Habitat Preferences of some Species of a Müllerian-mimicry Complex in Northern Venezuela, and their Effects on Evolution of Mimic-wing Pattern

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Abstract: A large mimicry complex occurring in the montane cloud forest of northern Venezuela was observed during the summer of 1967. Distinct preferences were shown by many of the species for specific microhabitats and light intensities. The dominant family in the complex was the Ithomiidae, and over 90% of the individuals in the complex were Müllerian mimics. Some species of the complex were shown to belong to more than one mimicry complex, with the pattern of the complex centered around the Ithomiidae and the behavior of other complexes.

It is concluded that the mimicry complex is much larger than usually thought and that members of a mimicry complex do not have to resemble each other perfectly. Habitat differences and the selective advantage of cryptic coloration favor the evolution of a generalized pattern. It is hypothesized that a predator would find it easier to learn a single generalized pattern than several specific ones.

During the summer of 1967, the author spent three months at the Rancho Grande experimental station in the montane cloud forest north of Maracay, Venezuela, observing the members of a large mimicry complex occurring there. Of particular interest were distinct preferences shown by many of the species for specific microhabitats and light intensities. It is my purpose to describe these habitat preferences and then discuss their possible significance in the evolution of the mimetic pattern and the extent of the mimicry complex.

METHODS

Most of the conclusions drawn are from field observations during 700 hours of field time from June to September of 1967. The best observations were made in a forest path while sitting in a chair. Most species of mimics, especially species of the dominant butterfly family Ithomiidae, were not distracted by my presence. Some of the moths listed were not observed in the field but were collected at mercury vapor light after dark. Some of the rarer Ithomiidae and Pericopidae

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were seen in the observation area only at Heliotrope plants used as bait. The use of *Heliotropum indicum* as an attractant for Ithomiidae, Pericopidae, Syntomidae, and Danaidae, has been described by Beebe (1955). No behavioral observations were made near the plants. Observations were confined to an area of about one-half kilometer in diameter. A description of the habitat at Rancho Grande has been given by Beebe and Crane (1947).

SPECIES COMPOSITION

The species I considered to belong to the mimicry complex are listed below and the majority figured in plates 1 and 2. The unorthodox combination of many different "types" is justified in the section discussing the evolution of the mimic wing pattern.

Both Batesian and Müllerian mimics are included in this complex, although it is not possible to state which are Batesian without testing them against possible predators. Species of the families Ithomiidae, Heliconiidae, Pericopidae, and Syntomidae are known to be distasteful to birds (Brower and Brower, 1964; Blest, 1964). Species of the family Ithomiidae made up over 85% of the total number of individuals and the Pericopidae about 5%. Of the total number of mimics, at least 90% were found to be Müllerian. Members of the mimicry complex formed the bulk of all diurnal Lepidoptera present, and only species of the butterfly family Satyridae were moderately common. The abundances and species diversity of the family Ithomiidae are being treated in another paper (Poole, m.s.).

HABITATS

A characteristic of tropical forest is the stratification of the trees (Richards, 1964). The herb layer at Rancho Grande is also structured into partially recognizable levels. For convenience, the herb layer was divided into three levels. Level one was defined as the plants occupying the area from the ground to about one foot. Level two was from one foot to two feet, and level three from two feet to six feet. Although each level was usually composed of characteristic species of plants, often smaller plants of levels three and two would be found in level one and so forth. Along the paths the average height of the ground cover decreased from the edge of the forest to the path. In open areas of the forest level three would be dominant and the other two levels almost absent. However, when the canopy was thick, all three levels were present but poorly developed.

I have attempted below to give a picture of the microhabitat preferences of the more common species of the mimicry complex (mostly ithomiids) occurring at Rancho Grande. Only species observed at least 25 times are included. The most common species were observed at least 100 times.

