ENERGETICS OF HOVERING FLIGHT IN HUMMINGBIRDS AND IN DROSOPHILA

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INTRODUCTION

The evolution of small birds and small insects appears to have proceeded from larger ancestors which made use of *fast forward flight* towards relatively small species which are able to remain airborne at low or negligible air speeds, i.e. to perform *hovering flight*. Although many existing insects require some forward air speed in order to lift their own weight, it appears justified to suggest that winged insects as a class (Pterygota) have conquered the small niches of the aerial biosphere as a consequence of being able to hover or to fly forwards very slowly. The same applies to humming-birds (sub-order Trochili within the order Apodiformes), which, like insects, hover and fly forwards or backwards with fully extended wings during the entire wing-stroke cycle. In contrast to this relatively simple type of wing movement, many small passerine birds (Brown, 1963), the African sunbirds (Nectariniidae; Zimmer, 1943) and some hovering bats (Chiroptera; Norberg, 1970) practise a different kind of hovering where the wings are flexed extensively, particularly during the upstroke.

From an aerodynamic point of view it is therefore possible to regard insects and hummingbirds as representatives of a single functional group which includes the majority of actively flying animals and which can be analysed within the same conceptual framework. As to size, two well-known extremes within this spectrum are hummingbirds and fruit flies belonging to the genus *Drosophila*. It is fortunate that a sufficient amount of observational data have been obtained in recent years to make possible realistic calculations of the forces involved in the hovering flight of these two groups.

Hovering flight is the most power-demanding type of locomotion in animals and is more expensive than ordinary flapping flight because, relative to the undisturbed air, the body has no accumulated kinetic energy. At any instant of time, the wings can therefore only produce lift when they are moved actively and they contribute little or nothing at the extremes of the wing stroke. During forward flight in birds, bats and insects lift is produced during the entire wing-stroke cycle and also when the angular movements are zero, the aerodynamic work being provided by the accumulated kinetic energy of the animal as a whole.

From an analytical point of view, true hovering flight on one spot is easier to handle than forward flight and, in the past, several attempts have been made to explain aerodynamic performance (for references other than those given in this paper, see Weis-Fogh & Jensen, 1956). However, I am unaware of any studies which are sufficiently complete to answer the following four questions with reasonable certainty:

(1) Is hovering flight consistent with *steady* or *quasi-steady aerodynamics* over the

relevant range of Reynolds numbers, i.e. from 10^2 in Drosophila to 10^4 in humming-birds?

(2) What is the *aerodynamic work and power* needed for hovering, using natural wings of known properties?

(3) How important is *wing-inertia* in the energy account?

(4) Is an *elastic system* similar to that found in locusts and other insects (Weis-Fogh, 1959, 1961, 1965) essential for insects and why does it appear to be absent in birds and other vertebrates?

As a result of the discussion it is argued that, in contrast to insects, those vertebrates which vibrate their limbs at high frequencies have not been able to make use of elastic storage and release of kinetic energy to any significant extent, the reason being that the only elastomer available to vertebrates, elastin, has a high internal damping as compared with resilin and insect cuticle. If substantiated by further studies, this has far-reaching consequences for our understanding of the form and function of some vertebrates.

PRINCIPLES, PROCEDURE AND MATERIAL

The primary aim is *not* to provide an analysis accurate in all detail but to offer quantitative estimates of force, work and power in large and small hovering animals respectively. If successful, we may then extend the inquiry to the whole spectrum of flying animals in order to unravel limiting or guiding features in the 'design' of the flight machinery of different groups. This may indicate where a fresh experimental approach is likely to result in new knowledge. For these reasons the flight data used must be as accurate as at all possible, but when approximations are introduced their effect should be to average out the results rather than to exaggerate them in one direction or the other. For instance, it is well known that the angular movement of the long wing-axis deviates from a sinusoidal movement in many insects (cf. locusts, Weis-Fogh, 1956; flies, Nachtigall, 1966) and that this tends to increase the bending moments caused by wing inertia as well as by the aerodynamic forces. However, it serves the present purpose best to use harmonic oscillations because we wish to know whether *a given type of construction* is able to fly on the basis of the simplest possible set of principles rather than to prove that a specific bird or insect is unable to do so unless it has resort to special tricks.

(a) Movements and forces

During hovering flight the resulting aerodynamic force is vertical and equal to the body weight when integrated over a whole wing-stroke. In hovering hummingbirds the movement of the long wing-axis is known to be almost sinusoidal with respect to angular displacements and, with good approximation, to be confined to a *stroke plane* which is slightly tilted relative to the horizontal by a small angle β both during the morphological downstroke and during the upstroke, so that the wing-tip describes a longish horizontal figure-of-eight (Fig. 2D). In all the calculations we disregard the movements normal to the stroke planes. The equation of angular movement is then

$$\gamma = \tfrac{1}{2}\pi + \tfrac{1}{2}\phi \sin\left(2\pi t/t_0\right), \tag{1}$$

where γ is the instantaneous *positional angle* of the long wing-axis in the stroke plane, ϕ is the angular excursion or the *stroke angle* (twice the amplitude), t is time and t_0 is

the fundamental period, so that $t_0 = 1/n$, where n is the *wing-stroke frequency*. The angular velocity is

$$dy/dt = \dot{y} = \pi\phi n \cos(2\pi n t). \tag{2}$$

The wing-speed of a wing-element r cm from the fulcrum caused by the flapping itself is $v_r = r\dot{y}$, and the aerodynamic force caused by this contribution is proportional to the square of the speed

$$v_r^2 = r^2\phi^2\pi^2 n^2 \cos^2(2\pi n t). \tag{3}$$

The angular acceleration is

$$d^2y/dt^2 = \ddot{y} = -2\phi\pi^2 n^2 \sin(2\pi n t), \tag{4}$$

so that the bending moment caused by the acceleration of the wing-mass in the stroke plane, i.e. the inertial torque, is

$$Q_i = I\ddot{y} = -2I\phi\pi^2 n^2 \sin(2\pi n t), \tag{5}$$

where I is the moment of inertia of the wing-mass with respect to the fulcrum. The bending moment caused by the wind forces is therefore $90°$ out of phase with the Q_i.

As to the total aerodynamic force, we must know the size and direction of the relative wind V_r at any given distance r from the fulcrum. It is composed of the flapping velocity v_r (equation 3) and of the *induced wind velocity*, w. An actuator disk is a conceptual device which accelerates the air in the direction normal to the plane of the disk and so that the flow is uniformly linear and without whirls. A well designed propeller or the rotor of a helicopter are examples of a physical approximation to this situation. During hovering in still air the disk is horizontal and the momentum which it imparts to the air must balance the weight W of the animal. According to the momentum theorem for an ideal actuator disk, the induced wind at the level of the disk itself is

$$w^2 = W/(2\pi\rho R^2), \tag{6}$$

where R is the radius of the disk, i.e. the wing-length, and ρ is the density of the air.

In flapping insects we know that w changes during the stroke (Wood, 1970), and the relatively large distance between the fulcra on the two sides, as well as the fact that the stroke angle ϕ is less than $180°$, mean that the system does not represent a uniform disk but two interrelated half-disks, as pointed out by Hertel (1966). Nevertheless, in the present quasi-steady approximation we shall assume that the induced wind is uniform across the stroke disk with respect to both distance and time, corresponding to equation (6). The justification is (*a*) that conservative estimates are to be preferred in this type of analysis, (*b*) that rough estimates indicate that the effect of deviations from uniformity will be relatively small, and the experimental finding (*c*) that the mean induced velocities measured by means of a hot-wire anemometer in the postulated critical case of a simulated beetle (*Melolontha vulgaris*) agree with the expected value deduced from the momentum theorem, in spite of the apparent non-steady conditions of flow (Bennett, 1966).

The magnitude of the resultant instantaneous force F_r acting on a wing-segment is assumed to depend on the square of the relative wind, V_r^2, on the area of the section A_r and on the coefficients of lift C_L and drag C_D, as in ordinary steady-state flight:

$$F_r = \tfrac{1}{2}\rho V_r^2 A_r(C_L^2 + C_D^2)^{\frac{1}{2}}. \tag{7}$$

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Since most previous work of this kind has been given in the technical force–length–time system we shall use it here, but the SI units are shown on the diagrams in addition to the g–cm–s units; at atmospheric pressure and room temperature, ρ equals $1\cdot25 \times 10^{-6}$ g cm^{-4} s^2. The lift is measured normal to the *relative* wind and the drag parallel to it. However, the forces which matter for the animal are the vertical component, or hovering force, H_r, and the component M_r parallel to the stroke plane because the latter determines the bending moment against which the wing must move. In order to calculate them we must know the *angle of tilt* β of the stroke plane relative to the horizontal, and also the approximate value of the *lift/drag ratio* within the effective range utilized during hovering. The last condition implies that one must make trial calculations in order to determine C_L (see later) and then study and choose the aerodynamic characteristics of actual wings or chosen airfoils.
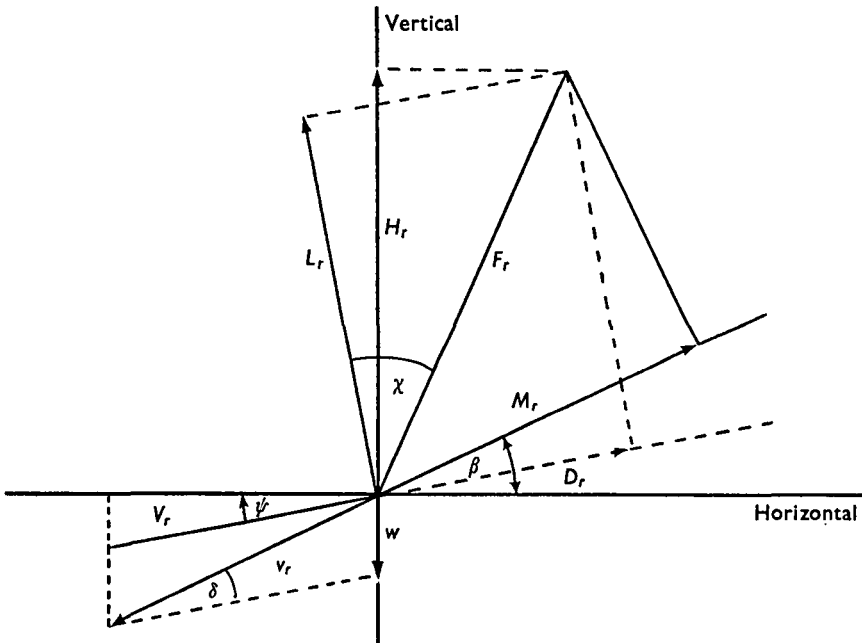

Fig. 1. The flapping velocity v_r and the induced wind velocity w acting on a wing-element at the distance r from the fulcrum during hovering in still air, together with the resulting aerodynamic force F_r and the various projections of this force (see the text).

