BIOMECHANICS OF FLIGHT IN NEOTROPICAL BUTTERFLIES: MORPHOMETRICS AND KINEMATICS

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Summary

Wing and body kinematics of free cruising flight are described for 37 species of Panamanian butterflies ranging over two orders of magnitude in body mass. Butterflies exhibit considerable diversity in body and wing shape, but morphological design is, in general, isometric. Wing loading and mean body diameter show positive allometry. The cruising flight of butterflies is characterized by low wingbeat frequencies (here averaging 11 Hz), stroke amplitudes averaging 103°, and forward speeds in excess of $1 \, \text{m s}^{-1}$. Body angles during flight are close to horizontal, and stroke plane angles are correspondingly high. Advance ratios are typically greater than 0.9, indicating that the forward and flapping velocity vectors are of comparable magnitude. Flight speed scales with morphological parameters in general accordance with predictions based on isometric design. Interspecifically, no consistent correlation exists between wing kinematics and absolute flight speed. However, maximum positional angle and stroke amplitude tend to increase while body angle decreases with increased relative flight speed.

Introduction

The wide diversity of wing size and shape in butterflies (Lepidoptera: Papilionoidea and Hesperioidea) suggests considerable variation in the biomechanics and aerodynamics of flight. Although variation in wing kinematics and the characteristic flight styles of particular butterfly species have been commented upon anecdotally, there is little quantitative description of these phenomena. Unlike most other insects, many butterflies exhibit considerable vertical oscillation during horizontal flight, giving rise to the characteristic fluttering flight path. The biomechanical implications of these oscillating flight paths have never been investigated. Similarly, the basic aerodynamics of butterfly flight has not been systematically studied. The low aspect ratio wings characteristic of many butterfly species are generally associated with a large induced drag and correspondingly high power requirements of flight. However, only a detailed analysis of the aerodynamic mechanisms operating during flight will permit a functional evaluation of butterfly wing shape.

The biomechanics and flight patterns of butterflies are also of considerable ecological interest. It has been suggested that the frequently erratic flight of butterflies helps them to evade would-be predators (e.g. Humphries and Driver, 1970; Edmunds, 1974). It has also been demonstrated that specific flight patterns and wing and body shapes are associated with unpalatability in tropical mimetic butterflies (Chai, 1986).

Recently, surveys of flight morphology and kinematics in bats and birds have helped to interpret flight styles and functional correlates of wing and body form (e.g. Norberg, 1981, 1986; Norberg and Rayner, 1987; Rayner, 1987; Viscor and Fuster, 1987). Equivalent studies for the diverse array of flying insects are not yet available. It is the purpose of this study to present kinematic data and a biomechanical interpretation of wing and body morphology for the butterfly superfamily Papilionoidea (Ackery, 1984). This paper describes, for an assemblage of Panamanian butterflies, wing and body motions determined using video filming and three-dimensional image reconstruction. Kinematic analysis is confined to wing motions relative to the butterfly body and to general body orientation in space; correlations between flight kinematics and various aspects of wing and body morphology are investigated. Additional papers will evaluate, for the same butterflies, vertical oscillations of the body and the aerodynamics and mechanical power requirements of flight.

Materials and methods

Study site and butterflies

All work was carried out on Barro Colorado Island, a research station located in Lake Gatun, Republic of Panama. The butterfly fauna of Barro Colorado Island is described by Huntington (1932). Butterflies chosen for the study belonged principally to the families Papilionidae, Pieridae and Nymphalidae (identifications following DeVries, 1987). However, one small riodinid butterfly and one skipper (Hesperioidea: Hesperiidae) were filmed. Butterflies were collected in either the laboratory clearing or the forest of Barro Colorado Island, and were generally filmed on the same day. Those butterflies filmed on the following day were kept overnight in small net cages and were fed a solution of sugar and water (1:1 v/v).

Filming procedures

Filming was carried out in a small screened insectary (3.4 m×3 m×2.1 m). Butterflies were released in the insectary and allowed to fly freely. A video camera (Panasonic AG-160) equipped with a high-speed electronic shutter (1/1000 s) was used to film at 30 frames s^{-1}; the high-speed shutter permitted sharp resolution of the moving wings. Butterflies generally cruised back and forth along one side of the insectary, opposite which the video camera was positioned horizontally using a spirit level. The camera was mounted on a tripod at a fixed height of about 1.5 m, and was generally 2 m from the insectary wall. Ambient temperatures in the insectary during filming ranged from 30 to 35°C and relative humidities from 82 to

95%. Ambient air motion in the screened insectary was negligible. After approximately 20 min of free flight, the butterfly was captured and killed by gently squeezing the thorax, with little or no hemolymph loss.

Morphological parameters

Morphological measurements on all butterflies were made within 10 min of filming; mass loss during this time was negligible. Basic morphological parameters determined for each insect included the following: body mass m (which includes the mass of both wing pairs), thoracic mass m_t (expressed in both absolute terms and as a fraction of body mass, $\hat{m}_t$), wing length R, body length $\hat{L}$ (expressed as a fraction of wing length) and total wing area S (the area of both wing pairs). Wing and body lengths were determined to ± 0.1 mm using dial calipers. Wing base separation was also measured to ± 0.1 mm, and was used to calculate the wingspan B (the distance between the extended wing tips) (see Norberg and Rayner, 1987). Wing area was determined with a leaf area meter (Delta-T Devices AMS), with the fore- and hindwings placed together in a position roughly equivalent to that observed in flapping flight (see Betts and Wootton, 1988). Areas of the fore- and hindwing were also determined separately (S_{fore} and S_{hind}, respectively), and their overlap during flapping flight S_{over} is given by ($S_{fore} + S_{hind} - S$). In many butterflies, a portion of the hindwing folds over part or all of the abdomen and does not noticeably move when the wings flap. This overlap of the hindwing onto the body, S_{body}, was determined by cutting and measuring this area separately from one of the two hindwings. Because this area does not function as part of the flapping wing surface, it was subtracted from the measurement of total wing area S. Wing loading p_w ($=mg/S$, where g is gravitational acceleration) and aspect ratio $\mathcal{R}$ ($=4R^2/S$) were calculated for each insect.

