

THE LYCAENID "FALSE HEAD" HYPOTHESIS: HISTORICAL REVIEW AND QUANTITATIVE ANALYSIS

ROBERT K. ROBBINS¹

Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama

ABSTRACT. The wing pattern and behavior of lycaenid butterflies putatively create the impression of a head at the posterior end of the insect, and deflect predator attacks from the real head. I review components of wing pattern and behavior which contribute to the appearance of a head, quantify two of these behaviors in the Neotropical "false head" lycaenid, *Arawacus aetolus*, and suggest that one behavior—landing head downwards—does not enhance the deceptiveness of a "false head". I then examine two kinds of evidence—predator inflicted wing damage and observations of predator attacks—which test the "false head" hypothesis.

The study of protective coloration in insects (e.g. mimicry, industrial melanism) has been instrumental in the development and testing of evolutionary theory. A fascinating proposed example of protective coloration is the hypothesis that the wing pattern and behavior of lycaenid butterflies (Lycaenidae) create the impression of a head at the posterior end of the insect, thus deceiving predators into attacking the less vulnerable end of the butterfly. This "false head" hypothesis is discussed in books on protective coloration of animals (e.g. Cott, 1940; Wickler, 1968; Edmunds, 1974a) and general works on butterflies (e.g. Klots, 1951; D'Abrera, 1971; Owen 1971), but has not been comprehensively reviewed. As a result, authors of popular books omit important information concerning the "false head" hypothesis, particularly observations of predators attacking lycaenids. Furthermore, behaviors which putatively enhance the deceptiveness of these insects were described qualitatively, and to varying degrees, inaccurately. The purposes of this paper are to review the development of the "false head" hypothesis, and to supplement this account with quantitative data on the Neotropical "false head" lycaenid, *Arawacus aetolus* Sulzer (= *Thecla togarna* Hew., = *Thecla linus* Sulzer [H. K. Clench, pers. comm.]) (Fig. 1).

Arawacus aetolus is a particularly appropriate experimental animal for studying the "false head" hypothesis. First, it is the most frequently cited species in discussions of the hypothesis (Longstaff, 1908; Salt, 1931; Curio, 1965; Wickler, 1968; Edmunds, 1974a). Second, unlike many other Neotropical lycaenids, males of this species are relatively easy to observe. Males occupy "territories" for most of the day during good weather (see Powell [1968] and Scott [1974a] for a discussion of this behavior), do not leave their "territory" even when

¹ Present address: 11 Bulaire Road, East Rockaway, New York 11518.



FIG. 1. Male of the Neotropical lycaenid, *Arawacus aetolus*. Notice the convergent dark-colored bands and white-tipped tails. I used the second dark-colored band (arrow) to measure the angle at which these butterflies land (see text).

disturbed repeatedly, and land within two meters of the ground. Third, *A. aetolus* is relatively common throughout the year in Gamboa, Republic of Panama, where I did this work.

This paper consists of two sections. The first part is an historical review and commentary on the components of lycaenid wing patterns and behaviors which hypothetically contribute to an impression of a head. Although descriptions of wing pattern components are straightforward, previous descriptions of three "false head" behaviors and of the circumstances under which they occur were sometimes contradictory. Thus, I augment this review with recent data on lycaenid behavior, particularly quantitative descriptions of the behavior of *A. aetolus*. The second part of the paper is an examination of the evidence supporting the "false head" hypothesis. I discuss the use of wing damage as indirect evidence of unsuccessful predator attacks, and the ways in which it can be used to test the "false head" hypoth-

esis. Finally, I summarize observations of predators attacking lycaenids under field conditions.

DEVELOPMENT OF THE HYPOTHESIS

Wing Pattern Components

A number of biologists (Kirby & Spence, 1818; Trimen, 1887; Poulton, 1890, 1902 & included references; Bell, 1906; Burn, 1906; Longstaff, 1905, 1906; Sibree, 1915; Mortensen, 1918; and Salt, 1931) have independently noted that the tails and spot of color at the anal angle of most lycaenid butterflies resemble antennae and eyespots, respectively (Fig. 1). The impression of a head is further strengthened by other aspects of wing pattern and morphology: 1) The anal angle is frequently everted at right angles to the wings so that the "head" has a three-dimensional appearance, particularly when viewed from above; 2) The tails are crossed so that they "flicker" when the hindwings are moved in a sagittal plane, and are white-tipped so that they are more conspicuous than the stationary real antennae; 3) The wings of some species have conspicuous lines converging (and presumably leading a predator's eye) towards the anal angle (Fig. 1). Although specimens illustrating the "false head" hypothesis in popular books have all of these characters, the number of such characters possessed by any one species varies considerably.