Fig. 1 shows the geometry, from which it is seen that

$$V_r^2 = v_r^2 + w^2 - 2wv_r \sin \beta. \qquad (8)$$

$$\text{Angle } \psi = \delta - \beta, \quad \text{where} \quad \sin \delta = w \cos \beta / V_r. \qquad (9, 10)$$

When $\tan \chi = C_D/C_L$ the resultant aerodynamic force is

$$F_r = (\tfrac{1}{2}\rho V_r^2 A_r) \, C_L/\cos \chi, \qquad (11)$$

so that the vertical component acting against gravity is

$$H_r = (\tfrac{1}{2}\rho V_r^2 A_r) \, C_L \cos (\chi + \psi)/\cos \chi. \qquad (12)$$

The component in the stroke plane is

$$M_r = (\tfrac{1}{2}\rho V_r^2 A_r)\, C_L \sin{(\chi + \psi + \beta)}/\cos{\chi}. \tag{13}$$

The aerodynamic torque attributed to the wing-segment is then

$$Q_{a,r} = r p_r C_L \sin{(\chi + \psi + \beta)}/\cos{\chi}, \tag{14}$$

where the potential dynamic pressure is $p_r = \tfrac{1}{2}\rho V_r^2 A_r$.

(b) Procedure

The wing of length R was divided transversely into three equally long sections, I–III, and the corresponding areas were measured. For each section a weighted average distance $\bar{r}$, the effective radius of gyration, was found by integration, so that the *dynamic pressure index* $p_r \cos{(\chi + \psi)}/\cos{\chi}$ could be estimated for ten time-equidistant points during a quarter stroke and for each of the three sections. By integrating the summed curves with respect to time (see Fig. 4), the average value of the product was found. When multiplied by the average lift coefficient $\bar{C}_L$ the result must equal the weight W of the hovering animal. For reasons given in the next section, the *average* lift coefficient $\bar{C}_L$ thus found is a good approximation to the true value throughout the stroke period both in hummingbirds and in Drosophila. The calculated $\bar{C}_L$ was therefore inserted in equation (14) in order to estimate the aerodynamic torque contributions Q_a as a function of time or positional angle. The total aerodynamic work during one wing-stroke is the sum of the work done during the upstroke and during the downstroke, and is

$$W_a = \int_{\gamma_{\min}}^{\gamma_{\max}} Q_a\, d\gamma + \int_{\gamma_{\max}}^{\gamma_{\min}} Q_a\, d\gamma. \tag{15}$$

The power expended against wind forces alone is then

$$P_a = n W_a. \tag{16}$$

Similar expressions apply to the inertial torque Q_i in equation (5) and the two contributions must be added for each instant of time or for each wing-position in order to determine the total work and power produced by the working thorax

$$P = n \int_{\gamma_{\min}}^{\gamma_{\max}} (Q_a + Q_i)\, d\gamma + n \int_{\gamma_{\max}}^{\gamma_{\min}} (Q_a + Q_i)\, d\gamma, \tag{17}$$

as is clear from the work diagrams in Figs. 6–8. P in equation (17) is then the total mechanical power imparted by the thorax to the wings and should be related to the metabolic rate of the hovering animal.

If we find that the average coefficient of lift $\bar{C}_L$ is higher than is consistent with the wing-profile and the Reynolds number in question, it would not be justified to apply the lift/drag relationship for a steady-state flow, and another approach would be needed. However, this was not the case in the present study. Also, one may subdivide the wing into more than three sections, but this is unlikely to represent a substantial improvement because we use weighted values for the radius of gyration. As to the lift-drag ratio, we use polar diagrams from real wings so that the induced drag is taken into account automatically. (This is one of the difficulties in Pennyquick's (1968) treatment of bird flight.) It is therefore meaningful to estimate the *aerodynamic*

efficiency of hovering as the ratio between the power estimated from the momentum theorem divided by the actual aerodynamic power P_a calculated from equation (16).

(c) Material and flight data

The flight parameters used are listed in Tables 1 and 2, but it is essential to discuss the selection of data in some detail; it is on this point that most studies of animal flight tend to err.

Hummingbirds (Trochili). No complete description is available for any species, but the flight system of the sub-order displays an unusually large degree of geometrical and dynamical similarity (Greenewalt, 1962). The precise measurements of the angular movements during true hovering in *Melanotrochilus fuscus* (Stolpe & Zimmer, 1939a; Hertel, 1966) and of wing-stroke frequencies in a large number of species (Greenewalt, 1960, 1962) therefore make it possible to estimate a consistent set of parameters for a given specimen.

Table 1. *Basic data for hovering flight in a hummingbird and in Drosophila*

(The figures in parentheses refer to the sources listed beneath the table. Various modifications are discussed in the text.)

Quantity:	Amazilia fimbriata fluviatilis		Drosophila virilis	
Body weight (g)	5·1	(1)	$2·0 \times 10^{-3}$	(2)
Wing-length (cm)	5·85	(1)	$3·0 \times 10^{-1}$	(2)
Wing-area, both wings (cm²)	17·0	(1)	$5·8 \times 10^{-2}$	(2)
Wing-weight, both wings (g)	0·309	(1)	$4·8 \times 10^{-6}$	(2)
I, moment of inertia of wing-mass, both wings (g cm s²)	$8·2 \times 10^{-4}$	(1)	$10·0 \times 10^{-10}$	(3)
ϕ, stroke angle (deg)	120	(4)	150	(2)
n, stroke frequency (sec^{-1})	35	(5)	240	(2, 6)
β, angle of tilt (deg)	11	(7)	20	(2, 8)
Adopted C_L/C_D ratio	1·8/0·3	(9)	0·86/0·54	(10)
Metabolic rate (cal g^{-1} h^{-1})	200	(11)	120	(12)
w, induced wind (cm sec^{-1})	137		76	
Average wing-load (kg/m²)	3		0·35	

(1) Present study; (2) Vogel, 1966; (3) Vogel, 1965; (4) Stolpe & Zimmer, 1939a; (5) Greenewalt, 1962; (6) Chadwick & Williams, 1949; (7) Stolpe & Zimmer, 1939b; (8) Vogel, 1967a; (9) Prandtl & Tietjens, 1934; (10) Vogel, 1967b; (11) Lasiewski, 1963; (12) Chadwick & Gilmour, 1940.

Table 2. *The area of the wing-sections A_r (cm²) and the weighted radius of gyration r (cm)*

	Amazilia fimbriata fluviatilis		Drosophila virilis	
	A_r	r	A_r	r
Section I (inner)	6·4	1·46	$1·1 \times 10^{-2}$	$0·75 \times 10^{-1}$
Section II (middle)	6·6	3·25	$2·7 \times 10^{-2}$	$1·65 \times 10^{-1}$
Section III (outer)	4·0	4·87	$2·0 \times 10^{-2}$	$2·50 \times 10^{-1}$

The specimen chosen was identified by Mr C. W. Benson as *Amazilia fimbriata fluviatilis* (Gould, 1861). It was purchased in Ecuador and given to me immediately after it suddenly died in the Copenhagen Zoo, where it had displayed normal flight activity at unknown wing-stroke frequency. Its geometry is shown in Fig. 2A and the

distribution of the wing-mass in Fig. 2B. An analysis of the angular movements was made from Fig. 3 of Stolpe & Zimmer (1939a) and is shown in Fig. 2C of this paper. It appears (a) that during hovering the morphological upstroke and downstroke are of almost equal duration, and (b) that the movements of the long wing-axis are almost sinusoidal when referred to the stroke plane, the small deviations being of no aerodynamic consequence. According to Stolpe & Zimmer's (1939b) accurate tracings the stroke plane is not horizontal but tilted by about 11° so that the wing-tip describes a
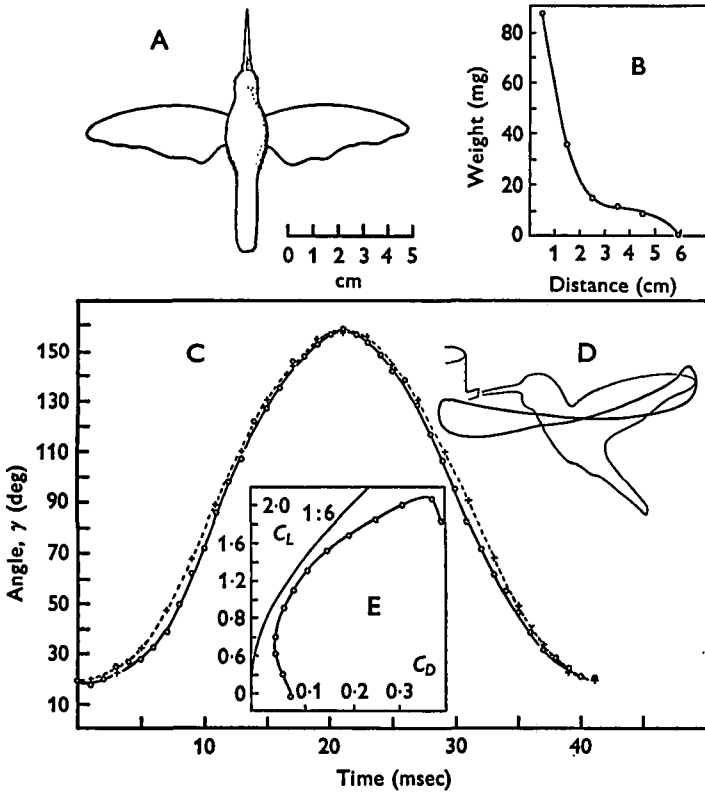

