AERODYNAMICS OF FLAPPING FLIGHT WITH APPLICATION TO INSECTS

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(With Fifteen Text-figures)

INTRODUCTION

The problem of natural flight is one of long-standing interest, both intrinsically and in connexion with mechanical flight. Rayleigh (1883) was perhaps the first to give a satisfactory explanation of the soaring flight of birds, and Walker (1927) gave a satisfactory quantitative discussion of the flapping flight of birds in a particular case. Hoff (1919), using the data of Demoll (1918), attempted to bring the flight of insects into the domain of conventional aerodynamics by showing that lift coefficients of reasonable value were required. He used only the linear velocity of flight to evaluate these coefficients and ignored the motion of the wings. He also pointed out the similarity between the flow pattern around an insect and around a propeller or actuator disk, a similarity which must hold from momentum considerations, independently of the action of the wings (Bairstow, 1939). Demoll (1919) indicated several errors and omissions in Hoff's work, so that in a number of cases the lift coefficients required were inordinately high. Finally, a most thorough experimental investigation was carried out by Magnan (1934), who was, however, unable to explain his results theoretically.

The difficulty of high lift coefficients has not been removed by other investigations which have indicated lift coefficients larger than those normally expected in wind-tunnel measurements. It has, therefore, been believed that insects must utilize some special mechanism in flight not present in conventional aerodynamic phenomena.

In this paper the mechanism of insect flight will be examined in detail in order to find some possible explanations for the high lift coefficients, as well as for other characteristic features of insect flight. General expressions will be obtained for the force acting on a wing surface element moving in an arbitrary manner. This force will be resolved into lift and drag components with respect to the relative wind, and integrated over the surface of the wing and averaged over the period of a wing beat in order to determine the total average vertical and horizontal forces exerted by the insect. The former is the required vertical force (weight of insect), the latter the required thrust (drag of insect's body). Average values of the lift and drag coefficients of the wings, $\bar{C}_L$ and $\bar{C}_D$, can then be determined, since there are two known forces given, and two unknown coefficients to be determined.

The scalar product of the vector force on the wing element into the vector velocity of the element with respect to the insect, integrated and averaged as before, gives the mechanical power exerted by the insect in flight.

The absolute magnitude of the total force on the wing element, integrated and averaged, will give a lower bound to the force coefficient for the average total force, $(\bar{C}_L^2 + \bar{C}_D^2)^{\frac{1}{2}}_{\min}$.

The power, the lift, drag and total force coefficients computed for the twenty-five insects for which data is available, will, when plotted against the other parameters of insect flight such as mass and ratio of flapping to linear velocity, reveal a number of interesting and systematic characteristics of insect flight. The flight data, summarized in Table 1 (p.   ), were taken from the work of Magnan, and were supplemented by measurements on specimens of the U.S. National Museum.

For those who wish to draw conclusions from this work without verifying the mathematical details, it may be said that the principal mathematical problem is to justify replacing the instantaneous velocities by suitably chosen averages over position and time. Once this process is admitted practically all of the qualitative conclusions may be reached by drawing vector diagrams similar to those of Fig. 4, with these average velocities for any particular case. In fact, if the averaging precepts are admitted, quantitative conclusions can be reached by drawing to scale, and with all small components such as v and w included, diagrams like Fig. 4.

DERIVATION OF THE FUNDAMENTAL FORMULAE

It is assumed that the lift force $d\mathbf{F}_s$ on an element of wing surface $c(r)dr$ is given by

$$d\mathbf{F}_s = (\tfrac{1}{2})\rho C_L c(r)\,dr\,|\,\mathbf{l} \times \mathbf{W}\,|^2\{(\mathbf{l} \times \mathbf{W})/|\,\mathbf{l} \times \mathbf{W}\,|\}, \tag{1}$$

and the drag force is given by

$$d\mathbf{F}_p = -(\tfrac{1}{2})\rho C_D c(r)\,dr\,|\,\mathbf{l} \times \mathbf{W}\,|^2\{(\mathbf{W} - \mathbf{W}.\mathbf{l}\mathbf{l})/|\,\mathbf{W} - \mathbf{W}.\mathbf{l}\mathbf{l}\,|\}. \tag{2}$$

The quantities which appear in these two formulae are defined as follows (see Fig. 1). Vectors are denoted by bold face, their scalar magnitude by two vertical lines.

$\mathbf{l}$, $\mathbf{m}$, $\mathbf{n}$ are mutually perpendicular unit vectors parallel to the axis of the wing, perpendicular to the axis of the wing in the instantaneous plane of beating, and perpendicular to this plane, respectively. The plane of beating is not the plane of the wing, but the plane in which its axis is moving. ρ is the air density. W is the relative wind or velocity of the surface element of the (right) wing with respect to the air, and is given by

$$\mathbf{W} = (\mathbf{n}\Omega \times \mathbf{l}r) - \mathbf{U}. \tag{3}$$

Ω is the instantaneous angular velocity of the wing element, and $\mathbf{U} = (0, -(V+v), -w)$ is the velocity of the air with respect to the insect's body. V is the velocity of flight and v, w are the induced velocities. $c(r)$ is the chord. r and t are the independent variables — distance along the wing and time. In the general case all of the quantities appearing in eqs. (1) and (2) (except ρ and $c(r)$) are functions of r and t. If the wing is assumed not to twist or bend, the unit vectors and Ω will be independent of r. C_D evidently represents the profile drag coefficient, since the relative wind includes the induced velocities.

Average values for the induced velocities v, w, or velocity increments of the slipstream, are given from momentum theory (Durand, 1935). They are independent of the mechanism of the wing action, and are obtained in first approximation by

requiring that v and w at the insect have one-half the final value necessary to provide the necessary vertical force and horizontal thrust:

$$\text{Lift (vertical force):} \quad L = Mg = \pi R^2 (V^2 + w^2)^{\frac{1}{2}} \, 2w, \tag{4}$$

$$\text{Thrust:} \quad T = (\tfrac{1}{2}) \, C_{Db} \, S_b \rho V^2 = \pi R^2 (V^2 + w^2)^{\frac{1}{2}} \, 2v. \tag{5}$$

R is the length of the wing, M is the mass of the insect, g is gravity, and S_b the body cross-section area and C_{Db} the body drag coefficient. Since, by division of the above,
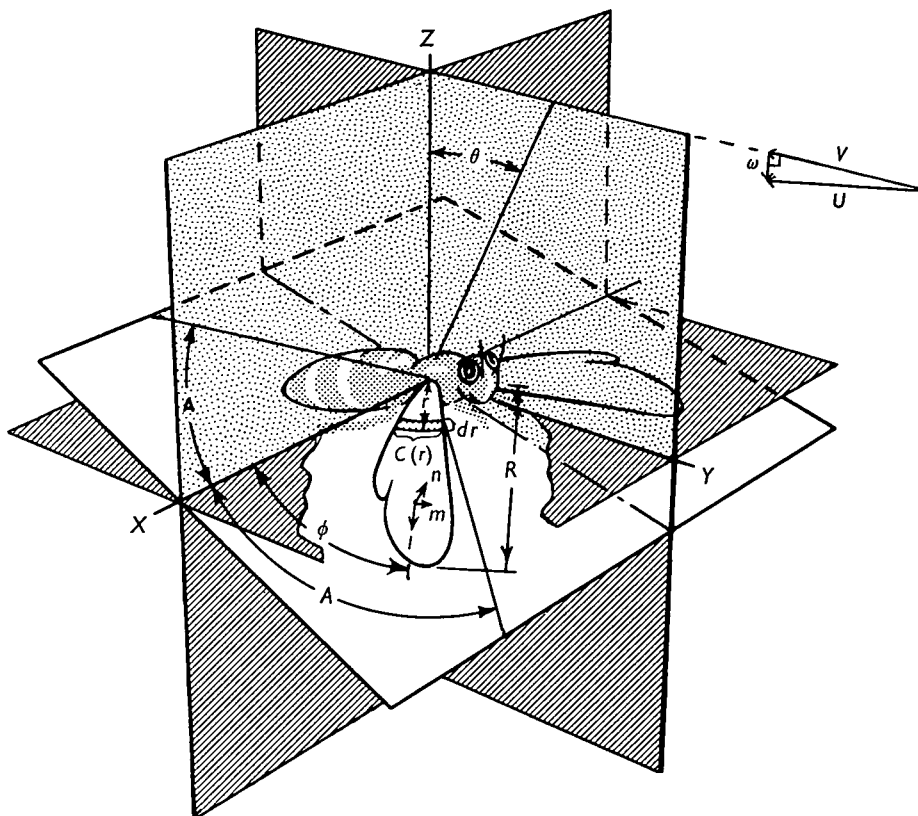

Fig. 1. Quantities defining motion of insect in flight.

$v/w = T/L$, and for the insects considered the thrust T is small compared to the vertical force L. v is small compared to w, and will be neglected, since w turns out to be small compared to the other velocities involved. The solution for w is given by

$$w^2 = V^2 \tfrac{1}{2} [-\mathrm{I} + (\mathrm{I} + L^2/\pi^2 \rho^2 R^4 V^4)^{\frac{1}{2}}]. \tag{6}$$

Eqs. (1) and (2) express the assumption that the determining velocity (squared) for both lift and drag is the component of the relative wind perpendicular to the axis of the wing, which is $|\mathbf{1} \times \mathbf{W}| = |\mathbf{W} - \mathbf{W} \cdot \mathbf{1} \mathbf{1}|$. The subscripts s and p indicate perpendicular (senkrecht) and parallel *to that component*, $\mathbf{W} - \mathbf{W} \cdot \mathbf{1} \mathbf{1}$. The last factor in braces gives the direction cosines of the forces. The drag is assumed to be perpendicular to the axis of the wing, hence the subtraction of the $\mathbf{1}$ component of $\mathbf{W}$, $\mathbf{W} \cdot \mathbf{1} \mathbf{1}$ in the

direction cosine. Forces along the length, or axis, of the wing tend to cancel for lift and thrust on the upper and lower half of a wing beat and overall between the right and left wing, since they are in opposite directions for opposite wings. Also they do not contribute to the power (eq. (8)) since they are perpendicular to the displacement of the wing elements, referred to the insect.