While such basic morphological data as body mass and wing area are essential for a biomechanical analysis of flight, several non-dimensional parameters are also useful in evaluating the functional consequences of wing and body shape. In particular, the present morphological analysis makes considerable use of the moments about the wing base (and their non-dimensional radii) of wing area, wing mass and wing virtual mass, which is the mass of air accelerated by the moving wings. For greater details of the theory and methods involved, see Ellington (1984b).

Wing mass $\hat{m}_w$ (the mass of both wing pairs) was measured to the nearest 0.1 mg and expressed as a percentage of the total body mass. The distribution of wing mass along the longitudinal wing axis was determined in the following manner. Beginning at the wing base, consecutive 5-mm strips were cut perpendicular to the wing length. Each strip was weighed to the nearest 0.1 mg. To correct for mass losses during the cutting and weighing procedure, the mass of each strip was multiplied by the ratio of the initial wing pair mass to the sum of masses of the individual strips. Non-dimensional radii of the first and second moments of wing mass [$\hat{r}_1(m)$ and $\hat{r}_2(m)$] were determined using the strip masses. Using tracings of the wing pair outline, non-dimensional radii for the first three moments of wing

area $[\hat{r}_1(S)$, $\hat{r}_2(S)$, $\hat{r}_3(S)]$ and of wing virtual mass $[\hat{r}_1(v)$, $\hat{r}_2(v)$, $\hat{r}_3(v)]$ were determined. Calculations of these area and virtual mass parameters were made using wing chords concentric to the wing base rather than chords perpendicular to the wing length, because of the low aspect ratio.of the wings (Betts and Wootton, 1988). A non-dimensional virtual wing mass $\hat{v}$ (equal to the ratio of the wing virtual mass to that of a wing of equal R but with a constant wing chord equal to the mean wing chord) was also calculated for each wing pair. Virtual mass estimates are only approximate as these calculations assume a perpendicular wing chord, not the circular chord used here. A mean wing thickness $\hat{h}$, expressed as a percentage of the wing length, was also calculated.

The center of mass of the body was determined from masses of five body regions (head, two thoracic sections and two abdominal sections), assuming mass to be homogeneously distributed within each section (see R. Dudley and P. J. DeVries, in preparation). This procedure assumes that the center of mass is located on the longitudinal body axis. Because body length is large relative to mean body diameter (see Results), this is an appropriate assumption. The distance of the center of mass from the anterior tip of the body is termed $\hat{l}$, while $\hat{l}_1$ is the distance of the center of mass to the wing base axis, and $\hat{l}_2$ is the radius of gyration for the moment of inertia of the body about the wing base axis. These three parameters were expressed non-dimensionally as a fraction of body length L, as was the mean body diameter $\hat{d}$ (Ellington, 1984b). Absolute values of the mean body diameter d were also calculated.

For comparison with results of previous workers, linear regressions were used to evaluate correlations between the body shape parameters $\hat{l}_1$ and $\hat{l}_2$, the wing shape parameters $\hat{r}_1(S)$ and $\hat{r}_2(S)$ and the wing mass parameters $\hat{r}_1(m)$ and $\hat{r}_2(m)$. Linear correlations between log-transformed values of the non-dimensional radii charac-terizing wing mass and shape were also performed to determine allometric power functions relating the different radii. Bivariate reduced major axis (RMA) correlations were determined between the log-transformed data of body mass and various wing and body dimensions to evaluate their allometry (see Rayner, 1985, for a discussion of appropriate statistical models in biomechanical analysis).

Flight kinematics

Video films were viewed using frame-by-frame playback on a video tape recorder (Hitachi VT 1570-A) connected to an AMDEK Video-300 VDU. For each butterfly, representative sequences of approximately horizontal, non-acceler-ating flight were identified through repeated viewing of the video tape. For each sequence, the following points on the butterfly image were manually digitized from each video frame: anterior and posterior tips of the body, wing base and both wing tips. The accuracy of the digitization process was checked by digitizing video images of variably sized circles. Typical distortion was approximately 4% of the true value for linear dimensions in the central regions of the screen where images were analyzed. Images near the screen edges were avoided. For all sequences, linear regressions of the coordinates of the wing base were used to determine the

angle ξ between the flight path and horizontal. Sequences in which the absolute value of ξ was greater than $15°$ were rejected.

Determination of wing motions and body orientation in three dimensions requires geometric reconstruction of the wing tip position using two-dimensional film images. Mathematical details of the reconstruction procedure used here can be found in Ellington (1984c), and will be briefly summarized. By considering the wing tip positions at both ends of a half-stroke, the three-dimensional motion of the wing tip relative to the body can be described. Points of interest on the insect's wing and body are transformed from a coordinate system based on the film image to a coordinate system based on the insect's body. Wing motions are assumed to be symmetrical with respect to the longitudinal body axis, which is the case in forward flight. A computer program which encoded the reconstruction procedure was written in MS-BASIC for use with a Macintosh Plus microcomputer.

For purposes of kinematic analysis, it was necessary to determine a reference length for each flight sequence. The low filming speed of the camera precluded use of the maximum projected wing length of a sequence as the reference length (cf. Ellington, 1984c). Instead, the projected body length was used. For all filming, the camera was nominally perpendicular to the flight path of the insect (see Results), and the projected body length was equivalent to the maximum possible projected length. An average projected body length was calculated for each flight sequence, and was used to estimate a maximum projected wing length by scaling appropriately from the morphological data. Occasionally, otherwise promising flight sequences could not be analyzed because the hindwing obscured the posterior tip of the body for a substantial number of frames.

