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# Vertical Stratification in Color Complexes of Ithomiine (Nymphalidae) Butterflies

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## ABSTRACT

Ithomiine (Nymphalidae) butterflies are vertically stratified by color pattern in neotropical forests. Each of the five color patterns recognized represents a mimicry complex of several sympatric species. Vertical stratification between color complexes of Ithomiines has been attributed to crypticity and host plant stratification. Here, I study stratification between the clearwing and golden-translucent complexes in Monteverde, Costa Rica. As in other studies, clearwings tend to fly lower than golden-translucents. Host plants do not correspond well to flight heights for these species, however. Within complexes species are also vertically stratified with most similar species tending to separate, possibly to aid in mate location.

## RESUMEN

Las mariposas Ithomiine (Nymphalidae) son verticalmente estratificadas por el patrón de color en los bosques neotropicales. Cada uno de los cinco patrones de color se reconocieron representando un complejo mimético de algunas especies simpátricas. La estratificación vertical entre el complejo de colores en Ithomiines se ha atribuido a ser críptico y la estratificación de la planta hospedera. Se estudió la estratificación entre los complejos de espejitos y oro-traslucidos en Monteverde, Costa Rica. Como en otros estudios, los espejitos tienden a volar más bajo que los oro-traslucidos. Las plantas hospederas no corresponden verticalmente a las alturas a la que vuelan estas especies. Entre los complejos de especies son también verticalmente estratificados con especies más similares tendiendo a separarse, posiblemente como ayuda en apareamiento.

## INTRODUCTION

The Ithomiinae (Nymphalidae) are a highly diverse subfamily of butterflies that range from Mexico through Central and South America (DeVries, 1987). This subfamily is entirely Neotropical and found in forest habitats in Costa Rica, with the highest diversity between 600-1500m (DeVries, 1987). Ithomiines derive pyrrolizidine alkaloids from plant sources which make them unpalatable to predators, and have tough, leathery bodies to prevent injury (Haber, 1978; Masters, 1990). Ithomiines exhibit Mullerian mimicry, in which their similar color patterns serve to “teach” birds, which are more likely to remember a single search image, associating a bad taste with that coloration (Brower, 1984).

These butterflies exhibit an aggregating behavior in which they collect into large, multi-species groups. This is a result of increased effectiveness of male scent scales which emit a mating pheromone (Haber, 1978). However, resources may vary and be distributed vertically, causing Ithomiines to be vertically stratified in the trees.

Papageorgis (1975) proposed that butterflies are vertically stratified into color complexes, which contain multiple species with similar color patterns. There is a trend toward increasing amounts of pigmentation in wing coloration from the forest floor into the canopy, where the more transparent complexes are found closer to the ground and become more opaque as height increases (Papageorgis, 1975).

There are five principle color complexes within the Ithomiinae including clearwings, black and yellow, tiger, black and rust, and golden-translucent (Haber, 1978). In the clearwing complex, the wings are transparent, with black margins and veins. Golden-translucent complexes have translucent wings marked with golden brown and smoky black shading (Haber, 1978). Each color pattern usually includes several sympatric species for a given location. Species within a given color complex have slight to substantial differences in wing patterns. All species, regardless of color, occur in similar ecological conditions in the forest, are subjected to the same predators and exhibit diurnal activity (Papageorgis, 1975) Flight height is the most likely reason for the segregation of complexes.

In several studies, the general pattern of stratification has been consistent, occurring in many areas (Ecuador: Drummond, 1976; Costa Rica: Haber, 1978; Peru: Papageorgis, 1994). Some researchers, however, have found substantially more overlap between the color complexes (Burd, 1994). Weather conditions, such as cloudy versus sunny days may impact the amount of stratification. Vertical stratification may not occur on cloudy days because crypticity may not be effective without sun (Edel, 1994).