The assumption that the force is proportional to the square of the relative wind component perpendicular to the axis of the wing is the conventional one in helicopter and sideslip performance calculations, and applies primarily to steady flow. Steady flow is far from realized in flapping flight, unless the variable or flapping components of velocity are small compared to the linear velocities, or the flapping velocity changes by a small fraction of itself over a displacement equal to the chord. The assumption of the steady state force formula is made primarily so that the computed results for C_L and C_D can be compared with conventional aerodynamic data, as will become apparent from the subsequent discussion. However, there is indirect evidence given below that this assumption is justified, at least in part, for the problem under consideration.

The total force on the surface element of the wing is

$$|\mathbf{dF}| = (|\mathbf{dF}_s|^2 + |\mathbf{dF}_p|^2)^{\frac{1}{2}}$$
$$= (\tfrac{1}{2})(C_L^2 + C_D^2)^{\frac{1}{2}} \rho c(r)\, dr\, |\mathbf{l} \times \mathbf{W}|^2. \tag{7}$$

The power expended in exerting the forces dF_s and dF_p is

$$dP = (\mathbf{dF}_s + \mathbf{dF}_p).(\mathbf{n}\Omega \times r\mathbf{l})$$
$$= dP_{F_s} + dP_{F_p}, \tag{8}$$

where P_{F_s} and P_{F_p} are the power contributions due to C_L and C_D forces.

The above formulae are general; the method of integrating and averaging them would depend on the particular example to which they were applied. In case the normal to the instantaneous plane of beating is the same for both wings, and remains in the yz plane, as in Fig. 1, the unit vectors $\mathbf{l}$, $\mathbf{m}$, $\mathbf{n}$ for the right wing are, in the x, y, z system,

$$\mathbf{l} = (\cos\phi,\ \sin\phi\cos\theta,\ -\sin\phi\sin\theta),$$
$$\mathbf{m} = (-\sin\phi,\ \cos\phi\cos\theta,\ -\cos\phi\sin\theta),\ \Big\} \tag{9}$$
$$\mathbf{n} = (0,\ \sin\theta,\ \cos\theta).$$

If θ, the inclination to the vertical of the normal to the instantaneous plane of beating (Fig. 1), is a constant, i.e. the wings beat in a plane, then $\Omega = d\phi/dt$. With these two specializations, eqs. (1) and (2) give (bars indicate average)

$$\overline{\mathbf{F}}_s = (\overline{X}_s,\ \overline{Y}_s,\ \overline{Z}_s) = \nu \iint\limits_{r,t} \mathbf{dF}_s(r,t)\, dr\, dt$$

$$= \nu \iint\limits_{r,t} (\tfrac{1}{2})\rho C_L\, 2c(r)(W_m^2 + W_n^2)^{\frac{1}{2}}\, dr\, dt$$

$$\times (w\sin\phi\cos\theta + V\sin\phi\sin\theta,$$
$$r(d\phi/dt)\sin\theta - w\cos\phi,$$
$$V\cos\phi + r(d\phi/dt)\cos\theta) \tag{10}$$

$$\overline{\mathbf{F}}_p = (\overline{X}_p, \overline{Y}_p, \overline{Z}_p) = \nu \iint\limits_{r,t} d\mathbf{F}_p(r,t)\, dr, dt$$

$$= -\nu \iint\limits_{r,t} (\tfrac{1}{2})\rho C_D 2c(r)\,(W_m^2 + W_n^2)^{\frac{1}{2}}\, dr\, dt$$

$$\times (-r(d\phi/dt)\sin\phi - V\sin\phi\cos\phi\cos\theta + w\sin\phi\sin\theta,$$
$$+ r(d\phi/dt)\cos\phi\cos\theta + V\sin^2\theta + V\cos^2\phi\cos^2\theta + w\sin^2\phi\sin\theta\cos\theta,$$
$$- r(d\phi/dt)\cos\phi\sin\theta + w\cos^2\theta + w\cos^2\phi\sin^2\theta + V\sin^2\phi\sin\theta\cos\theta). \qquad (11)$$

The range of integration over r is the length of the wing; o to R, and in t over the period $1/\nu$ of a wing beat, ν being the frequency of flapping.

In eqs. (10) and (11)

$$\left. \begin{aligned} W_m^2 + W_n^2 &\equiv |\,\mathbf{1} \times \mathbf{W}\,|^2 \equiv |\,\mathbf{W} - \mathbf{W}.\mathbf{ll}\,|^2 \equiv |\,\mathbf{W}.\mathbf{mm} + \mathbf{W}.\mathbf{nn}\,|^2, \\ W_m &= r(d\phi/dt) + (V\cos\theta - w\sin\theta)\cos\phi, \\ W_n &= V\sin\theta + w\cos\theta, \end{aligned} \right\} \qquad (12)$$

and the denominators of the direction cosines in eqs. (1) and (2) have been cancelled against the velocity-squared factor. The factor 2 before $c(r)$ takes account of left plus right wings.

The total average power* is from eq. (8)

$$\overline{P} = \{w\overline{Z}_s + V\overline{Y}_s\} + \nu \iint\limits_{r,t} d\mathbf{F}_p(r,t).\,(\mathbf{n}(d\phi/dt) \times r\mathbf{l})\, dr\, dt$$

$$= \{w\overline{Z}_s + V\overline{Y}_s\} + \nu \iint\limits_{r,t} (\tfrac{1}{2})\rho C_D 2c(r)\, dr\, dt\, (W_m^2 + W_n^2)^{\frac{1}{2}}\, r\, d\phi/dt$$

$$\times [r(d\phi/dt) + (V\cos\theta - w\sin\theta)\cos\phi]. \qquad (13)$$

Here the first term in the braces is the exact expression for P_{F_s}. The expression for power on the basis of the momentum theory (using eqs. (4) and (5)), is $VT + wL$, which is the rate of change in kinetic energy in the slipstream on passing the insect required in order to provide the net thrust $T = (\tfrac{1}{2})\rho C_{Db} S_b V^2$ and lift $L = Mg$. Thus when $C_D = 0$ ('ideal' fluid) the power determined from momentum theory and the power determined by integrating force × velocity (i.e. first term in { } of (13)) for each element of the wing agree exactly, as they should.

This is indirect evidence that the assumed formula for $\mathbf{F}_s$ (eq. (1)) gives a correct result when integrated in a case of periodic motion. The agreement between the formulae for the power computed by the two different methods corresponds, in the case of a simple lifting airfoil of finite span, to the agreement between the work done against induced drag, and the increase in kinetic energy of the trailing vortex sheet.

* By this is meant only the *mechanical* power (force × distance/time) expended by the insect. There is, of course, a much larger power loss in heating and chemical changes within the insect, as is true for any thermodynamic engine. No account is taken of this here.

In practice errors would be introduced by the fact that v and w are not constant in space and time, but the assumption of their constancy is a standard one in aerodynamic practice, and the error committed is not large.

The integration of eq. (7) can usually be carried out exactly, and by replacing the total force by $(T^2 + L^2)^{\frac{1}{2}}$ one can determine $\overline{(C_L^2 + C_D^2)^{\frac{1}{2}}}$. The result so obtained is a lower limit to the value of $(\overline{C}_L^2 + \overline{C}_D^2)^{\frac{1}{2}}$, since the integration effectively adds all the force elements in the same direction. One thus obtains

$$(\overline{C}_L^2 + \overline{C}_D^2)^{\frac{1}{2}}_{\text{min.}} = (L^2 + T^2)^{\frac{1}{2}}/(\tfrac{1}{2})\rho \iint\limits_{r,t} 2c(r)(W_m^2 + W_n^2)\, dr\, dt. \tag{14}$$

The explicit integration of eqs. (10), (11), (13) and (14) is tedious and the results somewhat lengthy. The steps will not be given here, but only an outline of the necessary additional assumptions and approximations. Eq. (14) can be integrated exactly.

The beating cycle is divided into two parts, the down beat, subscript 1, and the up beat, subscript 2. This was done since fairly constant conditions, particularly as to velocities, may obtain on a down or up beat alone, but not for the entire beating cycle. Hence averaging methods and approximations may be used for a single down or up stroke not valid for the entire cycle. Also, the explanation of some of the phenomena of flapping flight require differentiation between the up and down beat. Over the up or down beat θ, C_L, C_D are assumed to be constant with respect to r and t, and to have the values

$$
\begin{aligned}
C_{L1} &= \overline{C}_L(1+\xi), & C_{L2} &= \pm\, \overline{C}_L(1-\xi), \\
C_{D1} &= \overline{C}_D(1+\zeta), & C_{D2} &= \overline{C}_D(1-\zeta), \\
\theta_1 &= \overline{\theta} + \delta\theta, & \theta_2 &= \overline{\theta} - \delta\theta.
\end{aligned}
\tag{15}
$$

If P is the period of a wing beat, the subscripts 1 and 2 refer to the time intervals $0 < t < \pi/\omega_1$ (down beat) and $\pi/\omega_1 < t < P$ (up beat), respectively.