The kinematic analysis assumes that wing motions are confined to a stroke plane which forms an angle β relative to horizontal. The maximum positional angle ϕ_{max} and the minimum positional angle ϕ_{min} refer to the wing tip position in the stroke plane at the top and bottom of the half-stroke, respectively. Stroke amplitude Φ, the angular extent of motion in the stroke plane, is given by $\phi_{max} - \phi_{min}$; the mean positional angle $\bar{\phi}$ is equal to $(\phi_{max} + \phi_{min})/2$. Body angle χ is the angle relative to horizontal made by a line segment connecting the anterior and posterior tips of the body, when the insect is viewed laterally. Measurements of body angle were made when the wings were at the top (χ_t) and at the bottom (χ_b) of the half-stroke; the change in body angle through the half-stroke, $\Delta\chi$ ($=\chi_t - \chi_b$) and an average body angle $\bar{\chi} = (\chi_b + \chi_t)/2$ were also calculated.

Proper identification of two video frames representing the top and bottom of the half-stroke is critical for a correct determination of wingbeat kinematics. Because, in general, these frames did not immediately follow one another (unless the wingbeat frequency was exactly $15\,Hz$), it was necessary to analyze composite wingbeats formed from non-consecutive frames separated by intervening wingbeats. One frame was chosen which depicted the wing at the top of the half-stroke, and then the video tape was advanced frame by frame until the wing was shown at the bottom of the half-stroke. Video sequences were viewed repeatedly to guarantee correct identification of the frames containing the top and bottom of the

half-stroke. Multiple composite wingbeats were analyzed in each video sequence to evaluate short-term variation in kinematic parameters (see Results).

For each flight sequence, the wingbeat frequency n was determined by counting the number of video frames required to complete a wingbeat, with occasional visual estimation of the wing positional angle. Because of the filming speed of the video camera ($30\,\text{frames}\,\text{s}^{-1}$), the accuracy of this procedure was low, approximately $\pm 2\,\text{Hz}$. Five estimates of the wingbeat frequency were made and used to determine a mean value for each flight sequence. A similar frame counting procedure was also used for each sequence to determine the ratio of upstroke duration to downstroke duration ($US:DS$). For each butterfly, the number of frames in all analyzed sequences which depicted gliding flight (characterized by little or no wing motion from frame to frame) was determined. This quantity was divided by the total number of frames to determine the relative extent of gliding flight, G.

For all video filming, the optical axis of the camera was horizontal, so that the body angles and stroke plane angles determined by the kinematic analysis were expressed relative to true horizontal. Values of the roll η about the longitudinal body axis were calculated for each composite wingbeat (see Ellington, 1984c). Yaw α, which describes the rotation of the insect about the vertical axis, was also determined. Values of η are positive when the insect rolls away from the camera, and positive α indicates a yaw towards the camera. A yaw of $0°$ indicates that the longitudinal body axis is orthogonal to the camera. Non-zero yaw indicates that the actual projected body length deviates from the maximum possible projected length.

Relative flight speed $\hat{V}$ was determined by calculating the number of body lengths travelled horizontally by the wing base per second. Horizontal airspeed V was then expressed in absolute terms (m s^{-1}) by scaling with the measured body length. Flight speeds were related allometrically to wing and body morphology using RMA correlations on log-transformed data. RMA correlations were also used to evaluate the dependence of wing and body kinematics upon forward airspeed.

Errors arising from perspective effects in the three-dimensional reconstruction of the video image were estimated from the formulae given by Ellington (1984c). Representative values for horizontal coverage of the film image and for the distance from the object plane to the focus of the lens were about 7 and 75 wing lengths, respectively. Maximum error arising from the neglect of perspective in reconstructed spatial angles of the wings was calculated to be less than $1°$, and the deviation from true horizontal of the horizontal plane based on the image projection was less than $2°$.

Results

Butterfly identification and morphometrics

Morphological data were obtained for a total of 49 butterflies and one skipper,

Table 1. *Identification number (ID), species, sex, mass (m), wing length (R), aspect ratio (Æ), wing loading (p$_w$) and relative thoracic mass (m̂$_t$) of 15 butterflies for which three flight sequences were analyzed, and minimum, mean and maximum values of the same morphological parameters for the full sample of 50 butterflies*

ID	Species	Sex	m (mg)	R (mm)	Æ	p$_w$ (N m^{-2})	m̂$_t$
1	*Battus polydamas* (Linnaeus)	F	454.4	53.0	3.34	1.33	0.43
2	*Papilio thoas* Rothschild and Jordan	M	423.1	58.4	3.52	1.07	0.49
3	*Parides childrenae* (Gray)	M	373.1	46.1	3.86	1.66	0.41
4	*Aphrissa boisduvalii* (Felder)	F	138.3	32.5	2.09	0.67	0.55
5	*Itaballia demophile* Joicey and Talbot	F	88.6	28.4	2.47	0.66	0.37
6	*Archaeoprepona demophon* Fruhstorfer	F	1058.9	60.4	2.77	1.97	0.51
7	*Myscelia cyaniris* (Doubleday)	F	91.0	31.6	2.79	0.62	0.42
8	*Pyrrhogyra naerea* Godman and Salvin	F	111.7	30.6	2.35	0.69	0.35
9	*Siproeta stelenes* (Fruhstorfer)	F	239.5	40.9	2.78	0.98	0.42
10	*Dryas iulia* (Fabricius)	M	175.0	44.1	5.09	1.12	0.43
11	*Janatella leucodesma* (Felder and Felder)	M	24.0	18.1	2.66	0.48	0.44
12	*Morpho amathonte* Deyrolle	M	331.4	70.3	2.75	0.45	0.50
13	*Morpho peleides* Butler	F	357.7	60.5	2.60	0.62	0.45
14	*Caligo illioneus* Butler	M	1047.3	74.3	2.25	1.05	0.49
15	*Pierella luna* (Fabricius)	M	76.6	35.1	3.19	0.49	0.57
(N=50)	Minimum		17.4	17.1	1.92	0.26	0.23
	Mean		267.3	39.8	3.06	0.92	0.44
	Maximum		1841.2	82.3	5.09	1.97	0.59

representing 37 species. Seven species were represented by two individuals (generally a male and a female), and three species were represented by three individuals. The taxonomic distribution of species was as follows: Papilionidae, 4; Pieridae, 5; Nymphalidae: Charaxinae, 2; Nymphalidae: Nymphalinae, 9; Nymphalidae: Heliconiinae, 5; Nymphalidae: Melitaeinae, 1; Nymphalidae: Ithomiinae, 2; Nymphalidae: Morphinae, 2; Nymphalidae: Brassolinae, 1; Nymphalidae: Satyrinae, 4; Riodinidae, 1; Hesperiidae, 1. Most butterflies were fairly large (average mass 267 mg) to ensure an adequate image size during filming, and there was little representation of butterflies of mass less than 90 mg.