Along the paths through the forest, and sometimes in the forest proper, level

one of the vegetation was occupied by *Oleria makrena* and *Oleria phemonoe*, *O. phemonoe* flying in lighter and slightly more open areas than *O. makrena*. The pericopid *Hyalurga leucophaea* also flew in level one but only on very cloudy, dark days or in thick vegetation. The second level was occupied by *Pteronymia nubivaga* and *Pteronymia veia*, although *P. nubivaga* was usually restricted to the lower part of the second level. *P. veia* was the most variable ithomiid in terms of microhabitat preference. In the third level were *Oleria victorine, Hymenitis andromica, Pteronymia beebei,* and *Hymenitis dercetis*. *Hymenitis dercetis* occurred in darker wetter forest than the other three species and was much more common higher in the mountains. Of the three other species, *Pteronymia beebei* flew usually along open paths, but *Oleria victorine* and *Hymenitis andromica* were often found in the forest.

Species cited arranged by families

ITHOMIIDAE

Xanthocleis aedesia Doubleday and Hewitson
Mechanitis isthmia Bates
Hyalyris cana Haensch
Hypothyris euclea Godart
Ithomia agnosia Hewitson
Ithomia iphianassa Doubleday and Hewitson
Oleria victorine Hewitson
Oleria makrena Hewitson
Oleria phemonoe Doubleday and Hewitson
Dircenna jemina Geyer
Ceratinia tutia Hewitson
Pteronymia adina Hewitson
Pteronymia asopo Felder
Pteronymia beebei Fox and Fox
Pteronymia veia Hewitson
Pteronymia nubivaga Fox and Fox
Godyris kedema Hewitson
Hymenitis andromica Hewitson
Hymenitis dercetis Doubleday and Hewitson
Episcada sp.
Pseudoscada timna Hewitson

HELICONIIDAE

Heliconius clysonymus Latrielle

PIERIDAE

Dismorphia medora Doubleday
Dismorphia critomedia Hubner
Dismorphia theucharila Doubleday
Dismorphia nemesis Latrielle

PERICOPIDAE

Thyrgis militta Stoll
Eucyane excellens Walker
Eucyane diana Butler
Eucyane hystaspes Butler
Eucyane temperata Walker (?)
Pericopis marginalis Walker
Pericopis angulosa Walker
Pericopis hypoxantha Hubner
Phaloe cruenta Hubner
Hyalurga leucophaea Walker
Hyalurga fenestra Linnaeus
Hyalurga urioides Schaus
Crocomela intensa Walker

SYNTOMIDAE

Aclytia keber Cramer
Euagra cerymica Druce
Correbia fana Druce

DIOPTIDAE

Josia flavissima Walker (?)

GEOMETRIDAE

Heterusia sp.
Crocypus sp.

PYRALIDAE

Phostria seminitidalis Schaus
Sylepta dioptalis Walker
Sylepta reginalis Cramer
Diaphania confinis Druce
Diaphania sp.
Pilocrocis dioptoides Walker
Pilocrocis leucoplagalis Hampson

In open areas of the forest two species occurred, *Ithomia iphianassa* and *Godyris kedema*, with *I. iphianassa* flying in the lower part of the vegetation and *G. kedema* at higher levels. In very open areas, *Mechanitis isthmia* was common, but it rarely occurred in the forest or open areas in the forest. *Hypothyris euclea* also seemed to prefer open areas as a rule but was seen several times in thick forest. Of the three species of *Dismorphia* (Pieridae) seen in the sample area, *D. critomedia* flew in level three of the forest, *D. medora* flew in level two and the upper part of level one, and *D. theucharila* flew close to the ground and most often down the center of paths.

This ordination of the ithomiids into different levels and places in the forest is not absolute, but a set of probabilities, i.e. a particular species of ithomiid was more likely to be found in one place than in another. This variability made it impossible to quantify my observations. Habitat fidelity depended on the species and was a characteristic of each, with some species more restricted in microhabitat choice than others. The differentiation between forest and open areas in the forest was particularly vague. The stratification of the ground cover was important to the ithomiids, probably because of its correlation with light intensity. As the light intensity changed, the species moved up and down

