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NOTES

False Head Wing Pattern of the Burmese Junglequeen Butterfly and the Deception of Avian Predators

Key words: butterflies; false head; predation; rain forest; Vietnam; wing coloration.

MANY OF THE GREAT VARIETY of wing color patterns in butterflies are thought to have evolved because of the selective pressure exerted by visually hunting predators. Wing coloration may indicate distastefulness, mimic a dangerous creature, conceal the insect by matching it with its surroundings, or direct a predator's attack to those parts of the insect's body not essential for survival.

The "false head" hypothesis presumes that a certain pattern on the underside of the hindwing creates the impression of a head at the posterior of the butterfly. As with camouflage and mimicry patterns, many species are thought to possess a "false head," but confirmatory observations from natural ecosystems and critical experiments are almost completely lacking. The first speculations on the adaptive significance of "false head" patterns date from 1818 (Kirby & Spence 1818), and the first evidence that they work to deceive predators was presented by Van Someren (1922). Laboratory experiments by Wourms and Wasserman (1985), using artificially marked butterflies (*Pieris rapae*), showed that "false head" markings on the wings affect both the location and the success of bird attacks on butterflies. In the field, Robbins (1981) found a positive correlation between the frequency of symmetrical beak marks on the posterior hindwing area of 125 species of Lycaenidae and the number of "false head" components present there. A more straightforward way of testing the "false head" hypothesis is to compare the frequency of beak marks on different areas of the wings. This can be done only on larger butterflies. Yet so far only smaller species of Lycaenidae have been studied, preventing such an analysis (Robbins 1980, 1981). This paper presents evidence that the "false head" wing pattern is effective as an antipredator defense, a conclusion based on the distribution of wing damage in a species of large butterfly, *Stichophthalma louisa*.

The Burmese junglequeen butterfly, *Stichophthalma louisa* Wood-Mason 1877 (Lepidoptera: Nymphalidae, Morphinae), was used as the test species. It is a montane species that occurs in northern Indo-China. *Stichophthalma louisa* has a wing span of 10–11.5 cm and a wing area of 50–66 cm². Its appearance is cryptic, resembling a dead leaf in color. Its wings are rust-colored with black markings on the upper side, while the underside is greyish brown, sometimes with a green tinge. The underside shows a row of 11 eyespots. All spots but the hindmost are rusty and dark-rimmed, and have small white pupils. The remaining eyespot, located on the slightly prominent hind-tip of the hindwing, is black. Two roughly parallel black lines point to this spot (Fig. 1). Voucher specimens are available at the Institute of Entomology (České Budějovice).

The wings of *S. louisa* were divided into 13 sections (Fig. 1), and the distribution of wing damage inflicted by birds among these sections was assessed. Only deep, narrow, wedge-shaped gaps in the wings were considered to be wing damage caused by birds. Damage is of two types: asymmetrical, acquired probably in flight, and symmetrical, which could have resulted from attacks on butterflies resting with closed wings. No experiments were done to confirm that this damage is attributable to birds, but according to Robbins (1980), such an explanation is the most probable for symmetrical gaps, which could hardly be caused by wear and tear. The probability is very low that these symmetrical gaps could arise from damage separately inflicted on exactly corresponding areas of the left and right wings, as asymmetrical damage was comparatively rare.

The hypothesis tested was that the general color pattern, and in particular the lines and dark spot

