

WING SHAPE AND FLIGHT BEHAVIOUR IN BUTTERFLIES (LEPIDOPTERA: PAPILIONOIDEA AND HESPERIOIDEA): A PRELIMINARY ANALYSIS

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Summary

Representatives of six butterfly species, flying freely in the field or in simulated field conditions, were filmed with a high-speed ciné camera and subjected to kinematic and morphometric analysis. This is the first detailed investigation on an insect performing the varied patterns of 'natural' flight. Kinematic parameters in representative sequences of selected flight modes were calculated and compared, and wing shapes were characterized using aspect ratio and non-dimensional moment parameters.

The analyses and field observations of these and other butterflies suggest possible correlations between flight performance and wing shape. The behaviour of individual species conforms reasonably well with crude predictions based on aspect ratio, wing loading and wing inertia.

Introduction

Although several investigations have been carried out on the relationships between form and function in insect wings (e.g. R. A. Norberg, 1975; Pfau, 1978; Wootton, 1981; Newman, 1982; Brodsky & Ivanov, 1983; Betts, 1986*a,b,c*; Newman & Wootton, 1986), the significance of wing shape (= planform) has been neglected. In contrast, in birds and bats active work on this aspect is in progress (U. M. Norberg, 1981; U. M. Norberg & Rayner, 1987; Rayner, 1987). We have carried out a preliminary investigation on a small sample of a selection of butterfly species. Butterflies were chosen because of their diversity of size, wing shape and flight pattern, and because their large size and low wing beat frequencies make them relatively easy to film with a portable high-speed ciné camera in the field or in large enclosures, for later kinematic analysis. This was important: up to now almost all kinematic studies of insects have been restricted to tethered flight or to

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free flight in small laboratory enclosures, which inevitably limits the range of flight patterns performed and inhibits normal behaviour.

Wing design is often a compromise between several functions. The wings of butterflies may act in sexual and territorial display; in cryptic or warning defence; in thermoregulation (Kingsolver, 1985); and in a wide range of flight patterns reflecting their complex behaviour (e.g. Baker, 1972; Davies, 1978). Nachtigall (1976), Martin & Carpenter (1977), Bocharova-Messner & Aksyuk (1982), Ellington (1981, 1984*a,b*) and Brodsky & Ivanov (1984) have investigated the aerodynamics.

Wing shape is difficult to quantify and in much of the literature is presented simply in the form of the aspect ratio, which has serious shortcomings in describing insect wings. The value of the moments of area was stressed by Weis-Fogh (1973), and their use has been greatly extended by Ellington (1984*a*, part II), whose discussion of wing shape is a breakthrough in morphometric investigation. The non-dimensional moments of area are functions of wing shape in that they depend solely on the distribution of the non-dimensional chord along the wing; those of mass are rather less precise functions of three-dimensional shape. The radius of the first moment of area gives the position of the centroid, that of the first moment of mass the position of the centre of mass. Moments of area and mass also have mechanical significance: the first moment of mass is proportional to the inertial force on the flapping wings, and the second moment is the moment of inertia of the wing pair. The second moment of area is proportional to the mean lift force in a quasi-steady-state aerodynamic analysis, and the third moment to the mean profile power (Weis-Fogh, 1973).

Ellington (1984*a*, part II) has shown empirically for a range of flying animals – mostly insects, but including two birds and a bat – that for both area and mass the radii of the second and third moments are very closely correlated with the first moment. He did not include broad-winged Lepidoptera, and a secondary aim of the present investigation has been to test whether Ellington's conclusion holds for butterflies. If the relationship proves to be true for insects in general, then it becomes possible to characterize the shape of a wing with reference to a single, easily found parameter – the first moment of area – and the mass distribution similarly by the first moment of mass. A single value for the first moment does not precisely define a single wing shape as it cannot accurately show asymmetry about the longitudinal axis, but it does appear to represent the wing with respect to the mechanical effects of area distribution, and seems clearly preferable to any single mode of shape measurement previously employed.

Materials and methods

Definitions of terms

A *wing couple* consists of the forewing and hindwing on one side of the body.

A *wing pair* consists either of both forewings or of both hindwings.

A *flight mode* is a category of movement at more-or-less constant velocity, e.g. fast forward flight, slow forward flight, fast climb, hovering.

A *flight manoeuvre* is a change of velocity in flight, through alteration of speed, direction or both. One may distinguish *simple manoeuvres*, like turning or slowing down, and *compound manoeuvres* involving sequences of simple manoeuvres.

A *flight behaviour pattern* is a recognizable sequence of flight modes and manoeuvres, whose ecological significance may well be apparent.

Flight performance is the range of modes and manoeuvres of which an insect is capable.

The phrase 'flight category' is used to include both modes and manoeuvres.

Flight modes and simple manoeuvres are – in theory at least – easy to quantify, although there may be practical difficulties. Quantitative description of behaviour patterns is difficult, and has seldom been attempted, but it may prove possible by recording sequences of modes and manoeuvres.

Species selected

Four species of butterfly: *Troides rhadamantus* H. Lucas (TR), *Papilio rumanzovia* Eschscholtz (PR), *Pachliopta hector* Linnaeus (PH) and *Graphium sarpedon* Linnaeus (GS), showing a range of wing shapes and sizes, were obtained from a dealer for filming in this country. Eight more species were filmed and captured in and around the secondary rain forest at Ulu Gombak Field Station, Malaysia, and data from two of these, *Precis iphita* Cramer (PI) and *Idmon* sp. (ID), are included in the present study (Fig. 1). Further observations were made on butterflies in the wild in the UK and Malaysia.

Maintenance of adults

Four specimens each of four species of tropical butterfly were purchased as pupae from Entomological Livestock Supplies Ltd. Insects were placed in a netted enclosure ('Papronet': Direct Wire Ties Ltd) approximately 5 m × 2 m × 3 m, in a section of glasshouse maintained between 20°C and 28°C and between 45 % and 85 % relative humidity.

Filming

All ciné-films were taken using a tripod-mounted, battery-pack powered Photosonics high-speed ciné camera with a 72 mm Angenieux zoom lens and reflex viewing system.

