

BIOMECHANICS OF FLIGHT IN NEOTROPICAL BUTTERFLIES: AERODYNAMICS AND MECHANICAL POWER REQUIREMENTS

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Summary

A quasi-steady aerodynamic analysis of forward flight was performed on 15 species of neotropical butterflies for which kinematic and morphological data were available. Mean lift coefficients required for flight typically exceeded maximum values obtained on insect wings under conditions of steady flow, thereby implicating unsteady aerodynamic mechanisms even during fast forward flight of some butterflies. The downstroke produced vertical forces on average 18 % in excess of those necessary to support the body weight through the wingbeat, while the upstroke contributed minimal or negative vertical force. Estimated effective angles of incidence (α'_r) of the wings averaged 39° during the downstroke and -22° during the upstroke; spanwise variation in α'_r was greater than the average difference between half-strokes. Total mechanical power requirements of forward flight averaged 12.5 W kg^{-1} , for the case of perfect elastic storage of wing inertial energy, and 20.2 W kg^{-1} , assuming zero elastic energy storage. Energetic costs of the erratic trajectories during forward flight increased mechanical power requirements by an average of 43 %, assuming perfect elastic storage. Fluctuations in horizontal kinetic energy of the center of mass were principally responsible for this dramatic increase. When comparing different species, total mechanical power increased linearly with forward airspeed (assuming perfect elastic energy storage of inertial energy) and scaled with mass^{0.26}. If no elastic energy storage was assumed, mechanical power was independent of airspeed and was proportional to mass^{0.36}. Estimated metabolic rates during flight averaged 22 and $36 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, for the cases of perfect and zero elastic storage, respectively.

Introduction

The flight of butterflies is characterized by reduced wingbeat frequencies and often erratic flight trajectories. Compared to other pterygote insects, butterflies

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also possess lower aspect ratio wings and greater wing areas relative to body mass (Greenewalt, 1962; Betts and Wootton, 1988; Dudley, 1990). This paper evaluates the aerodynamic and biomechanical consequences of these attributes, using previously published kinematic and morphological data for 15 neotropical butterflies (Dudley, 1990). Mean lift coefficients necessary for flight are estimated using a quasi-steady aerodynamic analysis (see Ellington, 1984a). Recent studies of free forward flight in flies (Ennos, 1989) and bumblebees (Dudley and Ellington, 1990b) have demonstrated that quasi-steady aerodynamic mechanisms are inadequate to produce the forces required to offset the body weight (see also Zanker and Götz, 1990, for tethered *Drosophila*). By contrast, fast forward flight in the diurnal moth *Urania fulgens* (Uraniidae) may be consistent with quasi-steady aerodynamics (Dudley and DeVries, 1990), although the mean coefficients method does not unequivocally disallow unsteady mechanisms (Ellington, 1984a; see also Cloupeau *et al.* 1979). The precise means by which butterflies generate aerodynamic forces are not known, although during take-off and hovering of the cabbage white butterfly *Pieris brassicae*, pressure drag on the wings is the predominant force (Ellington, 1984a). One goal of this study is to evaluate the extent to which drag-based propulsion mechanisms are used by butterflies to effect forward flight.

From the results of a quasi-steady aerodynamic analysis, the total mechanical power required for flight can also be estimated. In bumblebees, both mechanical (Dudley and Ellington, 1990b) and metabolic (Ellington *et al.* 1990) power requirements are relatively independent of forward airspeed, up to $4\text{--}4.5\text{ m s}^{-1}$. In the moth *U. fulgens*, however, mechanical power requirements during flight increase substantially at higher airspeeds, because of a concomitant rise in the profile power associated with drag forces on the wings (Dudley and DeVries, 1990). This effect is less pronounced when the airspeed is low relative to the flapping velocity of the wings, and is thus reduced at lower advance ratios of the wings (Dudley and DeVries, 1990; see Ellington, 1984c, for a definition of advance ratio). Advance ratios for the butterflies considered here averaged 0.93 (Dudley, 1990), a value substantially lower than that for *U. fulgens* in both migratory and insectary flight. Correspondingly, the effect of changes in forward airspeed upon the relative velocity of the wings, profile drag and, thus, mechanical power requirements should be less pronounced. The quasi-steady aerodynamic analysis is used here to evaluate interspecifically the dependence of profile and total power requirements upon forward airspeed.

Unlike the typically rectilinear flight of most insects, the oscillating trajectories of many butterflies involve substantial changes in the kinetic and potential energy of the center of body mass. Erratic flight paths may therefore incur substantial energetic costs. The accelerations and vertical displacements of the center of mass during erratic flight are analogous to those occurring in the terrestrial locomotion of animals (e.g. Heglund *et al.* 1982a), and a similar approach is employed here to estimate the corresponding energetic costs for butterflies.

Materials and methods

Aerodynamics

The aerodynamic analysis of butterfly flight was identical to that used previously in studies of flight in bumblebees (Dudley and Ellington, 1990*b*) and in the moth *U. fulgens* (Dudley and DeVries, 1990). Following the quasi-steady assumption (Ellington, 1984*a*), the flapping wings were reduced to a set of spanwise wing sections operating, at successive intervals, under conditions of steady airflow. Lift and drag forces on wing sections were assumed to be proportional to the square of the component of relative air velocity perpendicular to the wing span. A mean lift coefficient $\overline{C_L}$ was determined such that the net vertical components of lift and drag, as summed along the wing span and through the wingbeat, offset the body weight. Wing motion was assumed to follow simple harmonic motion and to be confined to the stroke plane. Because the downstroke and upstroke were in general of unequal duration (Dudley, 1990), the angular motion of the wing in the stroke plane was expressed as two separate sinusoidal functions at different frequencies, the latter being determined from the upstroke:downstroke ratio and the average wingbeat frequency of the butterfly.

Morphological and kinematic data for each butterfly were taken from Dudley (1990). Species identifications for all 15 butterflies are given in Table 1. Three spanwise sections of the wing ($0-0.33R$, $0.33R-0.67R$ and $0.67R-1.0R$, where R is the wing length) were used in aerodynamic calculations; the area of each section was determined from an outline of the wing pair. The kinematic results given by Dudley (1990) are mean values derived from three separate flight sequences, each about 0.3 s in duration. The use of mean values for such kinematic parameters as stroke amplitude and wingbeat frequency is probably realistic for a quasi-steady aerodynamic analysis. However, because flight velocities of butterflies vary in both

Table 1. *Identification number (ID), species and sex of the 15 butterflies used in the quasi-steady aerodynamic analysis of forward flight*

ID	Species	Sex
1	<i>Battus polydamas</i> (Linnaeus)	Female
2	<i>Papilio thoas</i> Rothschild and Jordan	Male
3	<i>Parides childrenae</i> (Gray)	Male
4	<i>Aphrissa boisduvalii</i> (Felder)	Female
5	<i>Itaballia demophile</i> Joicey and Talbot	Female
6	<i>Archaeoprepona demophon</i> Fruhstorfer	Female
7	<i>Myscelia cyaniris</i> (Doubleday)	Female
8	<i>Pyrrogyra naerea</i> Godman and Salvin	Female
9	<i>Siproeta stelenes</i> (Fruhstorfer)	Female
10	<i>Dryas iulia</i> (Fabricius)	Male
11	<i>Janatella leucodesma</i> (Felder and Felder)	Male
12	<i>Morpho amathonte</i> Deyrolle	Male
13	<i>Morpho peleides</i> Butler	Female
14	<i>Caligo illioneus</i> Butler	Male
15	<i>Pierella luna</i> (Fabricius)	Male

the vertical and horizontal dimensions, assumption of a constant forward airspeed potentially introduces errors into the calculations of the magnitude and direction of the relative wind experienced by wing sections. For the butterflies considered here, the mean vertical component of the velocity of the center of mass averaged 16 % of the forward airspeed (range 10–30 %). Average deviation of the flight velocity vector from horizontal was thus approximately 11° , while its magnitude changed by 2 %. Average variation in the horizontal velocity of the center of mass was also small relative to the mean forward airspeed (19 %; range 12–27 %), but will cause a linear change in its magnitude. However, at the advance ratios under consideration, forward and flapping velocities are of comparable magnitude, and variation in the forward airspeed will result in a smaller change in the relative velocity of wing sections. Also, there was no correlation between vertical and horizontal deviations of the center of mass or between wing position and the center of mass for the flight sequences analyzed here (R. Dudley, in preparation). These considerations suggest that the use of an average horizontal airspeed will introduce only small errors into estimates of the relative velocity of wing sections and the associated aerodynamic forces. Incorporation of variation in forward airspeed into the quasi-steady analysis would, in any event, be difficult given the erratic character of the flight path.