Three separate flight sequences were analyzed for each of 15 individuals (see below), for which species identification, sex and general morphological parameters are given in Table 1. For the same butterflies, wing shape parameters are given in Table 2 and body parameters in Table 3. For comparative purposes, Tables 1–3 also include the minimum, mean and maximum values of all morphological parameters for the 50 butterflies examined. Because only one individual was generally used per species, intraspecific differences arising from geographical variation or sexual dimorphism were ignored. This variation is, however, likely to be small compared with the wide range of interspecific variation apparent in Tables 1–3.

Linear regressions were applied to the non-dimensional radii characterizing the

Table 2. *Wing parameters of the 15 butterflies for which three flight sequences were analyzed, and minimum, mean and maximum values of the same parameters for the full sample of 50 butterflies*

ID	$\hat{r}_1(S)$	$\hat{r}_2(S)$	$\hat{r}_3(S)$	$\hat{r}_1(v)$	$\hat{r}_2(v)$	$\hat{v}$	$\hat{m}_w$ (%)	$\hat{h}$ (%)	$\hat{r}_1(m)$	$\hat{r}_2(m)$
1	0.535	0.578	0.610	0.551	0.576	1.34	5.4	0.025	0.29	0.34
2	0.520	0.562	0.595	0.528	0.551	1.34	5.5	0.019	0.27	0.35
3	0.535	0.578	0.607	0.595	0.622	1.30	6.9	0.034	0.27	0.33
4	0.600	0.657	0.697	0.600	0.635	1.13	7.3	0.023	0.31	0.37
5	0.578	0.636	0.675	0.586	0.623	1.12	6.5	0.023	0.31	0.38
6	0.518	0.559	0.588	0.561	0.586	1.35	5.3	0.027	0.24	0.30
7	0.539	0.588	0.622	0.615	0.649	1.14	5.9	0.020	0.30	0.36
8	0.466	0.519	0.557	0.493	0.531	1.18	5.6	0.021	0.30	0.36
9	0.518	0.563	0.594	0.570	0.598	1.26	4.8	0.021	0.35	0.43
10	0.472	0.524	0.563	0.458	0.488	1.25	5.1	0.021	0.22	0.30
11	0.588	0.652	0.697	0.561	0.604	1.08	5.0	0.021	0.30	0.37
12	0.533	0.575	0.605	0.579	0.605	1.32	10.3	0.011	0.27	0.33
13	0.566	0.609	0.639	0.624	0.650	1.28	9.5	0.016	0.37	0.44
14	0.603	0.651	0.686	0.655	0.686	1.18	9.9	0.021	0.25	0.32
15	0.566	0.612	0.651	0.612	0.644	1.15	6.5	0.014	0.39	0.42
(N=50)										
Minimum	0.445	0.503	0.540	0.407	0.459	1.06	2.7	0.010	0.22	0.27
Mean	0.526	0.578	0.615	0.542	0.576	1.19	5.9	0.023	0.30	0.37
Maximum	0.626	0.678	0.713	0.655	0.686	1.35	10.3	0.074	0.44	0.52

$\hat{r}_1(S)$, $\hat{r}_2(S)$, $\hat{r}_3(S)$, first, second, and third non-dimensional radii of the moments of wing area; $\hat{r}_1(v)$, $\hat{r}_2(v)$, first and second non-dimensional radii of the moments of wing virtual mass; $\hat{v}$, non-dimensional virtual mass; $\hat{m}_w$, wing mass as a percentage of body mass; $\hat{h}$, mean wing thickness as a percentage of wing length; $\hat{r}_1(m)$, $\hat{r}_2(m)$, first and second non-dimensional radii of the moments of wing mass.

wing shape and mass distribution, to compare the relationships for butterflies alone with those determined by Ellington (1984b) for a set of insects from various orders. Regressions relating $\hat{r}_2(m)$ to $\hat{r}_1(m)$, $\hat{r}_3(S)$ to $\hat{r}_1(S)$ and $\hat{r}_2(v)$ to $\hat{r}_1(v)$ were all significant at $P<0.0001$, and their slopes did not differ significantly from those previously published. The regression of $\hat{r}_2(S)$ on $\hat{r}_1(S)$ was also highly significant ($P<0.0001$), but 95% confidence limits of the slope fell outside that given previously. Least-squares regression was also performed on the non-dimensional radii of the first and second moments of body mass about the wing base axis, $\hat{l}_1$ and $\hat{l}_2$. The resulting correlation was highly significant ($P<0.001$), and the slope of the regression did not differ significantly from that reported by Ellington (1984b).