In the field only natural light was used: in Malaysia exposures at around f4 were used for camera speeds between 250 and 300 frames per second (frames s⁻¹), which required force-processing of 150ASA rated film by 2 stops. In the UK f2.8–3 gave similar results. In the enclosure, natural light plus 6650 W of artificial light gave exposures at camera speeds of 250 frames s⁻¹ and f3–4 which required force-processing of 50ASA film by 2 stops for a grainy, but usable result. All filming in the enclosure used Ilford Pan-F (50ASA) black and white 16 mm film. In the field

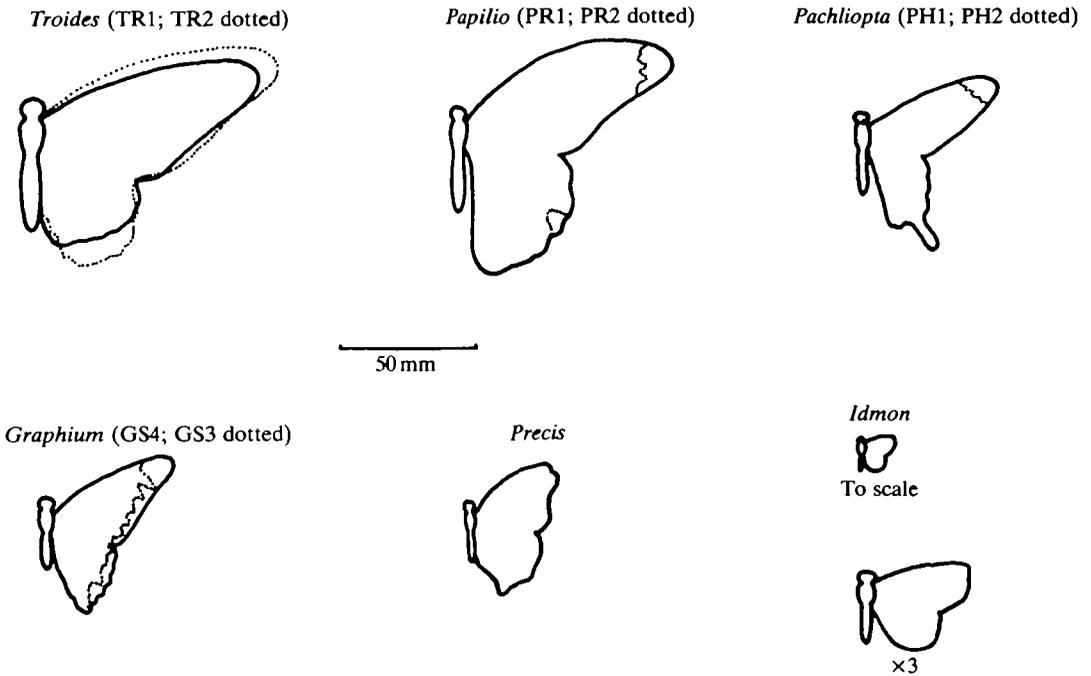


Fig. 1. Outlines to scale of the body and right-hand wing couple of the six species fully investigated.

Kodak 7240 tungsten-adjusted, colour reversal film (100–200ASA) was used with a Hoya 85A correction filter and a Hoya ultraviolet filter.

Ambient wind speeds were negligible at all times during filming.

Analysis

Morphological parameters

The following parameters were measured or calculated (see Fig. 2).

- (1) Total mass, m (g).
- (2) Body length, L (mm).
- (3) Wing length (forewing length as shown in Fig. 2), R (mm).
- (4) Wing area (total area of both pairs of forewings and hindwings when linked), S (mm^2).
- (5) Aspect ratio, AR ; given by $AR = 4R^2S^{-1}$.
- (6) Wing loading, P_w (N m^{-2}); given by $P_w = mS^{-1}$.
- (7) Moment of inertia of both wing couples, I_w (kgm^2).
- (8) Non-dimensional radius of the first moment of wing area, $\hat{r}_1(S)$; given by $\hat{r}_1(S) = \int_0^1 \hat{c} \hat{r} d\hat{f}$.
- (9) Non-dimensional radius of the second moment of wing area, $\hat{r}_2(S)$; given by $\hat{r}_2(S) = \int_0^1 \hat{c} \hat{r}^2 d\hat{f}$.

(10) Non-dimensional radius of the first moment of wing mass, $\hat{r}_1(m)$; given by $\hat{r}_1(m) = \int_0^1 \hat{m}' \hat{r} d\hat{r}$.

(11) Non-dimensional radius of the second moment of wing mass, $\hat{r}_2(m)$; given by $\hat{r}_2(m) = \int_0^1 \hat{m}' \hat{r}^2 d\hat{r}$.

(12) Non-dimensional radius of the first moment of virtual mass $\hat{r}_1(v)$; given by $\hat{r}_1(v) = 1/\hat{v} \int_0^1 \hat{c}^2 \hat{r} d\hat{r}$.

(13) Non-dimensional radius of the second moment of virtual mass, $\hat{r}_2(v)$; given by $\hat{r}_2(v) = 1/\hat{v} \int_0^1 \hat{c}^2 \hat{r}^2 d\hat{r}$.

Derivations of parameters 8–13 are given by Ellington (1984a). \hat{r} is the distance from the wing base of an element of the wing with non-dimensional chord \hat{c} and non-dimensional mass \hat{m}' . \hat{v} is the non-dimensional virtual mass of both wing couples. The virtual mass is the mass of air which is accelerated along with the wings during their motion.

All masses for 1, 7, 10 and 11 were taken from fresh specimens. Those collected in Malaysia could not be weighed fresh, and these parameters were therefore not available. Values for 7 and for the moment parameters 8–13 were found by strip analysis. For the moments of area, photographs of the fore- and hindwings, linked in the flight position, were divided into narrow strips concentric to the wing base (see Fig. 2, left-hand side). For 7 and for the moments of mass, the fore- and hindwing, linked as in flight, were cut into narrow, straight strips, parallel to the body axis (Fig. 2, right-hand side). The virtual masses of both wing couples, and the non-dimensional radii of their first and second moments were calculated for the sake of completeness, but are not discussed.