To determine effective angles of incidence of the wings through the wingbeat, it was first necessary to determine wing inclination relative to the horizontal. Wing orientation was not measured directly in this study, but an indirect estimate was possible. Particularly in palatable butterflies, a substantial portion of the hindwing overlaps onto the body, and the wing is maintained at a small positive angle to the longitudinal body axis. With one exception (no. 3), the butterflies examined here were all palatable (*sensu* Chai, 1986). Aerodynamic calculations were therefore performed assuming three possible wing inclinations during the wing beat: $\bar{\chi} + 5^\circ$, $\bar{\chi} + 10^\circ$ and $\bar{\chi} + 15^\circ$, where $\bar{\chi}$ is the mean body angle during flight (see Dudley, 1990). Substantial spanwise variation in wing inclination was not observed on the original video films, and no account was taken of possible wing twisting through the course of a wingbeat. It must be noted that a small spanwise reduction in geometric angle of attack is apparent for some butterflies, particularly at the beginning of the downstroke (see photographs in Dalton, 1975). Effective angles of attack of wing sections were obtained by adding the assumed wing inclination to the angle between the relative wing velocity vector and the horizontal (Dudley and Ellington, 1990*b*). The zero-lift angle of butterfly wings was assumed to be -5° (see Nachtigall, 1967), and this value was subtracted from the effective angle of attack to obtain the effective angle of incidence of the wing, α'_r (see Ellington, 1984*d*). Aerodynamic calculations were also performed using values of $\bar{\chi} + 5^\circ$ and $\bar{\chi} + 15^\circ$ for the inclination of the wing relative to the horizontal, but assuming that incidence angles within 10° of the zero-lift angle resulted in profile drag only (see below) and generated no lift. For each spanwise wing section and for the wing as a whole, mean values of α'_r for the downstroke ($\overline{\alpha'_{r,d}}$) and upstroke ($\overline{\alpha'_{r,u}}$) were determined.

Aerodynamic and inertial power requirements

The total mechanical power required for forward flight can be determined by examining the three components of aerodynamic power (parasite power P_{par} , induced power P_{ind} and profile power P_{pro}), and the inertial power during the first half of a half-stroke, P_{acc} . Parasite power is given by the product of the body drag and the forward airspeed V . Body drag D_b and body lift L_b were calculated using standard formulae (see Dudley and Ellington, 1990b). No data exist on the aerodynamic characteristics of butterfly bodies, and drag and lift coefficients were therefore taken from data for bumblebee bodies (Dudley and Ellington, 1990b) at the appropriate orientation and Reynolds number (Re). Bumblebee bodies operate at similar Re values to the butterflies considered here (1000–5000), and have similar non-dimensional body diameters (see Dudley, 1990). Parasite power was generally a small fraction of total power requirements (see Table 3), so estimates of the mechanical power required to fly were relatively insensitive to the choice of body drag coefficient. Also, body lift was in all cases less than 2 % of body weight, so that the vertical force balance was not seriously affected by the choice of body lift coefficient.

Following momentum jet theory, the induced power P_{ind} was determined from the product of the body weight (less body lift) and the induced velocity V_i , the latter calculated from the equation given in Dudley and DeVries (1990). The area swept out by the beating wings, ΦR^2 (where Φ , the stroke amplitude, is expressed in radians), was used as the actuator disc area in all calculations. Although in fast forward flight of animals a circle of radius R equal to the wing length (the wing disc) is generally used as the actuator disc (e.g. Pennycuik, 1975), use of ΦR^2 for the disc area (erroneously printed as $2\Phi R^2$ in Dudley and DeVries, 1990) is more appropriate, as it corresponds to the area across which the wings can impart vorticity to the wake (Ellington, 1984e). Moreover, use of the wing disc area can underestimate induced power at low airspeeds (see Ellington, 1984e). Ellington's formulation includes reduction of the disc area by the cosine of the stroke plane angle, to obtain the horizontal projection of the area swept out by the wings. This modification is not used here, because the high stroke plane angles (average of 67°; see Dudley, 1990) would reduce the actuator disc area by an excessive 60 %. Also, as was noted by Rayner (1979), wake momentum in forward flight is not perpendicular to the actuator disc, suggesting that a horizontal effective disc area is inadequate to model momentum flux with non-vertical components. Use of ΦR^2 as the actuator disc area is intended as a reasonable compromise between these diverse considerations.

Profile power P_{pro} was determined from the following equation (Dudley and Ellington, 1990b):

$$P_{\text{pro}} = \rho C_{D,\text{pro}} \int_0^R c(r) V_R^3 dr, \quad (1)$$

where ρ is the mass density of air, $C_{D,\text{pro}}$ is the profile drag coefficient of the wing, $c(r)$ is the wing chord (not wing area, as mistakenly given in Dudley and DeVries,

1990) at distance r from the wing base and V_R is the relative velocity of the wing at distance r . Equation 1 was evaluated by summing profile power requirements for each of the three aforementioned spanwise wing sections. The mean Re for the wingbeat of each wing section was determined from the mean chord and the average relative velocity of the section midpoint. From the mean value of Re , $C_{D,pro}$ was determined from the equation given by Ellington (1984d; equation 9) for wings operating at the Re and effective angles of incidence α'_t characteristic of insects in hovering flight, values of which are similar for butterflies in forward flight (see Table 2). Although the equation of Ellington (1984d) was derived from results for wings under conditions of steady flow, it is the best available approximation for drag coefficients in the Re range under consideration. Ellington (1984f) noted that in any case the appropriate data for unsteady drag coefficients on wings are not available. Mean profile power requirements averaged over the wingbeat were determined.

The inertial power during the first half of a half-stroke, P_{acc} , was estimated from the moment of inertia of the wing and the maximum angular velocity during the half-stroke (see Ellington, 1984f). The moment of inertia I of the wing mass and wing virtual mass was determined from morphological parameters given previously (see Dudley, 1990; Dudley and Ellington, 1990b). Maximum angular velocities were calculated separately for the downstroke and upstroke using the mean wingbeat frequency and the upstroke:downstroke ratio. Simple harmonic motion of the wing in the stroke plane was assumed. If the kinetic energy of the oscillating wing mass and virtual mass can be stored as elastic strain energy and later released, then inertial power requirements through the wingbeat will be zero. Mechanical power requirements (excluding power to oscillate the center of body mass) will in this case equal the aerodynamic power, $P_{aero} (=P_{par} + P_{ind} + P_{pro})$. Alternatively, if there is no elastic energy storage of wing inertial energy, then supplementary power will be required to accelerate the wing during the first half of a half-stroke. During the second half of the half-stroke, however, the negative power requirements that characterize wing deceleration are close to zero (Ellington, 1984f), while aerodynamic power requirements over the same period can be supplied by the kinetic energy of the decelerating wings. The power output averaged over the half-stroke will then be half the sum of P_{aero} and P_{acc} . For one butterfly (no. 8), P_{aero} was greater than P_{acc} (see Table 3). For this butterfly, power requirements averaged over the half-stroke were again simply P_{aero} , as aerodynamic power requirements during the second half of a half-stroke could not be completely supplied by the energy of the decelerating wing mass (see Dudley and DeVries, 1990).