There may be two possible reasons for vertical stratification to occur between color complexes. The colors of the complexes maximize crypticity of the butterflies, which combined with unpalatability will give an added advantage against predators (Papageorgis, 1975). Crypticity reduces the chance of being seen by predators in the first place, while unpalatability further reduces the chance of predation. For aposematic coloration to be effective, the butterfly does not have to be conspicuous, just recognizable as distasteful (Papageorgis, 1975).

Furthermore, if a butterfly happens to be attacked it must be able to quickly blend into the background when it flies away. Their cryptic coloration is intended to blend in with the background as it changes due to varying levels of light penetration at different heights (Papageorgis, 1975). At the lowest light level in the forest (0-2m), the background is comprised of low intensity light, with some small sunflecks. At this light level, transparent wings blend with the darkness and white spots on wings may look like sunflecks. As height increases, light patches increase in size and yellowish stripes on wings may look like sunny patches while darker stripes may blend into the background of the trees.

Another possible factor in the vertical stratification between color complexes is host plant stratification. In general, Lepidoptera tend to be host plant specialists, and

Ithomiines in particular are mostly associated with Solanaceae (Haber, 1978). The butterflies may assimilate the alkaloids found in these plants, making the butterflies unpalatable. Low-flying color complexes utilize only low-growing host plants while high-flying complexes use host plants at all heights, but show a preference for taller plants (Beccaloni, 1997). Females spend most of their time searching for host plants, therefore flying at the heights of their host species maximizes the probability of encountering the correct species (Beccaloni, 1997). Host plants that are visited by more than one butterfly species usually belong to the same host plant height group (Beccaloni, 1997). From this it can be suggested that species should be found at the same heights as their host plants, since females presumably locate their host plant by leaf size, shape, and chemicals.

Since vertical stratification has been shown to occur between color complexes, it seems logical that stratification may be further divided between species within the color complexes. In a previous study, this was shown within the golden-translucent color complex (Budny, 1998). If this is indeed true, there may be factors driving the species-level vertical stratification. It is possible that crypsis and host plant stratification are important but on a smaller scale. However, a third factor, mate location, may also affect vertical stratification within the color complexes.

Haber (1978) suggests that aggregating behavior is an adaptation for mate-seeking females so they can easily locate odors released by males. Males have long, hair-like scales on the anterior margin of the hindwing that emit a musky odor. Drummond (1976) concludes that both pheromones in scent scales and visual location are important in courtship. However, the effectiveness of the scales in recognition may be limited, as they may be used primarily in close-up mating associations (Haber, 1978). In Haber's (1978) experiment on male scent scales, 67.3% of Ithomiines tested were attracted to scent scales of a species other than their own. This suggests that the chemicals function to attract multiple species, and because they are not species-specific, visual cues may be necessary for identification. Visual location strategies provide further evidence for the need for vertical stratification because if species are located at different heights in the forest, mate location may be maximized.

The purpose of this study is to determine whether or not there is vertical stratification among species in two color complexes, golden-translucent and clearwings, in Monteverde, Costa Rica. If vertical stratification within the color complexes is shown, then there may be three possible reasons: crypsis, host plant preference, or mating behavior. I expect to find that clearwing and golden-translucent complexes will be further divided by vertical stratification within each complex. If crypsis is a factor, brightly colored species will fly higher. If larval host plant stratification is a factor, species should fly at the heights where the host plants normally occur. If species that share similar color patterns are found at different heights, mate-location is the most important factor. In general, clearwings are less variable in color within the complex, so this complex will be a particularly strong indicator of the niche partitioning of species.

If there is no further vertical stratification within the complexes, species will be flying at varying heights, with no apparent pattern. It may be possible that some species

occupy the entire range and others use only a portion. If this is true, other factors such as weather and temperature, or random positioning would be considered.