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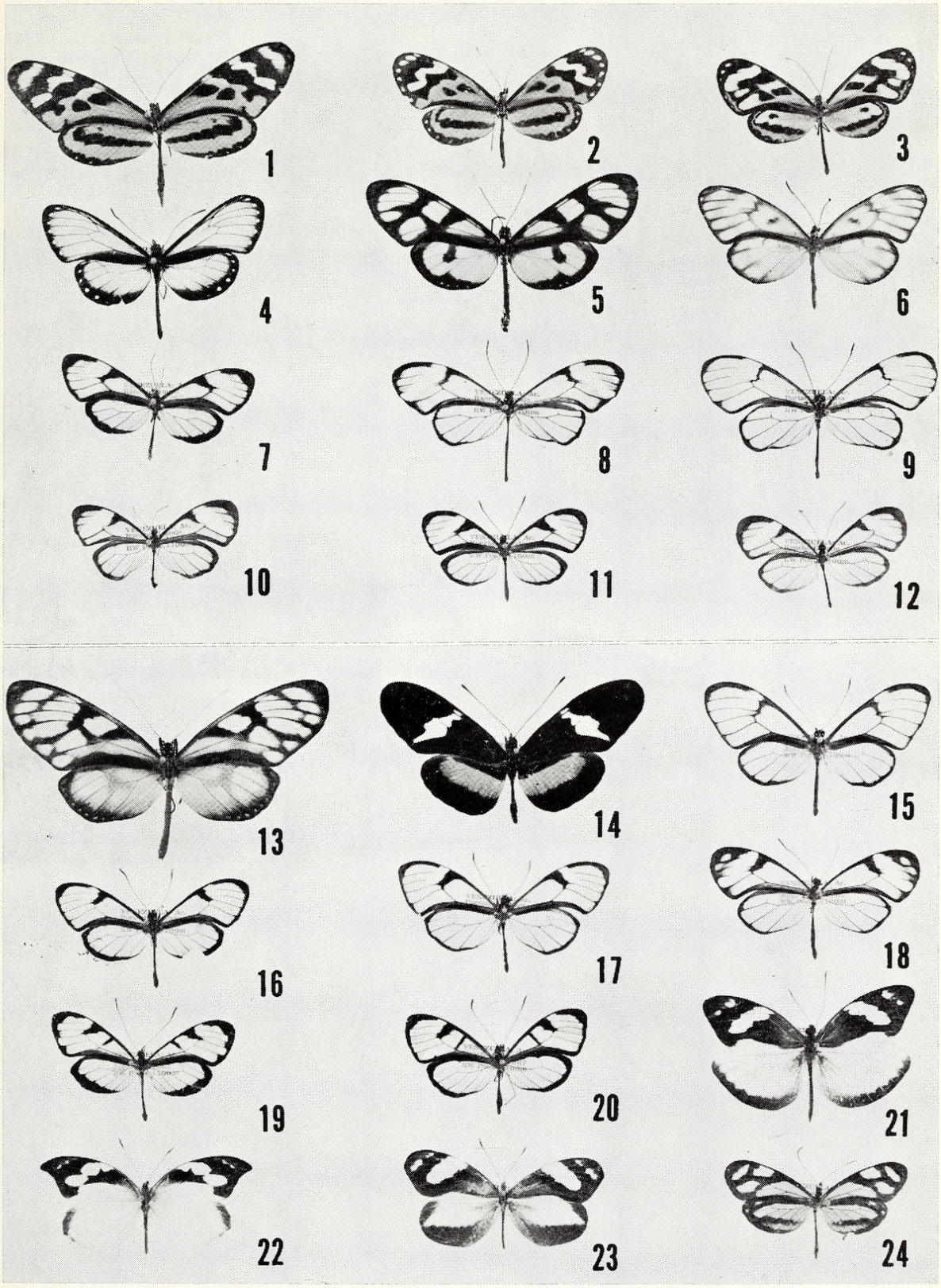
FIGS. 1–48. Members of the mimicry complex at Rancho Grande, Venezuela.