Energy changes of the center of mass

Changes in the potential and kinetic energies of the center of mass were estimated for each butterfly following the methods described in Heglund *et al.* (1982a). From the previously determined wing base position (x, y), the position of

the center of mass of the butterfly, $(x_{\text{cm}}, y_{\text{cm}})$, was determined using the following equations:

$$x_{\text{cm}} = x \pm \hat{I}_1 L' \cos \chi \quad (2)$$

and

$$y_{\text{cm}} = y - \hat{I}_1 L' \sin \chi, \quad (3)$$

where \hat{I}_1 is the non-dimensional distance of the center of mass from the wing base axis (see Ellington, 1984b), L' is the projected length of the body on the video image, and χ is the body angle in flight. The sign in equation 2 was positive when the butterfly was flying to the left and negative when it was flying to the right. Coordinates were then expressed in a horizontal system, (x', y') , by rotating the (x, y) system through ζ , the angle between the mean flight path and the horizontal (see Dudley, 1990). This transformation facilitated identification of vertical and horizontal motions of the center of mass as deviations in x' and y' from linear regressions of the two variables upon time. Because all flight sequences were characterized by absolute values of ζ of less than 15° (average 6.2°), distortion of the flight trajectory as a consequence of this transformation was small. Linear regressions of x' and y' upon time t were then used to determine residual deviations of the position of the center of body mass ($\Delta x'$ and $\Delta y'$, respectively), which were normalized by the mean body length for the flight sequence. Maximum and average values of $\Delta x'$ and $\Delta y'$ were determined for each butterfly by pooling absolute values from the three flight sequences.

For each of the three analyzed flight sequences of each butterfly, the trajectory of the center of mass in the (x', y') system was used to determine temporal variation in horizontal and vertical velocities. Horizontal and vertical kinetic energies and the gravitational potential energy of the center of mass were calculated and added to yield the total energy of the center of mass. The sum of positive increments in the total energy was divided by the total period of analyzed flight to obtain the associated mechanical power necessary to accelerate and lift the center of mass, P_{cm} . The percentage recovery of energy resulting from exchange between the kinetic and potential energies of the center of mass was estimated using the formula given by Heglund *et al.* (1982a). Mean values for P_{cm} and percentage energy recovery were determined by averaging the results from the three flight sequences for each butterfly.

Rotational kinetic energy associated with changes in body angle was estimated as $\frac{1}{2}[I_b - m(\hat{I}_1 L)^2]\omega^2$, where I_b is the moment of inertia of the body about the wing base axis, m is the body mass, L is the body length and ω is the angular velocity of the body (see Manter, 1938; Fedak *et al.* 1982; Ellington, 1984b). For each of the three flight sequences of a given butterfly, the sum of positive increments in rotational energy of the body was divided by the duration of analyzed flight to obtain the associated power requirements. The resulting values from the three flight sequences were pooled to obtain an average power.

Total power requirements

For each butterfly, the mechanical power requirements for the cases of perfect

elastic energy storage ($=P_{aero}$) and zero elastic energy storage [$=\frac{1}{2}(P_{aero}+P_{acc})$] were added to the power required to lift and accelerate the center of mass, P_{cm} , and to rotate the body. As for the aerial phases of running in animals (Heglund *et al.* 1982*b*), it was assumed that kinetic energy of the wings could not supplement the energy of the center of mass. This assumption was further supported by the absence of correlation between wing position and the position of the center of body mass, as mentioned previously. The total mechanical power for flight was divided by the body mass to obtain specific power requirements for the two cases of perfect (P_{per}^*) and zero (P_{zero}^*) elastic storage of wing inertial energy. Metabolic rates were then estimated for each butterfly by dividing total specific mechanical power by a flight muscle efficiency, η_m , and by assuming a standard conversion factor of $20 \text{ J ml}^{-1} \text{ O}_2$. Using a semi-isolated preparation, Mizisin and Josephson (1987) found for locust muscle that η_m was between 7.7 and 10.5 %, while Stevenson and Josephson (1990) estimated that η_m was approximately 10 % for hovering flight of the moth *Manduca sexta*. Neither of these results was dependent upon assumptions concerning elastic energy storage. Similar values for η_m characterize insects with asynchronous flight muscle in both hovering (Ellington, 1984*f*) and forward (Casey and Ellington, 1989) flight. Metabolic rates for butterflies in free flight were therefore estimated using a representative value of 10 % for the flight muscle efficiency. Insect flight metabolism is characterized by high factorial scopes (Kammer and Heinrich, 1978), so that basal metabolic activity was ignored in the energetic estimates, as were possibly heightened costs of respiration and circulation during flight.

Results

Aerodynamics

The mean coefficients method assumes that force coefficients, and hence effective angles of incidence (α'_r) of the wing, are constant throughout the wingbeat (Ellington, 1984*a*). This criterion was most closely met by the use of a wing inclination of $\bar{\chi}+5^\circ$ and the assumption that no lift forces were produced by relative airflow within 10° of the zero-lift angle. Given these stipulations, absolute values of α'_r averaged 39° during the downstroke and 22° during the upstroke (Table 2). The average difference in $|\alpha'_r|$ between the two half-strokes was 18° . By assuming that relative airflow produced lift and drag forces at all incidence angles, the disparity between mean downstroke and upstroke values of $|\alpha'_r|$ increased to 20° and 40° for wing inclinations of $\bar{\chi}+5^\circ$ and $\bar{\chi}+15^\circ$, respectively. By comparison, the difference in α'_r between proximal and distal wing sections averaged 25° and 29° for the downstroke and upstroke, respectively. Average spanwise variation in α'_r was thus greater than that between downstroke and upstroke. All aerodynamic calculations were therefore made using a wing inclination of $\bar{\chi}+5^\circ$ and assuming that no lift forces were generated by relative airflow within 10° of the zero-lift angle. The difference in $|\alpha'_r|$ between half-strokes is still substantial given these assumptions. However, butterfly wing polars tend to be relatively flat

Table 2. Aerodynamic results for 15 neotropical butterflies

ID	$\overline{C_L}$	$\overline{C_L}/\overline{C_D}$	V_i	\overline{Re}	$F_{\text{vert,d}}$	$\overline{\alpha'_{r,d}}$	$\overline{\alpha'_{r,u}}$	$ \Delta x' $	$ \Delta y' $
1	1.20	9.7	0.33	2330	0.97	36	-12	0.18	0.15
2	1.25	11.5	0.17	2690	1.18	40	-17	0.05	0.11
3	1.41	11.1	0.21	2060	1.10	34	-27	0.38	0.29
4	0.79	5.2	0.21	1960	1.25	43	-51	0.32	0.22
5	2.01	12.6	0.15	1330	1.24	31	-34	0.36	0.22
6	1.02	13.4	0.18	5300	1.18	29	-11	0.57	0.15
7	1.98	11.7	0.18	1120	1.06	28	-16	0.24	0.27
8	3.11	17.0	0.35	1110	1.06	32	-17	0.18	0.28
9	1.56	13.0	0.24	1960	1.26	33	-13	0.28	0.34
10	1.86	11.4	0.17	1290	1.15	56	-23	0.25	0.17
11	3.03	10.4	0.19	5000	1.03	42	-22	0.37	0.33
12	0.92	9.3	0.11	3300	1.41	49	-19	0.40	0.70
13	1.46	13.8	0.22	2500	1.22	37	-15	0.25	0.39
14	0.95	13.4	0.23	6010	1.27	49	-15	0.26	0.23
15	1.92	10.1	0.26	1040	1.28	42	-35	0.28	0.31
Mean	1.63	11.5	0.21	2300	1.18	39	-22	0.29	0.28

Mean lift coefficient required to offset the body weight, $\overline{C_L}$; ratio of $\overline{C_L}$ to the mean profile drag coefficient for the wingbeat, $\overline{C_L}/\overline{C_D}$; induced velocity, V_i , in m s^{-1} ; mean Reynolds number of three spanwise wing sections through the wingbeat, \overline{Re} ; vertical force production during the downstroke, $F_{\text{vert,d}}$, expressed as a fraction of total weight support required through the wingbeat; mean effective angle of incidence of wing sections during the downstroke, $\overline{\alpha'_{r,d}}$; mean effective angle of incidence during the upstroke, $\overline{\alpha'_{r,u}}$; and mean horizontal ($|\Delta x'|$) and vertical ($|\Delta y'|$) deviations of the center of mass from the mean flight path.