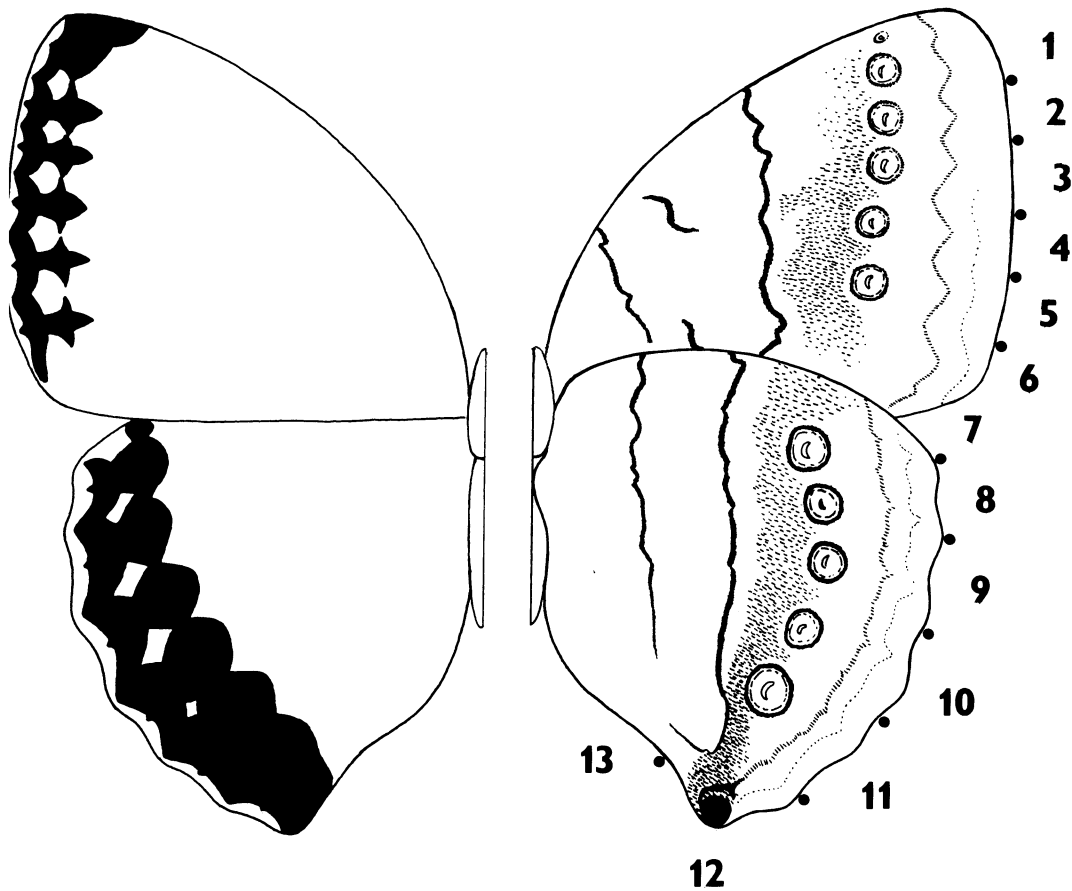


FIGURE 1. Wing pattern of the upper side (left) and the underside (right) of *Stichophthalma louisa*. Sections #1–13, referred to in Table 1, are demarcated by dots.

on the underside of the hindwings of *S. louisa*, deflect a bird's attack from the insect's head. The pattern of asymmetrical wing damage, inflicted when birds attack flying butterflies, is not likely to be influenced by the coloration of the wing underside. If birds do not respond to the supposed "false head" markings displayed by resting butterflies, the pattern of symmetrical and asymmetrical wing gaps should be similar. Consequently, the ratio of symmetrical and asymmetrical wing gaps would be independent of their location.

A large remnant of a montane monsoon forest (19,000 ha) in the Tam Dao Mountains (North Vietnam; 800–1000 m asl) was selected for the study. It is very rich in flora, without any conspicuously dominant species of tree. There was a tree layer with a dense continuous canopy, and epiphytes and climbers were numerous. Bamboo thickets prevailed on ridge tops and disturbed sites. The shrub and ground layers were fragmented.

The research was undertaken between 5 June and 7 July 1991, during the first half of the rainy season (the rainy season starts in June and ends in October). The study coincided with a period of high butterfly abundance, following a peak in emergence. The population of *S. louisa* was studied along a transect of 2 km demarcated in the forest. The transect was checked two times a day and all butterflies seen along the transect were captured. Each insect was marked by a label, had its wing damage recorded, and was released. The wing damage of recaptured butterflies, already bearing a label, was not taken into account, as the label could influence the potential location of bird attacks. In this way the sampling of butterflies from the population was probably random with respect to the location and the extent of the wing damage.