ϕ is assumed to vary sinusoidally over the up or down beat, where

$$\phi = A\sin\omega t, \quad \omega_1 = \overline{\omega}(1-\eta), \quad \omega_2 = \overline{\omega}(1+\eta), \quad \overline{\omega} = 2\pi\nu(1-\eta^2).$$

A is the amplitude of motion in the plane of beating, and $\eta = (a-1)/(a+1)$, where a is the ratio of duration of down beat to up beat. η and $\delta\theta$ are assumed small, but ξ, ζ are not so restricted. The double sign for C_{L_2} takes account of the possibility that leading and trailing edge of the wing, or pressure and suction side, may be interchanged on the up and down beat. This does not affect the sign of C_{D_2}.

The principal difficulty at this point is to obtain a satisfactory approximate expression for the radical $(W_m^2 + W_n^2)^{\frac{1}{2}}$; once this is obtained the integration is straightforward. No single approximation could be found which was satisfactory for all values of the ratio of the flapping to linear velocity $(rd\phi/dt)/V$ and the time. This ratio varies from zero to much greater than unity over the length of the wing and period of a wing beat, and becomes both positive and negative.

One method is to replace the variable terms in eqs. (10), (11) and (13) by averages. Two preliminary remarks are first necessary:

(1) If we have a complicated expression to integrate, $\int_0^P f(t)\, dt$, and we can guess in some way an average value $\bar{f}$, then $P\bar{f}$ is a good guess for value of the integral. If circumstances are such that we can guess average values over two parts of the range of integration o to a, and a to P, then the average value for the entire interval is given by

$$(a\bar{f}_{0,a} + (P-a)\bar{f}_{a,p})/P.$$

In what follows, P corresponds to the period of a wing beat and the two intervals to the period of the down and up beat, π/ω_1 and π/ω_2.

(2) Suppose $c(r)$ is a simple function, o at the end of an interval o to R, and positive in between, like a semi-elipse or a rectangle. We wish to integrate an expression of the form

$$I = \int_0^R (a_0 c(r) + a_1 r c(r) + a_2 r^2 c(r) + a_3 r^3 c(r) + \ldots)\, dr. \tag{16}$$

The a's are assumed such that the expression converges. Now if S is the area $\int_0^R c(r)\, dr$, I can be written

$$I = a_0 S + a_1 \bar{r} S + a_2 \overline{r^2} S + a_3 \overline{r^3} S + \ldots. \tag{17}$$

Now for a simple geometrical figure as above $\bar{r}, \overline{r^{2\frac{1}{2}}}, \overline{r^{3\frac{1}{2}}}$, etc., are all not so very different and one could approximate the desired integral by substituting a single average value for r for all those appearing, that is

$$I \simeq a_0 S + a_1 \overline{r^{2\frac{1}{2}}} S + a_2 \overline{r^2} S + a_3 \overline{r^{2\frac{1}{2}}} S + \ldots. \tag{18}$$

The best choice would be the one for which the corresponding a was the largest. In the above case presumably a_2 was the dominant coefficient.

To return to the integration of eqs. (10), (11) and (13). These are simply integrated by replacing the various variable terms by shrewdly chosen averages, the averages being chosen over two stretches as above, the down and up beat. The choice for average values is made in the following way. $(W_m^2 + W_n^2)^{\frac{1}{2}}$ was expanded under the two separate assumptions that the ratio $(rd\phi/dt)/V$ was (1) small, and (2) large, and the resulting expressions could then be integrated. In this way expressions corresponding to (16) above were obtained in which the coefficients $a_0, a_1, a_2, a_3, \ldots$ were constant or easily integrated trigonometrical functions of time. Average values were fixed for $r(\overline{r^{2\frac{1}{2}}}$ in (10) and (11), $\overline{r^{3\frac{1}{2}}}$ in (13)) which fitted both approximations moderately well. Also averages for $\cos\phi$, $\sin\phi$, $\cos\omega t$ were chosen which fitted both approximations moderately well. (Both expansions (1) and (2) above are still fairly good when $(rd\phi/dt)/V \sim 1$.) These selected averages were then substituted directly into the original eqs. (10), (11) and (13). As will be seen by comparing the equations below with eqs. (10), (11) and (13), this process simply amounts to replacing all the terms in eqs. (10), (11) and (13) by shrewdly chosen constant values and integrating in two steps. When this is done the results are as given below. S is the total area of both wings. Let the average velocity components in parentheses in eqs. (10) be indicated by

$$W_{sx} = \overline{\omega \sin\phi \cos\theta + V \sin\phi \sin\theta}, \quad W_{sy} = \overline{(rd\phi/dt)\sin\theta - \omega \cos\phi},$$
$$W_{sz} = \overline{V \cos\phi + (rd\phi/dt)\cos\theta},$$

and similarly for W_{px}, W_{py}, W_{pz} in eq. (11). $\bar{r}$, $\overline{r^2}$, $\overline{r^3}$ were determined by numerical integration over the wing form of each insect. Eq. (10) gives

$$
\begin{aligned}
\bar{X}_s &= 0, \\
\bar{Y}_s &= \bar{C}_L\{(\tfrac{1}{2})\rho v S[(\pi/\omega_1)(1+\xi)(W_{m_1}^2+W_{n_1}^2)^{\frac{1}{4}}W_{sy_1} \\
&\quad \pm (\pi/\omega_2)(1-\xi)(W_{m_2}^2+W_{n_2}^2)^{\frac{1}{4}}W_{sy_2}]\} \\
&= \bar{C}_L A \\
\bar{Z}_s &= \bar{C}_L\{(\tfrac{1}{2})\rho v S[(\pi/\omega_1)(1+\xi)(W_{m_1}^2+W_{n_1}^2)^{\frac{1}{4}}W_{sz_1} \\
&\quad \pm (\pi/\omega_2)(1-\xi)(W_{m_2}^2+W_{n_2}^2)^{\frac{1}{4}}W_{sz_2}]\} \\
&= \bar{C}_L B.
\end{aligned}
\tag{19}
$$

Eq. (11) gives

$$
\begin{aligned}
\bar{X}_p &= 0, \\
\bar{Y}_p &= -\bar{C}_D\{(\tfrac{1}{2})\rho v S[(\pi/\omega_1)(1+\zeta)(W_{m_1}^2+W_{n_1}^2)^{\frac{1}{4}}W_{py_1} \\
&\quad + (1-\zeta)(\pi/\omega_2)(W_{m_2}^2+W_{n_2}^2)^{\frac{1}{4}}W_{py_2}]\}, \\
&= \bar{C}_D C \\
\bar{Z}_p &= -\bar{C}_D\{(\tfrac{1}{2})\rho v S[(\pi/\omega_1)(1+\zeta)(W_{m_1}^2+W_{n_1}^2)^{\frac{1}{4}}W_{pz_1} \\
&\quad + (\pi/\omega_2)(1-\zeta)(W_{m_2}^2+W_{n_2}^2)^{\frac{1}{4}}W_{pz_2}]\} \\
&= \bar{C}_D D.
\end{aligned}
\tag{20}
$$

The quantities appearing in these two equations are defined as follows:

$$
\begin{aligned}
W_{m_1} &= (\overline{r^2}^{\frac{1}{4}} A\omega_1/2^{\frac{1}{4}}) + (V\cos\theta_1 - w\sin\theta_1)J_0(A), \\
W_{n_1} &= V\sin\theta_1 + w\cos\theta_1, \\
W_{m_2} &\doteq (-\overline{r^2}^{\frac{1}{4}} A\omega_2/2^{\frac{1}{4}}) + (V\cos\theta_2 - w\sin\theta_2)J_0(A), \\
W_{n_2} &= V\sin\theta_2 + w\cos\theta_2, \\
W_{sy_1} &= (\overline{r^2}^{\frac{1}{4}} A\omega_1/2^{\frac{1}{4}})\sin\theta_1 - wJ_0(A), \\
W_{sy_2} &= (-\overline{r_2}^{\frac{1}{4}} A\omega_2/2^{\frac{1}{4}})\sin\theta_2 - wJ_0(A), \\
W_{sz_1} &= (\overline{r^2}^{\frac{1}{4}} A\omega_1/2^{\frac{1}{4}})\cos\theta_1 + VJ_0(A), \\
W_{sz_2} &= (-\overline{r^2}^{\frac{1}{4}} A\omega_2/2^{\frac{1}{4}})\cos\theta_2 + VJ_0(A), \\
W_{py_1} &= (\overline{r^2}^{\frac{1}{4}} A\omega_1/2^{\frac{1}{4}})J_0(A)\cos\theta_1 + V\sin^2\theta_1 \\
&\quad + VJ_0^2(A)\cos^2\theta_1 + w(16J_1^2(A)/\pi^2)\sin\theta_1\cos\theta_1, \\
W_{py_2} &= (-\overline{r^2}^{\frac{1}{4}} A\omega_2/2^{\frac{1}{4}})J_0(A)\cos\theta_2 + V\sin^2\theta_2 \\
&\quad + VJ_0^2(A)\cos^2\theta_2 + w(16J_1^2(A)/\pi^2)\sin\theta_2\cos\theta_2, \\
W_{pz_1} &= (-\overline{r^2}^{\frac{1}{4}} A\omega_1/2^{\frac{1}{4}})\sin\theta_1 + w\cos^2\theta_1 \\
&\quad + wJ_0^2(A)\sin^2\theta_1 + V(16J_1^2(A)/\pi^2)\sin\theta_1\cos\theta_1, \\
W_{pz_2} &= (+\overline{r^2}^{\frac{1}{4}} A\omega_2/2^{\frac{1}{4}})\sin\theta_2 + w\cos^2\theta_2 \\
&\quad + wJ_0^2(A)\sin^2\theta_2 + V(16J_1^2(A)/\pi^2)\sin\theta_2\cos\theta_2.
\end{aligned}
\tag{21}
$$

$J_0(A)$ and $J_1(A)$ are Bessel's function of the first kind obtained from the expansion of $\cos\phi$, $\sin\phi$, where $\phi = A\sin\omega t$.