Wing inclination is assumed to equal $\bar{\chi}+5^\circ$, where $\bar{\chi}$ is the mean body angle in degrees.

Relative airflow within 10° of the zero-lift angle is assumed to produce drag forces only and no lift; see text for further details.

Values of $\overline{\alpha'_{r,d}}$ and $\overline{\alpha'_{r,u}}$ are given in degrees; negative values indicate that the relative airflow hits the dorsal surface of the wing.

Values of $|\Delta x'|$ and $|\Delta y'|$ are expressed non-dimensionally with respect to the body length.

Identification numbers (ID) refer to Table 1.

between 20° and 45° (see Nachtigall, 1967), indicating that the lift coefficient is fairly constant over the range of α'_r values considered here. Also, the majority of vertical forces are produced during the downstroke only. Thus, spanwise variation in α'_r and differences between the half-strokes should not affect the vertical force balance and the mean lift coefficient. However, profile drag (and power) can be affected by α'_r through the selection of the drag coefficient, $C_{D,\text{pro}}$. By estimating $C_{D,\text{pro}}$ solely from the Re of the wing section in question (see Materials and methods), effects of variation in Re are assumed to outweigh changes in wing angles of incidence through the course of a wingbeat. This is a likely outcome, given the flatness of butterfly wing polars, the substantial spanwise variation in flapping velocity and the asymmetry between half-strokes arising from the high stroke plane angles.

Mean lift coefficients required to support the body weight ($\overline{C_L}$) were high,

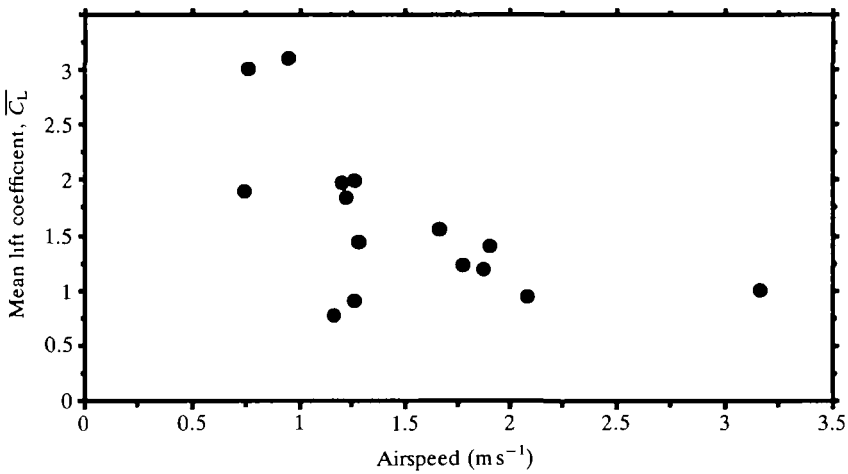


Fig. 1. Mean lift coefficient required for flight, $\overline{C_L}$, as a function of forward airspeed, V . Values of $\overline{C_L}$ were for most butterflies greater than those consistent with quasi-steady aerodynamic mechanisms.

exceeding 1.0 for 12 of the 15 butterflies, and for the other three butterflies averaging 0.89 (Table 2). Use of a wing inclination of $\bar{\chi} + 15^\circ$ (and assuming no lift forces within 10° of the zero-lift angle) changed mean lift coefficients on average by 19%. Interspecifically, $\overline{C_L}$ decreased markedly with increased airspeed (Fig. 1). Vertical force production during the downstroke, $F_{\text{vert,d}}$, was on average 18% in excess of that required to support the body weight (less body lift) through the entire wingbeat (Table 2). Correspondingly, the upstroke was for all butterflies except no. 1 characterized by negative vertical force production. There was no systematic change in $F_{\text{vert,d}}$ with forward airspeed. Of all the vertical forces produced during the downstroke, the proximal wing section was responsible for 29%, the medial section for 36% and the distal wing section for the remaining 35%. Aerodynamic efficiencies of flight, η_a , averaged 0.31 (range 0.13–0.63; see Dudley and Ellington, 1990b, p. 75, for a definition of η_a during forward flight).

Mechanical power requirements

Horizontal ($\Delta x'$) and vertical ($\Delta y'$) displacements of the center of body mass from the mean flight path were substantial fractions of the body length, with absolute values averaging $0.29L$ and $0.28L$, respectively, where L is body length (Table 2). Neither $|\Delta x'|$ nor $|\Delta y'|$ changed systematically with body mass m or with forward airspeed V . Vertical components of the velocity of the center of mass averaged 16% of the mean horizontal airspeed. Fluctuations in horizontal kinetic energy contributed the most to energy changes of the center of mass. Fluctuations in potential energy and vertical kinetic energy of the center of mass averaged 84% and 56%, respectively, of horizontal kinetic energy fluctuations. Percentage energy recovery averaged 29% (maximally 53%) and showed no interspecific correlation with forward airspeed. Specific mechanical power required to acceler-

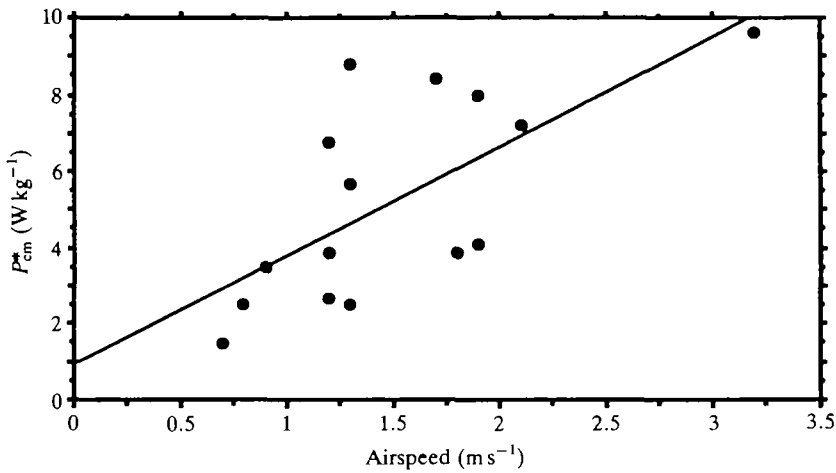


Fig. 2. Specific mechanical power required to lift and accelerate the center of body mass, P_{cm}^* , as a function of forward airspeed, V . The regression is given by: $P_{cm}^* = 2.84V + 1.01$ ($r = 0.67$, $P < 0.006$).