In addition to linear correlations between morphological parameters, bivariate linear regressions of log-transformed data were used to derive allometric relationships between the non-dimensional parameters characterizing wing shape. Such allometric relationships between the following sets of variables were highly significant ($P<0.001$): $\hat{r}_2(S)$ and $\hat{r}_1(S)$, $\hat{r}_3(S)$ and $\hat{r}_1(S)$, $\hat{r}_2(v)$ and $\hat{r}_1(v)$, $\hat{r}_2(m)$ and

Table 3. *Body parameters of the 15 butterflies for which three flight sequences were analyzed, and minimum, mean and maximum values of the same parameters for the full sample of 50 butterflies*

ID	$\hat{L}$	$\hat{d}$	$\hat{\imath}$	$\hat{\imath}_1$	$\hat{\imath}_2$
1	0.58	0.13	0.50	0.22	0.32
2	0.53	0.13	0.42	0.16	0.28
3	0.71	0.11	0.46	0.27	0.37
4	0.77	0.10	0.42	0.18	0.26
5	0.69	0.12	0.48	0.23	0.35
6	0.58	0.17	0.48	0.22	0.31
7	0.67	0.10	0.55	0.20	0.30
8	0.56	0.16	0.55	0.26	0.34
9	0.50	0.18	0.50	0.23	0.33
10	0.58	0.11	0.41	0.14	0.26
11	0.75	0.11	0.42	0.19	0.30
12	0.41	0.13	0.38	0.13	0.22
13	0.41	0.17	0.58	0.25	0.39
14	0.53	0.14	0.44	0.16	0.26
15	0.62	0.09	0.43	0.12	0.27
(*N*=50)					
Minimum	0.41	0.06	0.30	0.07	0.20
Mean	0.65	0.12	0.45	0.20	0.31
Maximum	1.04	0.20	0.60	0.42	0.50

$\hat{L}$, body length as a fraction of wing length; $\hat{d}$, mean body diameter as a fraction of body length; $\hat{\imath}$, distance of center of mass from anterior tip of body; $\hat{\imath}_1$, distance of center of mass from wing base axis; $\hat{\imath}_2$, radius of gyration of moment of inertia of the body about the wing base axis.

Values of $\hat{d}$, $\hat{\imath}$, $\hat{\imath}_1$ and $\hat{\imath}_2$ are expressed as a fraction of body length.

$\hat{r}_1(m)$, $\hat{r}_1(v)$ and $\hat{r}_1(S)$ and $\hat{r}_2(v)$ and $\hat{r}_1(S)$. Three of these regressions were characterized by exponents significantly different from those determined by Ellington (1984*b*) for a diverse group of insect wings from six orders: $\hat{r}_2(S)$ on $\hat{r}_1(S)$, $\hat{r}_2(v)$ on $\hat{r}_1(v)$ and $\hat{r}_1(v)$ on $\hat{r}_1(S)$. No significant correlation was found between log-transformed values of $\hat{r}_1(m)$ and $\hat{r}_1(S)$ or between $\hat{r}_2(m)$ and $\hat{r}_1(S)$.

For the full sample of 50 butterflies, the following morphological parameters increased isometrically with body mass ($P<0.001$): wingspan, wing length, body length, wing area, fore- and hindwing area, thoracic mass, wing mass, and fore- and hindwing mass. Wing loading (Fig. 1) and mean body diameter exhibited positive allometry. There was no significant correlation between aspect ratio and body mass ($P>0.05$).

Wing and body kinematics

Most butterfly species examined flew parallel to and within 20 cm of the sunlit side of the insectary. Typically, the butterfly cruised continuously back and forth for minutes on end, and flight sequences were taken from the center of the

Table 4. *Mean kinematic parameters of the 15 butterflies for which three flight sequences were analyzed, and average, minimum and maximum values of the same parameters for all analyzed sequences (44 butterflies)*

| ID	G	US:DS	n (Hz)	$\hat{V}$ (Ls^{-1})	V (ms^{-1})	J
1	0	1.14	12.4	60.5	1.87	1.33
2	0.27	0.9	9.5	57.1	1.77	0.93
3	0.12	0.59	12	58.0	1.90	0.95
4	0.31	0.76	13.7	46.5	1.16	0.61
5	0.13	0.94	11.7	64.1	1.26	0.81
6	0	1.06	8.9	89.9	3.16	1.43
7	0.17	1.08	9.1	56.3	1.20	1.23
8	0.08	1.35	10.7	55.4	0.94	1.04
9	0.13	0.96	10.7	81.0	1.66	1.30
10	0	1.22	13.9	48.1	1.22	0.55
11	0	1.28	13.3	56.0	0.76	0.77
12	0.35	1.17	6.4	43.9	1.26	0.72
13	0.13	1.03	6.9	52.0	1.28	1.09
14	0.16	1	9.6	52.0	2.07	0.90
15	0.57	0.5	13.7	34.0	0.74	0.63
(N=44)						
S.D.	–	0.1	1.2	7.3	0.19	0.08
Minimum	0.00	0.50	5.9	22.5	0.55	0.35
Mean	0.10	0.97	11.3	56.4	1.40	0.93
Maximum	0.57	1.35	23.0	139.8	3.16	2.03
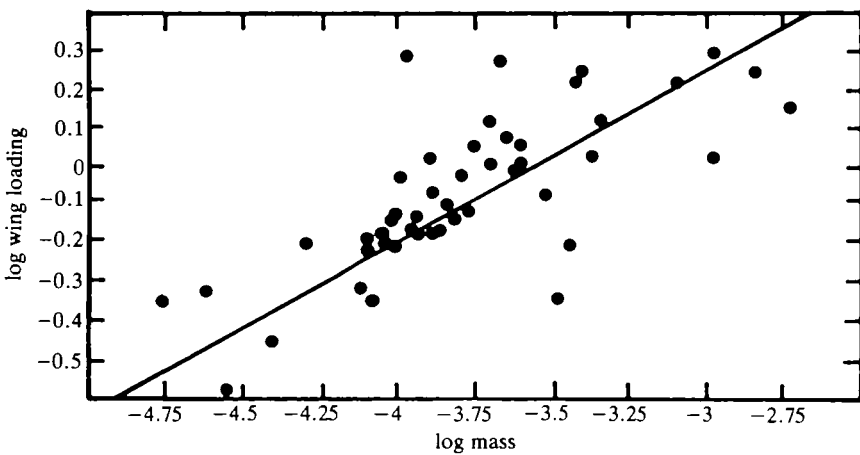
Fig. 1. Wing loading p_w (in N m^{-2}) *vs* body mass m (in kg) for 50 butterflies. The line shown is the reduced major axis correlation ($r=0.74$, $P<0.0001$); the equation is given by: $p_w=49.05m^{0.474}$. Wing loading exhibits positive allometry.