Several authors (Poulton, 1890; Bell, 1906; Burn, 1906; Sibree, 1915; Mortensen, 1918; Collenette, 1922) stated that the anal angle of lycaenid hindwings should break off if grabbed by a predator, so an attacked butterfly can escape (a situation analogous to lizards which autotomize their tails when grabbed). Van Someren (1922) confirmed that the anal angle of lycaenids breaks off when a lizard grabs it, and that the butterfly escapes unharmed. It is likely, therefore, that an enlarged or elongated anal angle area would be advantageous to the butterfly, and may be the adaptive significance of the angular hindwing shapes of many lycaenids, particularly "hairstreaks" (Theclinae).

Marshall (1902) and Van Someren (1922) suggested that the anal angle of lycaenid butterflies is an area of attraction to visual predators rather than a "false head." The primary evidence supporting this view is that the tails of some species do not resemble antennae. Although this argument is reasonable, these alternate views predict the same behavior by a predator, and cannot be distinguished.

Behavioral Components

One proposed "false head" behavior of lycaenid butterflies is moving their hindwings alternately back and forth along the cephalic-

caudal axis while resting. Trimen (1862–1866) and Niceville (1890) believed that all lycaenids move their hindwings, and there are records for species of Theclinae (“hairstreaks”) (e.g. Swainson, 1821–1822; Wallace, 1853; Belt, 1874; and Planter, 1903), Polyommatainae (“blues”) (e.g. Bell, 1906; Longstaff, 1908), and Lycaeninae (“coppers”) (e.g. Scott, 1974b) (see Eliot [1973] for taxonomy). However, not all species in these groups move their hindwings (e.g. *Lycaena phlaeas* L. in New England, pers. obs.). Also, observations in other lycaenid subfamilies (Lipteninae, Poritiinae, Liphyrinae, Miletinae, and Curetinae) do not explicitly mention whether this behavior occurs (Poulton, 1918). I have watched more than 100 Neotropical species of the closely related family, Riodinidae, and have never seen hindwing movements (although the tails of some species are blown by the wind).

The function of hindwing movements is generally interpreted as attracting the attention of predators to the “false head” (Trimen, 1887; Poulton, 1890; Mortensen, 1918; Salt, 1931; Curio, 1965), but there are two problems with this interpretation. First, tailless species lacking conspicuous spots at the anal angle also move their hindwings (Poulton, 1918; Klots, 1951). Poulton (1918) suggested that “the movements now observed in tailless Lycaenids had persisted from some ancestral time when tails were present” and perhaps secondarily direct attention to patterns on the hindwing margins. However, it might be advantageous for a butterfly to draw a predator’s attention to its hindwings whether or not the insect had a “false head.”

A second problem of interpretation is that hindwing movements occur sporadically. Poulton (1918) observed hindwing movements of *Satyrium w-album* Knoch. (= *Thecla w-album*) during “short rests, generally on flowers, between flights in hot sun.” Perkins (1918) corroborated this observation, but Mortensen (1918, 1919) observed no hindwing movements under similar conditions. Further, Poulton (1919) and Perkins (1919) noted that *Celastrina argiolus* L. (= *Cyaniris argiolus*) may move their hindwings during long (10-minute) rests. I have observed lycaenid butterflies occasionally moving their hindwings while walking (*A. aetolus*), while ovipositing (*Celastrina pseudargiolus* B. & L., *Incisalia augustinus* Westwood, *Strymon basilides* Geyer, and *A. aetolus*), and while apparently basking in the sun (*I. augustinus*, *Satyrium calanus* Hbn.). If hindwing movements attract the attention of predators, and I believe that they do, it remains to be shown that their sporadic and seemingly unpredictable occurrence is advantageous.