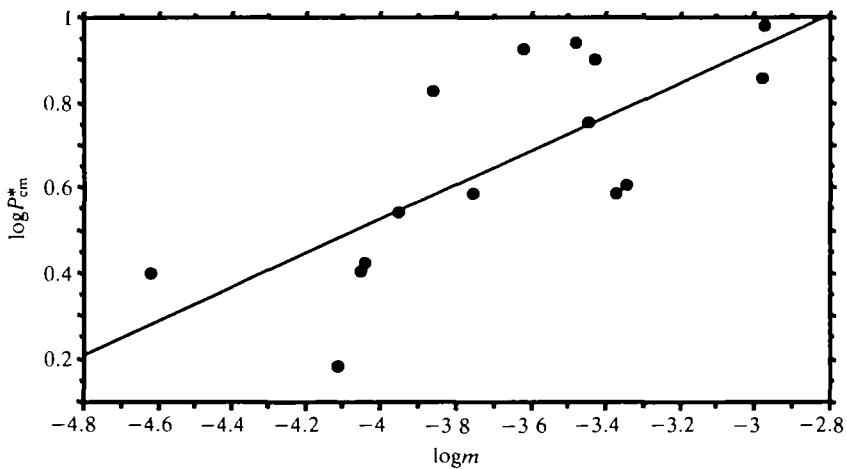


Fig. 3. Specific power required to lift and accelerate the center of body mass, P_{cm}^* (in W kg^{-1}), as a function of body mass, m (in kg). The regression is given by: $\log P_{cm}^* = 0.40 \log m + 2.13$ ($r = 0.73$, $P < 0.002$).

ate and lift the center of mass (P_{cm}^*) was high, averaging 43 % of total specific power requirements assuming perfect elastic energy storage, and 26 % for zero storage (see Table 3). Interspecifically, P_{cm}^* increased linearly with V (Fig. 2) and scaled with $m^{0.40}$ (Fig. 3). Energy costs associated with body rotations relative to the center of mass were in all cases less than 1 % of P_{cm}^* and were thus ignored in estimates of total mechanical power.

Estimates of the total mass-specific mechanical power required to fly ranged

Table 3. *Mass-specific mechanical power requirements of flight for 15 neotropical butterflies*

ID	P_{par}^*	P_{ind}^*	P_{pro}^*	P_{acc}^*	P_{cm}^*	P_{per}^*	P_{zero}^*	\dot{V}_{O_2}	
								Perfect	Zero
1	0.8	3.2	4.1	12.4	4.1	12.2	14.4	21.6	25.5
2	0.6	1.6	4.9	22.7	3.9	11.0	18.8	19.6	33.6
3	0.8	2.0	4.6	19.4	8.0	15.4	21.4	27.5	38.2
4	0.3	2.1	7.4	48.7	6.8	16.5	36.0	29.6	64.4
5	0.4	1.5	4.8	21.9	2.5	9.2	16.8	16.5	30.1
6	1.7	1.8	7.5	19.4	9.6	20.6	24.8	36.8	44.4
7	0.4	1.8	3.2	6.2	2.7	8.0	8.5	14.4	15.1
8	0.2	3.4	1.9	5.1	3.5	9.0	9.0	16.1	16.1
9	0.6	2.3	3.9	11.3	8.4	15.2	17.5	27.3	31.3
10	0.3	1.6	4.9	17.3	3.9	10.8	16.0	19.3	28.6
11	0.2	1.8	2.4	4.9	2.5	7.0	7.2	12.4	12.8
12	0.3	1.1	6.9	45.0	8.8	17.1	35.4	30.5	63.4
13	0.3	2.1	2.9	17.6	5.7	11.0	17.2	19.7	30.7
14	0.7	2.3	5.7	69.1	7.2	15.8	46.1	28.4	82.5
15	0.2	2.6	3.5	18.2	1.5	7.8	13.8	13.9	24.6
Mean	0.5	2.1	4.6	22.6	5.3	12.5	20.2	22.2	36.1

Parasite power, P_{par}^* ; induced power, P_{ind}^* ; profile power, P_{pro}^* ; inertial power requirements during the first half of a half-stroke, P_{acc}^* ; power required to accelerate and elevate the center of mass, P_{cm}^* ; total mechanical power requirements assuming perfect storage of elastic energy, P_{per}^* ($=P_{\text{par}}^*+P_{\text{ind}}^*+P_{\text{pro}}^*+P_{\text{cm}}^*$); total mechanical power requirements assuming zero storage of elastic energy, P_{zero}^* [$=\frac{1}{2}(P_{\text{par}}^*+P_{\text{ind}}^*+P_{\text{pro}}^*+P_{\text{acc}}^*)+P_{\text{cm}}^*$]; and estimated oxygen consumption during flight, \dot{V}_{O_2} , assuming perfect and zero storage of elastic energy.

Units of mass-specific power are W kg^{-1} ; metabolic rates are given in $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$.

Identification numbers (ID) refer to Table 1.

from 7 to 46 W kg^{-1} , depending on the extent of elastic energy storage (Table 3). The largest component of aerodynamic power requirements was typically the profile power (64 % on average), while parasite power requirements were always small, on average just 7 % of aerodynamic requirements. Interspecifically, both specific profile power and specific aerodynamic power requirements increased with airspeed to some power less than one ($\log P_{\text{pro}}^*=0.61\log V+0.54$, $r=0.60$, $P<0.02$; $\log P_{\text{aero}}^*=0.43\log V+0.78$, $r=0.70$, $P<0.01$). Inertial power required during the first half of a half-stroke typically exceeded aerodynamic power requirements by a factor of three. The total specific power required to fly increased linearly with airspeed only for the case of perfect elastic energy storage (P_{per}^* ; Fig. 4). Neither P_{per}^* nor the total specific power given zero storage, P_{zero}^* , were independent of body mass, scaling with $m^{0.26}$ and $m^{0.36}$, respectively (Fig. 5). Estimated metabolic rates during flight, \dot{V}_{O_2} , averaged $22.2 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, assuming perfect elastic energy storage, and $36.1 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, given zero elastic storage (Table 3).

Discussion

Aerodynamics

Mean lift coefficients for butterflies in forward flight are in general greater than one (Fig. 1; Table 2), whereas maximum lift coefficients for a variety of insect

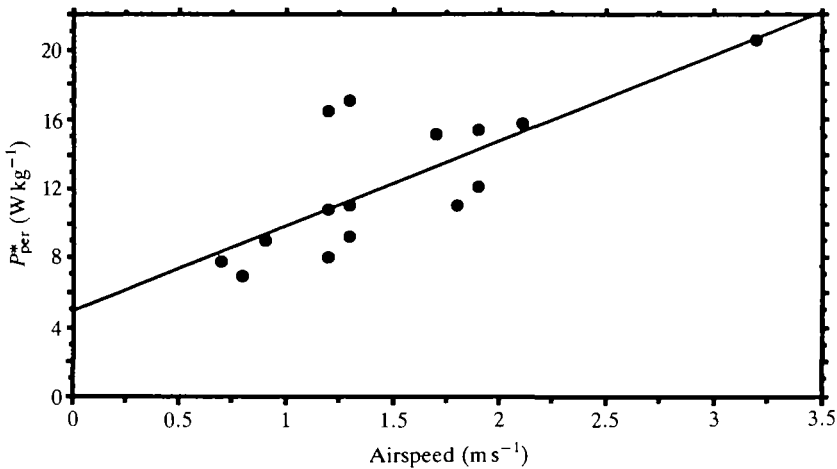


Fig. 4. Total specific mechanical power required to fly, given perfect elastic energy storage, P_{per}^* , as a function of airspeed, V . The regression is given by: $P_{\text{per}}^* = 4.88V + 5.11$ ($r = 0.76$, $P < 0.002$). The correlation between the total specific mechanical power required to fly, given zero elastic energy storage, P_{zero}^* , and V was not significant ($r = 0.41$, $P = 0.13$).