If the expression in braces in eqs. (19) and (20) is abbreviated by A, B, C and D one imposes the condition that the sum of the horizontal forces $\bar{Y}_p + \bar{Y}_s$ provide the required thrust $T = (\frac{1}{2})\rho C_{Db} S_b V^2$ and that the total vertical forces $\bar{Z}_s + \bar{Z}_p$ provides the lift $L = Mg$, then

$$T = \bar{C}_L A + \bar{C}_D C, \quad L = \bar{C}_L B + \bar{C}_D D. \tag{22}$$

Then by Cramer's rule,

$$\left. \begin{aligned} \bar{C}_L = \begin{vmatrix} T & C \\ L & D \end{vmatrix} \Big/ \begin{vmatrix} A & C \\ B & D \end{vmatrix}, \\ \bar{C}_D = \begin{vmatrix} A & T \\ B & L \end{vmatrix} \Big/ \begin{vmatrix} A & C \\ B & D \end{vmatrix}. \end{aligned} \right\} \tag{23}$$

This gives, using the substitution indicated for A, B, C, D, the expression for the average lift and drag coefficients $\bar{C}_L$ and $\bar{C}_D$ in terms of the observed flight parameter for any given insect.

In a similar manner one finds that the total power is

$$\left. \begin{aligned} P = w\bar{Z}_s &+ V\bar{Y}_s \\ &+ \bar{C}_D\{(\tfrac{1}{2})\rho v S[(\pi/\omega_1)(1+\zeta)(W_{m_1}^2 + W_{n_1}^2)^{\frac{1}{2}} Q_1 \\ &\qquad\qquad + (\pi/\omega_2)(1-\zeta)(W_{m_2}^2 + W_{n_2}^2)^{\frac{1}{2}} Q_2], \\ Q_1 = &\overline{r^{3\frac{1}{2}}} A\omega_1(\tfrac{4}{3}\pi)^{\frac{1}{2}} [\overline{r^{3\frac{1}{2}}} A\omega_1(\tfrac{4}{3}\pi)^{\frac{1}{2}} + (V\cos\theta_1 - w\sin\theta_1)\, 0.8 J_0(A)], \\ Q_2 = &-\overline{r^{3\frac{1}{2}}} A\omega_2(\tfrac{4}{3}\pi)^{\frac{1}{2}} [-\overline{r^{3\frac{1}{2}}} A\omega_2(\tfrac{4}{3}\pi)^{\frac{1}{2}} + (V\cos\theta_2 - w\sin\theta_2)\, 0.8 J_0(A)], \\ W_{m_1} = &\overline{r^{3\frac{1}{2}}} A\omega_1(\tfrac{4}{3}\pi)^{\frac{1}{2}} + (V\cos\theta_1 - w\sin\theta_1)\, 0.8 J_0(A), \\ W_{m_2} = &-\overline{r^{3\frac{1}{2}}} A\omega_2(\tfrac{4}{3}\pi)^{\frac{1}{2}} + (V\cos\theta_2 - w\sin\theta_2)\, 0.8 J_0(A), \\ W_{n_1} = &V\sin\theta_1 + w\cos\theta_1, \\ W_{n_2} = &V\sin\theta_2 + w\cos\theta_2. \end{aligned} \right\} \tag{24}$$

Notice that these are not the same averages as for eqs. (10) and (11). Cubic terms are more important in the power, square terms in the forces. The averages for r and the trigonometrical functions are chosen accordingly.

$\bar{C}_D$ and $\bar{Y}_s$, $\bar{Z}_s$ in (24) are computed from the eqs. (23) and (19).

Eq. (14) for the minimum total force coefficient can be integrated exactly. The result is

$$\left. \begin{aligned} (\bar{C}_L^2 + \bar{C}_D^2)_{\min.}^{\frac{1}{2}} = &(L^2 + T^2)/\{(\tfrac{1}{2})\rho S v[(\pi/\omega_1)(W_{m_1}^2 + W_{n_1}^2) \\ &\qquad + (\pi/\omega_2)(W_{m_2}^2 + W_{n_2}^2)\}, \\ W_{m_1}^2 = &\overline{r^2}A^2\omega_1^2/2 + 2(V\cos\theta_1 - w\sin\theta_1)\, \bar{r} A\omega_1(2/\pi)(J_0(A) + (\tfrac{2}{3})J_2(A)) \\ &+ (V\cos\theta_1 - w\sin\theta_1)^2 (J_0^2(A) + 2J_2^2(A)), \\ W_{m_2}^2 = &\overline{r^2}A\omega_2^2/2 - 2(V\cos\theta_2 - w\sin\theta_2)\, \bar{r} A\omega_2(2/\pi)(J_0(A) + 2J_2(A)/3) \\ &+ (V\cos\theta_2 - w\sin\theta_2)^2 (J_0^2(A) + 2J_2^2(A)), \\ W_{n_1}^2 = &(V\sin\theta_1 + w\cos\theta_1)^2, \\ W_{n_2}^2 = &(V\sin\theta_2 + w\cos\theta_2)^2. \end{aligned} \right\} \tag{25}$$

Note that this is again a different set of values for W_m and W_n, which here could be integrated exactly.

A second method of integrating (10), (11) and (14) replaced $(W_m^2 + W_n^2)^{\frac{1}{2}}$ by the sum of the absolute values of W_m and W_n, times a correction factor k which was a very slowly varying function of the ratio W_m/W_n, taken as constant. Thus

$$(W_m^2 + W_n^2)^{\frac{1}{2}} = (|W_m| + |W_n|)\, k.$$

From that step on the resulting integrations could be carried out almost exactly. The resulting formulae are exceedingly long, since a different set of formulae is required for each of the different sign possibilities for W_m, W_n and C_L on the up and down beat.

This second method has the advantage of showing analytically and directly the effect on the vertical force, thrust and power, of varying the flight parameters C_L, C_D, θ and ω on the up and down beat. The effect of independent variations appear as linear terms in ξ, ζ, η and $\delta\theta$, while the interactions appear as cross-products of ξ, ζ, η and $\delta\theta$.

Check computations by the two methods gave results in fair agreement. All of the numerical results given in this paper were obtained by the first method.

DETERMINATION OF FORCE COEFFICIENTS

Applications of eq. (23) to determine C_L and C_D for the twenty-five insects given in Table 1 were made under two assumptions: $\xi = \zeta = 0$, or equal force coefficients on the up and down beat, and $\xi = \zeta = 1$, or zero force coefficients on the up beat. It was felt that these represented the two limiting cases between which the actual practice must lie. The results are shown in Figs. 2 and 3, which give the average force coefficients for the entire wing beat or the value on the down beat, respectively. The length of the horizontal line represents the range of solution as the drag coefficient of the body varies between zero and unity, the points being plotted for zero-body drag coefficient.

It will be observed that for the case of zero force coefficients on the up beat the ratio of lift to drag does not exceed 3 or 4 to 1, which is quite acceptable aerodynamically. Hence large lift coefficients are always associated with large drag coefficients. All coefficients are positive, the largest lift and drag coefficients being 5·4 and 2·6, respectively. In the case of equal-force coefficients on the up and down beat, there are two instances of negative lift and drag coefficients, and six with zero or negative drag coefficient. The largest lift and drag coefficients are 11 and 20, respectively.

Under both assumptions, therefore, somewhat larger force coefficients are derived than are met with in conventional aerodynamics, but the assumption of equal-force coefficients on up and down beat leads to the additional anomalies of zero or negative drag and lift coefficients. It is, therefore, concluded that the assumption of zero force coefficients on the up beat must represent a much closer approximation to the truth than equal force coefficients on the up and down beat. In other words, the insect derives the great majority of the useful flying force on the down beat (Guidi, 1938; Holst & Kuckemann, 1942). This conclusion is reinforced by comparing points for the same insect on Figs. 2 and 3. The required lift coefficient for forces acting on the down beat alone is in most cases only slightly greater instead of twice