Ellington (1984a, part II) notes that for animals with $AR < 4$, the circular chord, as used here for the area parameters, gives more accurate values than the rectangular chord. Unfortunately, it was only possible to obtain rectangular strip values for analysis of wing mass. These still provide a sound basis for comparative study.

The positioning of the wings for strip analysis is important. Butterflies in

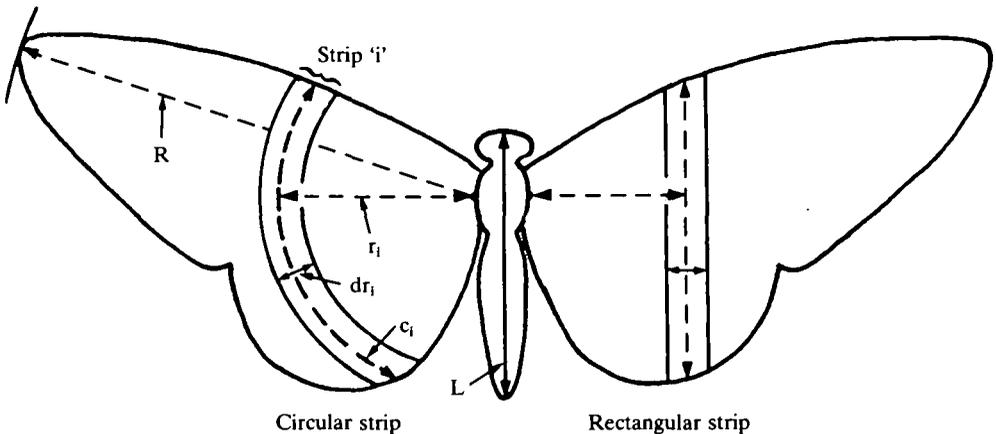


Fig. 2. Dimensions measured for the current study (see text for abbreviations).

collections are conventionally displayed with their wings fully extended. Observations from films suggest that this attitude is rarely achieved and is only transitory (at stroke extremes for instance): the attitudes of the wings in the outlines in Figs 1 and 2 are much more usual. Use of the circular chord eliminates the need to align the forewing other than extending it to its natural position. However, rectangular chord measurements and values for R would be affected by wing attitude: here measurements of R have all been made from wings aligned as in Fig. 2.

Film analysis

Timings of stroke intervals and tracings were all taken from images projected from an optical data analyser onto a flat surface using a front-silvered mirror.

Films were digitized for computer analysis using a PCD digital data reader, model ZAE 1E, incorporating a back projection screen and digitizer. Digitizer drift and frame distortion were negligible. The output was fed into an Apple II *via* a standard eight-bit analogue-digital converter. Programs developed by Newman (1982) were used to analyse the data. To summarize, the spatial relationships of the wing and body positions relative to the horizontal plane are calculated from the three-dimensional coordinates generated by computer for each digitized film frame. Changes in angular position of the wings and body can thus be accurately measured for the entire sequence and, by reference to a standard time-base, accelerations and relative velocities calculated. For further details of analysis procedures and notes on the form of the data produced by these programmes see Betts (1986c).

Parameters measured during film analysis (with abbreviations and units) were as follows (see Fig. 3).

- (i) Wing beat frequency, n (Hz).
- (ii) Mean angular velocity during downstroke, $\dot{\omega}$ (rad s^{-1}).
- (iii) Flight velocity, V (m s^{-1}) (presented in non-dimensional form in this

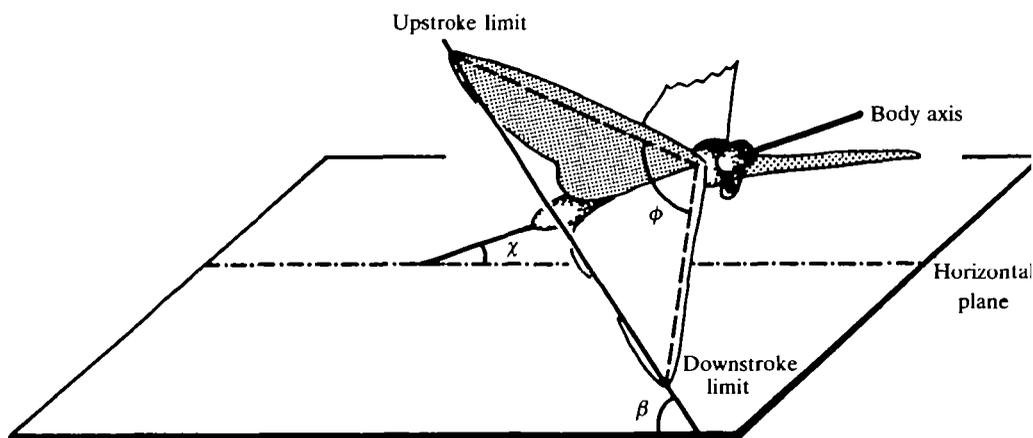


Fig. 3. Measurement of kinematic parameters (see text for symbol key).

study – \hat{V} ($= V/nR$) – representing number of wing lengths travelled per wing beat).

(iv) Advance ratio (ratio of the flight velocity to the mean flapping velocity of the wings), J ($= \hat{V}/2\phi$ where ϕ is in radians).

(v) Stroke plane angle (angle of extreme upstroke and downstroke limits relative to horizontal; see Fig. 3), β (presented as degrees in Table 2).

(vi) Stroke amplitude (angle described by extreme limits of wingstroke see Fig. 3), ϕ (presented as degrees in Table 2).

(vii) Body angle (angle of longitudinal body axis relative to horizontal), χ (presented as degrees in Table 2).

(viii) Pronation:supination ratio (ratio of time spent between end of upstroke and start of downstroke, to time spent between end of downstroke and start of upstroke), PRO: SUP.

(ix) Upstroke:downstroke ratio, US: DS.