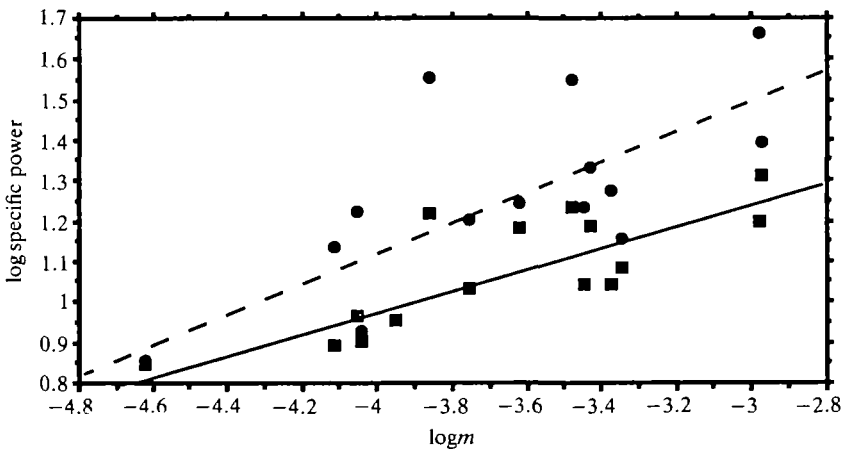


Fig. 5. Allometry of total specific power required to fly, given perfect elastic energy storage (P_{per}^* ; ■, solid line) and zero elastic energy storage (P_{zero}^* ; ●, dashed line). Units of specific power are W kg^{-1} ; mass, m , is in kg. The regressions are given by: $\log P_{\text{per}}^* = 0.26 \log m + 2.0$ ($r = 0.80$, $P < 0.001$) and $\log P_{\text{zero}}^* = 0.36 \log m + 2.57$ ($r = 0.70$, $P < 0.004$).

wings (e.g. Vogel, 1967; Nachtigall, 1977; Dudley and Ellington, 1990b; see also Ellington, 1984a) under conditions of steady flow are typically less than one. Consequently, butterflies must rely upon unsteady aerodynamic effects to generate the forces required for flight. Further support for this conclusion comes from consideration of lift-drag ratios, which averaged 11.5:1 for the butterflies under evaluation (Table 2). By contrast, maximum lift-drag ratios measured by Nachtigall (1967) on various lepidopteran wings were much lower, ranging from 2.2:1 to 3.6:1. Even for the faster-flying butterflies considered here, mean lift coefficients were close to one (Fig. 1). Several butterflies (nos 4, 12 and 14) were characterized by mean lift coefficients close to maximum values determined experimentally on fixed wings. As noted by Ellington (1984f), however, even an approximate agreement of mean lift coefficients and maximum values under steady conditions may implicate unsteady phenomena when the time-dependent growth of wing circulation (Wagner effect) is taken into account.

The conclusion that unsteady aerodynamic mechanisms characterize slow forward flight in butterflies is similar to recent results for various hovering insects (Ellington, 1984f; Ennos, 1989), the moth *U. fulgens* during slow flight (Dudley and DeVries, 1990) and bumblebees in forward flight up to 4.5 m s^{-1} (Dudley and Ellington, 1990b). In the fast forward flight of *U. fulgens* ($>3 \text{ m s}^{-1}$), however, mean lift coefficients are 0.5 or less, and are consistent with quasi-steady mechanisms. Fig. 1 suggests that this may also be the case for butterflies flying at speeds greater than the $1\text{--}2 \text{ m s}^{-1}$ considered here. Direct measurements of airspeeds under natural conditions have shown that palatable butterflies typically fly at $4\text{--}6 \text{ m s}^{-1}$ (R. B. Srygley and R. Dudley, unpublished data). Mean lift coefficients substantially below 0.5 would be expected at such airspeeds, given the quasi-steady dependence of aerodynamic force upon the square of wing relative velocity. Unsteady effects may, however, always characterize the flight of unpalatable heliconiine and ithomiine nymphalid butterflies, which have reduced wingbeat frequencies and low stroke amplitudes (Chai and Srygley, 1990; R. Dudley, personal observation), and in nature fly at airspeeds between 1 and 3 m s^{-1} (R. B. Srygley and R. Dudley, unpublished data).

Absolute values of incidence angles for butterfly wings during flight ranged from 20 to 40° . Together with the high mean lift coefficients and lift-drag ratios, such incidence angles indicate that butterflies are relying principally upon wing lift to support the body weight during forward flight. This result contrasts with the drag-based take-off and hovering described by Ellington (1984a) for the cabbage white butterfly. It would be of considerable interest to determine if the shift from drag- to lift-based weight support is a gradual function of forward airspeed or if there exist discrete gaits similar to those described by Rayner *et al.* (1986) in the flight of some bats. The estimated effective incidence angles for butterflies are remarkably similar to those for the moth *U. fulgens* ($19\text{--}29^\circ$; Dudley and DeVries, 1990), as well as for bumblebees ($20\text{--}40^\circ$; Dudley and Ellington, 1990b) at much higher wingbeat frequencies. In all of these cases, effective incidence angles are negative during the upstroke, indicating that wing circulation is reversed between half-

strokes. Aerodynamic configuration of insect wings is thus fairly similar for forward flight covering a wide range of airspeeds and advance ratios.

This similarity extends to partitioning of weight support and thrust generation between the down- and upstroke. In butterflies, the downstroke is responsible for the majority of vertical force production during the wingbeat, while lift forces during the upstroke are directed primarily downwards (negative vertical force production). Given negative incidence angles and estimated wing inclinations, wing lift must also be directed forwards during the butterfly upstroke, generating thrust. Similar patterns characterize forward flight in *U. fulgens* (Dudley and DeVries, 1990) and the fast forward flight of bumblebees (Dudley and Ellington, 1990b). For bumblebees in hovering flight, weight support is equally shared between the half-strokes (Ellington, 1984f), but the downstroke becomes progressively more dominant as airspeed increases (Dudley and Ellington, 1990b). Concomitantly, the upstroke produces thrust and little or negative vertical force. This consistent use for the upstroke by insects in forward flight probably reflects their comparative inability to reduce significantly through flexion the effective surface area of the wings. Vertebrate fliers, by contrast, can use the upstroke for various aerodynamic functions, depending upon the flight speed (Norberg, 1990). An analysis of butterfly flight at airspeeds higher than those considered here ($>3\text{ ms}^{-1}$) would be useful in determining whether the upstroke function gradually shifts to weight support as well as thrust generation. It should be emphasized that the deduced roles for down- and upstroke function in the forward flight of insects remain untested experimentally. Confirmation of the quasi-steady predictions, preferably by means of flow visualization during free flight (e.g. Kokshaysky, 1979; Rayner *et al.* 1986), is now required. Ellington (1980) used talcum powder to investigate the wake during take-off of the cabbage white butterfly (see also Brodskii and Ivanov, 1984, 1985), but flow visualization has not yet been used to study free forward flight in insects. Butterflies, with their low wingbeat frequencies, would be the most appropriate group for such investigations.