Table 1. Dimensions and performance data on insects

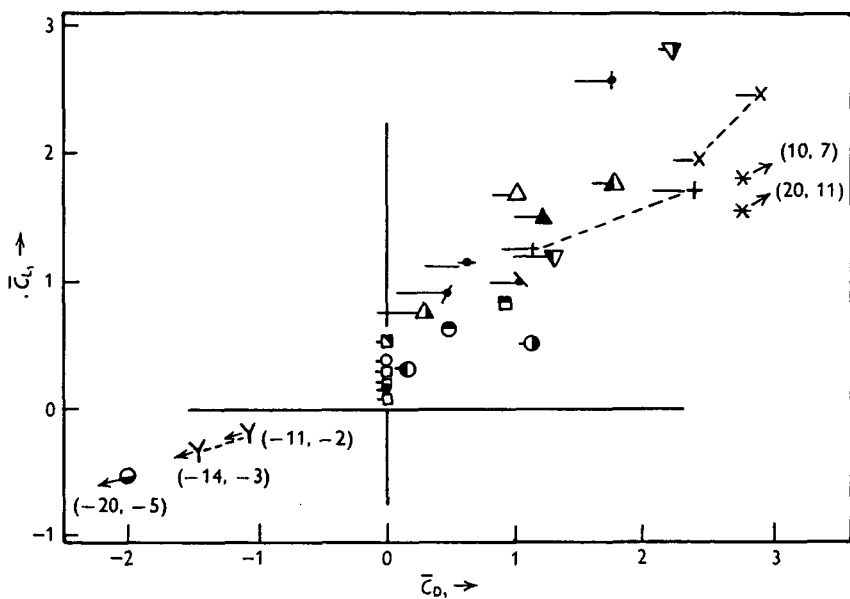| Name of insect	M Mass (mg.)	S Total wing area (mm.²)		S_b Body cross-section (mm.²)	R Length of longer wing (mm.)	ν Frequency of beating (sec.⁻¹)	V Velocity of flight (m./sec.)	a Ratio time of lowering to raising	2ψ Projected double amplitude xz plane (degrees)	A Adopted constant amplitude (radians)	Length of body (mm.)	θ Adopted inclination of plane of beating (degrees)
DIPTERA:												
Tabinus bovinus	276	184		63	15·5	96	4	1·5	90	—	23	(30)
Sarcophaga carnaria L.	45	36		12	7·0	160	2	1·5	75	—	12	(30)
Musca domestica	12	20		4·5	5·5	190		1·7	90	—	6·5	(30)
Volucella pellucens Meig.	73	78		39	12	120	3·5	1·2	75	—	13·5	(30)
HYMENOPTERA:												
Xylocope violacea	614	172		47	18	130	4	1·3	—	(1·0)	22	(30)
Bombus terrestris Fabr.	388	142		74	16	130	3	1·1	—	(1·0)	19·5	(30)
Vespa germanica	187	98		29	14	110	2·5	1·3	90	—	18	(30)
Vespa crabro L.	567	260		100	22·5	100	6	1·8	50	—	34	(30)
Apis mellifica L.	78	42		27	8·5	250	2·5	1·3	—	(1·0)	13	(30)
Amonophila sabulosa V. del	45	42		82	9·0	120	1·5	1·2	70	—	18	(30)
LEPIDOPTERA:												
Papilio podalirius	300	3600		52	37	10	3·5	—	140	—	25	(60)
Vanessa atalanta L.	134	1080		31	27	10	4	—	150	—	18	(60)
Pieris brassica L.	127	1840		35	31	12	2·5	—	—	(1·2)	23	(60)
Macroglossa stellatorum L.	345	400		68	20	85	5	1·3	80	—	28	(60)
Plusia gamma L.	144	440		36	18	48	1·5	1·1	120	—	19·5	(30)
COLEOPTERA:		mem. m. +ely.										
Melontha vulgaris Fabr.	961	402	642	100	28	46	2·5	1·5	130	(1·2)	28	(30)
Cetonia aurata	537	260	370	68	20	86	3	1·3	—	—	19	(30)
Lucanus corvus	2600	800	1220	250	36	33	1·5	1·0	160	—	54	(30)
Telephorus fuscus	109	116	166	20	12·5 anterior	72	0·8	1·4	145	—	16	(30)
NEUROPTERA:												
Brachytron pratense Mull.	557	1200		36	36·5	33	5	1·4	75	—	55	(30)
Calopteryx splendens Harr.	120	850		13	30	16	1·5	1·6	115	—	47	(30)
Pyrosoma ninium Harr.	38	355		8	25	27	0·6	1·2	100	—	32	(30)
Panorpa communis L.	30	176		8	14·5	28	0·5	1·6	150	—	17	(30)
Orthetrum caerulescens Fabr.	248	1080		22	32·5	20	4	—	—	(1·0)	42	(60)
Aeschna mixtra Latr.	530	1380		30	39·5	38	7	1·7	70	—	63·5	(60)

Fig. 2. Average lift *v*. drag coefficient for equal-force coefficients on up and down beat. $\xi = \zeta = 0$. Points with arrows fell outside the range of co-ordinates of the figure. The co-ordinates are in parentheses.
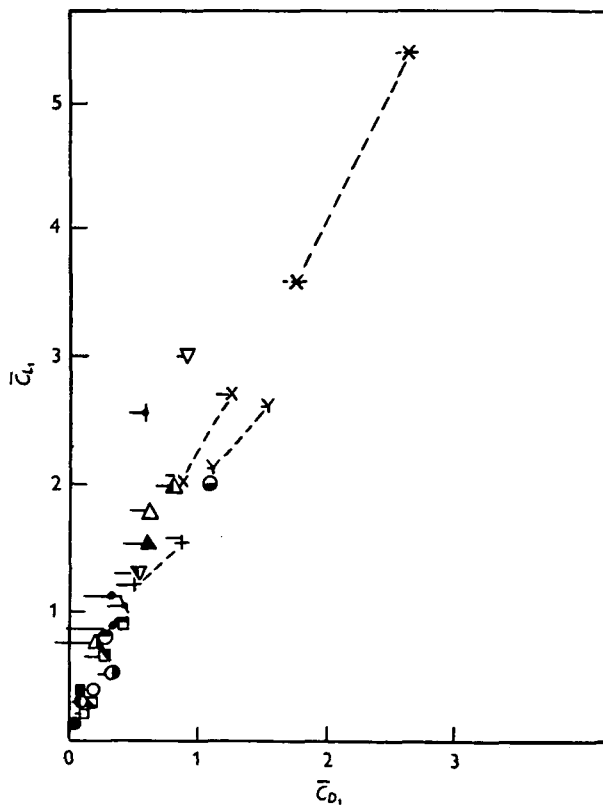

Fig. 3. Average lift *v*. drag coefficient for down beat for zero-force coefficients on up beat, $\xi = \zeta = 1$.

great, as might be expected, than when force acts on the wing during the entire beating cycle. In a few cases, it is less. Except for the 'anomalous cases', the drag coefficient is always a great deal less for the down beat alone than for the entire cycle.

There is a simple explanation for the conclusion that the great majority of the useful flying force must come on the down beat. One draws the components of the average (with respect to r and t) relative wind in the yz plane (Fig. 4). It is specified that the mean flapping velocity $V_F = \overline{(rd\phi/dt)^2}^{\frac{1}{2}} = \bar{r}^{2\frac{1}{2}} A\bar{w}/2^{\frac{1}{2}}$ is the same order of magnitude as the velocity of flight V, say, within a factor of 3 larger or smaller. This range covers most of the insects considered. Fig. 4 illustrates a number of such diagrams showing various choices ($1/3$, $1/1$, $3/1$) for the ratio of flapping velocity to the velocity $\bar{U}$, $V_F/\bar{U}$, and the inclination θ of the plane of beating. Fig. 4 is essentially a geometrical interpretation of eqs. (19) and (20). In this way one can determine to within a quadrant, referred to axes parallel and perpendicular to the relative wind, the direction in which the resultant force $\mathbf{F}_s + \mathbf{F}_p$ on the wing during the up or down beat must lie. Now the average resultant force for both up and down beat *must* provide the necessary vertical force Mg and thrust. This is a force which is predominantly up, with a small forward component. If it turns out, as is usually the case, that no matter how θ, the inclination of the plane of beating is chosen, that for the up beat *any* force within the 90° uncertainty has small or negative components in the direction in which the average resultant *must* lie, then *any* force acting during the up beat is undesirable. The insect will therefore tilt his wings to achieve as nearly zero force coefficients on the up beat as possible.

If the flapping velocity is larger than the linear velocity and θ is $\sim 30°$ or less (Fig. 4*e*), there is some advantage for the insect to reverse the direction of the lift (C_L force) on the up beat, by interchanging either the leading and trailing edge on the up and down beat or the pressure and suction side. In the calculations this assumption was made in those cases in Fig. 2 for which θ was taken to be 30°—all except the six on the $C_D = 0$ axis. There is some evidence that this 'reversed flapping' actually occurs, judging from the drawings and photographs in the literature. For 'reversed flapping' calculations the negative in the double sign in eqs. (15) and (19) is chosen.

When reversed flapping takes place there is also some advantage to the insect to move his wings in a tilted figure 8, with the steep side on the down beat ($\delta\theta > 0$). In this way the average resultant forces on the up and down beat more nearly approach parallelism, and the resultant on the up beat is more nearly in the desired direction. Observation is in agreement with this (Magnan, 1934; Schröder, 1928).

Fig. 4 also serves to show that the force perpendicular to the relative wind or C_L force is the one which most commonly provides the useful or flight-enabling force. Observations indicate (Guidi, 1939; Kukentahl & Krumbach, 1927–34, pp. 573–5; Magnan, 1935, pp. 61, 97, 104, 112, 114; Marey, 1890) that θ is usually 90° or slightly less when the ratio $\overline{(rd\phi/dt)^2}^{\frac{1}{2}}/V = \bar{r}^{2\frac{1}{2}} A\bar{w}/2^{\frac{1}{2}} V = V_F/V$ is small and can decrease as this ratio increases. Drawing the relative wind diagrams, as in Fig. 4, will show that the C_L force is more nearly in the direction in which the average resultant must lie; the C_D force is at best usually at right angles to the necessary resultant. For an
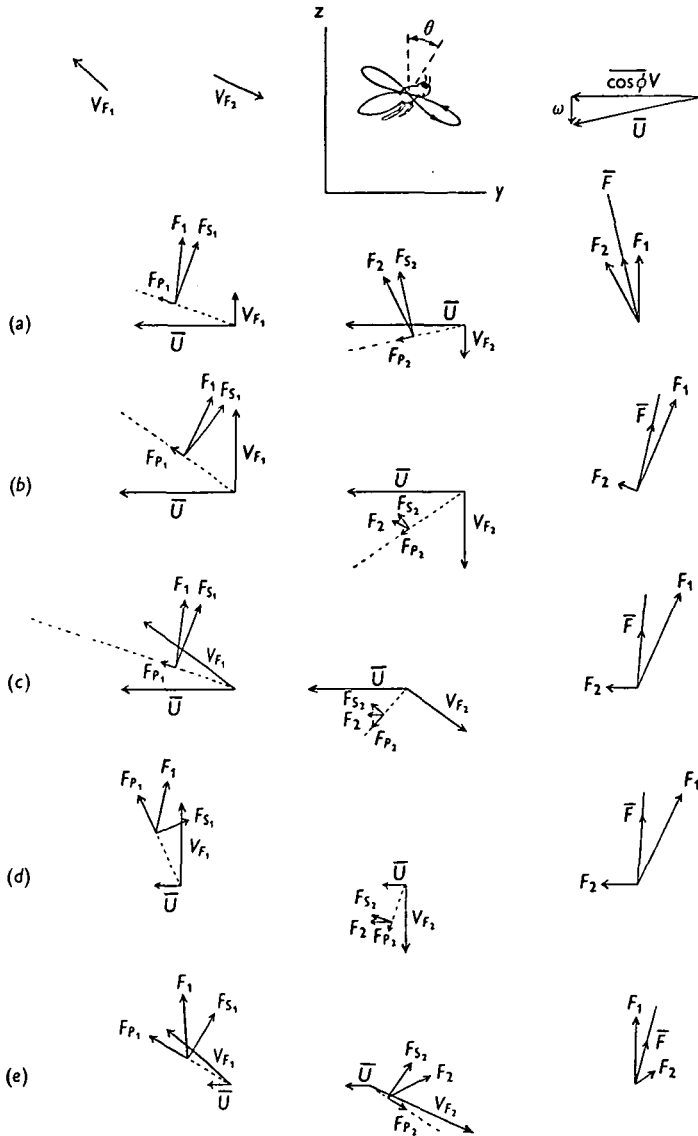
Fig. 4. Graphical determination of forces on up and down beat in YZ plane and average resultant force. V_{F_1} or V_{F_2} = root-mean-square flapping velocity. F_s, F_p = forces perpendicular and parallel to relative wind. F_1, F_2 = average resultant force on down and up beat. F = average of F_1 and F_2. $\overline{U}$ = average velocity of air with respect to insect. The magnitude of the induced velocity w is exaggerated in the vector diagram to the right of the insect. It is always very small compared to at least one of the velocities V_F or U, and is so drawn in (a) to (e).