FIG. 1. *Mechanitis isthmia.*
FIG. 2. *Hypothyris euclea.*
FIG. 3. *Ithomia iphianassa.*
FIG. 4. *Hyalyris cana.*
FIG. 5. *Xanthocleis aedesia.*
FIG. 6. *Godyris kedema.*
FIG. 7. *Pteronymia veia.*
FIG. 8. *Hymenitis andromica.*
FIG. 9. *Hymenitis dercetis.*
FIG. 10 *Pteronymia asopo.*
FIG. 11. *Pseudoscada timna.*
FIG. 12. *Ithomia agnosia.*
FIG. 13. *Dircenna jemina.*
FIG. 14. *Heliconius clysonymus.*
FIG. 15. *Episcada* sp.
FIG. 16. *Pteronymia nubivaga.*
FIG. 17. *Pteronymia beebei.*
FIG. 18. *Oleria victorine.*
FIG. 19. *Oleria phemonoe.*
FIG. 20. *Oleria makrena.*
FIG. 21. *Dismorphia critomedia.*
FIG. 22. *Dismorphia nemesis.*
FIG. 23. *Dismorphia medora.*
FIG. 24. *Dismorphia theucharila.*
FIG. 25. *Pericopis angulosa.*
FIG. 26. *Pericopis hypoxantha.*
FIG. 27. *Pericopis marginalis.*
FIG. 28. *Hyalurga fenestra.*
FIG. 29. *Hyalurga urioides.*
FIG. 30. *Phaloe cruenta.*
FIG. 31. *Eucyane excellens.*
FIG. 32. *Eucyane temperata.*
FIG. 33. *Eucyane hystaspes.*
FIG. 34. *Eucyane diana.*
FIG. 35. *Thyrgis militta.*
FIG. 36. *Euagra cerymica.*
FIG. 37. *Phostria seminitidalis.*
FIG. 38. *Diaphania confinis.*
FIG. 39. *Crocypus* sp.
FIG. 40. *Pilocrocis dioptoides.*
FIG. 41. *Pilocrocis leucoplagalis.*
FIG. 42. *Sylepta dioptalis.*
FIG. 43. *Diaphania* sp.
FIG. 44. *Sylepta reginalis.*
FIG. 45. *Aclytia keber.*
FIG. 46. *Correbia fana.*
FIG. 47. *Josia flavissima.*
FIG. 48. *Hyalurga leucophaea.*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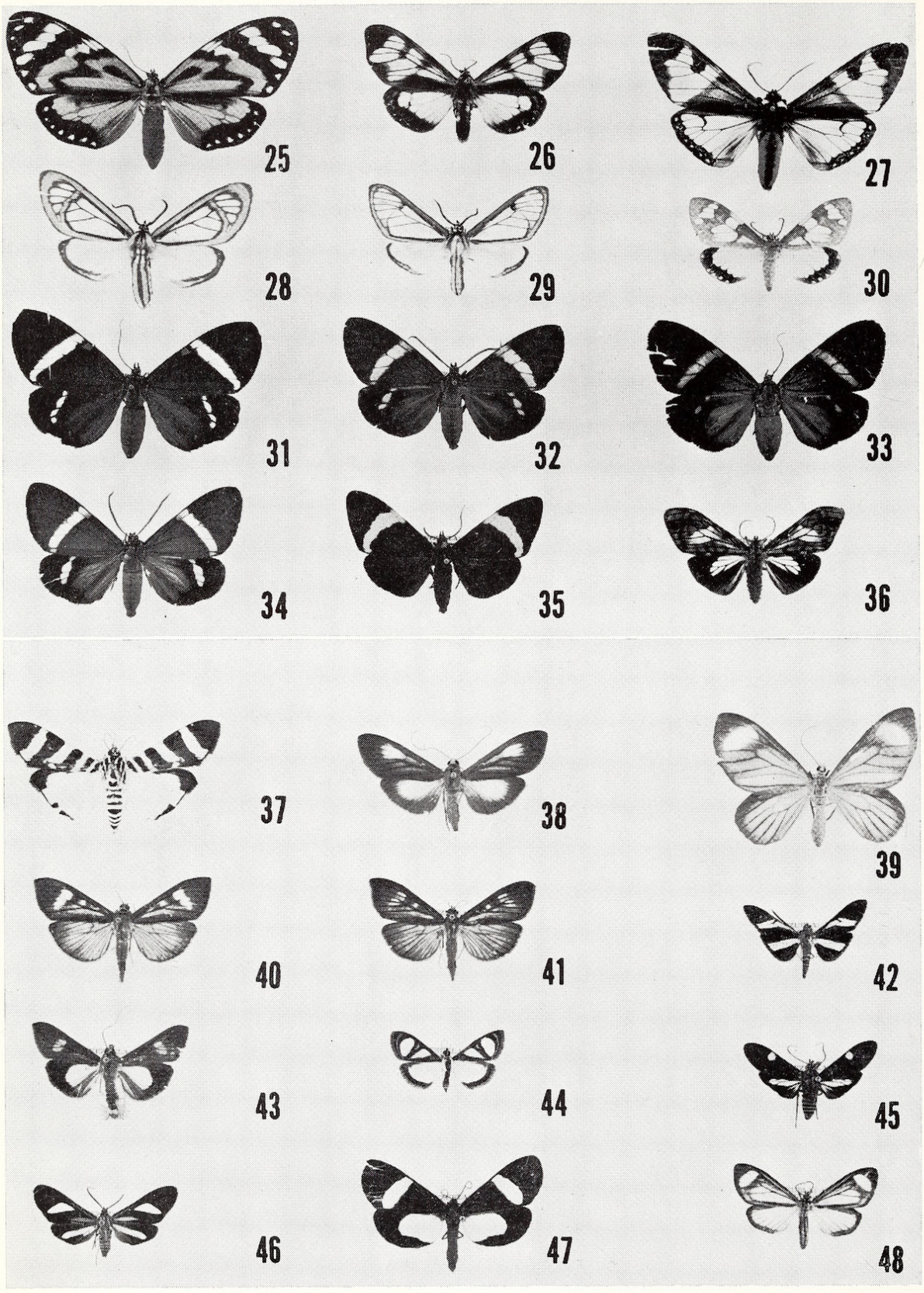
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in the cover. The apparent determining factor was light intensity and not an attraction to the level or place in which the species is normally found. One result of this response to light intensity was that many species of Ithomiidae flew at a lower level along a path than they did when flying in the forest. The Satyridae at Rancho Grande also exhibited this inclination to move up and down depending on light intensity. The tendency of the Ithomiidae to fly at different levels in the forest has also been noted by Brown and Mielke (1967) in Brazil.