TABLE 1. *Distribution of wing gaps on the wings of Stichophthalma lousia.*

Wing section	Wing gaps	
	Asymmetrical	Symmetrical
Forewings		
1	6	1
2	4	0
3	5	2
4	11	0
5	5	0
6	9	2
Hindwings		
7	13	1
8	10	1
9	12	2
10	11	5
11	14	8
12	10	22
13	2	7
Outside FHA	46	9
Inside FHA	26	37

Wing sections #1 through #13 are demarcated in Figure 1. FHA = the "false head" area, *i.e.*, wing sections #11–13. Difference in the asymmetrical/symmetrical wing gap ratio between the FHA area and the rest of hind wing area is significant ($\chi^2 = 22.16$, $P < 0.001$, $df = 1$). Altogether 227 specimens were examined.

Stichophthalma lousia is confined to the forest, and its population density there was estimated as approximately 15 individuals per hectare. The forest edge represents a barrier which the butterflies rarely cross. Open sites within the forest habitat (such as glades), although small in size, were avoided by the butterflies as well. Likewise, butterflies were rarely observed in very dense patches of bamboo. On the other hand, butterflies were more frequently observed flying in "tunnels" in vegetation along brooks and in gullies than in the surrounding dense forest. *Stichophthalma lousia* was never seen visiting flowers. The only observed source of food for butterflies was sap bleeding from injured trees of various species. *Stichophthalma lousia* did not form large aggregations in any type of forest habitat. No hilltopping or response to other landmarks was observed, nor any "puddling behavior." The butterfly's activity did not reveal a consistent daily pattern. At night, the butterflies roosted singly in the vegetation. When flying, a butterfly slowly glided in a zigzag course through the vegetation, like a falling leaf. Butterflies closed their wings when resting on vegetation. They frequently landed on the ground as well as on tree trunks.

Of the 227 specimens checked, the wings of 149 were damaged only by wear and tear, or undamaged, while 78 bore wing gaps, sometimes several, presumably inflicted by birds. The distribution of these gaps is summarized in Table 1. Symmetrical wing gaps are obviously concentrated on the hindwing section with the dark spot on the underside (#12). The difference in the asymmetrical/symmetrical wing-gap ratio between the "false head" area (sections #11–13) and the rest of hindwing area is significant (Table 1).

We consider that the pattern of wing gaps shown by *S. lousia* supports the "false head" hypothesis. The importance of this antipredator mechanism is indicated in part by the fact that attacks on almost all of the 42 specimens bearing symmetrical wing gaps occurred in this area. The observed pattern of wing damage represents the distribution of unsuccessful bird attacks (Edmunds 1974). This pattern might arise either from a higher frequency of bird attacks to the "false head" area than to other parts of the hindwing, or from the lower success of attacks to this area. Laboratory experiments by Wourms and Wasserman (1985) indicate that both possibilities may be valid. According to Vermeij (1982), it is unsuccessful predation which may be important in the evolution of antipredator adaptations.

In *S. lousia*, the “false head” pattern is uniquely combined with a row of eyespots, which is also found in many other species from the monophyletic group consisting of the Morphinae, Brassolinae, and Satyrinae (Young 1979, Nijhout 1991). They are assumed to contribute to the cryptic appearance of a butterfly, to discourage potential predators, or to misdirect attacks (Blest 1957; Stradling 1976; Young 1979, 1980; Wourms & Wasserman 1985). Eyespots, both those supposedly intimidating and those deflective, may combine with cryptic background coloration in a complex defense system (Stradling 1976, Brakefield & Larsen 1984).