(a) $V_F \cong 3\overline{U}$, $\theta = 90°$. $\xi = \zeta = 0$. The necessary thrust is not provided unless $F_2 \ll F_1$.

(b) $V_F \cong \overline{U}$, $\theta = 90°$.

(c) $V_F \cong \overline{U}$, $\theta = 45°$.

(d) $V_F \cong \overline{U}/3$, $\theta = 90°$.

(e) $V_F \cong \overline{U}/3$, $\theta_1 = 45°$, $\theta_2 = 30°$. Reversed flapping.

exception to this statement, see *d*, Fig. 4, down beat. Here both C_L and C_D forces are nearly equal and equally useful. Thus the insect, in common with all successful flying machines, primarily depends on the force at right angles to the relative wind for flight. Magnan (1934) sketches one exceptional insect, the *Syrphus* fly, for which the C_D force is the useful one. Use of the C_D force is one way to obtain very large force coefficients at the price of considerable power. Other examples of the use of the C_D force will undoubtedly be found when more experimental data is obtained. They will occur when θ is near 90° when hovering, or greater than 90° in forward flight. In
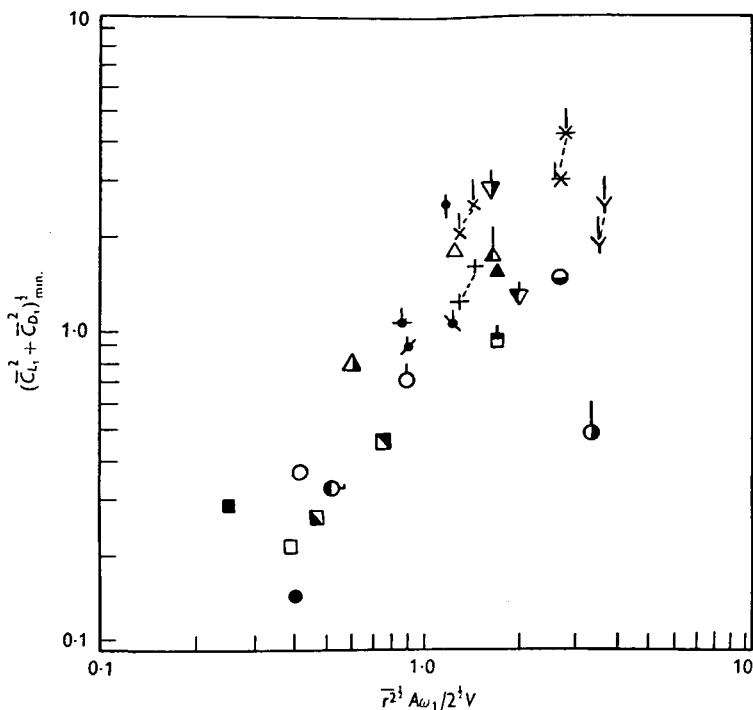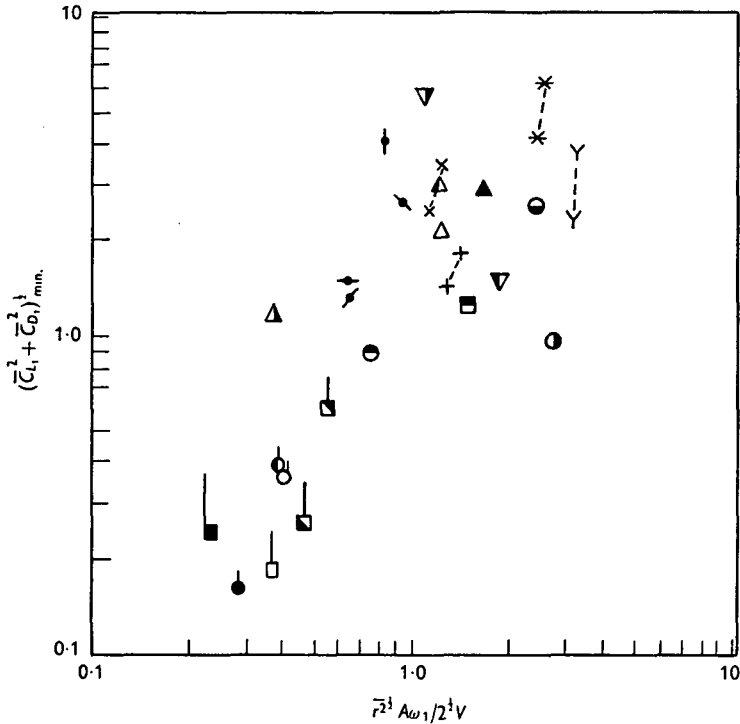

Fig. 5. Minimum total force coefficient on down beat coefficient *v*. ratio of root-mean-square flapping velocity to velocity of flight. $\theta = 30°$, $\xi = \zeta = 1$.

any case the significant force, perpendicular or parallel to the relative wind, can always be determined for any given mode of flight by drawing the relative wind diagram as in Fig. 4.

There remains to explain the occasional large lift and drag coefficients which appear in Figs. 2 and 3. To this end reference is made to Figs. 5 and 6 in which the minimum total force coefficient, determined from eq. (25), is plotted against the ratio of the root-mean-square (with respect to *r* and *t*) flapping velocity to the velocity of flight. This ratio measures the importance of the acceleration or inertia forces; when small the inertia forces are negligible. It will be observed that there is a distinct correlation between this ratio and the total force coefficient; when this ratio is small the force coefficient does not exceed those values normally expected in aerodynamic practice.

Thus the abnormally large lift coefficients derived by previous investigators must be attributed to acceleration effects. Both theoretically and practically there is no upper limit to the force coefficient referred to the velocity squared if acceleration forces are permitted. Thus for an impulsive start from rest, as in the case of an oar which is jerked, the terminal velocity may be very small and the force large. Hence the force' coefficient referred to the square of the average velocity will be very large. This conclusion holds for both potential and non-potential flow, though in the former case the motion must not be perfectly cyclic.

Fig. 6. Minimum total force coefficient on down beat v. ratio of root-mean-square flapping velocity to velocity of flight. $\theta = 60°$, $\xi = \zeta = 1$.

Part of the high lift coefficient may be due to a slotted wing or flap effect. For those insects with two pairs of wings which overlap, the anterior always overlay the posterior, which is the correct arrangement for a slotted wing. In some cases the posterior is hinged by hooks to the anterior, in which case the posterior may act as a flap.

In Figs. 5 and 6 the vertical lines run up to the values of $(\bar{C}_L^2 + \bar{C}_D^2)^{\frac{1}{2}}$, as determined from the separately derived values of $\bar{C}_L$ and $\bar{C}_D$ given in Fig. 3. Computations of $(\bar{C}_L^2 + \bar{C}_D^2)^{\frac{1}{2}}_{\min}$ were also made for the case of equal force coefficients on the up and down beat ($\xi = \zeta = 0$) and for assumed $\theta = 90°$ and $0°$ (not given here), and all led to essentially the conclusions above. In the case of the remaining figures in this paper,

they all refer to zero-force coefficients on the up beat ($\xi = \zeta = 1$). Calculations were also made for $\xi = \zeta = 0$ but are not given, since they indicated in some cases too small or negative values for the power, corresponding to the zero or negative values of C_D.