Results

Morphometrics and wing shape

Table 1 summarizes morphometric data for the specimens filmed. Mean values have not been calculated because of the small sample sizes. Fig. 4 presents the relationship between the position of the centroid of wing area [$\hat{r}_1(S)$] and its radius of gyration [$\hat{r}_2(S)$] using data from this study. Data from Ellington (1984a, part II) are also included and the curve plotted represents the geometric relationship established by Ellington (1981, equation 38). Fig. 5 presents the equivalent relationship for wing mass and includes data and the curve representing the geometric relationship from Ellington (1981, equation 43). Figs 4 and 5 compare the geometric and empirical relationships.

Kinematics

Table 2 summarizes all the kinematic data from the film sequences analysed by computer. The butterflies displayed a wide range of complex flight patterns, each being a sequence of modes and rapid manoeuvres. In the course of filming and analysis four flight modes were distinguished: (1) fast climb (*FC); (2) slow forward flight (*SF); (3) fast forward flight (*FF); (4) hovering (*H). In the discussion which follows, two manoeuvres (tight turns and glides) are also recognized, but not analysed.

The flight modes were distinguished using ranges of values for J , the advance ratio, which proved to be the most consistent kinematic parameter (Table 2). Where $J < 0.1$ the insect was considered to be hovering, as in Ellington (1984a, part III). The remaining limits have been decided by repeated visual analysis of film sequences. Fast forward flight and fast climb or take-off were separated by an additional variable, the ratio of horizontal to vertical movement, describing the flight angle of the specimen. Sequences with values of this variable less than 2 represented a steep climb or take-off. Take-off was easily recognized visually.

Table 1. *Morphometric data of specimens examined*

| Species code | R (mm) | m (g) | L (mm) | P_w (Nm^{-2}) | S (mm^2) | AR | I_w ($kgm^2 \times 10^{-7}$) | $\hat{f}_1(S)$ | $\hat{f}_2(S)$ | $\hat{f}_1(m)$ | $\hat{f}_2(m)$ | \hat{v} | $f_1(v)$ | $f_2(v)$ |
|--------------|--------|--------|--------|---------------------|--------------|------|----------------------------------|----------------|----------------|----------------|----------------|-----------|----------|----------|
| TR1 | 67 | 0.725 | 45 | 1.43 | 4950 | 3.63 | 10.4 | 0.378 | 0.440 | 0.301 | 0.359 | 1.16 | 0.458 | 0.477 |
| TR2 | 63 | 0.629 | 47 | 1.51 | 4069 | 3.90 | 9.19 | 0.393 | 0.474 | 0.362 | 0.435 | 0.947 | 0.499 | 0.524 |
| PR1 | 67 | 0.435 | 36 | 0.957 | 4454 | 4.03 | 8.01 | 0.343 | 0.414 | 0.458 | 0.522 | 1.05 | 0.470 | 0.487 |
| PR2 | 55 | 0.328 | 33 | 0.852 | 3778 | 3.20 | NA | 0.497 | 0.546 | 0.312 | 0.375 | 1.33 | 0.546 | 0.570 |
| GS2 | 40 | 0.350 | 24 | 1.785 | 1925 | 3.32 | 3.05 | 0.437 | 0.491 | 0.276 | 0.372 | 0.874 | 0.534 | 0.553 |
| GS3 | 27 | 0.202 | 27 | 1.334 | 1487 | 1.96 | NA | 0.619 | 0.669 | 0.368 | 0.463 | 1.42 | 0.748 | 0.777 |
| GS4 | 40 | 0.149* | 26 | 0.743 | 1969 | 3.25 | NA | 0.463 | 0.509 | 0.369 | 0.439 | 1.25 | 0.508 | 0.529 |
| PH1 | 48 | 0.232 | 28 | 0.831 | 2739 | 3.36 | 4.10 | 0.439 | 0.491 | 0.407 | 0.490 | 1.19 | 0.496 | 0.549 |
| PH2 | 40 | 0.190 | 27 | 0.956 | 1949 | 3.28 | NA | 0.461 | 0.529 | 0.415 | 0.490 | 1.00 | 0.566 | 0.587 |
| PI | 33 | NA | 21 | NA | 1976 | 2.20 | NA | 0.528 | 0.569 | NA | NA | 1.31 | 0.565 | 0.590 |
| ID | 15 | NA | 11 | NA | 250.1 | 3.60 | NA | 0.533 | 0.576 | NA | NA | 1.03 | 0.555 | 0.581 |

* Value is unreliable as specimen was not freshly killed; NA, not available.

TR, *Troides radamanthus*; PR, *Papilio rumanzovia*; GS, *Graphium sarpedon*; PH, *Pachliopta hector*; PI, *Precis iphita*; ID, *Idmon* sp.