Robbins (1981) identified four “false head” components: contrasting coloration at the anal wing angle, lines pointing to the anal spot, presence of tails, and the anal angle everted at right angles so that the “head” seems three-dimensional. Our data show that even the imperfect “false head” of *S. lousia*, *i.e.*, one lacking tails and everted wing angles, was preferred by birds as a target for attacks to the row of eyespots, though the latter is very conspicuous to a human observer. The wing coloration of *S. lousia* may represent a unique combination of three antipredator mechanisms. It is cryptic; if revealed, however, it menaces the predator (by means of eyespots); and, if the insect is attacked, the markings direct the attacker to a false target (*i.e.*, the “false head”). Alternatively, eyespots may contribute to the cryptic appearance of a butterfly and not deflect predators.

Vermeij (1982) distinguishes three phases of a predator-prey encounter: detection, pursuit (or escape), and subjugation (or resistance). The cryptic background coloration, behavior, and possibly also the eyespots of *S. lousia* may be important during the detection phase. Eyespots may furthermore be discouraging, which is important during the pursuit phase. Finally, the “false head” pattern may increase the likelihood of escape, particularly during handling (Robbins 1980, Wourms & Wasserman 1985).

We are aware of the difficulties of deducing mechanisms from observed patterns: perhaps the increased frequency of symmetrical wing gaps in the supposed “false head” area could result from other factors, *e.g.*, its hindmost position on the hindwing. Nevertheless, in the absence of hard evidence from manipulative experiments, which are extremely difficult to execute in natural situations, our observations tend to support the “false head” hypothesis.

Quantitative tests of the ecological functions of wing coloration are necessary. As indicated by this study, even patterns that are relatively inconspicuous to the human eye may play a significant ecological role. Consequently, the functions of wing color patterns in butterflies may be more complicated (and/or quite different) than our anthropocentric speculations suggest.

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Ballistic Pollen Release in Australian Members of the Moraceae

Key words: ballistic pollen discharge; Malaisia; Moraceae; *Streblus*; subtropical rain forest; wind pollination.

IN TEMPERATE DECIDUOUS FORESTS many canopy trees are wind pollinated (Faegri & van der Pijl 1979). However, in evergreen tropical forests wind pollination has been more rarely recorded (Bawa & Crisp 1980). Explanations for its assumed rarity include the reduced impact and reliability of wind in the understory synusiae, impaction of pollen on the dense evergreen canopy with consequent inefficiencies in pollen transference to widely spaced conspecific plants in species-rich tropical forest communities, and adverse impacts of rain removing pollen from the air. Ashton (1969) found that only one species (not given) out of 760 in a study plot in Brunei rain forest was wind pollinated and this was restricted to high ridges.

We record here observations of ballistic pollen release, with inferred possible wind pollination, in two species of Australian Moraceae; a small tree *Streblus brunonianus* (Endl.) F. Muell. and a vine *Malaisia scandens* (Lour.) Planchon. All observations were from lowland subtropical rain forests in the Manning Valley on the north coast of New South Wales.

Streblus brunonianus is distributed north from the south coast of New South Wales to North Queensland and is also found in Papua New Guinea and the Pacific Islands (Floyd 1989). In New South Wales *S. brunonianus* occurs in a variety of lowland rain forest types. It is primarily an understory species, often in association with watercourses (Harden 1990), but also occurs on rain forest margins and in depauperate secondary regrowth and remnant rain forests where it may be common. It is dioecious and the greenish white flowers are borne in dense spikes (Fig. 1). The genus *Malaisia* is monotypic and is recorded in eastern Australian, Pacific Islands, and Southeast Asian rain forests (Harden 1990) and occurs clumped in light gaps, and along watercourses and rain forest margins. *Malaisia scandens* is either monoecious or dioecious and produces small creamish-white flowers (Fig. 2). Both species flower in late spring–late summer (Nov.–Feb.) but the flowers are not conspicuous.

Populations of *Streblus brunonianus* were observed in subtropical riverine and riparian rain forest remnants at Wingham (31°52'40"S, 152°22'00"E), Woko National Park near Gloucester (31°49'00"S,