To what extent is the analysis of butterfly flight by quasi-steady means justifiable? The requirement of the quasi-steady analysis that effective angles of incidence be fairly constant through the wingbeat was satisfied, given reasonable assumptions concerning wing orientation. However, advance ratios of butterflies in flight were close to one (Dudley, 1990), indicating that forward and mean flapping velocities are of comparable magnitude. Clearly, unsteady aerodynamic phenomena must be a prominent feature of butterfly flight. Ellington (1984d) discussed various unsteady mechanisms that may influence lift production during insect flight (e.g. delayed stall, rotational effects, clap-and-fling, peel). The temporal resolution of video filming was inadequate to assess the likelihood of these mechanisms operating for the butterflies examined here, although the possibility of extensive wing rotation at the ends of half-strokes was eliminated (Dudley, 1990). Given the estimated effective angles of incidence and reversal of circulation at the end of each half-stroke, delayed wing stall is also unlikely to

enhance lift production during forward flight. Moreover, the relatively large chords of butterfly wings suggest that lift production will be seriously diminished by the Wagner effect. The most likely means of lift enhancement in butterflies involve the effects of opposite wing interference, particularly at the beginning of the downstroke. Maximum positional angles averaged a high 69° for the butterflies considered here (Dudley, 1990), with correspondingly reduced distances between the two wing pairs. Ellington (1984*c,d*) suggested for butterflies that such low wing separations (the near clap-and-fling), as well as full contact and subsequent chordwise separation of opposite wing surfaces (the peel), could have advantageous aerodynamic consequences, generating high lift forces in a manner similar, but not identical to, the Weis-Fogh clap-and-fling (Weis-Fogh, 1973). While such kinematic mechanisms are also suitable candidates for investigation by means of flow visualization, the high lift coefficients estimated for the forward flight of butterflies simply underscore the present inadequacy of aerodynamic theory for evaluating large-amplitude flapping in low aspect ratio wings. Lacking the appropriate analytical tools, the quasi-steady approach remains the only means of estimating force production and the concomitant mechanical power requirements of flight.

Butterflies studied here spanned almost two orders of magnitude in body mass (Dudley, 1990), and consideration of the effects of size change upon aerodynamic force production is appropriate. In particular, wing loading of butterflies increased faster than predicted by isometry, in proportion to $m^{0.47}$. Higher wing loadings indicate a reduction in relative wing area, and if stroke amplitude remains constant, the relative velocity of wing sections must correspondingly increase if body support is to be maintained. Stroke amplitude showed no interspecific trend with respect to body mass, while wingbeat frequency during forward flight scaled with $m^{-0.26}$ and flight speed increased approximately with $m^{0.38}$ (Dudley, 1990). At the average advance ratio of 0.93, forward and flapping velocities contribute approximately equally to the wing relative velocity during the downstroke. Vertical force production during the upstroke is minimal, while the low induced velocities will not contribute substantially to the wing relative velocity at any stage of the wingbeat (see Table 2). The decline in flapping velocity with body mass is thus more than compensated for by the increase in forward airspeed, and relative velocity during the downstroke will show a slight positive allometry. In the quasi-steady analysis, aerodynamic forces are proportional to the wing area and the square of relative velocity. The allometric increase in wing relative velocity combines with the reduction in relative wing area to result in an approximately constant vertical force production. Pennycuik (1975) observed that minimum wingbeat frequencies of animals in forward flight will scale with body mass to the power -0.16 , and that flapping frequency of wings with negative taper, a characteristic of many butterflies, will decrease even faster. The high positive allometry of flight speeds in butterflies may, in part, be necessitated by this reduction in wingbeat frequency. Generation of thrust has not been evaluated here, because body drag is very small relative to the vertical forces required during

flight. Detailed analysis of thrust production would require a more precise characterization of wing orientation and relative velocities than is currently available (see Dudley and Ellington, 1990*b*).

Power requirements of flight

Vertical body displacements during the flight of butterflies are substantial (Table 2), and the specific mechanical power costs associated with oscillations of the center of mass (P_{cm}^*) are high (Table 3). By contrast, vertical and horizontal displacements during hovering flight of insect fliers with asynchronous flight muscles are much smaller, with maximum values typically equal to 1–2 % of the wing length (Ellington, 1984*c*). Because kinetic energy is proportional to the square of velocity, such body displacements will result in much smaller changes in kinetic energy and associated power. The results presented here for butterflies are more akin to the findings for running in terrestrial arthropods (e.g. Blickhan and Full, 1987; Full and Tu, 1990), for which oscillation of the center of mass represents the majority of total power requirements during locomotion. In running cockroaches, changes in horizontal kinetic energy and in potential energy are of similar magnitude at low speeds. At high speeds, mechanical power is dominated by fluctuation in horizontal kinetic energy (Full and Tu, 1990), a characteristic of the erratic flight of butterflies in the 1–3 ms⁻¹ airspeed range considered here. A recent quantitative assessment of irregular flight paths in butterflies emphasized the contribution of vertical displacements of the body to the total distance flown (Chai and Srygley, 1990). It is, however, curious that changes in the horizontal component of body velocity constitute the primary energetic expense during erratic flight. Unpredictable variability in both vertical and horizontal dimensions may be an essential feature of protean flight paths designed to evade aerial predators.

The high costs of body oscillations during locomotion may be mitigated in part by maintaining fluctuations in kinetic and potential energy out of phase (Heglund *et al.* 1982*a*). Percentage energy recovery by such means averaged 29 % for butterflies in forward flight, indicating that a pendulum-type mechanism to exchange kinetic and potential energies of the center of mass is at least partially effective. Higher rates of recovery would require tighter phase relationships between vertical and horizontal body displacements, which would probably be incompatible with maintenance of an unpredictable and erratic flight trajectory. Because the video filming of Dudley (1990) investigated only two-dimensional projections of butterfly flight paths, lateral displacements during flight have been ignored in the present estimates of total power requirements. Moreover, the filming frequency relative to the wingbeat frequency was not sufficiently high to determine curvature of flight trajectories in detail, and linear interpolation of flight paths undoubtedly results in underestimates of the total distance travelled. The values given in Table 3 are thus conservative estimates of the mechanical power required to maintain fluctuations in the kinetic and potential energy of the center of mass. For some butterflies, the energetic costs of flight could be higher,

particularly if there are pronounced lateral components to the flight path (e.g. fast-flying pierids). However, it is probable that changes in the lateral components of kinetic energy will be similar in magnitude to changes in the vertical components. Because changes in these latter components are typically smaller than horizontal fluctuations in kinetic energy, lateral displacements during forward flight are unlikely to cause a substantial increase in the mechanical power required to oscillate the center of mass.

Mechanical power requirements of flight at $1\text{--}3\text{ ms}^{-1}$ are much lower in butterflies (Table 3) than in bumblebees of comparable body mass (see Dudley and Ellington, 1990b). For both bumblebees and butterflies flying at such speeds, parasite power is small relative to other components of the power curve. Correspondingly, streamlined aerodynamic design of the body is probably of little consequence. Wingbeat frequencies are typically an order of magnitude lower in butterflies than in insects with asynchronous flight muscles flying at the same airspeeds (e.g. flies: Ennos, 1989; bumblebees: Dudley and Ellington, 1990a). Because profile power is proportional to the cube of wing relative velocity, the low wingbeat frequencies of butterflies result in much reduced profile power requirements. Induced power, of course, increases because of the low aspect ratio wings in butterflies, but this effect is countered by their very low wing loadings. Thus, aerodynamic power requirements for butterflies are dominated by the relatively low profile power, resulting in total mechanical power requirements substantially lower than those for asynchronous fliers.

The linear dependence of power required to fly upon forward airspeed (Fig. 4) arises primarily from increases in profile power and power to oscillate the center of mass, while the concomitant decrease in induced power is of lesser importance. This linear variation of total power requirements (assuming perfect elastic energy storage) with airspeed contrasts with the sharp increase in profile and total mechanical power deduced for different individuals of the moth *U. fulgens* (Dudley and DeVries, 1990). The lower advance ratios of butterflies compared to *U. fulgens* (see Introduction) suggest that profile drag and hence power are less dependent upon the forward airspeed. This possibility was substantiated by the finding that profile power in butterflies varies interspecifically with airspeed to the power 0.61 (see Results). Estimates of mechanical power requirements for an individual butterfly flying at different airspeeds would further clarify the relationships between profile power, advance ratio and speed of flight. Wing kinematics may well be constrained by optimal strain rates and contraction frequencies of the flight muscle and thoracic apparatus (Dudley and Ellington, 1990b), in which case profile power requirements would not exhibit a dramatic change over a range of airspeeds.