Fig. 2. Hovering flight of a hummingbird. (A) Outline of the specimen used in this study, *Amazilia fimbriata fluviatilis* (Gould, 1861). (B) Distribution of the wing-weight as a function of distance from the shoulder joint. (C) Comparison between the angular movements of the long wing-axis in the stroke plane of *Melanotrochilus fuscus* (full curve) and a sinusoidal movement (broken curve), as analysed from Fig. 3 in Stolpe & Zimmer (1939a). (D) The wing-tip curve of a hovering *M. fuscus* (from Stolpe & Zimmer, 1939b). (E) Polar diagram for a high-lift wing of aspect ratio 1:6, the parabolic curve for the induced drag being indicated by the left-hand curve (from Prandtl & Tietjens, 1934).

horizontal figure-of-eight when seen from the side (Fig. 2D; also reproduced by Gray, 1968). Apparently Hertel (1966) had access to the slow-motion films from which the original analysis was made and confirmed that the movement is sinusoidal. In addition, he found that the wing is twisted like a propeller blade during both upstroke and downstroke so that each section along the wing-axis has the same instantaneous geometrical angle of attack (his fig. 91) and, also, that the average effective angle of attack is attained almost instantaneously at either end of the stroke and remains almost

constant until the wing reaches the other extreme. This is seen from his fig. 92 which, when integrated, indicates that the mean angle of attack is 23° during both phases of the stroke, the induced wind being taken into account.

These findings are in accordance with the less-detailed records by Greenewalt (1960), mainly obtained from *Archilochus colubris*, but Greenewalt (1962) also provides accurate information on the wing-stroke frequency in relation to size. According to his fig. 11 (right) my specimen, which is of medium weight and wing-length as hummingbirds go, should hover at a frequency of about 35 strokes/sec. The less accurate data obtained by means of a mechanical stroboscope and during very brief chance observations indicate a somewhat lower frequency (his fig. 11, left). I have therefore calculated C_L for 29, 35 and 39 strokes/sec.

The *Amazilia* wing has an aspect ratio of about 1:6, and at a distance 0.7 R from the fulcrum it works at a Reynolds number of 7500 during the middle part of the stroke. Since the angles of attack are high and uniform, it is justified to choose a wing with aspect ratio 1:6 and of high-lift profile, such as the slotted wing in Prandtl & Tietjens (1934, fig. 90; see Fig. 2E). When the angle of attack is about 20°, and if we allow for the somewhat higher induced drag caused by the wind gradient along the wing, the ratio $C_L/C_D = 1.8/0.3 = 6$ appears to be justified. Lift coefficients of this magnitude are common in flapping birds (Pennycuick, 1968) but are smaller during gliding and soaring (Tucker & Parrott, 1970; Parrott, 1970).

Compared with other hummingbirds, the present specimen has a high average wing load (3.0 kg/m²). According to Greenewalt (1962) the area is 40 % less than should be expected by comparison with the smaller species *Archilochus colubris* (3.0 g, 13 cm², 2.3 kg/m², $R = 3.9$ cm, $n = 60$ sec⁻¹) and *Eupherusa eximia* (2.9 g, 15 cm², 1.9 kg/m², $R = 5.1$ cm). The true wing-stroke frequency of the hovering *Amazilia* specimen may therefore be higher than 35 sec⁻¹; the effect of wing inertia will therefore hardly be overestimated.

Drosophila and similar insects. The majority of the data derive from Vogel's beautiful studies of tethered rather than free flight. We are therefore forced to deduce a consistent set of data applicable to free hovering. Although the resulting lift and thrust have been shown to depend on the square of the wing-velocity in *Drosophila virilis* (Vogel, 1967a), the lift/drag diagram measured at a Reynolds number of 250 clearly indicates that the viscous forces seriously influence its shape and reduce the lift coefficient (Vogel, 1967b; cf. Fig. 3 F). During the morphological downstroke the wing is slightly cambered (oblique curve), whereas it is flat during the upstroke (Fig. 3E); during either phase the wing remains untwisted, so that all sections are set at the same geometrical angle of pitch relative to the stroke plane; the pitch changes abruptly at either end of the stroke and remains almost constant during more than two-thirds of the sweep (Vogel, 1967a; cf. Fig. 3B). Another important factor is that the lift varies little with the angle of attack from 20° to 50°, as originally pointed out by Thom & Swart (1940) and by Horridge (1956) and verified experimentally in Drosophila b; Vogel (1967b). This explains why the wings are not twisted. In the case of *symmetrical hovering* (see below), I have chosen a lift/drag ratio of 0.86/0.54 = 1.6, corresponding to an angle of 25°. For *unsymmetrical hovering*, the same figure applies to the downstroke when the wing is cambered, but it declines to 0.61/0.54 = 1.1 during the upstroke when the wing is flat. According to my calculations the middle and outer

wing-sections (II and III) produce more than 95% of the lift and drag, and their Reynolds number varies between 200 and 500, so that the lift/drag ratio may be somewhat improved during natural hovering. Because of the induced wind the effective angles of attack from base to tip differ from the geometrical angles, but the differences amount to only 8° in sections II and III. As in hummingbirds, it is therefore justified to use average force coefficients.
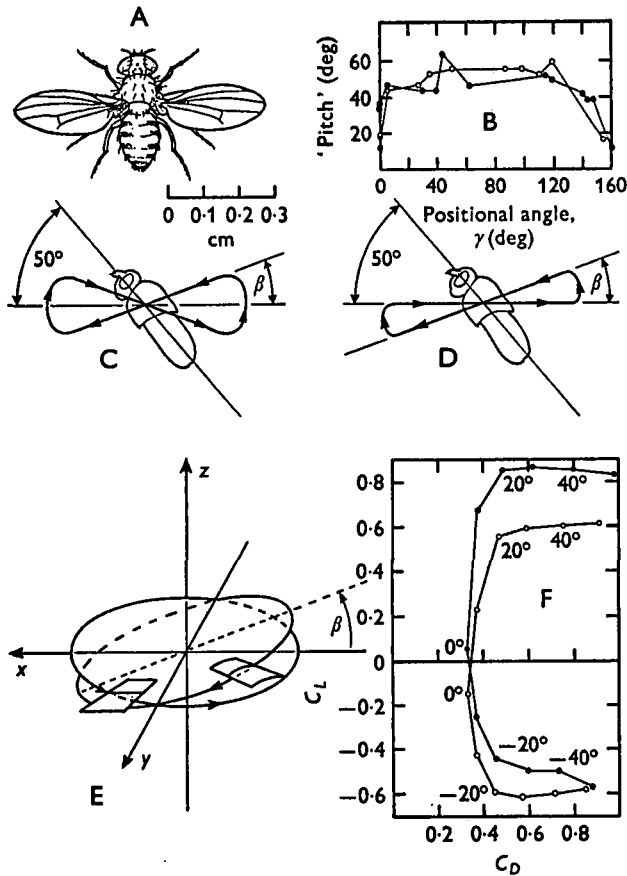

Fig. 3. Hovering flight of Drosophila. (A) Outline of a *Drosophila* sp. (B) The angular setting ('pitch') of the non-twisted wing-surface relative to an arbitrary plane as a function of the positional angle during tethered flight in still air (open circles) and at a wind speed of 200 cm/s (filled circles), from Vogel (1967a). (C) Wing-tip curve during symmetrical hovering and (D) during asymmetrical hovering. (E) the movement of a cambered wing-section during the morphological downstroke at $\beta = 20°$ and of a flat wing-section during the horizontal upstroke when $\beta = 0°$ during asymmetrical hovering. (F) Polar diagrams of wings of *Drosophila virilis* when cambered (filled circles) and flat (open circles), from Vogel (1967b).

The most difficult choice concerns the angular movements. Like other higher Diptera, Drosophila is a 'visual' creature, and when the visual field of a suspended fly is moved the frequency, the stroke angle and the aerodynamic force are significantly increased (Götz, 1968). Vogel's (1966) figures for standard flight of *Drosophila virilis* were taken during sustained performances of tethered flies with no visual stimulation and at wind speeds from zero to 250 cm sec^{-1}. The vertical lifting force H was a maximum

when the body angle was 50° which, in still air, corresponds to the stroke plane being tilted so that $\beta = 20°$ relative to the horizontal (Vogel, 1967a). As to frequency n, the steady-state value in Vogel's experiments was 195 sec^{-1} ± 10 % but the temperature was not reported. It is well known that n decreases with time, by 20–25 % during the first 15 min after start in *D. repleta* (Chadwick, 1939), which would bring the initial frequency of *D. virilis* up to about 240 sec^{-1}. It is also known that n increases significantly with temperature within this genus (Chadwick, 1939; Sotavalta, 1952a), and Chadwick & Williams (1949) found that shortly after the start the value in a tethered *D. virilis* was 183 sec^{-1} at 19·3 °C and 229 sec^{-1} at 25·9 °C. From an aerodynamical point of view, start and hovering flight are the most critical performances of the insect; they occur spontaneously and they are usually accompanied by changes in the visual field. It is therefore to be expected that both frequency and stroke angle are higher than during enforced sustained performances in a wind-tunnel and may well exceed the values seen in Table 1.