Table 2. Kinematic data from film analysis

| Species code | Film sequence | Flight mode | n (Hz) | $\dot{\omega}$ (rad s ⁻¹) | J | \dot{V} | ϕ (degrees) | β (degrees) | χ (range, degrees) | PRO: SUP | US: DS |
|--------------|---------------|-------------|--------|---------------------------------------|--------|-----------|------------------|-------------------|-------------------------|----------|--------|
| TR1 | LC9b1 | *FF | 7.3 | NA | 0.674 | 2.59 | 69 | 110* | 7-30 | 1 | 0.416 |
| | LC9b2 | *FF | 9.8 | 39.7 | 0.458 | 1.60 | 68 | 100 | 10-26 | 0.666 | 0.500 |
| | LC9b3 | *H | 6.3 | NA | 0.054 | 0.262 | 24* | 140* | NA | 0.666 | 0.800 |
| | LC161 | *SF | 9.1 | 60.6 | 0.241 | 0.866 | 49 | 103 | 17-48 | 1 | 0.620 |
| PR1 | LC101 | *FF | 9.1 | 29.7 | 0.369 | 1.52 | 30 | 118 | 18-50 | 1 | 0.438 |
| | LC102 | *SF | 5.1 | 32.0 | 0.198 | 0.864 | 45 | 125 | 18-52 | 1 | 0.960 |
| | LC111 | *FF | 9.6 | NA | NA | NA | NA | NA | NA | 0.666* | 0.500 |
| | LC141 | *H | 9.8 | 62.2 | 0.059 | 0.172 | 64 | 84 | 0-33 | 0.500 | 0.920 |
| GS3 | LC151 | *H | 19 | 145 | 0.091 | 0.362 | 35 | 114 | 0-11 | 1 | 0.800 |
| | LC152 | *FC | 21 | 60.9 | 0.833 | 2.52 | 59 | 86.7 | 22-51 | 0.666* | 0.500 |
| | LC153 | *H | 13 | NA | 0 | 0 | 62* | NA | 15* | 1* | 1 |
| | LC162 | *SF | 17 | 126 | 0.159 | 0.537 | 70 | 97 | 14-30 | 1* | 1.10 |
| GS4 | LC171 | *H | 19 | NA | 0.071 | 0.320 | 28* | 130* | 68* | 1* | 0.800 |
| | LC201 | *H | 12 | 51.4 | 0.052 | 0.186 | 87 | 102 | 10-20 | 1 | 0.820 |
| PH1 | LC202 | *FF | 16 | 53.9 | 1.06 | 3.47 | 79 | 94.2 | 44-56 | 0.500 | 1 |
| | LC203 | *SF | 13 | 36.9 | 0.177 | 0.642 | 67 | 104 | 13-33 | 1 | 0.820 |
| | LC204 | *FF | 13 | NA | 0.314 | 1.31 | 55* | 110* | 40* | 1 | 0.820 |
| | LC211 | *H | 14 | 51.1 | 0.069 | 0.359 | 45 | 148 | 14-28 | 1 | 1 |
| PH2 | LC211 | *H | 14 | 51.1 | 0.069 | 0.359 | 45 | 148 | 14-28 | 1 | 1 |
| | LC221 | *FF | 12 | NA | 0.249† | 0.911 | 20 | 105* | 67* | 1 | 0.875 |
| ID | LM51 | *FC | 19 | 330 | 0.314 | 1.71 | 53 | 156 | 14-45 | 6 | 1 |
| | LM52 | *FF | 14 | 209 | 0.615 | 2.75 | 61 | 128 | 26-48 | 4 | 0.571 |
| PI | LM61 | *FC | 9.4 | 43.4 | 2.11 | 3.83 | 90 | 52 | 19-42 | 2 | 1.42 |
| | LM62 | *FF | 14 | NA | 0.866 | 5.44 | 69* | 180* | 8* | 1* | 1.30 |

* Visual estimation; NA, not available; †, ?slow climb.

Data are mean values of three successive wingbeats.

For details of species codes see Table 1, and for details of flight modes see text.

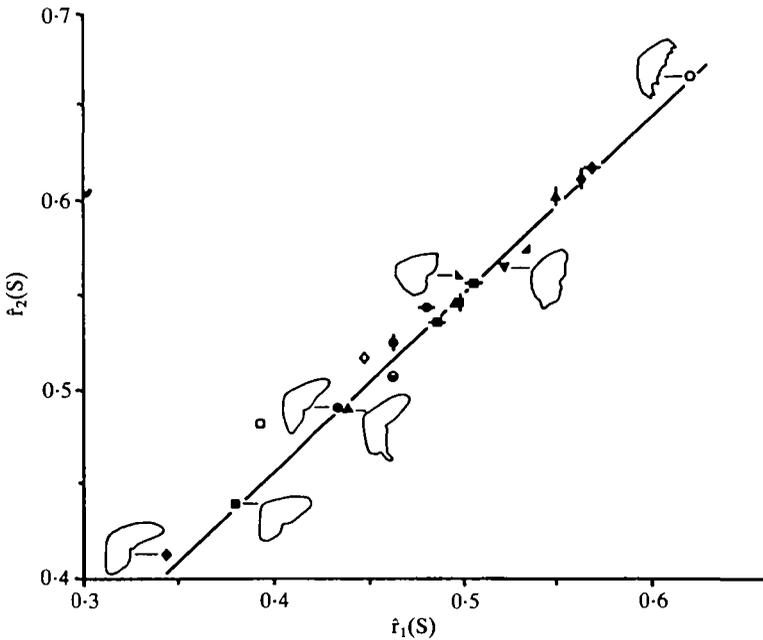


Fig. 4. Graph representing the relationship between shape parameters $\hat{f}_1(S)$ and $\hat{f}_2(S)$. Wing planforms are given for data plotted from the current study, to show how shape varies along the curve. The equations for the regression on this data and for the curve plotted (the geometric relationship of Ellington, 1981) are compared below.

| Geometric relationship (Ellington, 1981) | Empirical relationship (current study) | S.D. ($P = 0.05$) |
|---------------------------------------------|--------------------------------------------|------------------------|
| $\hat{f}_2(S) = 0.153 + 0.847\hat{f}_1(S)$ | $\hat{f}_2(S) = 0.116 + 0.881\hat{f}_1(S)$ | NS |

Key to symbols: \blacklozenge PR1; \diamond PR2; \blacksquare TR1; \square TR2; \bullet GS2; \circ GS3; \odot GS4; \blacktriangle PH1; \triangle PH2; \blacktriangledown PI; \blacktriangleright ID; \blacklozenge Odonata (*Aeshna* forewing)*; \blacklozenge Neuroptera (*Pterocroce*)*; \blacktriangle Diptera (*Tipula*)*; \bullet Hymenoptera (*Apis*)*; \bullet Coleoptera (*Coccinella*)*; \blacktriangle Heteroptera (*Palomena*)**; \blacksquare bat (*Plecotus auritus*)*; \blacksquare birds (*Amazilia fimbriata fluvialis* and *Ficedula hypoleuca*)*.

* Ellington, 1984a, part II; ** C. R. Betts (unpublished data).