DISCUSSION

In my opinion all of the species listed are members of one mimicry complex. Each different wing pattern is usually thought to represent a separate complex, but because of the significant selective advantage of an increased density of mimics (Holling, 1965) and the existence of an interspecific pheremone used to keep the various Müllerian members of the complex aggregated (Poole, m.s.), the existence of many separate Müllerian complexes is improbable. Schmidt (1958) working with chicks as predators and their reaction to artificial models and mimics found that a very incomplete resemblance between model and mimic caused avoidance. Many birds respond to generalized shapes or colors (releasers) rather than to details or specific patterns in instinctive behavior (Welty, 1962). In experiments with rats, Lashley (1938) found that many patterns were equivalent to the rats, even some dissimilar ones and states, "the animal reacts to a limited part of the total visual field and disregards variations in the remainder." Holling (1965) has shown mathematically that even small resemblances of pattern between model and mimic or two models will have a selective advantage.

Some elements of the wing patterns appear to be constant throughout the complex. These can be compared between the species in plates 1 and 2. In the forewing the pattern consists of a light patch set next to a dark one. The hindwing pattern consists of a dark border around a light center. The light area in the hindwing is achieved in several ways. In some ithomiids, for example *Oleria makrena*, the area is transparent; in others, such as *Mechanitis isthmia*, orange. In the pericopid genus *Eucyane*, the light area consists of metallic blue scaling. In many of the ithomiids, the central vein of the hindwing is conspicuous because of the transparency of the wing. In those species with orange hindwings, this vein is usually marked with black and well set off.

When ithomiids rest, the wings are folded over the back, and the lower surface of the wing is the pattern that serves as the signal to any insect predator. The optimal way of displaying a pattern at rest will probably be different than when moving since the lower wing pattern is different in some respects from the upper. The lower pattern consists of a row of white dots in a reddish to brown margin around the wings. The white dots are obscure in some members of this group, particularly those that fly under the lowest light conditions. At Rancho Grande

the pericopids *Hyalurga leucophaea* and *Pericopis* spp. sit with the wings held flat against the leaf and, when sitting, it is the upper surface rather than the lower surface that shows. In these moths the upper surface has the pattern of the lower surface of the ithomiids, with the upper wing pattern of the ithomiids superimposed.