There is no precise information about the angular movements in Drosophila, but Nachtigall (1966) has published extensive measurements based on cinematography of a large calliphorine fly *Phormia regina*. When the fly was tethered in still air, the angular movement approached that of an harmonic oscillation but with a difference in duration between upstroke and downstroke amounting to up/down = 0·8. We shall therefore discuss both (*a*) *symmetrical hovering* (see Table 1, Fig. 3C), where the two phases are equally long, symmetrical with respect to the $y–z$ plane, $\beta = 20°$, and $n = 240$ sec^{-1}, and (*b*) *unsymmetrical hovering* (Fig. 3D, E) where up/down = 0·8, the upstroke is horizontal ($\beta = 0$) and the wing flat, the downstroke plane is tilted ($\beta = 20°$) and the wing is cambered, the over-all frequency is $n = 267$ sec^{-1} so that the effective frequency during the downstroke is 240 sec^{-1} (as before) and 300 sec^{-1} during the upstroke. It is not known whether *Drosophila virilis* in fact behaves in this way, but other small insects of similar dimensions may well do so.

<div align="center">RESULTS</div>

<div align="center">(a) Dynamic pressure index</div>

The variation with time of the dynamic pressure index $p_r \cos (\chi + \psi)/\cos \chi$ is seen in Fig. 4. At the relative time $T = 0$ the wing passes the middle position ($\gamma = 90°$) where the angular velocity is maximum, and at $T = 10$ the wing is at the extreme position where the velocity is zero. When the stroke plane is tilted ($\beta \neq 0$) there is a vertical component at the extreme ends caused by the induced wind but it is too small significantly to influence the shape of the curves, which are similar in the two animals although not identical. As one should expect, the inner third of the wing has very little aerodynamic effect in Drosophila (2·5 %) but it contributes significantly in the hummingbird (7·8 %) due to the broadening of the wing near the base. As is the case in other birds, and in hawk moths, locusts, etc., the broad wing-base is important for lift production during forward flight (of which hummingbirds are equally capable) but is of relatively little use during hovering or slow flight. In some Diptera it has even become modified into squamae which protect the halteres mechanically but appear to be without direct aerodynamic significance (Diptera Calypterae).

The area under the summed curve (full line) represents a product of pressure with

time, as integrated over one-quarter of a complete stroke cycle. When multiplied by the lift coefficients it must equal the body weight if free hovering in still air is to result. The curves are used to estimate the average lift coefficient $\bar{C}_L$ needed to make the animals airborne. The body weights are shown by an open circle on the ordinate, and a straight line has been drawn from it to $T = 10$. It is then immediately apparent that *Amazilia* must have an average lift coefficient near to but smaller than 2, and that the value for Drosophila is significantly smaller than 1.
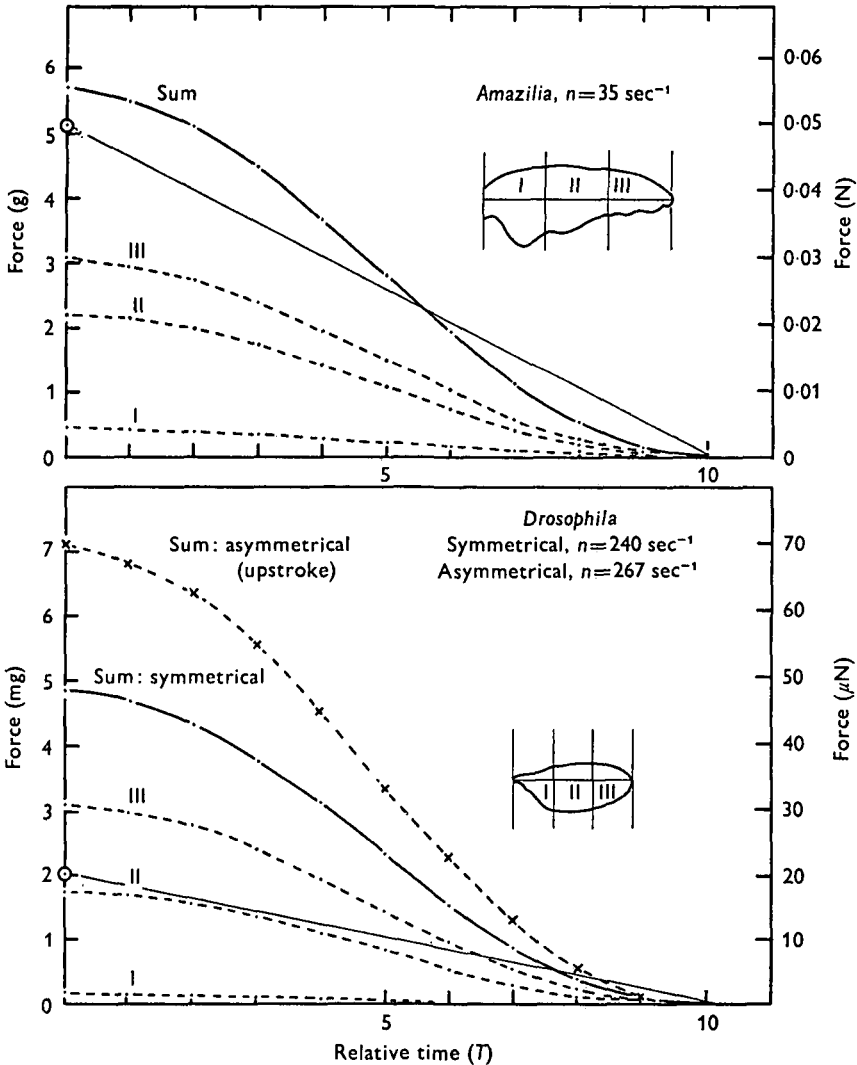

Fig. 4. The three wing-sections I–III in *Amazilia* and in Drosophila, and the vertical dynamic pressure index for each section as it varies with relative time T during a quarter stroke of symmetrical hovering (dots and broken curves). The summed curve is drawn in full line and the weight of the animal is indicated by an open circle on the ordinate axis. The summed curve for the upstroke of Drosophila during asymmetrical hovering is shown by crosses connected with dashed lines.

(b) The hummingbird

Coefficient of lift. At the typical wing-stroke frequency of 35 sec^{-1}, the lift coefficient for *Amazilia* was 1·82, which is very close to the value estimated for the ruby-throated hummingbird *Archilochus colubris* on the basis of Greenewalt's cinematographic flight data (1·86; Pennycuick, 1968). It also makes room for sudden changes up or down and therefore for manoeuvres. However, if we use the less reliable value of 29 sec^{-1} discussed earlier, $\bar{C}_L$ would increase to 2·7, which does not seem possible according to quasi-steady aerodynamics in a wing which is relatively thin and not multi-slotted (Savile, 1950). It is obvious from slow-motion films that hummingbirds increase the frequency somewhat when they break away from hovering. At 39 strokes per second $\bar{C}_L$ is reduced to 1·5, which offers ample scope for the aerobatics described by Greenewalt (1960).
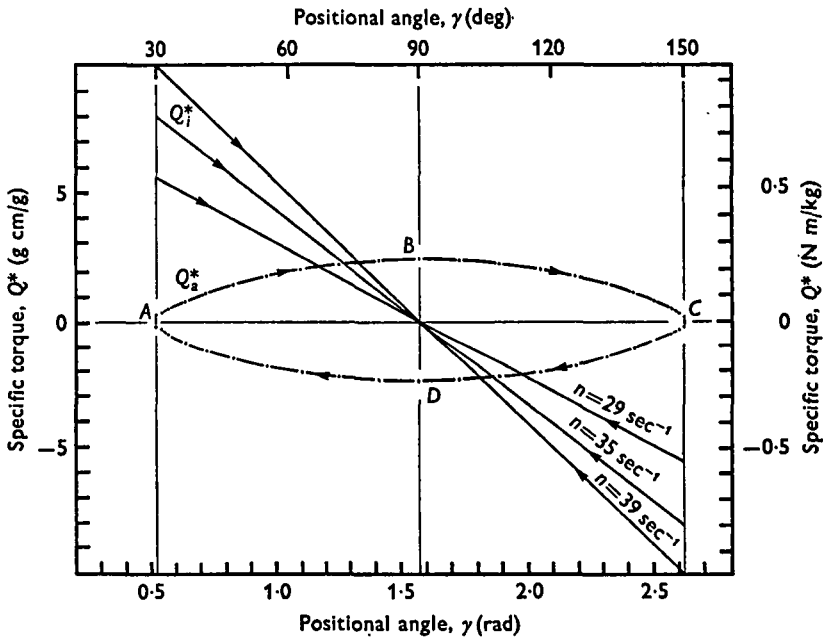

Fig. 5. Work diagram of a hovering hummingbird. The variation of the specific aerodynamic torque (Q_a^*) and of the specific inertial torque (Q_i^*) during a complete wing-stroke of *Amazilia fimbriata fluviatilis* when the wing-stroke frequency is $n = 35$ sec^{-1}. The inertial torques are also indicated for $n = 29$ sec^{-1} and $n = 39$ sec^{-1}. In this and the remaining figures the torque is of positive sign when it tends to turn the wing in the morphologically downwards direction.

Work diagram and aerodynamic torque. When we calculate the aerodynamic torque, the above variations in frequency do not result in any drastic change and the aerodynamic power remains at the same magnitude because a change in frequency in one direction is more or less balanced by a change in drag in the opposite direction. However, there is a very substantial alteration in the inertial torque Q_i. This is seen from the work diagram in Fig. 5 in which the specific torques Q_a^* and Q_i^* are illustrated, i.e. the *bending moments per unit body weight*. Results from animals of different shape and size can then be directly compared. The lens-shaped figure *ABCD* shows the variation of the specific aerodynamic torque Q_a^* during one complete cycle, the

'thickened' ends being caused by the induced wind. In this and the following diagrams the torque is of positive sign when it tends to turn the wing downwards. The area enclosed by the curve is therefore the positive aerodynamic work done; during the upstroke (γ_{min} to γ_{max}) the area above the zero line *ABC* represents positive work because the two factors to be multiplied, Q_a and $d\gamma$, are both positive; during the downstroke (γ_{max} to γ_{min}) the corresponding area *CDA* below the zero line also represents positive aerodynamic work because the values are both negative (cf. equation 15).