Table 4. *Continued*

ID	χ_t	χ_b	$\Delta\chi$	$\bar{\chi}$	β	$\beta+\chi$	ϕ_{max}	ϕ_{min}	Φ	$\bar{\phi}$
1	31	14	18	22	64	86	50	−12	61	19
2	21	12	9	16	79	95	62	−37	98	13
3	17	7	10	12	73	85	76	−27	104	25
4	41	14	27	27	42	69	73	−51	123	11
5	31	−18	49	7	67	74	75	−58	133	9
6	15	4	11	9	80	89	75	−42	118	16
7	18	−1	18	8	81	89	64	−33	97	15
8	21	13	7	17	77	94	55	−24	79	15
9	15	17	−2	16	76	91	59	−25	84	17
10	31	14	17	23	71	93	67	−36	103	15
11	24	11	13	18	68	86	75	−43	118	16
12	18	20	−3	19	73	92	61	−50	111	6
13	18	18	1	18	71	89	65	−15	81	25
14	32	18	14	25	71	96	76	−16	92	30
15	47	9	38	28	65	93	48	−22	70	13
($N=44$)										
S.D.	7	8	9	7	7	7	7	9	11	5
Minimum	8	−18	−3	3	39	46	48	−12	61	6
Mean	23	8	14	16	67	83	69	−33	103	18
Maximum	47	28	49	32	86	104	86	−66	144	30

Also included are the mean standard deviations for all kinematic parameters except for gliding, which was determined using all sequences for a given butterfly.

G, relative extent of gliding flight; $US:DS$, ratio of upstroke duration to downstroke duration; n, wingbeat frequency; $\hat{V}$, relative flight speed based on body length, L; V, absolute flight speed; J, advance ratio; χ_t, body angle at top of half-stroke; χ_b, body angle at bottom of half-stroke; $\Delta\chi$, change in body angle through half-stroke; $\bar{\chi}$, average body angle over half-stroke; β, stroke plane angle; ϕ_{max}, maximum positional angle; ϕ_{min}, minimum positional angle; Φ, stroke amplitude; $\bar{\phi}$, mean positional angle.

All angles are given in degrees.

generally horizontal flight trajectory. For six individuals, only weak fluttering flights in the corners of the insectary were filmed, and these butterflies were therefore used for morphological data only. From the other butterflies, one flight sequence was analyzed for each of 15 individuals, two such sequences for 14 individuals, and three flight sequences were analyzed for each of the remaining 15 butterflies. The mean number of video frames per analyzed flight sequence was 8.4 (equivalent to about 0.3 s of flight). Mean values of kinematic parameters for each sequence were calculated using an average of 2.4 composite wingbeats. Whenever either two or three separate flight sequences of a particular butterfly were analyzed, kinematic results from these sequences were averaged to yield representative values of the flight speed and other kinematic parameters. In such cases, statistical analysis was also performed separately using the kinematic data

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Table 5. *Allometric relationships between forward airspeed V and morphological parameters for the sample of 15 butterflies each with three analyzed flight sequences*

	Equation for V	Expected scaling	Correlation coefficient
m	$32.97m^{0.378}*$	1/6	0.89
m_t	$39.80m_t^{0.363}*$	1/6	0.86
B	$15.14B^{0.997}$	1/2	0.71
R	$29.47R^{0.984}$	1/2	0.7
L	$191.51L^{1.338}*$	1/2	0.8
d	$56.71d^{1.825}$	1/2	0.53
S	$25.59S^{0.496}$	1/4	0.67
$\mathcal{R}$	$0.11\mathcal{R}^{1.720}$	0	0.1 (NS)
p_w	$1.589p_w^{0.848}*$	1/2	0.86

All relationships were determined using RMA correlations of log-transformed data; all units are kg, m or s.

Significant differences from isometric scaling are indicated with an asterisk; NS, not significant.

m, mass; m_t, thoracic mass; B, wingspan; R, wing length; L, body length; d, body diameter; S, total wing area; $\mathcal{R}$, aspect ratio; p_w, wing loading.

obtained for sequences showing the lowest, intermediate (if it existed) and highest flight speed.

For the 15 butterflies with three analyzed sequences each, average values of wing and body kinematic parameters are given in Table 4, as are mean values of the advance ratio J $(=V/2\Phi nR)$. For each kinematic parameter, standard deviations were derived from the three sequences of each butterfly, and mean values of these are also given in Table 4, as are means of the kinematic data and the range for all butterflies $(N=44)$ for which at least one flight sequence was analyzed. Flight sequences used for analysis generally displayed non-rolled flight perpendicular to the camera axis. For all analyzed wingbeats, the average absolute values of the roll η and yaw α were 8° and 9°, respectively.

Kinematics and morphology

For the sample of 15 butterflies with three analyzed flight sequences, forward airspeed was positively correlated with a variety of morphological parameters, including body mass, thoracic mass, wing length, wingspan, body length, mean body diameter, wing area and wing loading (Table 5). No significant correlation was found between aspect ratio and forward airspeed $(P>0.05)$. When these correlations were performed using alternately the lowest, intermediate or highest airspeeds (and the corresponding kinematic results) determined for each butterfly, the results were unchanged. Table 5 includes the predicted scaling of flight speed given isometric design (see Norberg and Rayner, 1987). The allometric dependence of flight speed on body mass, thoracic mass, body length and wing loading differed significantly from predicted values.
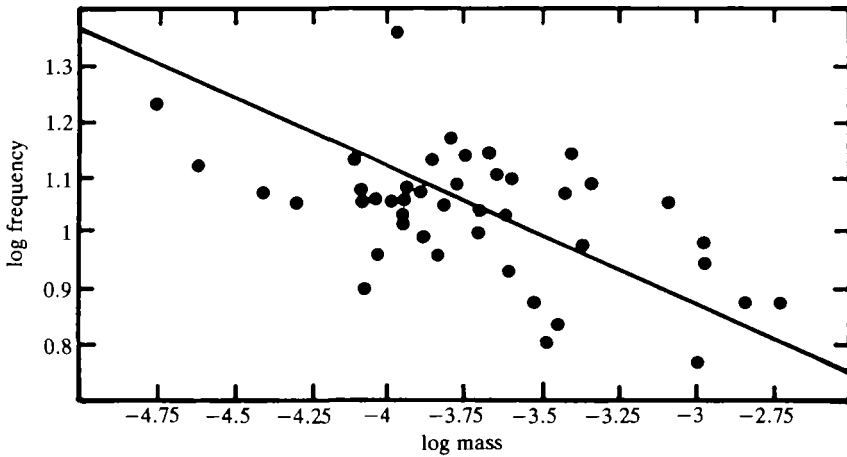
Fig. 2. Wingbeat frequency n (in Hz) *vs* body mass m (in kg) for 44 butterflies. The line shown is the reduced major axis correlation ($r=0.52$, $P<0.001$); the equation is given by: $n=1.194m^{-0.258}$.