Other possible functions of hindwing movements are that the “rubbing” of the wings produces sounds or disperses pheromones. Swin-

ton (1878) suggested that the anal vein of the ventral forewing is a stridulating organ. Scudder (1889) rejected this suggestion, but described a patch of scales on the inner margin of lycaenids which might function similarly. Evidence for pheromone dispersal is that males of many species have specialized "scent" scales where the wings overlap (Eliot, 1973). However, hindwing movements have not been noted to occur during courtship (Powell, 1968; Gorelick, 1971; Scott, 1974b; Lundgren & Bergstrom, 1975; pers. obs. of *C. pseudargiolus*, *I. augustinus*, *Strymon melinus* Hbn., *Satyrium edwardsii* Saunders, *Theritis mavors* Hbn., and *A. aetolus*), and it is unlikely that any sounds or pheromones produced by hindwing movements function during courtship.

A second behavior which presumably enhances deceptiveness of lycaenid butterflies is landing head-downwards. Observations of this behavior have been contradictory, perhaps because few species land on vertical substrates, such as tree trunks, on which head position can be unequivocally recorded. Longstaff (1906, 1908) and Collenette (1922) noted head-downwards resting postures, with few exceptions, among lycaenids in England, Jamaica, Trinidad, South Africa, Ceylon, and Malaya. On the other hand, Mortensen (1918) reported that Panamanian lycaenids land horizontally. Further, Johnson & Borgo (1976) recorded the resting postures of males of *Callophrys gryneus* Hbn. perching on red cedar (*Juniperus virginiana*) as "head up," "horizontal," or "head down," and found no statistical difference in the frequency of "head up" and "head down" positions. Butterflies do not land exactly horizontally, of course, and the "horizontal" of one author may have been the "head-downwards" of another.

I measured the angle of inclination at landing (with respect to the horizontal) of *A. aetolus* males, which normally land on "horizontal" leaves, and *S. basilides* males, which often land on tree trunks and other vertical surfaces, as a preliminary attempt to resolve these conflicting reports with quantitative data. I measured this angle to the nearest degree for 211 landings of 11 individuals of *A. aetolus* (Fig. 2) with a Brunton compass using the second discal black band on the ventral wing surfaces (Fig. 1) as the butterfly's "horizontal axis." I calculated a mean angle of 7.0° downwards, $s = 21.42^\circ$, and a 95% confidence interval for the mean angle of 9.9° downwards to 4.1° downwards. The probability that the parametric mean is 0° (horizontal) or upwards is less than 0.001. Thus, there is a statistical bias towards landing head-downwards in *A. aetolus*. I also observed 50 landings of *S. basilides* during which the butterflies landed at right angles to the ground with their head downwards 47 times. The other three times, the butterfly landed at an acute angle to the perpendicular, and

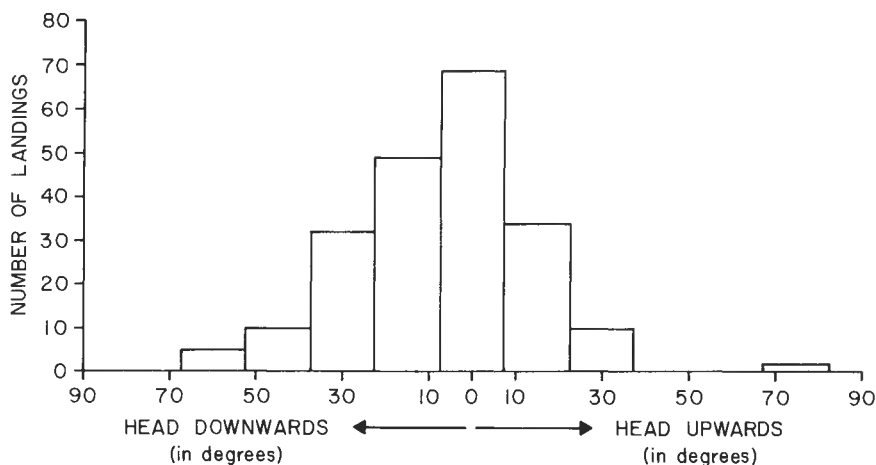


FIG. 2. The angle of inclination (with respect to the horizontal) upon landing of males of *A. aetolus*. The mean angle is 7.0° downwards with a standard deviation of 21.42° ($n = 211$).

immediately turned head downwards. If the resting postures of *S. basilides*, *A. aetolus*, and *C. gryneus* are indicative of other lycaenids, I tentatively conclude that lycaenids which rest on vertical surfaces land head-downwards, lycaenids which rest on broad leaves land head-downwards "on average," and lycaenids which rest on the scale-like foliage of some gymnosperms show no statistical preference for head-downwards or head-upwards.