Discussion

Wing shape

The moment parameters usefully characterize wing shape. They can also give aerodynamic information (for which they were originally designed) and, in conjunction with other morphometric data, yield some interesting observations on overall wing design. Figs 4 and 5 show that data from the current study fit Ellington's (1984a, part II) geometrical laws very closely (no significant statistical difference). This is even true when the wings are badly worn (*Graphium* 3, *Papilio* 2, *Pachliopta* 2) suggesting that, although substantial areas of the wing margin can be lost during normal flying life (25% for *Graphium* 3), this wear can

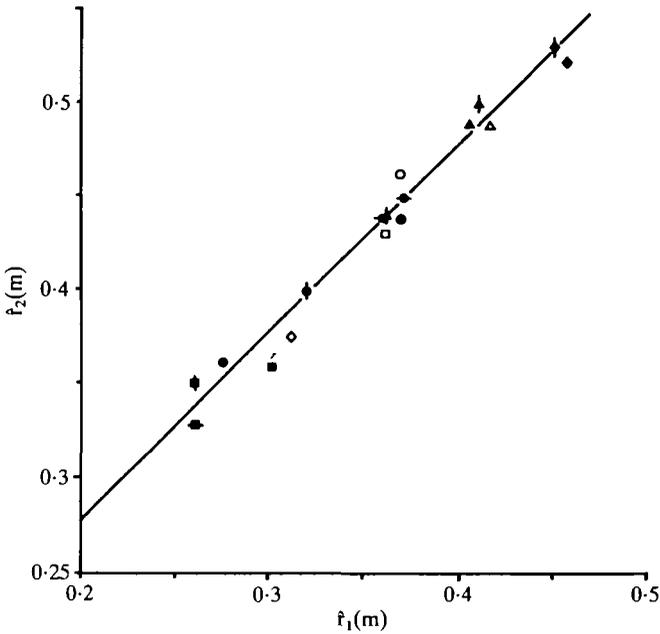


Fig. 5. Graph representing the relationship between shape parameters $\hat{r}_1(m)$ and $\hat{r}_2(m)$. The equation for the regression on this data and that for the curve plotted (geometric relationship of Ellington, 1981) are compared below. See Fig. 4 for symbols.

| Geometric relationship (Ellington, 1981) | Empirical relationship (current study) | S.D. ($P = 0.05$) |
|---------------------------------------------|-------------------------------------------|------------------------|
| $\hat{r}_2(m) = 0.093 + 0.971\hat{r}_1(m)$ | $\hat{r}_2(m) = 0.040 + 1.09\hat{r}_1(m)$ | NS |

be uniform, so that wing shape remains symmetrical. The large spread of values on both graphs is both inter- and intraspecific in origin. Wing damage may account for some of the variation; and males and females can also have different wing shapes (compare *Troides* 1, male, and *Troides* 2, female, in Fig. 1). In the intact individuals examined, wing area is concentrated quite near the base, with the larger specimens having the lowest $\hat{r}_1(S)$ values (0.4–0.45). Low values are characteristic of flying animals with broad wing bases, like most papilionid butterflies. The distribution of wing mass is much more variable, some specimens having it concentrated towards the wing base (*Troides*, *Graphium*), others where the centre of wing mass is more distal, comparable to dragonflies (intact *Papilio* 1 and *Pachliopta*).

Wing loading in the butterflies examined is also very low, at the bottom end of the range of flying animals (see data in Ellington, 1984a).

Of those examined, intact specimens of *Papilio* and *Troides* have the most similar wing shape and size. Their flight behaviour, however, is very different, and there are structural differences. Intact *Papilio* 1 has more wing area concentrated

basally [$\hat{r}_1(S) = 0.343$; average *Troides* values = 0.381] but relatively more mass concentrated distally [$\hat{r}_1(m) = 0.458$; average *Troides* values = 0.331]. *Papilio* is much lighter than *Troides*, and the wing loading of both specimens is 20 % lower than in *Troides*.

Kinematics

It is possible to characterize each flight mode using the kinematic parameters described earlier (see values of J in Table 2). Although there are inconsistencies, due both to flight versatility and analysis error, some patterns are still discernible from the data, and from extensive qualitative observation, and unlisted measurements from other sequences.

Fast forward flight

The kinematics of *Troides* and *Papilio* were notably different through the range of flight behaviour. During fast forward flight *Papilio* had a lower mean angular velocity than *Troides*, but comparable wing beat frequency and greater stroke amplitude. Body angle was continually changing in all species recorded, with a good deal of vertical motion and pitching. Stroke plane angle is affected by altering the body angle; and the greater the stroke plane angle, the faster the flight speed (Ellington, 1984a: part III). In fast flight, *Papilio* adopted a higher range of body angles than *Troides*, and the stroke plane was consequently shallower. In contrast, *Pachliopta* adopted a steep stroke plane angle and greater wing beat frequency and mean angular velocity than *Troides* and *Papilio*.

Precis had the highest non-dimensional flight velocity in this mode, employing a near-vertical stroke plane with a shallow body angle. Both stroke amplitude (visual estimate) and upstroke/downstroke ratio were by far the highest among the butterflies studied and may indicate the aerodynamic mechanism employed (see next section).

Slow forward flight

During slow forward flight both *Papilio* and *Graphium* had greater stroke amplitude, mean angular wing velocity and stroke plane angle, but lower wing beat frequency than in fast flight. *Troides* also increased its mean angular wing velocity, but in contrast reduced its stroke plane angle. This variation between species in change of stroke plane angle suggests different flight strategies. In all three species, the consistent increase in mean angular wing velocity was accompanied by an increase in the US:DS ratio; these latter changes appeared to continue as flight speed decreased, culminating in the extreme values seen during hovering.

Pachliopta, most frequently seen in this flight mode, showed little consistent kinematic change between modes.

Hovering

During hovering, in most sequences analysed, a mean body angle of around 15°

was maintained, associated in all species except *Troides* with a steeply inclined stroke plane. Although a horizontal stroke plane was certainly used on occasions, particularly by *Graphium*, this was more the exception than the rule. Indeed an inclined stroke plane may well be more common in other hovering insects than previously supposed (A. R. Ennos, personal communication). Stroke amplitude varied but mean angular velocity was greater for *Papilio* and *Graphium* than in their other flight modes. There was a relative increase in upstroke times during hovering except in *Pachliopta*, which retained a US:DS ratio of about 0.8:1 throughout the range of flight modes. A high US:DS ratio has been recorded in other hovering animals (Ellington, 1984a, part III). *Pachliopta* and *Graphium* were probably the most accurate and frequent hoverers. *Troides* was rarely recorded hovering; the analysed sequence shows a shallow stroke plane as is consistent with the reduction in stroke plane angle with flight speed recorded above.

