THE "FALSE HEAD" HYPOTHESIS: PREDATION AND WING PATTERN VARIATION OF LYCAENID BUTTERFLIES

Camouflage, mimicry, and other forms of deceptive appearances have presumably evolved under selective pressures from predators who hunt by sight (e.g., Cott 1940). A fascinating example of deceptive coloration is the hypothesis that the ventral wing pattern of lycaenid butterflies (Lepidoptera: Lycaenidae) creates an impression of a head at the posterior end of the butterfly that diverts predator attacks towards the less vulnerable end of the insect (reviewed in Robbins 1980). Predators may direct their attacks towards "eyespot" markings on lepidopteran wings (Poulton 1890; Swynnerton 1926; Blest 1957), and lizards preferentially attack the "false head" of lycaenid butterflies, frequently getting a mouthful of hindwing while the butterfly escapes otherwise unharmed (Van Someren 1922). The components of wing pattern and morphology that contribute to an impression of a head, however, vary markedly among lycaenid species. Consequently, the deceptiveness of these wing patterns should vary and should be positively correlated with the frequency of deflected predator attacks. Here I present evidence confirming this correlation and supporting the hypothesis that predation influences the evolution of wing patterns among lycaenid butterflies. I then discuss possible explanations for the diversity of lycaenid wing patterns.

To compare the frequency of deflected attacks with deceptiveness as predicted by the "false head" hypothesis, I used two samples of lycaenid butterflies (Eumaeini). The first sample consisted of more than 1,000 specimens of about 125 species collected on a small hill (0.5 km², 500 m elevation) within 5 wk at Villavicencio, Meta, Colombia. The second sample consisted of almost 400 specimens of about 75 species collected in Panama Province, Panama, during 3 mo (June–August). Every lycaenid specimen seen was chased until captured or lost.

As a measure of predicted deceptiveness, I scored specimens for the following components of false-head wing patterns (fig. 1; Robbins 1980): (1) the presence of two or more contrasting lines converging, and leading a predator's eye, to the eyespot at the anal angle (caudal end) of the hindwings, (2) the occurrence of an anal angle of less than 65° as measured from the base of the hindwing to the anal lobe (end of vein Cu_2) to the end of vein M_1, (3) the presence of anal angle coloration contrasting with the ground coloration, and (4) the presence of tails, which presumably represent false antennae. I then placed species with all four of the above characters in rank 1, those with three characters in rank 2, those with two characters in rank 3, and those with one or zero characters in rank 4.

Predators sensitive to UV radiation might see these aspects of wing patterns differently. Thus I examined 75 of these lycaenid species with a television camera modified for viewing UV wing patterns (Eisner et al. 1969), but found no differences between the UV wing pattern and the visible light wing pattern.

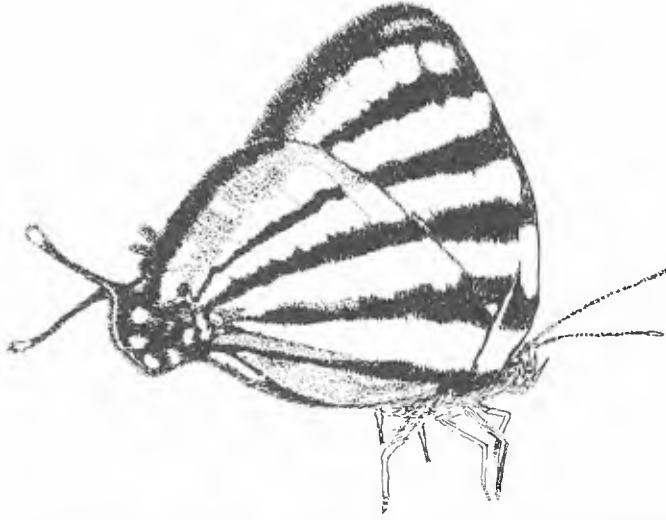Species placed in rank 1 have been considered classic examples of false-head

Fɪɢ. 1.—The "false head" butterfly, *Arawacus aetolus*. Note the tails (false antennae) and enlarged anal lobe with white highlights (false head) at the posterior end of the butterfly. The dark bands and wing outlines converge at the anal angle.

butterflies, and are illustrated in popular books on protective coloration (e.g., Cott 1940; Wickler 1968). Species in rank 2 typically are similar to rank 1 wing patterns, but have more rounded hindwings. Species in rank 3 usually have a tail and colored eyespot, but lack convergent lines and sharply tapered anal angles. The majority of species in the samples have rank 3 wing patterns as do many widespread holarctic species (e.g., most *Satyrium* spp., =*Strymonidia*, =*Nordmania* [Clench 1978]). Species in rank 4 typically have rounded hindwings that lack linear markings.