Considering all butterflies for which at least one flight was analyzed, correlations of airspeed with wing length, mean body diameter, wing area and aspect ratio were not significant ($P>0.05$). Correlations of airspeed with body mass, thoracic mass, body length, wingspan and wing loading were, however, significant ($P<0.01$), although characterized by correlation coefficients much lower than those for correlations using the sample of 15 butterflies with three flight sequences each.

Of the kinematic parameters in Table 4, only the maximum positional angle ϕ_{max} was significantly correlated with mean forward airspeed V for the sample of 44 butterflies ($P<0.02$). For the 15 butterflies with mean airspeeds and kinematic parameters derived from three separate sequences, none of the kinematic parameters in Table 4 was positively correlated with forward airspeed. For both samples, mean body angle $\bar{\chi}$ and relative speed $\hat{V}$ were negatively correlated ($P<0.05$). For the sample of 15 butterflies, no other kinematic parameters were significantly correlated with $\hat{V}$, while for the sample of 44 butterflies only ϕ_{max} and the stroke amplitude Φ showed a significant increase with V ($P<0.05$).

Mean wingbeat frequency decreased with body mass to the power -0.24 for the sample of 15 butterflies, and with mass to the power -0.26 for the sample of 44 butterflies (Fig. 2); both of these exponents were significantly less than 0 ($P<0.05$). For neither sample, however, was there a significant correlation between wingbeat frequency and wing loading ($P>0.05$).

Many butterflies glided frequently and, of the species examined here, 60% glided to some extent (Table 4). Betts and Wootton (1988) noted that, in papilionid butterflies, the fore- and hindwings are generally separated during gliding. Because of the video camera orientation used here, it was not possible to evaluate in detail the separation between the fore- and hindwings in gliding butterflies. In most species, however, this separation did not appear to be

substantial and, particularly in the Pieridae and in the satyrine nymphalid *Pierella luna*, fore- and hindwings appeared to overlap during gliding flight. Overlap of the hindwings onto the body may improve aerodynamic flow and reduce body drag in either flapping or gliding flight. However, no significant correlation was found between the relative overlap of the wings on the body ($=S_{body}/S$) and either forward airspeed or the extent of gliding ($P>0.05$).

Because of the low filming frequency of the video camera, detailed analysis of wing orientation and deformation at the ends of half-strokes was not possible. Wing rotation at the ends of half-strokes was not, however, particularly pronounced in most flight sequences examined. Particularly for those butterflies with a significant overlap of the hindwing onto the body, the wing appeared to be maintained at an angle relative to horizontal close to that of the mean body angle throughout the wingbeat. Wing deformation during each half-stroke appeared to be minimal. At the beginning of the wingbeat, a pronounced clap and subsequent peeling apart of the two wing pairs was apparent in many butterflies (see Ellington, 1984*a*). This was most evident in the Pieridae (e.g. *Aphrissa boisduvalii*).

Discussion

Butterflies are far from morphologically uniform, as even a cursory examination of Tables 1–3 will reveal. Masses of the butterflies examined here range over two orders of magnitude, and there is considerable variation in wing and body shape parameters. Nonetheless, wing loading and aspect ratio are, in general, lower in butterflies than in other insects. Thus, wing areas relative to body mass are higher and wings are generally broader. Correspondingly, relative wing mass is substantially higher in butterflies than in other insect orders. Wing lengths typically exceed body lengths by 54 %, mean body diameters of butterflies average 12 % of the body length, and the center of mass of the body is located in the generally elongated abdomen. With the exception of mean body diameter and wing loading, morphological parameters increase isometrically with body mass. Wing loading in butterflies exhibits positive allometry, which has also been found by Norberg and Rayner (1987) for bats over a wide mass range.

In the sample of 50 butterflies analyzed for morphology, allometric relationships between the non-dimensional radii of wing area, wing mass and wing virtual mass are, in general, the same as those found by Ellington (1984*b*). However, there are exceptions, particularly the correlation between $\hat{r}_1(S)$ and $\hat{r}_2(S)$, which also differs from a linear regression derived from the area radii of Betts and Wootton (1988) for 11 butterflies. For the butterflies examined here, wing area is typically much more skewed distally [higher $\hat{r}_1(S)$; see Table 2] than in the insects examined by Ellington (1984*b*) and Betts and Wootton (1988). The butterflies examined by Betts and Wootton (1988) were primarily papilionids, whose broad wing bases tend to reduce the radius of the centroid of wing area. However, the correlation relating $\hat{r}_1(m)$ to $\hat{r}_2(m)$ does not differ significantly from that of Ellington (1984*b*) or from that of Betts and Wootton (1988). Also, no significant correlations were

found relating $\hat{r}_1(m)$ and $\hat{r}_2(m)$ to $\hat{r}_1(S)$, and such correlations are not significant for the butterfly mass and area radii given in Betts and Wootton (1988). These results suggest that, while wing mass distributions may be conservative across the Insecta, wing area distributions are not necessarily so.