Although lycaenids tend to land head-downwards, the advantage of this behavior for butterflies with "false head" wing patterns is obscure. Longstaff (1905, 1906) stated that the resemblance of a "false head" to a real head would be more "striking if . . . Lycaenids . . . habitually rest with the head downwards," but stated no explicit reasons for this proposal. He (Longstaff, 1908) reported proposals of Sidgwick that a butterfly which rests "head downwards is less conspicuous than one in the opposite position" and of Marshall that "the head-down position gives the insect a much better opportunity of launching into a rapid flight, and thus evading attack . . ." Neither of these proposals, however, explains how landing head-downwards would increase the resemblance of a "false head" to a real head. Later authors (e.g. Nicholson, 1927; Wickler, 1968) suggested that most butterflies rest head-upwards, and as a result, predators would be likely to attack the posterior end of lycaenids which rest head-downwards. Evidence indicates, however, that most butterflies, like lycaenids, rest head-downwards: Longstaff (1908) and Marshall (cited in Longstaff,

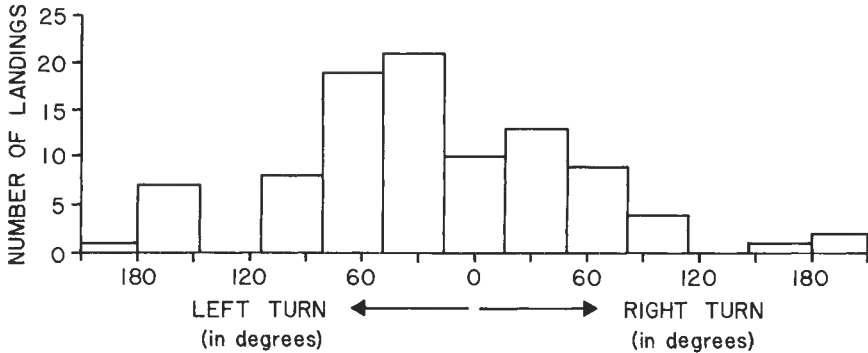


FIG. 3. The angle through which males of *A. aetolus* turned within five seconds of landing. Landings on which a male did not turn are not recorded. The mean angle turned is 19.1° left with a standard deviation of 83.25° ($n = 95$).

1908) noted that nymphalids (with the exception of the Danaidae and Acraeidae) land head-downwards; in Panama, all nymphalids (e.g. *Prepona*, *Historis*, *Catagramma*, *Colobura*, *Hamadryas*) and riodinids (e.g. *Thisbe lycorias* Hew., *Calociasma lilina* Btlr.) which I observed on vertical surfaces also rested head-downwards. Further, I did not see any species which consistently rested head-upwards. A predator, then, would not "expect" a lycaenid to be resting head-upwards, and landing head-downwards probably should be removed from the repertoire of presumed "false head" behaviors.

A third behavior which hypothetically enhances the deceptiveness of lycaenid butterflies is turning around immediately upon landing. This behavior has been noted in *Talicauda nyseus* Guer. (Longstaff, 1906), *A. aetolus* (Curio, 1965), and *Atlides halesus* Cr. (Winkler, 1977). Curio suggested that turning around upon landing might deceive a visually-hunting predator which saw the direction in which the butterfly landed. I observed 231 landings of 17 males of *A. aetolus* to more accurately describe this behavior. On 131 (58%) occasions, the individual did not turn within 5 sec of landing. I measured the angle and direction through which the butterfly did turn in the other 95 (42%) landings using a hand-held protractor (Fig. 3). There is a curious bias towards turning to the left, which is illustrated by the mean angle turned (19.1° left from initial landing position) and a 95% confidence interval for this mean (36.1° left to 2.2° left). I also found that turning may occur after long rests, when an object such as a camera lens is moved towards the butterfly's real head, when a walking butterfly reaches the edge of a leaf, or while a female is looking for an oviposition site on a leaf or stem of its larval foodplant. Indi-

viduals of other species, however, such as *S. basilides*, turn around infrequently (less than 10% of the times they land). If turning around upon landing is deceptive, then the variance in frequency of this behavior must be explained.