## METHODS

The study took place in secondary forest interior in Bajo del Tigre reserve in premontane wet forest, and also river forest and forest edge near La Estación Biológica in lower montane wet forest. The study took place in Monteverde, Puntarenas, Costa Rica from October 21, 1999 to November 19, 1999. The Ithomiine aggregations were not present throughout the study, probably due to weather, so the exact location of study sites varied. Each morning an aggregation was located, data was collected, provided conducive weather conditions. The aggregations returned to the same general area each day until they completely disappeared from the area. Ithomiines were usually found in areas with sunlight, such as treefall gaps.

Upon locating the butterfly, the basic behavior which consisted of flying or perching, was noted. A standard butterfly net was used to capture the species lower to the ground, and a double pole-length net was constructed to capture butterflies at greater heights. I then captured the butterflies and measured the height at which they were captured. A tape measure was used to determine the height. The butterflies were marked using non-toxic permanent marker on the underside of the wing to prevent recapture. Sex was determined and the individual was identified to species and released unharmed. Weather conditions, ranging from rainy and overcast to sunny, were also noted. More butterflies were present on sunny days.

## RESULTS

Over the course of seventeen days, 255 butterflies were collected, belonging to fourteen species. In data analysis, seven species were used, three golden-translucent and four clearwings due to inadequate sample sizes of the other species (Table 1). These species were *Ithomia heraldica*, *Pteronymia fulvescens*, *Pteronymia notilla*, *Pteronymia simplex*, *Oleria vicina*, *Greta nero*, and *Greta annette* (Figure 1). Species with a sample size less than ten were not used including *Pteronymia artena*, *Dircenna relata*, *Godyris zygis*, *Pteronymia fulvimargo*, *Ithomia xenos*, *Pteronymia lonera*, and *Dircenna chiriquensis*.

### Crypsis and Mate Location

Overall, the golden-translucent complex had a significantly higher flight height than clearwings (T-test;  $df = 242$ ;  $t = 2.463$ ;  $p = .0145$ ) (Figure 2). The mean flight height for the golden-translucent complex was 125.336cm (SE = 7.024) and 100.061cm (SE = 6.881) for the clearwing complex.

Differences were shown in flight heights between seven species (ANOVA  $p = .0194$ ), although not all species were significantly different. The data clearly show mean height differences between species in the golden-translucent complex. *I. heraldica* and *P.*

*notilla* as well as *P. fulvescens* and *P. notilla* fly at different heights, while *I. heraldica* and *P. fulvescens* fly at the same heights (Figure 3). *P. fulvescens* and *P. notilla* look very similar while both differ in appearance from *I. heraldica*. Furthermore, the four clearwing species do not show a statistical difference in heights. There is an obvious trend, however, toward differences in mean heights within the complex. The mean heights of *P. simplex* and *G. nero* are similar (mean = 111.81, 109.06), while they have obvious differences in coloration. The same is true for *G. annette* and *O. vicina* (mean = 84.64, 80.13) which also differ from each other in coloration and have similar mean flight heights. *P. simplex* and *G. annette* look similar and show different mean heights (mean = 111.81, 84.64) as well as *G. nero* and *O. vicina* which also show similarities in appearance (mean = 109.06, 80.13).

A two-way ANOVA was performed without *G. annette*, because this species only had one female. Although it showed no significant difference ( $f = 2.120$ ;  $p = .0643$ ), between all species, it also showed that there is no height difference between sexes ( $f = 3.046$ ;  $p = .0824$ ). A 3-way ANOVA of species, behavior, and sex with *P. fulvescens* and *P. notilla* shows a highly significant height difference between the species ( $p = .0035$ ). All of the butterflies tend to fly higher than they perch ( $f = 7.692$ ;  $p = .0069$ ) (Figure 4), and there is no difference in heights between sexes ( $f = .034$ ;  $p = .8543$ ).

## Host Plants

There is no significant correlation between the mean height of the butterflies and their host plants (Spearman Rank, tied  $z = .218$ ; Rho corrected = .060) (Figure 5).