Some species belong to more than one Müllerian complex. The genus *Eucyane* and the three species of Syntomidae have the generalized pattern of this complex but also the metallic blue and behavioral patterns of another complex based on the wasp subfamily Pepsinae. The pericopid, *Pericopis marginalis*, has the pattern of the ithomiid complex, but the behavioral actions of a complex of arctiids, syntomids, saturnids, and noctuids that, when disturbed, lift the wings to display contrasting bands on the tergites of the curled-up abdomen. This display, studied by Blest (1964), probably represents a Müllerian complex based on a behavioral mechanism.

The pattern of each species will represent a compromise between convergence to a common "complex mimicry pattern" and adaptation to the habitat in which the species occurs. Light intensity and vegetation structuring are different from microhabitat to microhabitat, and in each microhabitat there will be an optimal wing pattern and way of presenting it. If two species occur in the same microhabitat, a perfect resemblance can be selected for. However, if the two species occur in different microhabitats, the resemblance, beyond a generalized pattern, will be a compromise between selection for better mimicry and selection for cryptic coloration. Aposematic coloration was not noticeable or did not occur in this complex at Rancho Grande. Most species of ithomiids were difficult to observe, particularly on cloudy or foggy days (cloud forest is foggy a large part of the time). If specific components of the pattern are not important to the predators, selection for cryptic coloration will probably be the stronger of the two pressures. In the ithomiids I noticed that those species occurring in the same general microhabitat tended to resemble each other most. For example, yellow, orange, and black species usually occurred in open areas, but the black, transparent species occurred in the forest. In the transparent species, those with yellow or white bands flew at higher levels in the vegetation than those with little or no yellow or white.

The generalized pattern has many advantages. It enables the species of the complex to adapt to its microhabitat and become cryptic as well as mimetic. A predator would probably find it easier to learn a generalized pattern than a complicated one. It would definitely be easier to learn one generalized pattern than several specific ones.

Literature Cited

BEEBE, W. 1955. Two little-known selective insect attractants. Zoologica, **40:** 27–32.

———, AND J. CRANE. 1947. Ecology of Rancho Grande, a subtropical cloud forest in northern Venezuela. Zoologica, **32:** 43–59.

BLEST, A. D. 1964. Protective display and sound production in some New World arctiid and ctenuchid moths. Zoologica, **49**: 161–181.

BROWER, L. B., AND J. Z. BROWER. 1964. Birds, butterflies, and plant poisons. A study in ecological chemistry. Zoologica, **49**: 137–159.

BROWN, K. S., AND O. H. MIELKE. 1967. Lepidoptera of the central Brazil plateau. I. Preliminary list of Rhopalocera: Introduction, Nymphalidae, Libytheidae. J. Lepid. Soc., **21**: 77–106.

HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Canada, no. 45, 65 pp.

LASHLEY, K. 1938. The mechanism of vision. XV. Preliminary studies of the rat's capacity for detail vision. J. Genet. Psychol., **18**: 123–193.

RICHARDS, P. W. 1964. The tropical rain forest. University Press, Cambridge. 450 pp.

SCHMIDT, R. S. 1958. Behavioral evidence on the evolution of Batesian mimicry. Animal Behavior, **6**: 129–138.

WELTY, J. C. 1962. The life of birds. Saunders, Philadelphia. 546 pp.

BUTTERFLY SPECIMENS WANTED

W. V. Krivda (P.O. Box 864, The Pas, Manitoba, Canada) wishes to obtain for his research specimens of *Limenitis* or *Basilarchia* from the contact zone of *L. arthemis* and *L. a. astyanax*. He especially hopes for the "hybrids" between the two. The condition of the specimens is not important.

In exchange he can offer northern Canadian butterflies, or population samples of species in his locality.

Poole, Robert W. 1970. "Habitat Preferences of Some Species of a Müllerian-Mimicry Complex in Northern Venezuela, and Their Effects on Evolution of Mimic-Wing Pattern." *Journal of the New York Entomological Society* 78, 121–129.

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