Take-off and climb

All species were capable of high non-dimensional flight speeds during take-off and rapid climbs: *Papilio* was the slowest, *Graphium* and *Idmon* the fastest by far. The latter two species stand out by having such high mean angular wing velocities during take-off and hovering – between two and five times as high as any of the other species.

Aerodynamic considerations

Despite notable recent advances (Weis-Fogh, 1973; Ellington, 1978, 1984b; Rayner, 1979) there is still much to be learnt about the aerodynamics of flapping flight. The clap-and-fling mechanism of Weis-Fogh (1973) is now well known. Ellington (1984b) presents some additional aerodynamic lift-generating mechanisms for some insects for which the ‘quasi-steady assumption’ (where instantaneous forces generated by a moving wing are explained in terms of a conventional steady, not-flapping, aerofoil) fails. These mechanisms all rely on vortex shedding during rotational motion of the wing at stroke extremes. The ‘peel’ and ‘partial peel’ rely on the wings meeting and then moving rapidly apart, leading edge first, creating circulation about each wing. The large stroke amplitude and wing deformations seen during sequences of hovering, slow forward and fast forward flight in *Precis*, *Graphium* 2 and *Graphium* 4, and especially *Idmon*, suggest they may be using the peel or partial peel to generate lift at stroke reversal. Bocharova-Messner & Aksyuk (1982), studying the flight of *Gonopteryx rhamni*, have also suggested that the wing alignment when the wings meet at stroke extremes creates a ‘tunnel’, which could act as a funnel for the production of ‘jet-forces’. The attitude of the wings at stroke reversal would direct the action of the aerodynamic forces generated in this way and so determine the relative proportion of lift and thrust components.

The quasi-steady assumption may be enough to explain the flight of many animals (although the use of alternative mechanisms can never be ruled out) and

may be adequate for the low-frequency, large-amplitude wing beats exhibited by most butterflies. Rotational mechanisms may also be operating, particularly in those butterflies where strong wing twisting is observed (e.g. *Pachliopta*, *Graphium*, *Idmon*).

The vertical stroke plane seen in *Pieris* during take-off and hovering (Ellington, 1984b) has also been seen in some film sequences of *Pachliopta*, *Graphium* and *Papilio* and during fast forward flight in *Precis*. In the case of *Precis* and *Pachliopta* in particular, the insect gives the appearance of rowing through the air (similar to that seen in Heteroptera; Betts, 1986c). A pressure-drag mechanism of force-generation proposed by Ellington (1984b) is used to explain this phenomenon. Film of *Pieris* flying in the wild shows that, like the other species, it does not always employ a vertical stroke plane and a large stroke amplitude during fast forward flight; and it may well prove to be similarly variable when hovering, using inclined, vertical or horizontal stroke planes.

Many butterflies use a 'flap-glide' technique where fast forward flight is interspersed with significant periods of gliding. This is rarely used by other insects (Kingsolver, 1985) although recorded for locusts by Baker & Cooter (1979) and for some dragonflies. Butterflies may be able to optimize their gliding performance by smoothing the airflow over their wings. Martin & Carpenter (1977) established empirically that the wing 'tails' of some species enhanced the airflow over the wing surface by stabilizing the shed tip-vorticity. In their experiments, Martin & Carpenter used specimens and scale models with linked wings acting as single aerofoils. In all the gliding sequences analysed here the wings of each specimen appeared to be unlinked during gliding (Fig. 6). By permitting airflow between the

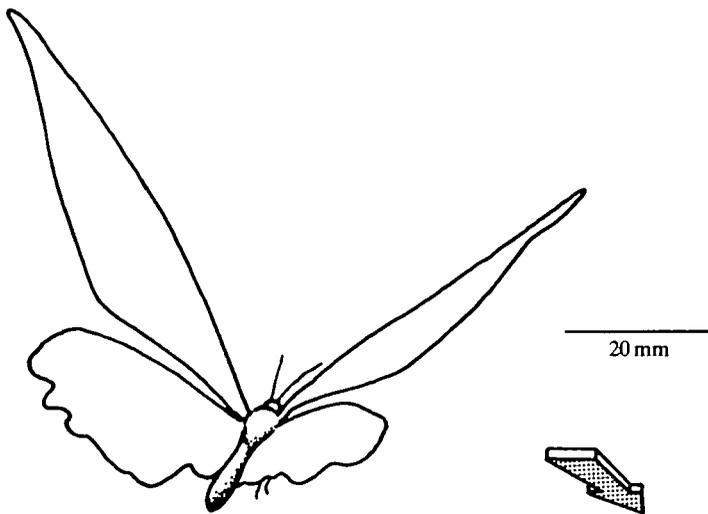


Fig. 6. Tracing from high-speed ciné film of *Papilio rumanzovia* during a glide, showing the unlinked fore- and hindwings. Its direction of motion is indicated by the arrow.

fore- and hindwings, the flow over the whole aerofoil may perhaps be improved by a slotting effect, delaying stalling at low speeds and/or high angles of attack.

Flight behaviour and wing form

Predictions

Our knowledge of the relationship between wing shape and flight performance in animals comes mainly from birds and bats (e.g. Norberg, 1981; Norberg & Rayner, 1987; Rayner, 1987). Butterfly wing planforms are very different from those of vertebrates; their wing loadings are several orders of magnitude lower, and they probably make far more use of non-steady aerodynamic mechanisms. Nonetheless, it is useful to list some simple predictive generalizations, based on theory and on vertebrate studies, against which our observations can be tested.

In general, high wing loading is associated with fast flight, low wing loading with slow flight and sometimes hovering. A high aspect ratio goes with power economy; low aspect ratios allow low loadings in comparatively short wings, when there are environmental constraints on span, or advantages in minimizing inertial and bending moments.

A low moment of inertia (second moment of mass) tends to minimize power consumption in flapping flight, and may also aid agility – particularly in animals where direction changes and accelerations occur in the course of one or two wing beats.