Furthermore, host plant data lists show species overlap of Ithomiines on their host plant species (Haber, 1978) (Table 2). Congeneric species share the same larval host plants, specifically *P. fulvescens*, *P. notilla*, *P. simplex* and *G. annette*, *G. nero* in this data set. *P. notilla* and *P. simplex* use *Solanum arboretum* and all three Pteronymia species share *Solanum brenesii*... Several species share larval host plants but were found to have different mean flight heights. The average host plant heights are not consistent with the mean flight heights of the butterflies collected in this study (Table 2).

## DISCUSSION

As demonstrated by several studies, I also found distinct differences in the vertical stratification of color complexes, with the golden-translucent residing at a higher level in the forest understory than clearwings. This confirms Papageorgis' (1975) idea that on the level of color complexes, the strategy of vertical stratification enhances crypticity and also that host plant specificity may determine the vertical heights. On a finer scale, however, the strategies become more complex at the species level.

There were significant differences in the vertical stratification between species in the golden-translucent complex and a trend toward differences in the clearwing complex. There is evidence that crypsis is a determining factor in which the more colorful species fly higher. *I. heraldica* is darker than both *P. fulvescens* and *P. notilla*, and *P. fulvescens*

is slightly more colorful than *P. notilla*... Therefore, the prediction is true that *I. heraldica* is higher than *P. fulvescens* which is higher than *P. notilla* ( $I_h > P_f > P_n$ ).

The evidence for host plant stratification as an important factor is not convincing in this study. Primarily, these data showed no relationship between the mean flight heights of the butterfly species and the average height of their appropriate host plants. Since congeneric species are all sharing the same host plants but are found at different heights it is evident that there is a more important driving force in their flight heights than host plant height (Figure 2). These data are especially interesting for *P. fulvescens* and *P. notilla* because these two species are essentially the same color pattern, share the same host plant *S. brenesii*, but are found at different heights. The same is true for *G. nero* and *G. annette* and their host plant, *Cestrum sp.*... Although their appearances differ more, it may still indicate that host plant location is not a factor in the vertical stratification of species. Some Ithomiine species have mean flight heights that differ greatly from their respective host plants. For example, host plant heights were often greater than four meters; however, none of the individual butterflies were collected higher than four meters (Table 2).

Within the two color complexes, mate location seems to be an important factor in the vertical stratification between species, and the golden-translucent complex showed this statistically. In agreement with this hypothesis, species that look similar, *P. notilla* and *P. fulvescens*, fly at different heights from each other. This improves their abilities to visually locate the correct species for mating. *I. heraldica* and *P. fulvescens* look very different and in accordance with mate-location, can reside at similar heights. These color differences allow them to fly together because mates will easily distinguish between species. Although my results do not show a difference statistically between the clearwings, the data show a trend suggesting that mate location is the major determining factor in flight height. Also there are two different height levels within this clearwing complex, however due to large vertical ranges this difference cannot be shown statistically.

In accordance with mate location, Ithomiines tend to fly higher than they perch. This may be because it improves their ability to locate mating sites. By flying higher, they can visually assess the vegetation underneath. This is evidence of the importance of visual strategies in these butterflies.

Also following the mate location hypothesis, females and males fly at similar heights, which can be explained in two ways. Males may be waiting at the same height that females fly at for better mating opportunities, or females may be attracted to males' pheromones and thus fly to the height in which male occur.

In conclusion, a combination of crypsis and mate location seem to be the factors driving the structure of Ithomiine communities at the species level in two color complexes, golden-translucent and clearwing. Although host plants are not important at the species level in this study, they may exhibit greater importance on a larger scale, between color complexes. The results of this study are interesting because on a larger scale, crypticity seems to play a major role in vertical stratification, but between species the patterns become more complex, suggesting that mate location is also a factor. The

Ithomiines are an example of the complexity of biological interactions, with vertical stratification occurring even at a fine scale of species-level.