Inertial torque. In contrast to this, the specific inertial torque Q_i^* and the inertial work change sign. Since the oscillation is assumed to be harmonic it varies linearly with the positional angle γ. Two important features of hovering flight now become clear. (*a*) Since the inertial torque is maximum at the extreme positions where the only wind component is the induced wind and Q_a^* approaches zero, it is impossible to avoid some loss of the energy needed to accelerate the wing-mass; we shall estimate the loss below. (*b*) Without an elastic system (see later) the only way to reduce the loss is to reduce Q_i^* by decreasing the frequency n and the mass moment of inertia I within the limits set by aerodynamic requirements and material strength, respectively.

Hummingbirds have shorter wing-length R relative to body weight than other birds (Greenewalt, 1962, fig. 1), and since $I \propto R^5$, one must assume that, during evolution, the moment of inertia has become reduced as much as is functionally possible in this group. We have already seen that in *Amazilia n* cannot be smaller than 35 sec^{-1} if the bird should be left with any aerodynamic safety margin at all. Nevertheless, at this frequency Fig. 5 shows that the inertial torque is very considerable and that the energy loss from accelerations must be substantial. The straight lines for $n = 39$ sec^{-1} and $n = 29$ sec^{-1} are also drawn for comparison, and it is clear that hummingbirds must use up considerably more energy during hovering than is needed for the aerodynamic work alone unless elastic forces are introduced.

Total work. The torque and work which the thorax has to produce is found by adding the two torque components for every wing-position separately, as in Fig. 6, where the frequency is 35 sec^{-1}. To estimate the total work one must make a decision. Starting at the beginning of the upstroke ($\gamma_{min} = 30° = 0.52$ rad), there is no problem about the positive work which the thorax must deliver to the wings and which is represented by the shaded area *EAB*, but after 1.86 rad and until the end of the upstroke ($\gamma_{max} = 150° = 2.62$ rad), the work becomes negative and the thorax has to brake the movement and absorb the excess kinetic energy of the wings indicated by the dotted triangular area *BFC* under the zero line. In the absence of an elastic system the absorption of energy must be achieved by stretching the activated striated downstroke muscles of the bird, i.e. the muscles must do so-called negative work, the positive sign being reserved for work done during shortening. It is a characteristic of striated muscle that negative work costs considerably less chemical energy than an equal numerical amount of positive work, about 20 times less in a cycling man during the most favourable circumstances (Asmussen, 1952), and there is no indication that the chemical reaction can be driven backwards by a stretch and ATP actually synthesized; it is only possible to reduce the expense (Hill & Howarth, 1959). Even if no external work is done, positive or negative, it costs energy to activate a muscle. In our case it is the activated downstroke muscles which brake the upstroke and thereafter start a phase of positive downstroke work in the course of a single twitch. They are

therefore going to be activated anyway, and it is reasonable to assume that the cost
of negative work may approach zero in a well-designed reciprocating system like that
of a flying bird, bat or insect. In order not to exaggerate our estimate of work and
power, we therefore decide to disregard the cost of negative work. It should also be
noted that any viscous braking in addition to active muscle braking is then automatically
taken into account.

During symmetrical hovering the downstroke is similar to the upstroke but now
the dotted triangular area FCB represents positive work in excess of the useful aero-
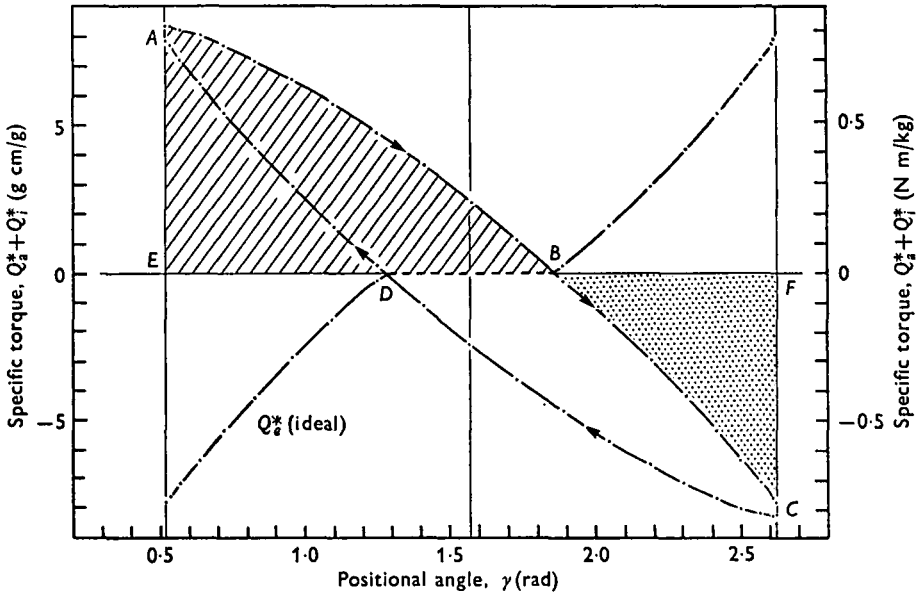dynamic work CDB, in the same way as the triangular part of the shaded area EAD

Fig. 6. The summed specific torque $(Q_a^* + Q_i^*)$ which the thorax must impart upon the wings
during a complete stroke of a hummingbird hovering at $n = 35$ sec^{-1}. The work diagram and
the specific elastic torque Q_e^* which could prevent unnecessary dissipation of energy are
explained in the text. The shaded area is the positive muscular work and the dotted area the
negative muscular work during an upstroke, provided that there is no elastic counter-torque
$(Q_e^* = 0)$.

is wasted as far as hovering is concerned. However, the area FCB of course represents
energy which could be useful to the bird in the form of an instantaneous pool for sudden
manoeuvres. However, if the bird were to hover without energy waste caused by
wing-inertia, it must be able effectively to store kinetic energy in a passive elastic
system and pay it back during the succeeding phase of the stroke. In the case of Fig. 6
such an *ideal elastic system* is characterized by the dashed curve Q_e^* (ideal), which is a
mirror image about the zero line of a curve corresponding to $ADBC$. It will be discussed
later. I have been unable to find any trace of such a system in the two recently dead
hummingbirds I have examined, and to my knowledge nobody has ever described a
passive elastic system in other birds. We are therefore forced to conclude that the
minimum amount of work per wing-stroke in a hovering *Amazilia* is represented by
the shaded area EAB plus its counterpart during the morphological downstroke DFC.

Work and power. During a complete wing-stroke the specific positive aerodynamic

work in Fig. 5 is $W_a^* = 7\cdot48$ g cm/g body weight and the inertial work is $W_i^* = 8\cdot42$ g cm/g, the direct sum being $15\cdot9$ g cm/g. In actual fact, kinetic energy is of course being converted into useful aerodynamic work to some extent so that the true expense $(W_a^* + W_i^*)$ from Fig. 6 and equation (17) is $13\cdot1$ g cm/g. About $5\cdot6$ g cm/g, or 43% of the total mechanical work, is therefore wasted.

The total *mechanical power output* of the wing muscles is $P^* = 13\cdot1 \times 35 = 459$ g cm sec^{-1}/g body weight. Since 1 g cm sec$^{-1} = 0\cdot845 \times 10^{-1}$ cal h^{-1}, the power output expressed in more familiar units is $38\cdot8$ cal g^{-1} h^{-1}. Lasiewski (1963) measured the *metabolic rate* of five species of hovering hummingbirds. In the case of *Calypte costae* a male weighing $3\cdot0$ g hovered continuously for 50 min and its average metabolic rate over 35 min of that period was $42\cdot4$ ml O$_2$ g^{-1} h^{-1}, or about 200 cal g^{-1} h^{-1} if fat was the main fuel. In our case this gives a *mechanical efficiency* of a hovering *Amazilia* of $38\cdot8/200 = 0\cdot19$, which is very plausible. Lasiewsky also noted that during brief bursts of flight in this and other hovering species the rate may increase by a factor 2 or 3. There is therefore ample surplus for paying the extra cost caused by an increase in wing-stroke frequency or stroke angle during less steady performances. For example, in the case of *Selasphorus rufus* ($4\cdot5$ g weight) the size is similar to that of my *Amazilia* and, during brief periods of hovering, the metabolic rate ranged from 200 to 610 cal g^{-1} h^{-1}.

Aerodynamic efficiency. The induced wind is 137 cm sec^{-1}, so that the momentum imparted to the air *per g body weight* is 137 g cm sec^{-1}. The actual specific aerodynamic power P_a^* is $7\cdot48 \times 35 = 262$ g cm sec^{-1}/g. As compared with an ideal actuator disk the aerodynamic efficiency of a hovering hummingbird is therefore $136/262 = 0\cdot52$. This is not bad for an oscillating system.

Conclusion. In hummingbirds the calculated lift coefficient, the work, the power, and the mechanical and aerodynamic efficiencies all fit together and match independent observations of other aspects of hovering flight. There is therefore no reason to believe that non-steady aerodynamics is involved to any significant extent or that the method of calculation developed here is seriously at fault. The third major conclusion is that hovering hummingbirds must waste a substantial amount of power in order to vibrate the wing-mass. The loss amounts to 43% of the total expenditure at the normal frequency of 35 sec^{-1}, but since the inertial power increases with the cube of the frequency, P_i^* would increase from 25 to 34 cal g^{-1} h^{-1} at 39 strokes/sec. About 60% of the mechanical power would then be wasted and the metabolic rate would have to be increased from 200 to at least 260 cal g^{-1} h^{-1}. Wing-inertia is clearly a major factor in hovering birds.