Paralleling the morphological diversity of butterflies is substantial diversity in wing and body kinematics (Table 4). Several general trends are nonetheless apparent. Body angles during free flight are close to horizontal (averaging 16°), and stroke plane angles are correspondingly high (averaging 67°). Through the course of a wingbeat, body angles tend to vary, at times substantially, and on average decrease by 14° from top to bottom of the half-stroke. Stroke amplitudes are not particularly high, typically being close to 100°, although maximum positional angles are large (average 69°). Wingbeat frequencies of butterflies are low, averaging here around 11 Hz. In the insectary, butterflies flew at airspeeds generally in excess of $1 \, \mathrm{m \, s^{-1}}$, and the advance ratio of the wings averaged 0.93. The magnitude of the forward velocity vector was thus comparable to that of the flapping velocity vector. In contrast, the advance ratios for two bumblebee workers flying at $1 \, \mathrm{m \, s^{-1}}$ were 0.13 and 0.16, and the effects of flapping dominated flow over the wings (Dudley and Ellington, 1990).

Allometric relationships between forward airspeed and various morphological parameters generally corresponded to expectations based on isometric scaling (Table 5). Correlations were strongest when multiple flight sequences were averaged for each individual. For the sample of 15 butterflies each with three analyzed flight sequences, several correlations deviated significantly from the expected relationship based on isometry, most notably the variation of airspeed with body mass and wing loading. For flying animals in general, higher airspeeds are correlated with increased wing loadings. Chai and Srygley (1990) also found for 52 butterfly species in Costa Rica that airspeed was positively correlated with wing loading. No significant correlation was found here between flight speed and aspect ratio. In bats, Norberg and Rayner (1987) found that field airspeeds increased with aspect ratio, but suggested that this was an indirect effect arising from a positive correlation of aspect ratio with wing loading.

No systematic variation in wing kinematics with absolute flight speed is apparent in butterflies, although in some cases maximum positional angles and stroke amplitudes do show a significant increase with *relative* flight airspeed. Mean body angles decrease significantly with relative, but not with absolute, flight speeds. Betts and Wootton (1988) found for individual papilionid butterflies that slower flight was characterized by an increase in the stroke amplitude, stroke plane angle and upstroke: downstroke ratio, and by a decrease in the wingbeat frequency. Chai and Srygley (1990) suggested that fast-flying butterflies have deeper wingbeats, but no correlation was found here between stroke amplitude or minimum positional angle and flight speed. The highest relative flight speed observed here was attained by a riodinid (*Thisbe irenea*), which flew at $140 \, L \, \mathrm{s^{-1}}$. Its mean body angle was 7° and the stroke plane angle 65°; stroke amplitude was fairly high at 123°. The fastest (in non-dimensional terms) butterfly studied by

Betts and Wootton (1988) was *Precis iphita* (Nymphalidae), which flew at a low body angle and high stroke plane angle, and exhibited the highest stroke amplitude and upstroke:downstroke ratio of those butterflies studied. In absolute terms, the fastest butterfly studied here was *Archaeoprepona demophon* (Nymphalidae: Charaxinae), which in one sequence flew at $3.2\,\mathrm{m\,s^{-1}}$. At this speed, the body angle was $8°$ and the stroke plane angle was $85°$. Stroke amplitude ($111°$) was, however, only slightly greater than the sample average ($103°$). Interestingly, wing aspect ratio in *A. demophon* was below the sample average. Betts and Wootton (1988) suggested that low aspect ratio wings would be associated with slow flight but, as mentioned above, no such relationship was found here.

Filming in an enclosed insectary raises the possibility that flight behavior is not normal or is modified in some way unknown to the experimenter. This proposition is difficult to evaluate, given the absence of knowledge concerning flight behavior under natural conditions. There is little evidence to suggest, however, that the insectary dimensions seriously constrained flight activity or speeds. Butterflies cruised continuously in the insectary for minutes on end. The highest airspeeds measured in the insectary are substantial; as mentioned previously, the fastest flier (*A. demophon*) attained a speed of $3.2\,\mathrm{m\,s^{-1}}$. The butterfly *Caligo illioneus* (Nymphalidae: Brassolinae) is of comparable mass ($>800\,\mathrm{mg}$) to *A. demophon*, and in the insectary was on average slower by 54% ($N=2$ for each species). Field observations confirm that cruising flight in this species is much slower than in *A. demophon*. In the same subfamily as *A. demophon* is the mimetic butterfly *Consul fabius*, which unlike other charaxines has a fairly slow cruising flight (DeVries, 1987). The one filmed individual of this species flew in the insectary much more slowly than did *A. demophon* (average of $1.6\,\mathrm{m\,s^{-1}}$ *vs* $2.9\,\mathrm{m\,s^{-1}}$). While these comparisons are suggestive, only direct measurements of airspeeds for butterflies in natural free flight will evaluate the validity of studying flight behavior in an enclosed space.

Individual butterflies possess a considerable diversity of flight modes (*sensu* Betts and Wootton, 1988), ranging from hovering (at flowers or during mate selection and oviposition) to fast forward flight. Hovering in butterflies appears to be much more poorly controlled than in many dipterans and hymenopterans, with considerable lateral and vertical oscillation of the body. Slow deliberate flight characterizes butterflies in search of oviposition or nectar sites, while startled or migrating butterflies are probably much faster (see also Nikolaev, 1974). Here, the cruising flight of butterflies in the insectary corresponds to the fast forward flight mode described by Betts and Wootton (1988). Advance ratios of this flight mode are high, averaging 0.9 (Table 4). Because butterflies are capable of such variation in flight modes and performance, it is correspondingly difficult to determine a 'typical' flight speed for a given species. Additionally, intraspecific differences may exist in flight speed between the sexes, and in wing and body morphology depending upon nutritional state and age. By confining analysis of different butterflies to typical cruising flight in the same insectary and under approximately equivalent microclimatic conditions, flight behavior is operationally standardized.

Even then, analysis of multiple flight sequences for any one individual is appropriate. The strong correlations between flight speed and morphology which emerge here suggest that at least some degree of realism and standardization in flight behavior has been attained.

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