In addition to aerodynamic power, inertial power requirements of butterflies were also much lower than those estimated for asynchronous insect fliers (see Ellington, 1984f; Dudley and Ellington, 1990b). Although radii of gyration for butterfly wings are comparable to those of other insects (see Ellington, 1984b), inertial power requirements are small in butterflies because of their very low

wingbeat frequencies. Wing mass and virtual mass in butterflies are relatively high (Dudley, 1990), but this is counterbalanced by the dependence of inertial power upon the square of wingbeat frequency. Even so, inertial power requirements typically exceeded aerodynamic power requirements of flight for butterflies (Table 3). Inertial power requirements can be eliminated if the flight muscles or other elastic elements can store the kinetic energy of the oscillating wing mass at the end of one half-stroke and then release it in the following half-stroke. Maximum elastic energy storage of synchronous flight muscle was estimated to be about 1.4 J kg^{-1} muscle, using the formula and data of Alexander and Bennet-Clark (1977), but assuming a maximum stress for synchronous muscle of 200 kN m^{-2} (Ellington, 1985). The amount of required energy storage during flight (see Ellington, 1984f) averaged 0.93 J kg^{-1} for all butterflies, considerably less than the estimated maximum capacity for synchronous muscle. In three butterflies (nos 4, 12 and 14), however, the required energy storage was in excess of 1.4 J kg^{-1} . For these insects, elastic components supplementary to the flight muscle would be necessary if inertial power requirements were to be completely eliminated.

Estimates of power requirements for forward flight in bumblebees suggest that the power output of flight muscle is adequate for flight even if there is no elastic storage of wing inertial energy (Dudley and Ellington, 1990b). Because maximum power output of asynchronous flight muscle is probably higher than that of synchronous muscle (Ellington, 1985), a comparable estimate for butterflies is appropriate. Mizisin and Josephson (1987) found that mechanical power output of a locust flight muscle in an *in vivo* preparation averaged about 50 W kg^{-1} muscle, increasing to about 73 W kg^{-1} muscle with multiple stimulation per contraction cycle. Working with a flight muscle in the sphingid *Manduca sexta*, Stevenson and Josephson (1990) obtained mechanical power output averaging 90 W kg^{-1} muscle (maximally 130 W kg^{-1}). Flight muscle mass for the butterflies considered here was estimated using the relative thoracic mass given in Dudley (1990) and assuming that flight muscle constituted 90% of the thorax. Power output of the flight muscle then averaged 36 W kg^{-1} body mass, which for all but one butterfly (no. 14) was well in excess of that required to fly even assuming no elastic storage of inertial energy (see Table 3). Accordingly, slow flight does not require elastic storage of wing inertial energy, although at higher airspeeds ($>3 \text{ m s}^{-1}$) some storage would probably be required.

It is of interest to compare the estimated metabolic rates for butterflies (average values of $22\text{--}36 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$; see Table 3) with existing data on lepidopteran flight energetics. Zebe (1954) measured metabolic rates of some temperate-zone butterflies engaging in vigorous activity inside a flight chamber, and obtained values between 40 and $100 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, although these results do not refer to controlled forward flight. Mass-specific rates of oxygen consumption during hovering flight of various moths typically range from 43 to $60 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (see Casey, 1989), although values as high as $126 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ have been reported (Casey, 1981). The only available energetic data for free forward flight in insects

are those made on two species of bumblebee (Ellington *et al.* 1990). Metabolic rates averaged about $65 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ over the range of hovering up to a forward airspeed of 4 ms^{-1} , although a value as low as $43 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ was recorded. Metabolic rates estimated here for butterflies are much lower than those for bumblebees in forward flight, and are also reduced compared to the rates measured for hovering moths. If butterflies in hovering flight exhibit metabolic rates similar to those of moths, the power curve relating cost of flight to airspeed would be similar to the 'U-shaped' power curve postulated by Pennycuik (1975). Such a curve would contrast markedly with the relatively flat power curve described by Ellington *et al.* (1990) for bumblebees. Given the low wing loadings of butterflies, however, hovering metabolism might well be comparable to the values estimated for forward flight, and the power curve would then be fairly flat. Measuring the flight metabolism of butterflies in hovering or near-hovering flight is probably feasible experimentally, as many male butterflies are capable of hovering for extended periods during courtship.

Total costs of flight are low in butterflies because of their much reduced wingbeat frequencies coupled with very low wing loadings. Dudley (1991) suggested that the enlarged wings of Lepidoptera have become partially decoupled from their aerodynamic functions, assuming such diverse roles as thermoregulation, sexual communication and camouflage. Concomitantly, however, increased wing size results in heightened apparency to visually oriented predators, and the antipredatory mechanisms in the Lepidoptera have been correspondingly enhanced. Most moths fly only at night, while butterflies tend to be either erratic fliers or to be slow-flying, aposematic and unpalatable (as are many diurnal moths). While the costs of sequestering toxic plant compounds and maintenance of unpalatability can only be conjectured (e.g. Brower, 1984; Huheey, 1984), it is possible to assess quantitatively the energetic costs of irregular flight paths. The results presented here indicate that, while the absolute power requirements of flight may be low in butterflies (particularly at low airspeeds), the relative energetic costs of maintaining an erratic flight trajectory are high.

Appendix

An asterisk following any of the symbols that represent mechanical power requirements (i.e. P_{aero} , P_{cm} , P_{ind} , P_{par} , P_{per} , P_{pro} and P_{zero}) indicates mechanical power per unit body mass.

$c(r)$	Wing chord at distance r from wing base
$\overline{C_D}$	Mean drag coefficient
$C_{D,\text{pro}}$	Profile drag coefficient
$\overline{C_L}$	Mean lift coefficient
D_b	Body drag
$F_{\text{vert,d}}$	Vertical force production during the downstroke
I	Moment of inertia of the wing mass and wing virtual mass
I_b	Moment of inertia of the body about the wing base axis

\hat{l}_1	Non-dimensional distance of the center of body mass from the wing base axis
L	Body length
L'	Projected body length
L_b	Body lift
m	Body mass
P_{acc}	Inertial power requirements during the first half of a half-stroke
P_{aero}	Aerodynamic power requirements ($=P_{par}+P_{ind}+P_{pro}$)
P_{cm}	Mechanical power necessary to lift and accelerate the center of body mass
P_{ind}	Induced power requirements
P_{par}	Parasite power requirements
P_{per}	Total mechanical power requirements given perfect elastic energy storage
P_{pro}	Profile power requirements
P_{zero}	Total mechanical power requirements given zero elastic energy storage
r	Radial position along wing
R	Wing length
Re	Reynolds number
t	Time
V	Forward airspeed
V_i	Induced velocity
V_R	Relative velocity
\dot{V}_{O_2}	Estimated oxygen consumption during flight
x_{cm}	Horizontal position of the center of body mass in the (x,y) coordinate system
$\Delta x'$	Horizontal deviation of the center of body mass from the mean flight path
$ \overline{\Delta x'} $	Mean absolute value of $\Delta x'$
y_{cm}	Vertical position of the center of body mass in the (x,y) coordinate system
$\Delta y'$	Vertical deviation of the center of body mass from the mean flight path
$ \overline{\Delta y'} $	Mean absolute value of $\Delta y'$
$\overline{\alpha_{r,d}}$	Effective angle of incidence
$\overline{\alpha'_{r,u}}$	Mean effective angle of incidence during the downstroke
$\alpha'_{r,u}$	Mean effective angle of incidence during the upstroke
ζ	Angle between mean flight path and the horizontal
η_a	Aerodynamic efficiency
η_m	Muscle efficiency
ρ	Mass density of air
Φ	Stroke amplitude
χ	Body angle in flight
$\bar{\chi}$	Mean body angle
ω	Angular velocity of the body

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