(c) Drosophila and similar insects

Apart from the geometrical shape and the ability to hover and to fly slowly about, hummingbirds and Drosophila are as different as can be. Drosophila is small, works at low Reynolds numbers, has a poor lift/drag diagram due to the relatively large effect of the viscous terms of the flow as compared with the inertia terms, and the appearance of the insect is that of an aircraft working at the limit of its ability with almost nothing to spare for manoeuvres. Compared with other insects, Drosophila is also economical with respect to metabolic rate. As explained earlier, the available flight data are not as relevant for free flight as is the case with hummingbirds, and the present results therefore need checking as new observations become available.

Symmetrical hovering. This mode is characterized by symmetry with respect to the main axes of the animal, to relative time, and to forces. Although the stroke plane is tilted by 20°, the resultant propulsive wind forces during upstroke and downstroke will balance and the animal will hover on the spot or climb or descend vertically. In two respects this performance is somewhat unrealistic for Drosophila because Vogel (1967a) has shown that the wing is cambered during the morphological downstroke and flat during the upstroke, and that the durations of the two phases differ. However, it is instructive to analyse this performance as an example of what a small insect may do when power economy is a major concern.
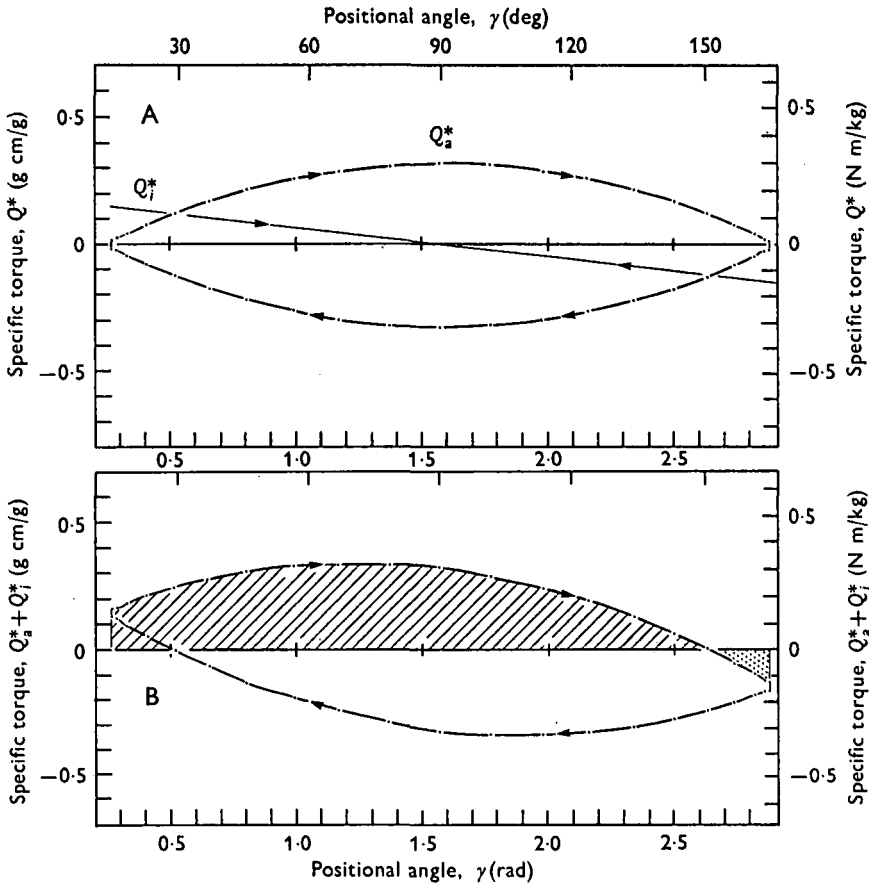

Fig. 7. Work diagrams for Drosophila during symmetrical hovering. Compare with Fig. 5 for *Amazilia* and with Fig. 6. Note that the negative muscular work is small in Drosophila because the frequency n is about 3 times smaller than in most other insects of similar size; otherwise, the inertial torque would have been 9 times larger and would be a significant factor in the balance sheets for energy and power.

The *average lift coefficient* $\bar{C}_L$ was found to be 0·83, which is close to the maximum possible and reasonable in view of the fact that, according to the lift/drag diagram, C_L only varies between 0·80 and 0·85 when the angle of attack changes from 15° to 50° (see Fig. 3F).

The *specific aerodynamic and inertial torques* are seen separately in Fig. 7A and

combined in the work diagram of Fig. 7B. The units on the vertical axis are 10 times smaller than in the corresponding diagrams for *Amazilia*. The *aerodynamic* curve is of the same general shape in the two animals, as was to be expected, but the similarity goes farther. The specific maximum torque is 7·8 times larger in the hummingbird than in the insect. In a series of *similarly built* hovering animals $Q_a^* \propto n^2 l^2$ where l is a representative length, say the wing-length (Weis-Fogh, 1972*b*). The ratio of the aerodynamic torques in the hummingbird and in Drosophila should then be $(35 \times 5 \cdot 9 / 240 \times 0 \cdot 3)^2 = 8 \cdot 2$, i.e. very close to the value found. This degree of similarity may appear surprising in view of the considerable difference as to wing-construction, flow conditions and wing-loading, but it remains a fact.

Also with respect to *specific aerodynamic power* the similarity is striking. In Fig. 7A, $W_a^* = 1 \cdot 16$ g cm/g; at 240 strokes/sec this corresponds to $P_a^* = 23 \cdot 5$ cal g^{-1} h^{-1}, as against 22·2 in *Amazilia*. It is obvious that the specific power for hovering need not vary much with absolute size, as will be discussed elsewhere (Weis-Fogh, 1971*b*).

The *inertial torque and power*, on the other hand, are so small compared with those in *Amazilia* as to be of little significance in Drosophila, although the general trend is the same and the triangular areas representing the wasted work are still discernible (Fig. 7B). The total power output $(P_a^* + P_i^*)$ is 24·2 cal g^{-1} h^{-1}, so that the loss caused by wing inertia is only 3%. Evidently Drosophila is designed for maximum aerodynamic output per unit energy used. However, small inertial torques are not characteristic of insects in general (Sotavalta, 1952*b*), and, as already pointed out, the wing-stroke frequency of Drosophila compared with other insects of similar size is three times smaller. If n was increased to what is normal for an insect of the size of Drosophila the inertial P_i^* would approach 100 cal g^{-1} h^{-1} and would really matter in the energy account.

The *aerodynamic efficiency* is $76/278 = 0 \cdot 27$ and is fair for an oscillating system working against relatively high viscous forces. It is more difficult to estimate the *mechanical efficiency* of the wing muscles. If we use the average steady-state metabolic rate for tethered flies, it is $24 \cdot 2/106 = 0 \cdot 23$; but this may be too high, and the metabolic rate of 140 cal g^{-1} h^{-1} at the beginning of flight is probably more realistic for free hovering, giving an efficiency of 0·17. Anyway, there can be no doubt that the aerodynamic system of Drosophila requires practically all the available energy and that it appears to be as efficient as can be designed at the low Reynolds number in question.

It should be noted that the inertial forces in a flying Drosophila are so small that they cannot provide the mechanical conditions necessary for the oscillation of myogenic muscles (Pringle, 1967). In this genus the sterno-pleural muscles are unusually large (cf. Pringle, 1968) and it must be their action on the thorax elasticity which provides the necessary phase change between force and movement.

Asymmetrical hovering. Strictly speaking, this is not stationary flight on one spot because the morphological downstroke with cambered wings is identical with that of the previous example, while the faster horizontal upstroke with flat wings was calculated for a lift coefficient of 0·60 when 0·58 would have been sufficient. This means that there is a slight surplus of lift as well as an average forward thrust. In other words, the work diagram in Fig. 8 illustrates the energetics of a Drosophila-like insect during steep forward climb which is so characteristic for the start of many small species. The increase in frequency from 240 to 267 sec^{-1} has a negligible effect on the expense,

but the impaired lift/drag ratio is significant. The *specific upstroke work* (area *EAB*)
is 0.923 g cm/g and the downstroke work (area *FCD*) is 0·597 g cm/g, or a total of
1·52 g cm/g body weight. The *specific power* is 34·2 cal g^{-1} h^{-1}. This is 41 % more
than during symmetrical hovering, and the *aerodynamic efficiency* is 0·19. Again, the
mechanical efficiency of the wing muscles is uncertain but may be as high as 34·2/
140 = 0·24.

Conclusion. The assumption of a succession of steady-flow situations is able to explain
the flight and energetics also of a hovering or climbing *Drosophila virilis*. Admittedly,
the wing-stroke frequency during asymmetrical hovering, i.e. during a steep climb,
had to be 11 % higher than hitherto reported from tethered animals, so that it is
desirable to obtain more detailed measurements on freely flying insects. However,
there is no reason to doubt that the present procedure represents a good qualitative
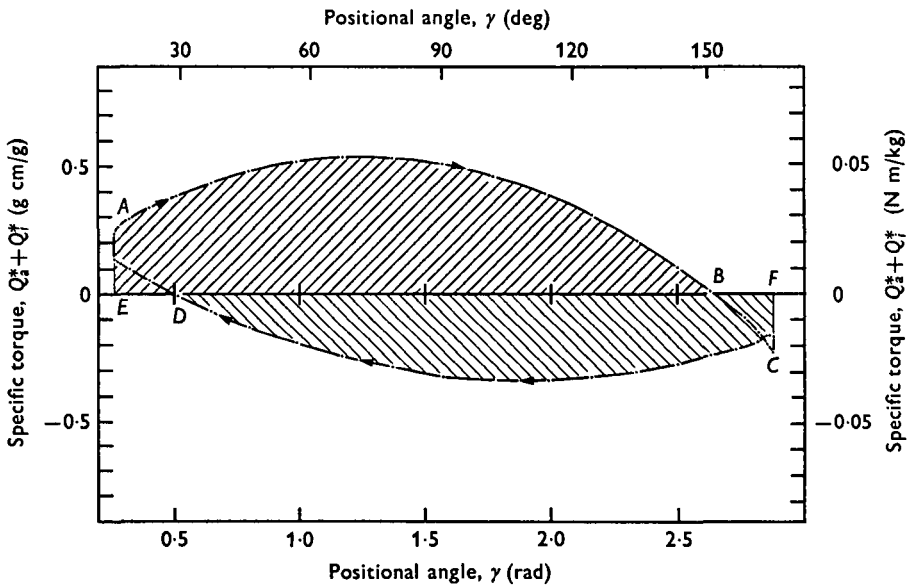and quantitative approximation to the true flight.