Other factors may complicate the conclusions. As Burd (1994) argues, flight ranges of some mimicry complexes overlap considerably. *P. notilla* has a lower mean height than the other golden-transluents with overlaps into the clearwing complex. It seems unreasonable to infer that the butterflies would have a strict dividing line between the flying ranges of the complexes.

This study could be improved with a larger sample size, especially in the clearwing complex, which may then show a significant difference between those species. Consistency in external variables will also improve this study such as only sampling on sunny days, and using only one study site.

Further studies could compare the differences in vertical stratification between complexes and species in various habitat types. It would also be interesting to study the effects of elevation as it relates to the vertical stratification of Ithomiines, or to study differences in other color complexes.

## ACKNOWLEDGEMENTS

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Table 1. Species list of Ithomiines and number of individuals collected for all study sites over seventeen days in Monteverde, Costa Rica .

<u>Species</u>	<u>Sample size</u>
<i>Dircenna chiriquensis</i>	1
<i>Dircenna relata</i>	2
<i>Godyris zygis</i>	2
* <i>Greta arnette</i>	22
* <i>Greta nero</i>	17
* <i>Ithomia heraldica</i>	56
<i>Ithomia xenos</i>	1
* <i>Oleria vicina</i>	16
<i>Pteronymia artena</i>	1
<i>Pteronymia fulvimargo</i>	3
<i>Pteronymia lonera</i>	1
* <i>Pteronymia notilla</i>	26
* <i>Pteronymia simplex simplex</i>	43
* <i>Pteronymia fulvescens</i>	64
<hr/> Total = 14	<hr/> Total = 255

\*species used in statistical analysis

Table 2. Seven Ithomiine species and their host plants in Monteverde, Costa Rica. The host plant vegetation types and host plant heights (m) are also included.

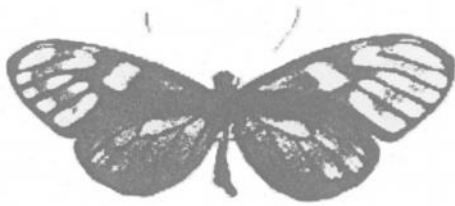
<u>Ithomiine species</u>	<u>Host plant species</u>	<u>Host plant veg. type</u>	<u>Host plant height (m)</u>
<i>Greta annette</i>	<i>Cestrum sp.</i>	treelet	1-3
	<i>S. cordovense</i>	treelet	4-5
<i>Greta nero</i>	<i>Cestrum sp.</i>	treelet	4-5
<i>Ithomia heraldica</i>	<i>Acnistus arborescens</i>	small tree	8
	<i>W. riparia</i>	small tree	4
	<i>W. morii</i>	small tree	4
<i>Oleria vicina</i>	<i>Lycianthes multiflora</i>	liana	15
	<i>S. tricygum</i>	herb	1
<i>Pteronymia fulvescens</i>	<i>S. brensii</i>	small tree	6
<i>Pteronymia notilla</i>	<i>S. arboreum</i>	small tree	6
	<i>S. brensii</i>	small tree	6
<i>Pteronymia simplex</i>	<i>S. antillarum</i>	small tree	3-5
	<i>S. arboreum</i>	small tree	3-5
	<i>S. brensii</i>	small tree	3-5