Species in the samples with wing patterns typical of those placed in each rank of predicted deceptiveness are as follows: rank 1—*Arawacus aetolus* (=*linus*, =*togarna*), *Cycnus phaleros*, and *"Thecla" gibberosa;* rank 2—*Thereus palegon*, *Rekoa meton*, and *Atlides atys* (=*scamander*); rank 3—*Calycopis isobeon* (=*beon* of some authors), *"Thecla" orcynia*, *"Thecla" ericusa*, and *"Thecla" empusa* (=*halciones*); rank 4—*Strymon bazochii*, *Polyniphes dumenilii*, and *"Thecla" una*. These species are illustrated in Seitz (1907–1924) and in Lewis (1973).

As a measure of deflected predator attacks, I counted the number of specimens in each rank that showed evidence of an unsuccessful predator attack directed to the anal angle of a butterfly's hindwings. I scored as predator-damaged those specimens that were missing a symmetrical piece of hindwing or that had beak marks (impressions of beaks on wing surfaces) on their hindwings. Such wing damage has been used previously as evidence of unsuccessful predator attacks on lycaenids (e.g., Poulton 1890; Collenette 1922) and other Lepidoptera (e.g., Carpenter 1935, 1937; Collenette 1935; Smith 1979). In addition, three lines of evidence strengthen the argument that such wing damage is the result of an unsuc-

TABLE 1

COMPARISON OF RANK OF PREDICTED DECEPTIVENESS OF LYCAENID BUTTERFLY WING PATTERNS
WITH THE TIME OF DAY AND HEIGHT ABOVE THE GROUND AT WHICH SPECIMENS WERE SAMPLED

	Ranks 1 & 2	Ranks 3 & 4
Time of day		
Morning	16	138
Afternoon	11	221
Height above ground		
0–1 m	11	181
Greater than 1 m	12	155

NOTE.—$\chi^2_{[1]} = 4.54$, $.05 > P > .025$, for time of day, and $\chi^2_{[1]} = .316$, $P > .05$, for height above ground.

cessful predator attack. First, Van Someren's (1922) illustrations prove that predators inflict this kind of wing damage on lycaenid butterflies. Second, Robbins (1980) monitored marked individuals of Neotropical lycaenids in the field and found that this kind of wing damage is not the result of gradual wear. Third, Robbins (1980) confined lycaenid specimens in net bags over plants with numerous thorns to confirm that sharp objects in the environment did not cause such observed wing damage.

The use of wing damage as a measure of deflected predator attacks to species in different ranks assumes that species in different ranks have equivalent life spans and behave similarly (Edmunds 1974). Available evidence supports these assumptions. I marked and released 20 field-caught and 22 reared males of *Arawacus aetolus* Sulzer over 4 mo to determine whether this species, the most common rank 1 species in both samples, has a longer life span than other lycaenids. I compared maximum life spans rather than average life spans because estimates of average life spans from mark-recapture data assume equal recapture probabilities (Seber 1973), an invalid assumption for these "territorial" butterflies. I recorded a maximum life span of 37 days for reared males and 31 days for field-caught males of *A. aetolus*. This result can be compared with a maximum life span of 23 days for field-caught males of a Nearctic species of Eumaeini in rank 4 (Robbins 1978), and a maximum life span of 31 days for field-caught males of a Neotropical species in the related family, Riodinidae (Callaghan 1978). Although these data are scanty, it seems likely that the life spans of species in rank 1 are similar to those in other ranks.