Fig. 8. Work diagram of Drosophila during asymmetrical hovering or during slow steep climb.

As to inertia terms, Vogel (1962) has pointed out that the boundary layer of small
insects may add significantly to the effective moment of inertia of the oscillating wings,
about 50 % in the case of Drosophila. Since the total effect of wing inertia is so small
compared with the aerodynamic terms in this particular group of insects, the present
results are not affected to any significant extent. This also means that the marked
effect of changes in air density on the wing-stroke of Drosophila cannot be explained
by changes in the mass of the boundary layer as suggested by Vogel, but must be
caused by changes in the completely dominating aerodynamic drag forces, as suggested
by Chadwick & Williams (1949) and Chadwick (1951). In other small insects with
higher relative wing-stroke frequencies, Vogel's argument remains valid.

DISCUSSION

We know that steady-state aerodynamics is adequate to explain the fast forward flight of locusts with considerable accuracy (wing-length $R = 6$ cm; Jensen, 1956) and we have good theoretical evidence that, in principle, this also applies to a horse-fly (1·4 cm) and to a mosquito (0·4 cm; Weis-Fogh & Jensen, 1956). We have now seen that the more exacting task of hovering on the spot or of climbing steeply is possible in hummingbirds (6 cm) as well as in Drosophila (0·3 cm) without involving non-steady principles. We are therefore in a position to discuss the mechanics and energetics of a whole range of flying animals on a unified basis, as will be done elsewhere (Weis-Fogh, 1972a). However, these *average* results do not exclude non-steady flow during certain phases of the wing-stroke, nor do they rule out that certain species regularly exploit such situations, as has been suggested by Osborne (1951) and Bennett (1966, 1970) with particular reference to the large lamellicorn beetles *Lucanus* (stag beetle) and *Melolontha* (cockchafer). Until new reliable observations of *free flight* in these and other species become available it is not possible to decide how important these effects may be, although my estimates of $\bar{C}_L$ in *Melolontha* and in the large elephant-dung beetle *Heliocopris* indicate that they are negligible (Weis-Fogh, 1972a). However, the general problem remains, that of non-steady periods within an essentially steady-flow pattern.

(a) Non-steady flow

The two main phenomena are probably delayed stall and the time needed to build up circulation after a change of angle of attack, the so-called Wagner effect. They arise because it takes time to exchange energy for boundary-layer separation and for vortex formation respectively. These phenomena have opposite effects with respect to fluctuating lift production. The delayed stall means that a given wing can work at high lift coefficients without stalling shortly after an increase in the angle of attack, but the effect is over after the wing has travelled 2–3 chord lengths (cf. Goldstein, 1938). The Wagner effect is operative whether the angle of attack is increased stepwise (cf. Goldstein, 1938) or sinusoidally (cf. Garrick, 1957), and under both conditions it takes 2–3 chord lengths to attain about 80 % of the steady-state lift. At present it is not possible accurately to evaluate the opposing tendencies in a hovering animal, but the following is worth noting. During hovering the *average* length travelled by a wing chord situated 0·7R from the fulcrum is 6 chord lengths in *Amazilia* and 5 in *Drosophila virilis*. Delayed stall and the Wagner effect may therefore be of some importance in the beginning of each half-stroke. Since they work against each other, the combined result may well approach the steady-state value. An anlysis by experts is clearly desirable.

In this context it is worth pointing out that the characteristic *wing-tip curve* during hovering, the horizontal figure-of-eight, may have three advantageous effects. The first and the second are obvious from Fig. 1. (1) The *tilted stroke plane* counteracts the adverse downwards direction of the relative wind caused by the induced wind and therefore increases the vertical lifting force. The tilt could be considered as a useful adaptation to the aerodynamic effect of the induced wind both in animals with a high and a low lift/drag ratio. (2) If the lift/drag ratio is relatively small, as it is bound to be in small insects working at low Reynolds numbers, the resultant aerodynamic

force F_r is considerably larger than the lift L_r and the stroke plane must be tilted by
a relatively big angle in order for the vertical force H_r to become as large as possible.
(3) The third effect is not well understood at present but is worth pointing out.
Although the angular movements in the stroke plane itself approach zero at the extreme
positions and although the kinetic energy of the wings is small (Stolpe & Zimmer,
1939a; Jensen, 1956; Nachtigall, 1966), the wings do not cease moving but are swung
upwards simultaneously with a brisk alteration of the wing-twist in preparation for
the next half stroke. It must be remembered that it takes time for circulation not only
to build up but also to become reduced. Towards each extreme wing-position the
preceding circulation actually ought to be annihilated since the reverse stroke must
produce a bound vortex of the opposite sense. The upwards movements at the ends
of the horizontal figure-of-eight may therefore represent periods when the wings move
away from the vortex which has to be shed at the end of each half-stroke so as to escape
the adverse effect of the shed vortex. This problem obviously deserves some attention
by specialists.

(b) Wing-inertia and wing-elasticity in insects

In most insects the maximum specific inertial torque amounts to 2–4 g cm/g body
weight during harmonic oscillations. In small and medium-sized insects with a high
wing-stroke frequency this would lead to a very considerable waste of power (Sotavalta,
1952b; Weis-Fogh, 1972a). However, to a considerable extent the loss is avoided by
means of a complex elastic system for storage and release of kinetic energy; it is
characterized by a low degree of mechanical damping and will be analysed in detail
elsewhere (preliminary reports, see Weis-Fogh, 1959, 1961, 1965), but one result is
shown in Fig. 9. The ordinate is the specific elastic torque Q_e^* of a large male dragonfly
Aeshna grandis L. (0·7 g body weight) and the abscissa is the positional angle γ, the
maximum and minimum values being indicated for each pair of wings when the flying
insect lifted its own weight and the frequency was 29 sec^{-1}. The steepest curves are
from the intact, non-stimulated thorax after removal of the central nervous system.
The similarity between the shape of the curves and that of the ideal elastic curve for
the hummingbird in Fig. 6 is remarkable. In each pair of wings the maximum elastic
torque Q_e^* amounts to 1–2 g cm/g in *Aeshna grandis* and corresponds to a natural
frequency of the wing-system of about 20 sec^{-1}, i.e. the fluttering frequency which I
observed when the animal increased its thoracic temperature before taking to the wing
at 29 sec^{-1}. The specific elastic torque was of the same magnitude in locusts (*Schistocerca
gregaria*, 1–2 g cm/g for each wing pair), and in a privet hawk moth (*Sphinx ligustri*,
4 g cm/g for all four wings). In these insects the major contribution to the elastic
torque derives from the sclerotized cuticle of the thoracic box and from the rubber-like
ligaments whose main component is the protein resilin (Weis-Fogh, 1965). In the
dragonfly, however, about 75 % of the energy is stored in and released from passive-
elastic elements in the wing muscles themselves. In locusts the elastic efficiency of
non-active flight muscle was found to be 0·8 ± 0·2 so that a substantial saving is possible
from this tissue alone. Although dragonflies appear to be unique as to the *relative*
importance of muscle as storage compartments for elastic energy, the main point of
Fig. 9 is that insects have used at least three different materials for the construction of
an elastic wing-system: (1) the solid skeletal cuticle, (2) a typical elastomer in the form
of the protein resilin and (3) an elastic component in the myofibrils themselves which

still remains unidentified chemically and structurally. It is present inside fibres of both neurogenic and myogenic wing muscles (Buchthal & Weis-Fogh, 1956).

