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WING DECOUPLING IN HOVERING FLIGHT OF SWALLOWTAIL BUTTERFLIES (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT.– Wing uncoupling during hovering flight is described in Papilionidae, with *Parides neophilus* (Geyer), from Trinidad, as a particular example. Energy expenditures and predation dangers for hovering butterflies are also discussed.

KEY WORDS: behavior, Eriocraniidae, flight, Heliconiinae, *Heliconius*, Hepialidae, Hesperiidae, Ithomiinae, Lycaenidae, Malvaceae, *Mechanitis*, Melitaeinae, Micropterigidae, morphology, Musaceae, Nymphalidae, *Papilio*, Papilionidae, Papilioninae, *Parides*, Pieridae, Riodinidae, Verbenaceae.

Moths and butterflies are usually regarded as functionally two-winged insects with amplexiform wing coupling. The primitive moth families Eriocraniidae, Hepialidae, and Micropterigidae are exceptions, with uncoupled wings that perform strokes of different amplitudes (Kozlov *et al.*, 1986). In this paper we describe another example of lepidopteran wing uncoupling, not in moths but rather in papilionid butterflies. A Bolex Super-8 camera operated at 24 frames/s was used to obtain films of an individual Trinidadian *Parides neophilus* (Geyer) (Papilionidae: Papilioninae) flying to and feeding from *Lantana* (Verbenaceae) flowers under greenhouse conditions. While hovering at and feeding from a flower, the *Parides* hindwings were held open and stationary, thereby displaying prominently an aposematic red patch in the center of each hindwing (Figure 1; see also genus account in DeVries, 1987). Aerodynamic force production was achieved entirely by means of forewing strokes at high frequencies. Ornithopteran butterflies feeding at flowers display similar forewing motions (BBC Film Productions, "Butterflies," 1979), as does *Papilio torquatus* Cramer under greenhouse conditions. In the film sequence of *Parides neophilus,* complete wingbeats cannot be resolved in film playback, indicating that frequency of motion was substantially greater than the 24 Hz filming frequency. In general, butterflies are characterized by very low wing loadings and correspondingly reduced wingbeat frequencies, about 12-15 Hz for butterflies comparable in size to the aforementioned *Parides* spp. (Dudley, 1990).

Fig. 1. *Parides neophilus* hovering at *Lantana.* Hindwings are held stationary and display the aposematic red patch, while forewings beat at a high frequency.

Similarly, force production predominantly by the forewings was observed in films of a wild *Papilio zelicaon* Lucas male hovering at dead grass heads used as perches in its hilltop territory. However, once the butterfly resumed investigative or pursuit flights in response to intruding butterflies, fore- and hindwings were fully coupled. In both cases, the angular extent of motion of the forewings during hovering appeared to be 90-100°. Therefore, these papilionids can behave as morphologically two-winged insects but with the hindwings completely dissociated from force production. Because the effective wing loading will increase in this configuration, power expenditure during hovering will increase relative to flight with normal amplexiform coupling (Pennycuick, 1975). Analogous to physical decoupling of homologous wing pairs, extreme differentiation of dorsal and

ventral wing coloration occurs in many mimetic thecline lycaenids (Johnson, 1986; Constantino *et al.*, 1993) and in many palatable butterflies generally (see DeVries, 1987).

What is the basis for an apparently unnecessary increased power expenditure in papilionids during hovering around flowers and territorial perches? Clearly, selective forces other than immediate energetic gain must be proposed to explain the observed behavior. Analysis of single traits for single functions means little outside the broader context of understanding a complex set of interrelated functions which characterize the whole organism (Rasnitsyn, 1987). In the context of flower visitation, it is likely that a diversity of morphological and behavioral strategies has evolved in response to increased exposure to predators. Compared to aposematic papilionids, certain other butterflies that visit flowers are generally, 1) small, fast, or of minimal energetic value to vertebrate predators (lycaenids, riodinids, small pierids), 2) medium to large sized unpalatable, aposematic, or mimetic butterflies (ithomiines, heliconiines, melitaeines), or 3) of medium size, palatable, and disruptively or cryptically colored (some pierids and nymphalids). Smaller butterflies may obtain more nectar per unit body weight at any given flower, and in general tend to visit inflorescences with many flowers in a cluster or platform. Large butterflies, however, have greater nectar demands and must move frequently, placing them at considerable risk of predation by birds and other vertebrates. The erratic flight of palatable butterflies (Chai, 1986) may be incompatible with rapid local movements among florets of an inflorescence, suggesting that the flight patterns of many papilionids has evolved under the multiple selective forces of efficient interfloral movement and rapid response to predators. Other large butterflies (certain pierids and hesperiids) possess very long probosces and are able to exploit bird flowers (*Heliconia* (Musaceae), *Malvaviscus* (Malvaceae)) that contain greater nectar rewards per flower than do butterfly flowers. Infrequent flights between long bouts of perching on flowers may be an effective foraging tactic for such species.

By contrast, medium to large aposematically colored papilionids may be at reduced risk of attack when feeding at flowers, provided that warning coloration is still visible. Selection for evolution of warning colors in these butterflies has however not been sufficiently strong as to restructure flight patterns, which remain erratic relative to those of butterflies such as the nymphalids *Heliconius* or *Mechanitis*. In papilionids, display of hindwing coloration during hovering at flowers can be viewed as a behavioral response superimposed upon the biomechanical means of force production that may enhance overall survivorship. A phylogenetic survey of flower visitation behavior in papilionid butterflies would provide further assessment of the evolutionary forces acting to promote aposematic display in this diverse and colorful taxon.

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