**A. *Ithomia heraldica***



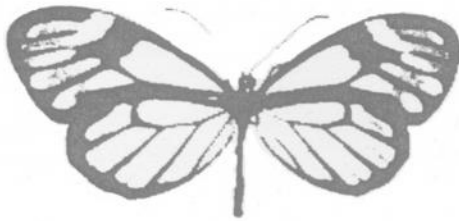
**B. *Pteronymia notilla***



**C. *Pteronymia fulvescens***



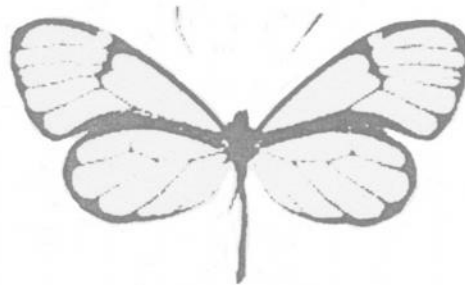
**D. *Oleria vicina***



**E. *Greta nero***

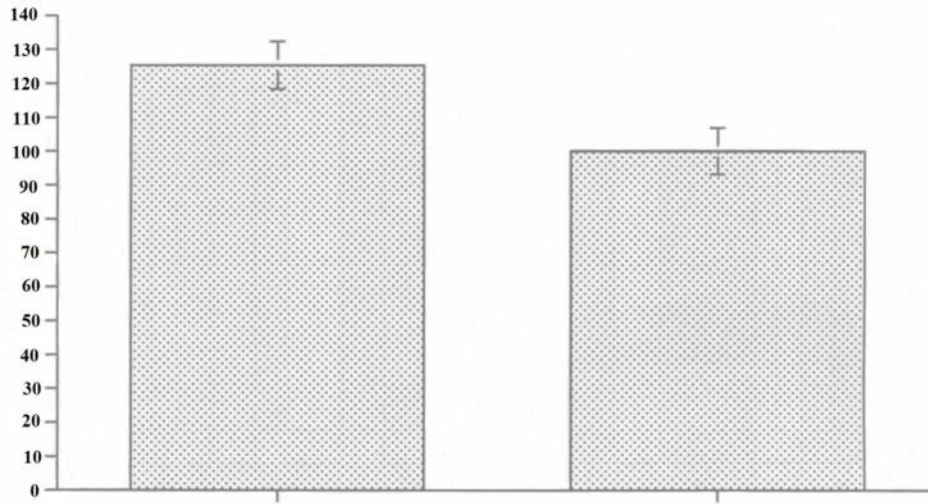


**F. *Pteronymia simplex***



**G. *Greta anette***

**Figure 1. Common ithomiine butterflies from the Golden Translucent complex (A-C) and the Clear Wing complex (D-G) captured in Monteverde, Costa Rica.**



**Figure 2.** Mean flight heights between two color complexes. The golden complex consists of three species and the clearing complex consists of four species. Data was collected over a period of seventeen days.