TESTING THE "FALSE HEAD" HYPOTHESIS

There are three proposed mechanisms by which a "false head" at the posterior end of a lycaenid might provide protection from predators. First, Kirby & Spence (1818), Trimen (1887), and Bell (1906) suggested that "false head" wing patterns alarm or menace potential predators. This hypothesis is probably not true for mantids (Burn, 1906), and is clearly not true for lizards (Van Someren, 1922) which preferentially direct their attacks towards the "false head" of lycaenids. Second, Kirby & Spence (1818) and Poulton (1890) suggested that the apparent presence of two heads confuses potential predators. Once again, the directed attack of lizards towards the "false head" falsifies this hypothesis, at least for the species Van Someren observed. There are some Neotropical species, however, which have an "eyespot" at the base of the hindwings (near the thorax), as well as a "false head" (e.g. *Rekoa meton* Cr., "*Thecla*" *atesa* Hew., *Atlides inachus* Cr.), and it is possible that such wing patterns confuse predators. A third suggestion is that "false head" wing patterns deflect predator attacks towards the less vulnerable posterior end of the butterfly. I devote the remainder of this paper to a discussion of the evidence bearing on this last hypothesis.

Hindwing Damage by Predators

A number of authors (Poulton, 1902 & included references; Burn, 1906; Longstaff, 1906; Collenette, 1922) considered lycaenid butterflies with the anal angle (or adjacent areas) of both hindwings broken off (Fig. 4) to be indirect evidence of a predator's unsuccessful attack directed at the "false head." Three lines of evidence support this proposal. First, Van Someren (1922) confirmed that the unsuccessful attacks of lizards produce this kind of wing damage. Second, I marked individuals of *A. aetolus* using felt-tip markers, and monitored them under field conditions for several weeks to determine whether symmetrically missing pieces of hindwing can result from gradual wear. I found that hindwing margins gradually frayed with age, rather than breaking cleanly to produce the symmetrical damage shown in Fig. 4. Third, I confined six *A. aetolus* females in net bags (for an average of three days each) over plants with recurved spines on branches and both leaf surfaces (*Solanum lancaiefolium*) to determine whether sharp objects, such as thorns, might cause symmetric gaps in hind-

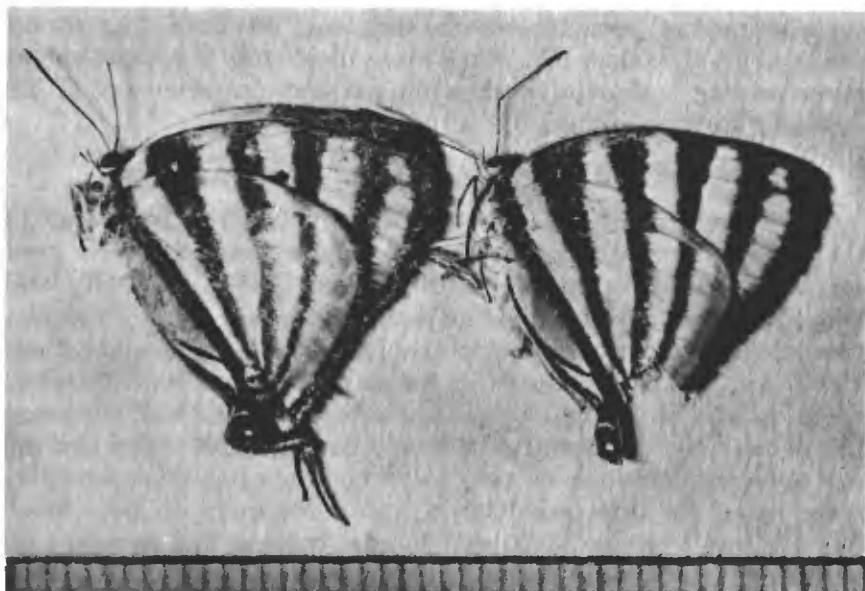


FIG. 4. Individuals of *A. aetolus* before and after sustaining symmetrical hindwing damage. Individual on the right had no damage to its hindwings four days prior to its capture. Scale in mm.

wing margins. Although wing margins of these individuals frayed rapidly, as is usually the case with butterflies confined by net bags, I found no symmetrical damage. Thus, I conclude that the rate at which lycaenid butterflies sustain symmetrical damage to their hindwings is a relative measure of the frequency of unsuccessful predator attacks.