The behavior of lycaenids in different ranks is similar. First, species in all ranks move their hindwings alternately back and forth in the sagittal plane, a behavior that presumably enhances the deceptiveness of false-head wing patterns by drawing attention towards the posterior end (Robbins 1980). Second, species of all ranks land on leaves or flowers, and not on the ground (three exceptions) or on tree trunks (two exceptions). Third, available data on time of activity and height above the ground of activity for the Panamanian sample (table 1) show only minor differences in behavior. (Specimens in ranks 1 and 2 were more active in the morning than specimens in ranks 3 and 4, but this difference is only marginally

TABLE 2

Number and Percentage of Specimens with Symmetrical Damage to the Hindwings for Ranks of Predicted Deceptiveness

Rank	1	2	3	4
No. of specimens without damage	51	257	528	107
No. of specimens with damage	15	36	26	4
% of specimens with damage	22.7	12.3	4.7	3.6

Note.—A goodness-of-fit test shows a significant deviation from random expectations. $\chi^2_{[3]} = 38.3$, $P < .001$.

significant.) Thus, frequency of wing damage appears to be a valid comparative measure of the rate of deflected predator attacks to species in different ranks.

Comparison of the frequency of deflected predator attacks with rank of predicted deceptiveness for the Colombian sample (table 2, $\chi^2_{[3]} = 38.3$, $P < .001$) confirms the prediction of the "false head" hypothesis, and shows that predators attack various wing patterns differently. Results for the smaller Panamanian sample are nearly identical (Robbins 1978). Species with classic false-head wing patterns (rank 1) are five times as likely to have sustained wing damage from a deflected predator attack than species with average false-head wing patterns (rank 3). Further, the small differences observed in life spans or times of activity could not account for the fivefold differences between ranks 1 and 3.

If species with rank 1 wing patterns are more deceptive than species with other wing patterns, as the "false head" hypothesis predicts, then why have not more lycaenid species evolved rank 1 wing patterns? One explanation is that genetic processes such as pleiotropy (Manley 1978) or a lack of genetic variation over evolutionary time have retarded changes in wing patterns. Although this explanation may be valid for some species, evidence indicates that ventral wing patterns undergo evolutionary change frequently. For instance, rank 1 wing patterns evolved independently at least six times in the Neotropics (R. K. Robbins, unpublished data), and very closely related species may have significantly different wing patterns (e.g., *Panthiades battus*, rank 1; *P. bitias*, rank 3 [Nicolay 1976]). In addition, there are numerous other cases of convergent wing pattern evolution among Neotropical lycaenids (R. K. Robbins, unpublished data).

A second explanation is that ecological factors are responsible for maintaining wing pattern variation among lycaenid butterflies, a situation that could arise in several ways. First, contrasting black and white rank 1 wing patterns may be more conspicuous than other wing patterns to visually hunting predators, but more deceptive once the butterfly is detected. In this case, the advantages of deceptiveness might be balanced by the disadvantages of conspicuousness. Second, wing patterns may be correlated with palatability. Although unpalatable butterflies are usually "tough" in order to survive the attack of a naive predator (Trimen 1869), an unpalatable lycaenid would have an alternative strategy available to it. If such insects evolved conspicuous, but deceptive, wing patterns and sequestered some noxious compounds in their wings, as monarch butterflies do (Brower and Glazier

1975), then naive predators would grab a piece of distasteful hindwing, not otherwise harm the butterfly, and learn to avoid that wing pattern. Third, the aspect diversity hypothesis (Rand 1967; Ricklefs and O'Rourke 1975) and the anomaly hypothesis (Sargent 1973) predict that a diversity of wing patterns decreases predator efficiency by confusing or surprising predators. Fourth, ventral wing patterns may result from selection by forces other than predation, such as thermoregulation and sexual selection. If the first three processes are important determinants of wing pattern variation, then it will be necessary to modify the "false head" hypothesis as presently stated and to reformulate the mechanism by which predators exert selection on these butterflies. However, the data in this paper show that predators attack the various wing patterns differently. Thus the conclusion that predation influences the evolution of lycaenid wing pattern diversity is valid irrespective of possible modifications to the "false head" hypothesis.

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ROBERT K. ROBBINS

DEPARTMENT OF ENTOMOLOGY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C. 20560