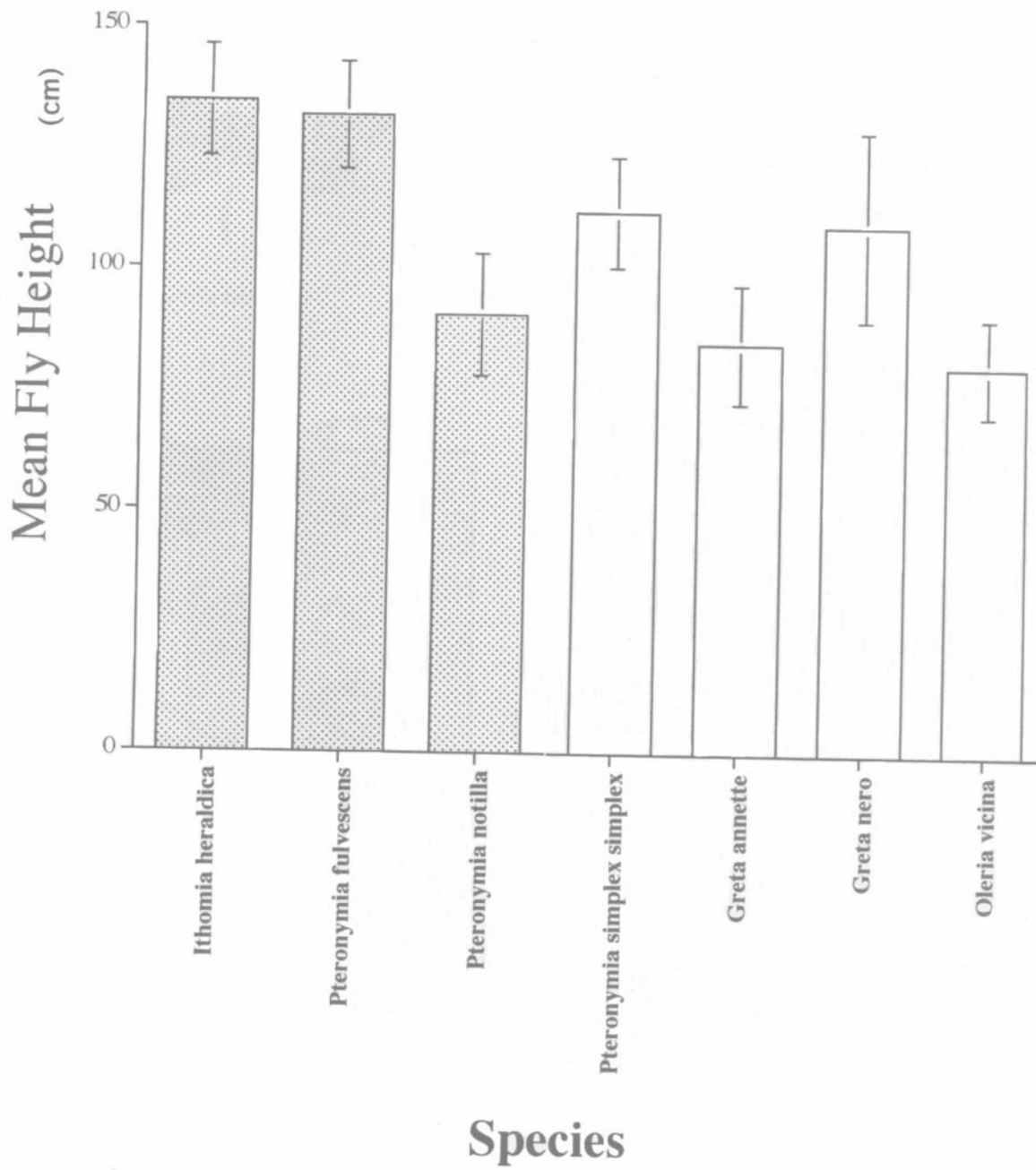
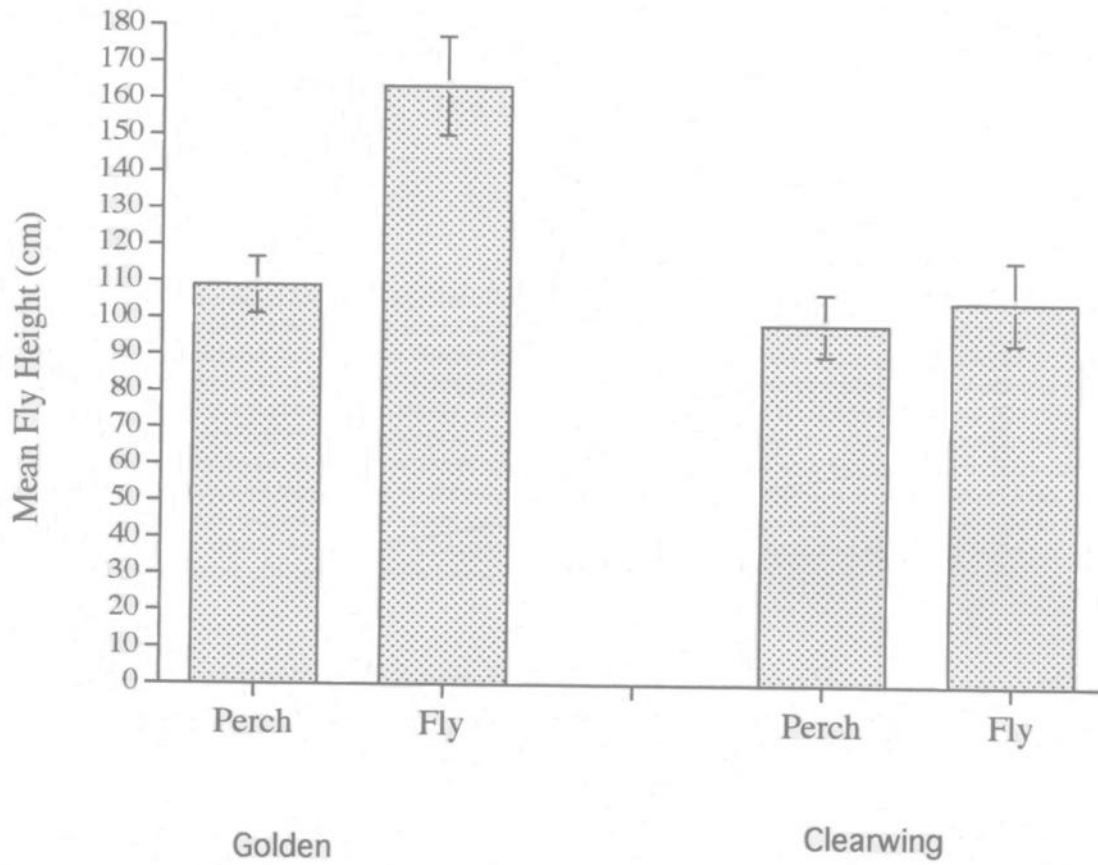
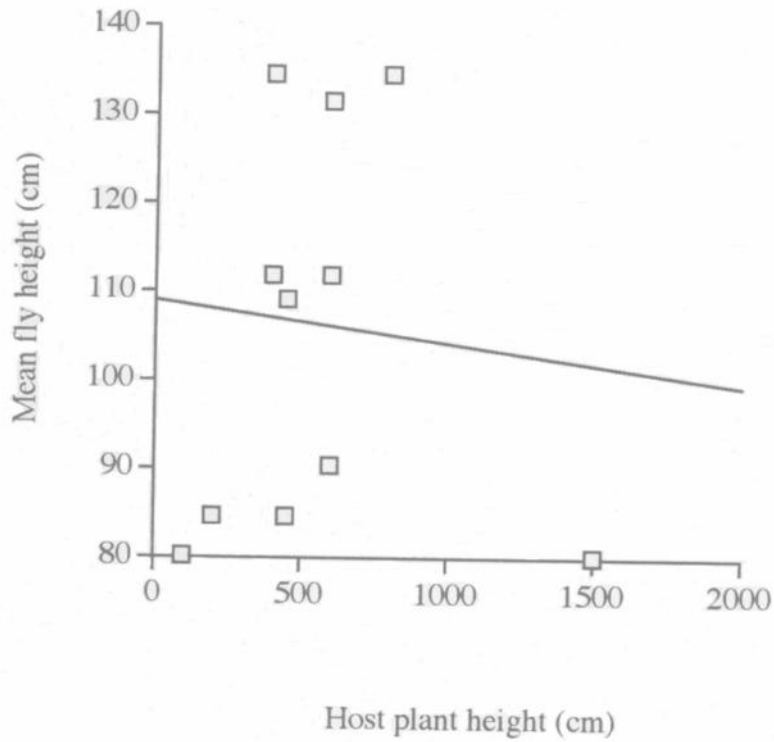


Figure 3. Mean heights for seven species of Ithomiines in two color complexes. Three species are golden and four species are clearwing.



**Figure 4. Mean heights for perched and flying butterflies for two color complexes, golden and clearwing. Overall flight heights are significantly greater than overall perch heights ( $f = 7.475$ ,  $p = .0068$ )**



**Figure 5. Mean flying height of seven species of Ithomiine butterflies against their appropriate host plant heights. The results show no significant correlation (tied  $z = .218$ ,  $Rho = .060$ ).**