Since the observations did not provide values of θ they had to be assumed, though in some cases they could be inferred from the drawings of Magnan. This assumed
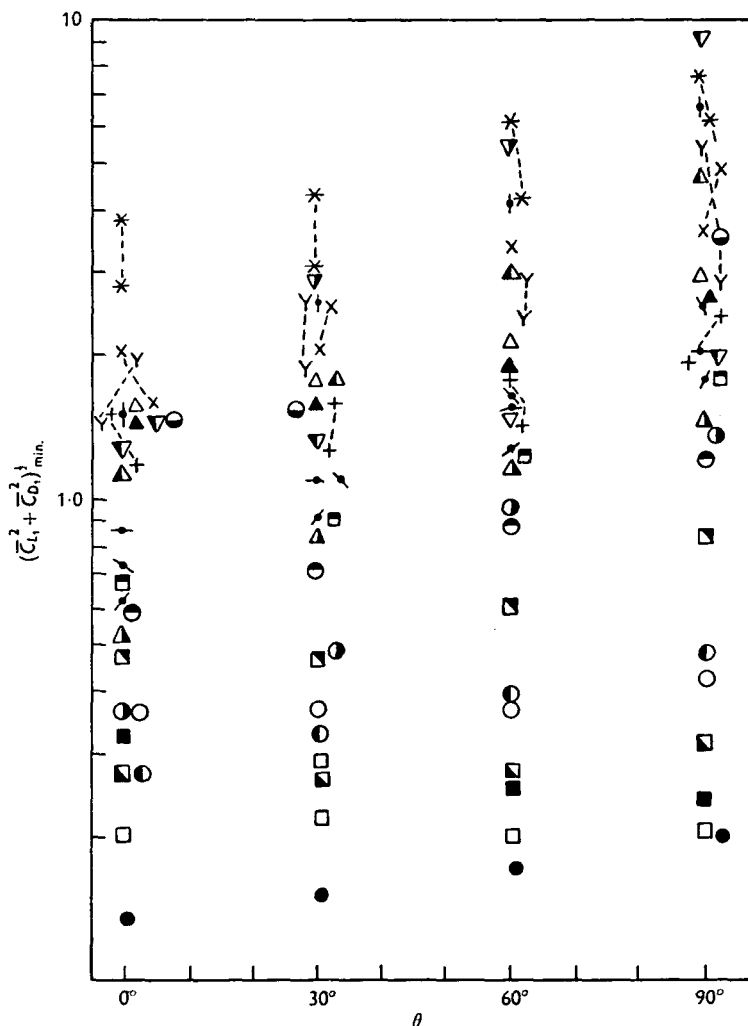

Fig. 7. Minimum total force coefficient on down beat as a function of the assumed inclination θ of the plane of beating. $\xi = \zeta = 1$.

value influenced the value of the double amplitude $2A$ of the wing motion in the plane of beating, since the double amplitude projected on the vertical (xz) plane, 2ψ, was the observed quantity given by Magnan. Hence the smaller the assumed θ, the larger the derived $2A$, which would vary between its projected value and $180°$ as θ varied from $90°$ to $0°$. The effect of the assumed θ on the derived minimum total

force coefficient is shown in Fig. 7, where it can be observed by tracing out a curve
for a single insect that the force coefficient can at most increase by a factor of 4 or 5
to 1 as θ varies from 0 to 90°. The variation is much less for those insects with
a projected double amplitude close to 180° and for those insects for which no pro-
jected amplitude was given, so that a constant amplitude in the plane of beating had
to be assumed. The range of solution for $0 < C_{Db} < 1$ is not given in Fig. 7; the range
was negligible. Assumed values of θ and A in Table 1 are in parentheses.

The actual values of θ as used for the computations of C_L, C_D (Figs. 2 and 3) and
the remaining figures involving the power were chosen as indicated in Table 1.
In general, for $\overline{(r(d\phi/dt))^2}^{\frac{1}{2}}/V \gtrsim 1$, θ was assumed to be 30°, whereas if this ratio were
much less than 1, $\theta = 60°$ was assumed. The values of θ chosen by this rule were
the least values compatible with the available drawings of Magnan and others. The
consequence of such a choice is that A is a little too large, and the derived values of
$\bar{C}_L$, $\bar{C}_D$ and $\bar{C}_D/\bar{C}_L$ and the power a little too small. This is considered to be 'advan-
tageous' to the insect in that the necessary power is a minimum. The range of solution
as θ is varied can be estimated from Fig. 6.

From another standpoint also the derived average values of $\bar{C}_L$, $\bar{C}_D$ and $(\bar{C}_L^2 + \bar{C}_D^2)^{\frac{1}{4}}$
are minimum values. Since the actual instantaneous values of these quantities must
vary with r and t, at some time the instantaneous values must exceed their averages.

According to Table 1, col. 8, it will be observed that the down beat is slower than
the up beat, or $\omega_1 < \omega_2$ (see also Marey, 1895, p. 228; Guidi, 1938, p. 1108). This is
an 'advantageous' mode of flight to the insect, in that it tends to reduce the power
for fixed frequency of flapping and fixed requirements of vertical force and thrust.
Since the down beat *must* provide most of the force, and since the force goes up as the
velocity squared of the wing while the power goes up as the velocity cubed, it requires
less power for the same average force when a smaller force is exerted over a longer
time ($\omega_1 < \omega_2$) than a larger force over a shorter time ($\omega_1 > \omega_2$).

GEOMETRICAL SIMILARITY AND POWER

The degree of geometrical similarity of the insects considered can be examined in
Figs. 8 and 9. Here the wing length and area are plotted against the mass. The dotted
line in each figure indicates the expected slope for geometrical similarity, i.e. the
quantities plotted should be proportional to $M^{\frac{1}{3}}$, $M^{\frac{2}{3}}$ respectively. Geometrical
similarity is realized with considerable dispersion except possibly for the wing area,
which seems to increase slightly faster than $M^{\frac{2}{3}}$. Fig. 9 also shows that the Lepidoptera
and Neuroptera (squares and circles), which tended to have smaller force coefficients,
have relatively larger wing areas for their masses.

In contrast to the large individual departures from geometrical similarity for the
wing area, the power as a function of the mass shows surprisingly small dispersion
(Fig. 10). The power is very nearly proportional to the mass (dotted line indicates
proportionality). This proportionality is reasonable from the standpoint of meta-
bolism, and is also in keeping with the observation that the wing area increases
slightly faster than $M^{\frac{2}{3}}$. From aerodynamic considerations it can be shown that
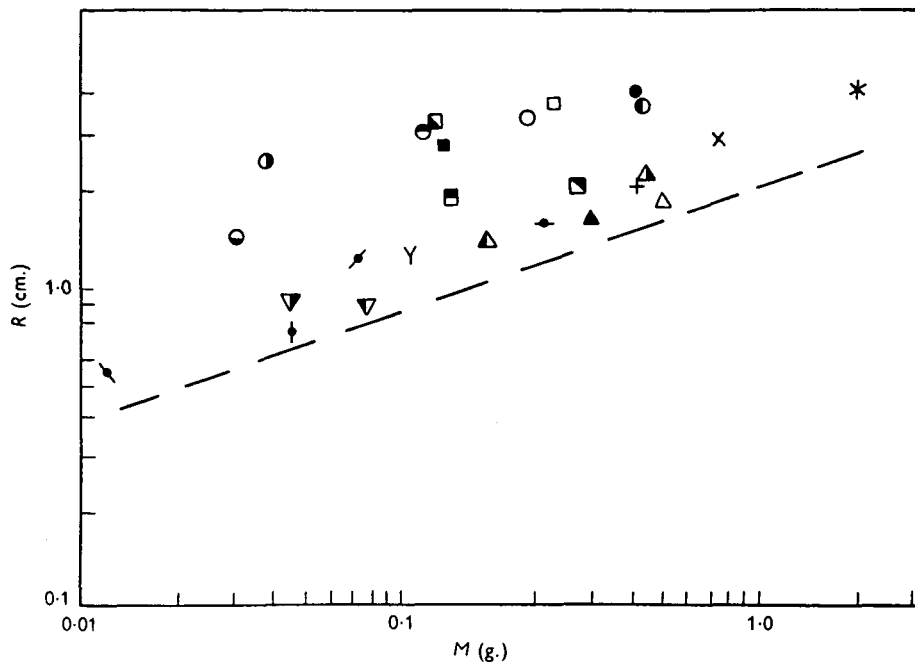
Fig. 8. Wing length *v.* mass of insect. The dotted line indicates the slope for geometrical similarity,
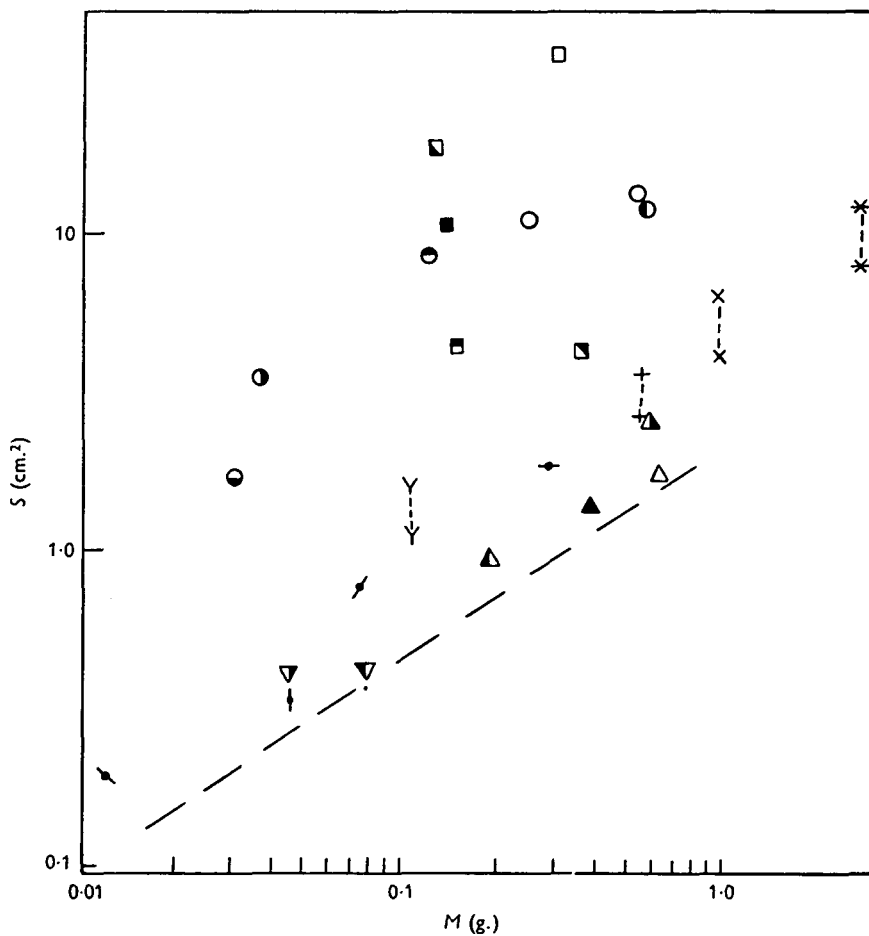$R \propto M^{\frac{1}{3}}$.