(c) *Elastic recoil in vertebrates*

An internal skeleton which is mineralized and therefore essentially brittle does not lend itself to absorption and release of substantial amounts of elastic energy. In this respect an external skeleton of tough and flexible cuticle is far superior (Jensen & Weis-Fogh, 1962). The possibility of including the elasticity in the myofibrils of the power-producing muscles themselves remains open in principle although there is no
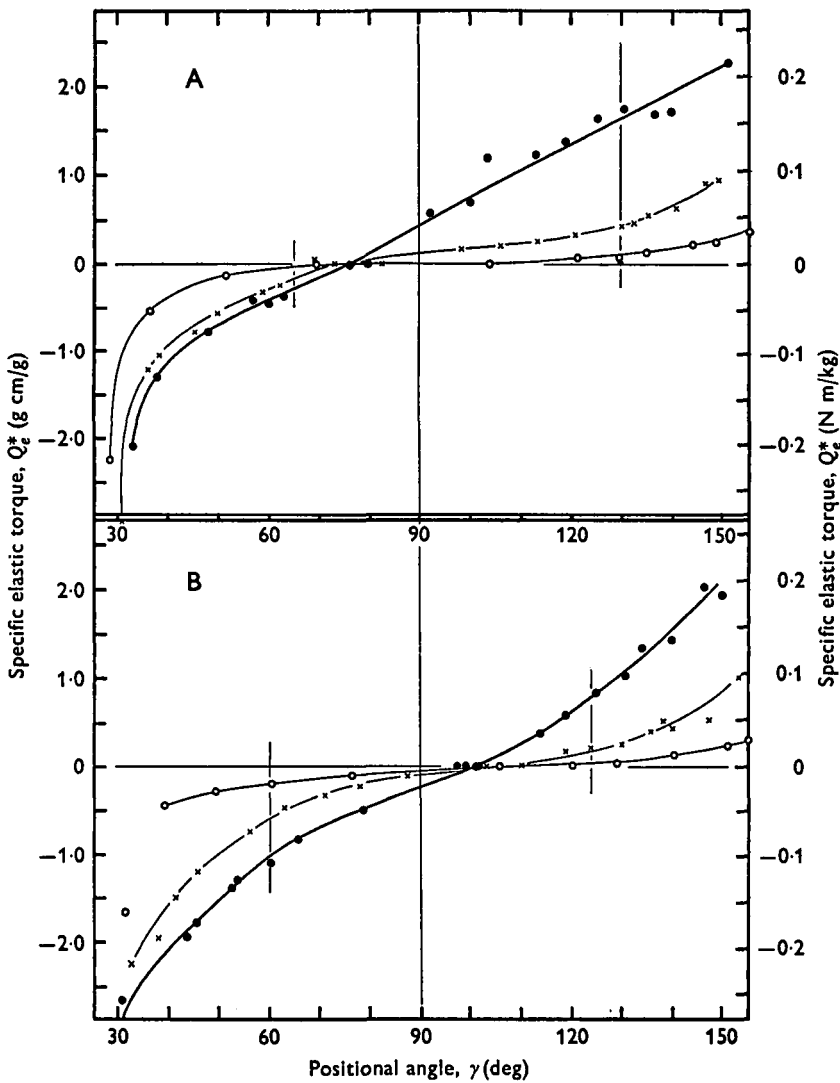

Fig. 9. Measured specific elastic torques (Q_e^*) in a male dragonfly (*Aeshna grandis*), (A) for two forewings and (B) for two hindwings. Filled circles: intact thorax with central nervous system removed, 30 °C. Crosses: intact thoracic box after removal of all flight muscles. Open circles: the elastic wing-ligaments alone.

sign of it in relaxed or dead hummingbirds or in other vertebrates which I have examined. In insects the elasticity is manifest in relaxed muscle and acts in parallel with the contractile machinery when the muscle shortens (Buchthal, Weis-Fogh & Rosenfalck, 1957); it is extraordinarily strong in some myogenic muscles (Pringle, 1967). For the time being one cannot with certainty exclude that wing muscles of hummingbirds contain unusually compliant and elastic A-filaments or I-filaments in which a substantial amount of energy can be stored when the muscle is activated, but this possibility has no experimental basis and appears highly unlikely. One may ask why the elastic muscle type known from insects has not evolved within the vertebrate group. First of all, this type of solution is known only from insects where it is found either in the flight system or in the tympanal organ of some cicadas (Pringle, 1967, 1968), i.e. from systems where the muscles have but one function, work at an almost constant frequency, and are suspended in a cuticular box whose dimensions remain constant after the final moult. Under such conditions one can imagine that the muscle filaments are assembled with or around intracellular, stable, elastic structures, whereas a similar system is difficult to reconcile both with the large range of speed and movement of vertebrate limbs and with the fact that the growth of all chordates is continuous and not confined to discrete steps as in arthropods.

Nevertheless, hummingbirds resemble insects in so far as their wings are moved at an almost constant frequency irrespective of whether they hover, fly backwards or are in continuous forward flight at top speed (Greenewalt, 1960). In other words, if avian muscle had the potential to develop elastic components similar to those in insect wing muscle, both hummingbirds and other birds would have gained substantially during evolution. The absence of such a system indicates that the potential was lost at an early stage, if it was ever present.

The third possibility is to make use of the extracellular elastomer which is characteristic for chordates as a phylum, the protein elastin.

(d) Elastin and vertebrate locomotion

Let us first consider a flying hummingbird like *Amazilia*. We have seen that in the absence of an elastic system it wastes about 6 g cm of energy per g body weight per wing stroke. We have also seen that metabolically it is actually able to meet this cost and quite a bit more when need be. However, it would undoubtedly be of selective advantage if the bird could save a substantial amount of power, and the question is whether this could be done by making use of elastin, remembering that any addition would increase the weight of the animal. According to Meyer (1950), the elastic coefficient of ox ligamentum nuchae is 14 kg/cm^2 in the region of 10–50% extension where the work diagram is almost linear (Weis-Fogh & Andersen, 1970). If we stretch a centimetre cube from side length 1·00 to 1·25 cm, the maximum force will be 3·5 kg per cm^2 original cross-sectional area, and it will have stored about 440 g cm/cm^3. In order to store 6 g cm, we should need 6/440 cm^3 elastin, or about 15 mg elastin (density 1·1 g/cm^3) per g body weight. This is only 1·5% of the weight of the bird and 5% of the weight of the flight muscles (30% flight muscle, Greenewalt, 1962). In other words, an addition in weight of only 1·5% could save 40% in energy during normal hovering and considerably more when the frequency is increased during manoeuvres.

One may argue that this solution would result in lack of fine control of the wing-beat, but this need not be so. If the elastin was arranged as a tendon in series with a mechanically *slow* muscle which could adjust the *average* length of the tendon and could resist a force of 3·5 kg/cm², the bird would have gained a distinct advantage as to energetics and speed of movement. The principle of a slow muscle in series with a resilin tendon is in fact utilized by dragonflies (Weis-Fogh, 1960; Neville, 1960). If the muscle is of the same length, weight and cross-sectional area as the tendon, complete control of the elastic system could be obtained at a total cost of about 3 % increase in weight. A wider but shorter muscle could offer good control for extensions of the tendon of up to 50% and it could then store four times more energy than before. Has this obvious possibility been made use of during the long competitive evolution of birds and other fast moving vertebrates ? The answer must be given in two parts.

In some large mammals elastin appears to be incorporated in parallel with muscle fibres because in the ox Bendall (1967) has shown that the epimysium and perimysium of the longissimus dorsi of the forelegs and the semitendinosus of the hind legs contain large and abundant elastin fibres. During a fast gallop these powerful muscles swing the extended legs backwards and assist propulsion. During the forward swing the legs are partially flexed and the inertial torque reduced. The maximum level speed of large fast-running mammals is limited by limb inertia (see discussion in Gray, 1968); the more the backward swing is assisted, the smaller the cost of energy will be and the larger the frequency and the higher the speed. In the ox about 2% of the dry weight of these muscles consist of elastin which may reduce the effect of limb inertia significantly although quantitative estimates are still lacking. According to Gray's (1968) figure 10·20 of a galloping horse and a cheetah, the shortening of these muscles would be about 25 % of the extended length in the horse and 50% in the cheetah. In both animals the maximum frequency is 2·5 sec^{-1}. In other words, at this rate of deformation the evidence is that some large mammals make use of elastin as a means of counteracting the adverse effect of limb inertia, although more detailed studies are needed in order to evaluate the effect quantitatively.

The other part of the answer is related to the damping properties of elastin as a function of frequency and amplitude. We have recently proposed a new functional model for elastin as an elastomer, called a liquid-drop model (Weis-Fogh & Andersen, 1970) and this has led us to a comparison between mechanical and thermodynamic hysteresis in samples which are subject to sinusoidal extensions. It turns out that at a peak-to-peak amplitude of 25%, elastin has little damping at small frequencies (2–5 sec^{-1}) but the ratio between the heat dissipated per cycle and the stored energy increases steadily with frequency and exceeds 10% at about 30 sec^{-1} (Gosline & Weis-Fogh, unpublished). It therefore looks as if elastin as a material is unsuited for the construction of oscillating systems working at high rates of deformation. Since elastin is found in all chordates it must have evolved at an early stage of evolution and long before fast running or flying became part of the vertebrate repertoire.

If it had been possible for small and medium-sized reptiles, birds or mammals to take advantage of an effective elastic system, the frequency of oscillation and the speed of movement might have been increased relative to those of known species. Many forms of construction would then have been different from the ones we know and crash-proofing would be a major problem.

SUMMARY

1. Expressions have been derived for an estimate of the average coefficient of lift, for the variation in bending moment or torque caused by wind forces and by inertia forces, and for the power output during hovering flight on one spot when the wings move according to a horizontal figure-of-eight.

2. In both hummingbirds and Drosophila the flight is consistent with steady-state aerodynamics, the average lift coefficient being 1·8 in the hummingbird and 0·8 in Drosophila.

3. The aerodynamic or hydraulic efficiency is 0·5 in the hummingbird and 0·3 in Drosophila, and in both types the aerodynamic power output is 22–24 cal/g body weight/h.

4. The total mechanical power output is 39 cal $g^{-1} h^{-1}$ in the hummingbird because of the extra energy needed to accelerate the wing-mass. It is 24 cal $g^{-1} h^{-1}$ in Drosophila in which the inertia term is negligible because the wing-stroke frequency is reduced to the lowest possible value for sustained flight.

5. In both animals the mechanical efficiency of the flight muscles is 0·2.

6. It is argued that the tilt of the stroke plane relative to the horizontal is an adaptation to the geometrically unfavourable induced wind and to the relatively large lift/drag ratio seen in many insects. The vertical movements at the extreme ends may serve to reduce the interaction between the shed 'stopping' vortex and the new bound vortex of opposite sense which has to be built up during the early part of the return stroke.

7. Two additional non-steady flow situations may exist at either end of the stroke, delayed stall and delayed build-up of circulation (Wagner effect), but since they have opposite effects it is probable that the resultant force is of about the same magnitude as that estimated for a steady-state situation.

8. Most insects have an effective elastic system to counteract the adverse effect of wing-inertia, but small fast-moving vertebrates have not. It is argued that the only material available for this purpose in this group is elastin and that it is unsuited at the rates of deformation required because recent measurements have shown that the damping is relatively high, probably due to molecular factors.

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