants, treat the forest edge as the canopy come to the ground. Light is considered to be an important factor in maintaining stratification in some forest and marine communities (Bainbridge et al. 1966; Allee et al. 1969), yet the effect the forest edge or disturbed forests have on stratification has not been addressed in tropical forest insects. If differences in light levels are important for maintaining stratification in rainforest butterflies, we might predict that in habitats without pronounced differences in light levels (i.e., disturbed forest, in deciduous forest during the dry season, or along the forest edge), stratification will not be as distinct as in closed canopy forest. The study of fruit-feeding nymphalids across various forest successional stages with the methods described herein may provide the necessary tools for understanding the role of light levels and forest structure in the maintenance of stratification of rainforest butterflies.

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