The following "baseline data" are reported for frequencies of symmetrical hindwing damage. Collenette (1922) reported that the percentage of lycaenid specimens in Malaya with symmetrical hindwing damage was as high as 10% in worn specimens. Robbins (1978) found 7.9% ($n = 1024$) of hairstreak butterfly specimens (Eumaeini) from Villavicencio, Meta, Colombia, and 7.0% ($n = 386$) of such specimens from the Republic of Panama with such hindwing damage. Such data are easy to collect, but have the disadvantage of being dependent on lifespans since old individuals are more likely to have sustained wing damage than young ones (Edmunds, 1974b). As an alternative, I estimated the rate at which individuals of *A. aetolus* sustain hindwing damage. Each time I re-sighted a marked individual of *A. aetolus*, I recorded the number of days since the previous sighting and whether hindwing damage had been sustained since that previous sighting (Table I). From these data, I estimate (see Appendix) a 2.7% proba-

TABLE 1. The number of marked individuals of *Arawacus aetolus* with and without new hindwing damage (since the previous sighting) as a function of the number of days since that previous sighting. The number of days since the previous sighting was omitted from the table if there were no individuals found after that interval of days. From these data, I estimated the probability that an individual sustained wing damage was 2.7% per day.

No. of days since previous sighting	No. of sightings with no wing damage	No. of sightings with wing damage	Total no. of sightings
1	18	0	18
2	12	0	12
3	6	1	7
4	7	1	8
5	1	0	1
6	2	0	2
7	2	0	2
9	0	1	1
14	0	1	1
17	1	0	1
19	1	0	1
20	0	1	1
30	1	0	1
34	0	1	1

bility of sustaining hindwing damage per day for surviving individuals of *A. aetolus*. Although these data are too scanty to test the assumptions of the model (Appendix) or to reasonably estimate a variance for this probability, this figure is probably a good first estimate of the true rate at which individuals of *A. aetolus* sustain wing damage. In addition, this method might be used profitably on locally abundant species for which larger sample sizes could be collected. I emphasize, however, that frequency of hindwing damage is a relative measure of unsuccessful predator attacks, and not of successful ones (for which one first would have to make assumptions such as age-independent mortality).

Tests of Deflected Attacks by Predators

One way to test whether "false head" wing patterns deflect predator attacks is to compare the frequency of specimens with damage at their anal angle to the frequency of specimens with damage to other parts of the wings. If "false head" wing patterns do deflect predator attacks, then the frequency of predator-inflicted damage should be greatest at the "false head." Such a comparison assumes that the wings of lycaenid butterflies will break off wherever grabbed. To test this assumption, I measured the force needed to break different parts of lycaenid wings using an artificial "beak" apparatus (Fig. 5). I found