In butterflies it might therefore be expected that: (1) short, broad (low AR) wings would favour slow, agile flight, and would be common among forms that frequently fly in restricted spaces or dense vegetation; (2) long, slender (high AR) wings would be associated with species that fly extensively, but available speeds would depend on wing loading, which would be low in forms that hover frequently and high in species that fly fast and use shallow glides; (3) forewings with extended, narrow tips would gain some of the benefits of a high aspect ratio while maintaining reasonably low moments of area and mass, and hence high agility.

Conclusions

How far do our results (Tables 1, 2) match these predictions?

Troides radamantus consistently performed prolonged, fast flights, travelling the full expanse of the area, occasionally climbing or visiting flowers, but rarely hovering or executing rapid manoeuvres. This fits well with predictions: the high aspect ratio and high wing loading together favouring fast extended flight, and the high moment of wing inertia discouraging manoeuvrability and hovering. However, the insects may not have shown their full range of flight patterns in the rather small enclosure. In Malaysia, *Troides ?helena* flew similarly, but seemed to glide more frequently and for greater distances (original observation); and males of this species have been seen performing fast turns and accurate hovering during sexual display (R. Vane-Wright, personal communication). But in general fast, pro-

longed, relatively unmanoeuvrable flight seems to be characteristic of many birdwing butterflies. In Malaysia, *Trogonoptera brookiana* males (AR = 5) appeared to fly even faster than *Troides*, at steady speeds along uniform paths performing occasional steep climbs and tight turns.

Papilio rumanzovia, superficially rather similar in size and shape to *Troides* but with a markedly lower wing loading and moment of wing inertia, presents a nice contrast in flight pattern, which fits well with expectation. The individuals studied flew more slowly and with far greater manoeuvrability, showing rapid accelerations and extended tight turns, and hovering at flowers.

Pachliopta hector is a smaller species – about half the mass and wing area of *P. rumanzovia* and so with a similar wing loading – and has a lower moment of wing inertia. The aspect ratio is distinctly lower than that of the intact *Papilio*; but the moments of area are higher, probably reflecting the elongate and rather broad forewing, and illustrating the limitations of describing butterfly wing shape solely in terms of aspect ratio. The manoeuvrability, generally low flight speed, and frequent hovering conform with predictions, but the insect was capable on occasion of flying nearly as fast as *Troides*.

The wing area of *Graphium sarpedon* is about 17% lower than that of *Pachliopta*, and the wing loading of the intact male was markedly higher. Aspect ratio and area moments are similar despite the obvious difference in shape: the forewing has a narrower elongate tip, and the hindwing no tail. The moments of inertia are far lower, reflecting the basal concentration of wing mass.

The flight of *Graphium* was very different from the other species studied. Both in the enclosure and in the wild it was a fast, agile flier capable of repeated rapid manoeuvres and skilful accurate hovering. Individuals often settled, and executed short, fast flights between perches – as did the smaller nymphalid, *Polyura*, which occurs in the same situations. *Polyura* has broader wings than *Graphium*, but shares the conspicuously narrow and produced forewing tip.

Again performance matches well with expectation, particularly with prediction 3 above. The high wing loading conforms with the generally rapid flight, and low moment of wing inertia with manoeuvrability and frequent hovering. Interestingly, wing clapping and the high angular accelerations at stroke reversal tended to fray the lightly constructed distal margins, so that it was possible to monitor the effect of a more-or-less isometric reduction in wing area. Loss of 25% of the wing of *Graphium* 3 increased the beat frequency, lowered the speed, and reduced the capacity to hover and turn accurately, and prevented sustained flight.

Precis iphita has a low aspect ratio and high area moments: it is broad-winged, with a large distal chord. The filmed individual flew with a lower beat frequency and mean angular velocity than did *Graphium*, using its short, stiff wings for rapid manoeuvring and extended slow glides – predictable from the wing shape – but was capable of remarkable and unexpected bursts of speed, using a steep stroke plane and a sharply increased amplitude and frequency.

Hesperiidae (skippers) are taxonomically and morphologically distinct from other butterflies. Most are small, though some approach hawk-moth size and look

rather similar, but with broader wings. *Idmon*'s aspect ratio is moderate, with a large distal chord. We have no figure for wing-loading, but the bodies are stout and values are probably high.

Skippers are capable of very fast flight, are extremely manoeuvrable, and hover well. In Malaysia *Idmon* was difficult to follow in flight: it may not have reached full speed on film. The wing bases are stout, and the tips are strongly deformed at stroke reversal; this is not surprising since the mean angular velocities reached are comparable with those of some asynchronous flight systems (Betts, 1986*b*). The unremarkable value for wing beat frequency is misleading, since one wing beat occupied only 20 ms followed by a delay of about 40 ms before the next downstroke. Throughout this interval the skipper was propelled forward with wings closed over its abdomen. Manoeuvres could be accurately performed within a half-stroke.

In summary, the flight patterns of the butterflies studied broadly agree with predictions based on theory and on experience of the effects of wing loading, aspect ratio and wing inertial moments in vertebrates. However, this is clearly a simplistic approach. Butterflies sometimes perform in unexpected ways: witness the bursts of high-speed flight in *Precis* and *Pachliopta*, and the hovering of male *Troides* in courtship. There is an overall impression of great versatility, with individuals being capable of switching between flight modes and manoeuvres by startling shifts in frequency, amplitude and stroke plane angle, in a manner quite unlike that of most insects whose flight has been investigated. Inter- and intraspecific differences in kinematic parameters suggest that a wide variety of aerodynamic tricks are in use, whose implications on wing design are quite unknown.

The quantitative description of wing form remains a problem. Aspect ratio, a mainstay of bird and bat morphometrics, is evidently quite inadequate to describe the complex shapes of butterfly wings. Non-dimensional moment parameters are far more promising, though still imperfect, and other measures of shape may be devised. However described, the significance of wing form will only emerge through multivariate analysis of the flight and morphology of a wide range of species, and from a rigorous study of their aerodynamics. Both are now under way.

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