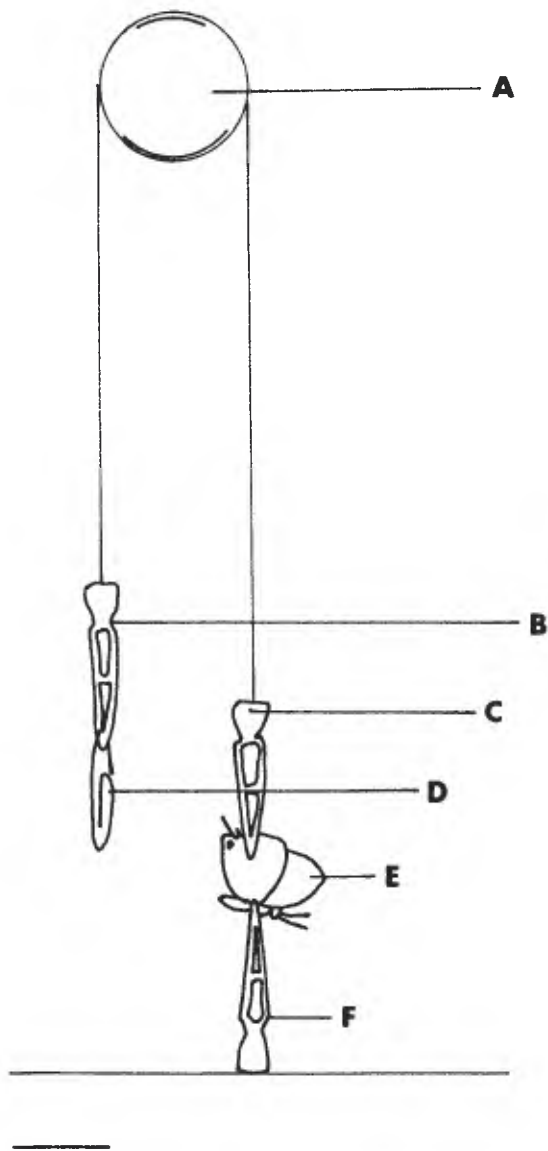


FIG. 5. Artificial "beak" apparatus. a, pulley; b, hair pin; c, hair pin used as a beak; d, paper clip weights; e, butterfly; f, attachment to butterfly. The force needed to break part of the wings being tested was measured by the weight of paper clips needed to break the wings. Scale line (lower left) = 2 cm.

that the outer margins of both wings and the hindwings adjacent to the anal angle break the most easily, while the forewing costal vein and the area where all four wings overlap are the most resistant to breakage (more than four times stronger than the anal angle area). These results are corroborated by the incidence of beak marks (impressions of beaks on butterfly wing surfaces) on lycaenid butterflies. The majority of beak-marked individuals which I have seen had been grabbed by all four wings or across the forewing costal vein. This result indicates that wings do not break when grabbed in these areas. Thus, frequencies of predator-inflicted wing damage to different areas of the wings cannot be used to test the "false head" hypothesis. However, these results also indicate that, in terms of probability of escape, it is most advantageous for the butterfly to be grabbed at its "false head."

A second way to test whether "false head" wing patterns deflect predator attacks is to compare the predicted and observed deceptiveness of a wide range of lycaenid wing patterns. If "false head" wing patterns do deflect predator attacks, then species possessing more of the proposed components of "false head" wing patterns should have a higher frequency of predator-inflicted hindwing damage. I made such a comparison (Robbins, 1978; 1980), and the results were consistent with those predicted by the "false head" hypothesis. This test also raises the question of why, if some "false head" wing patterns are particularly deceptive, all species have not evolved these wing patterns.

A third, more direct way to test whether "false head" wing patterns deflect predator attacks is to watch how predators attack lycaenid butterflies. Such systems are difficult, at best, to set up in the lab (e.g. Collenette 1922), and there is only one report of predators attacking lycaenids under field conditions. In a remarkable, yet little known paper, Van Someren (1922) reported his observations of lizards attacking lycaenids. He found that lizards invariably attacked the posterior end of these insects, and did not attack when the real head of the butterfly was closest to the lizard. Further, Van Someren reported that lizards were successful only if they grabbed part of the butterfly's body; otherwise they got a piece of hindwing, and the butterfly flew off. Thus, Van Someren confirmed that the "false head" of a lycaenid butterfly can deflect predator attacks to its posterior end, and as a result, the butterfly may escape unharmed.

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APPENDIX

The following model can be used to estimate the rate per day at which surviving butterfly individuals sustain symmetrical hindwing damage. It assumes that this rate is age-independent, an assumption which is probably accurate except for very old individuals. This model is unlikely to be original, but I have been unable to find it published elsewhere.

Let u be the probability that a butterfly survives and does not sustain hindwing damage within one day.

$p(i)$ be the probability that a sighted, marked individual was last sighted i days ago.

$N(i)$ be the number of individuals sampled which were re-sighted after i days.

$n(i)$ be the number of individuals sampled which were re-sighted after i days and which had no new hindwing damage since the last sighting.

The probability of re-sighting an individual after i days with no new wing damage is $p(i)u^i$ and the probability with wing damage is $p(i)(1 - u^i)$.

The log-likelihood equation is

$$\ln(L) = \sum [N(i)\ln(p(i)) + n(i)\ln(u^i) + (N(i) - n(i))\ln(1 - u^i)]$$

Taking the partial derivative with respect to u , and setting it equal to zero yields the following equation for u^* , the maximum likelihood estimate of u .

$$\sum \frac{iN(i)u^{*i} - in(i)}{(1 - u^{*i})} = 0$$

This equation can be solved numerically for u^* , and the maximum likelihood estimate of $(1 - u)$ is $(1 - u^*)$. With sufficient data and with estimates for the $p(i)$, this model can be tested by a goodness of fit test.