Fig. 9. Wing area *v.* mass of insect. The dotted line indicates the slope for geometrical similarity,
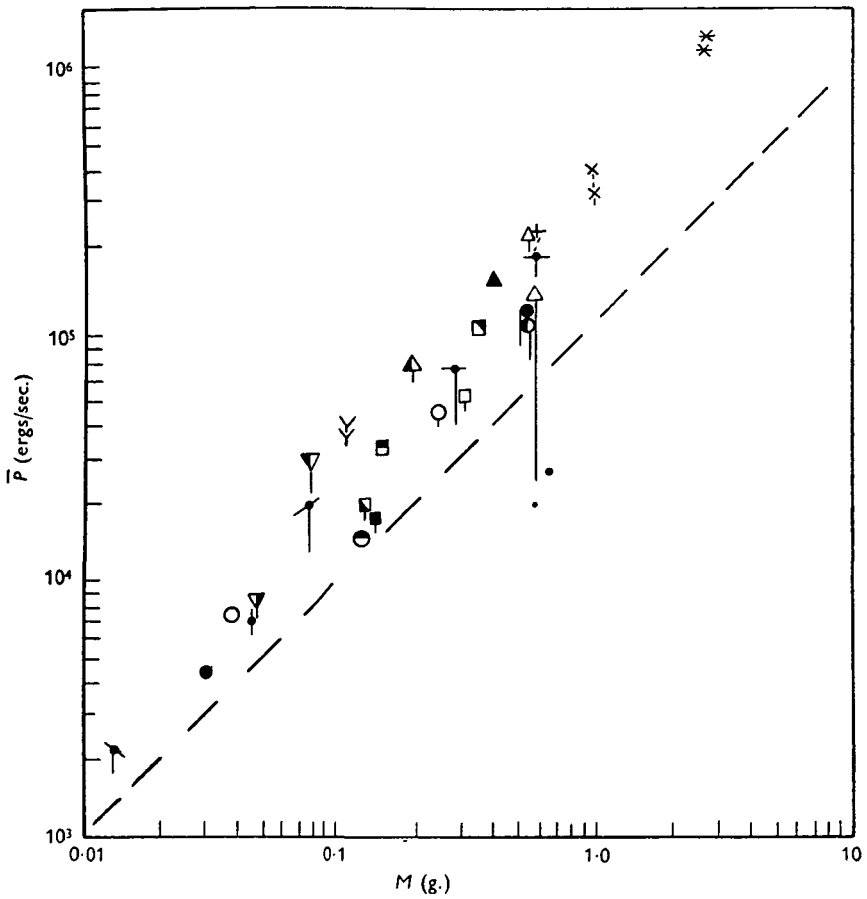$S \propto M^{\frac{2}{3}}$

Fig. 10. Power v. mass, $\xi = \zeta = 1$. The dotted line indicates the slope for simple proportionality.
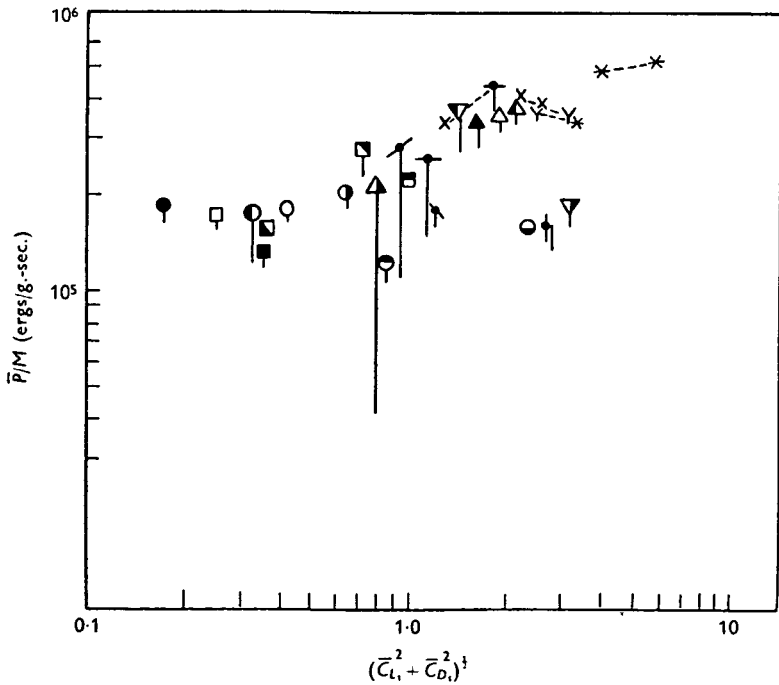

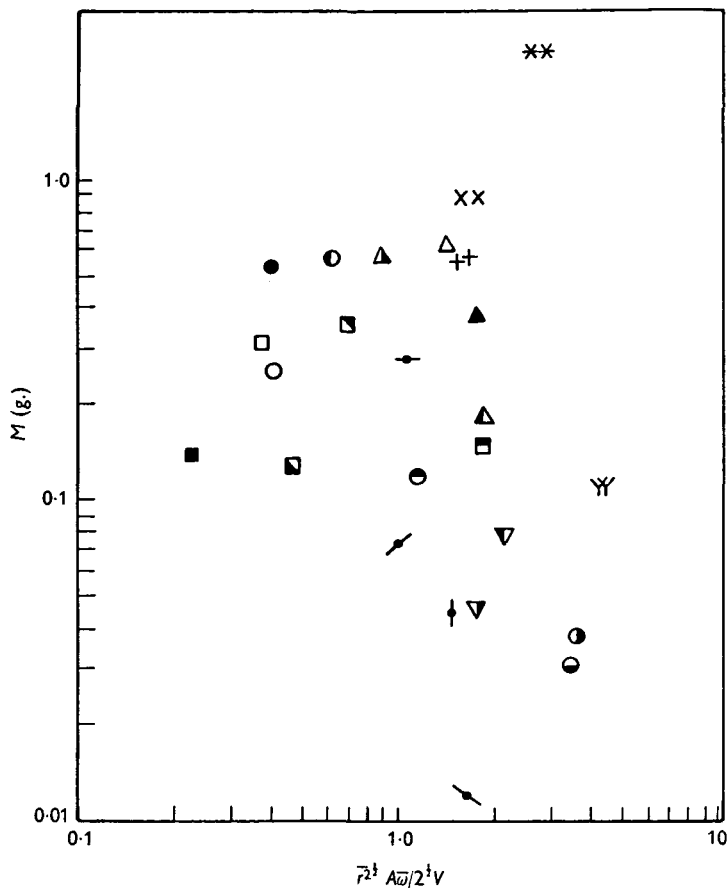Fig. 11. Power per gram as a function of the total force coefficient. $\xi = \zeta = 1$.

Fig. 12. Mass v. ratio of root-mean-square flapping velocity to velocity of flight.
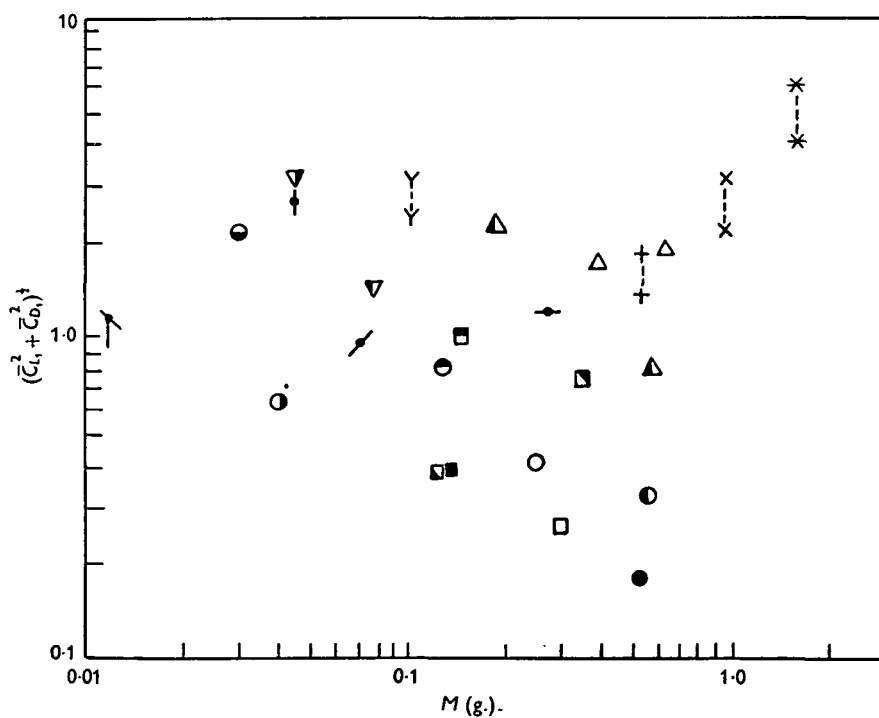

Fig. 13. Total force coefficient on down beat v. mass. $\xi = \zeta = 1$.

other things being equal, either the wing area must increase faster than is required by dimensional similarity, the power increase faster than the mass, or both, as seems indicated in the present case. The uncertainty of the data renders this conclusion as yet only tentative.
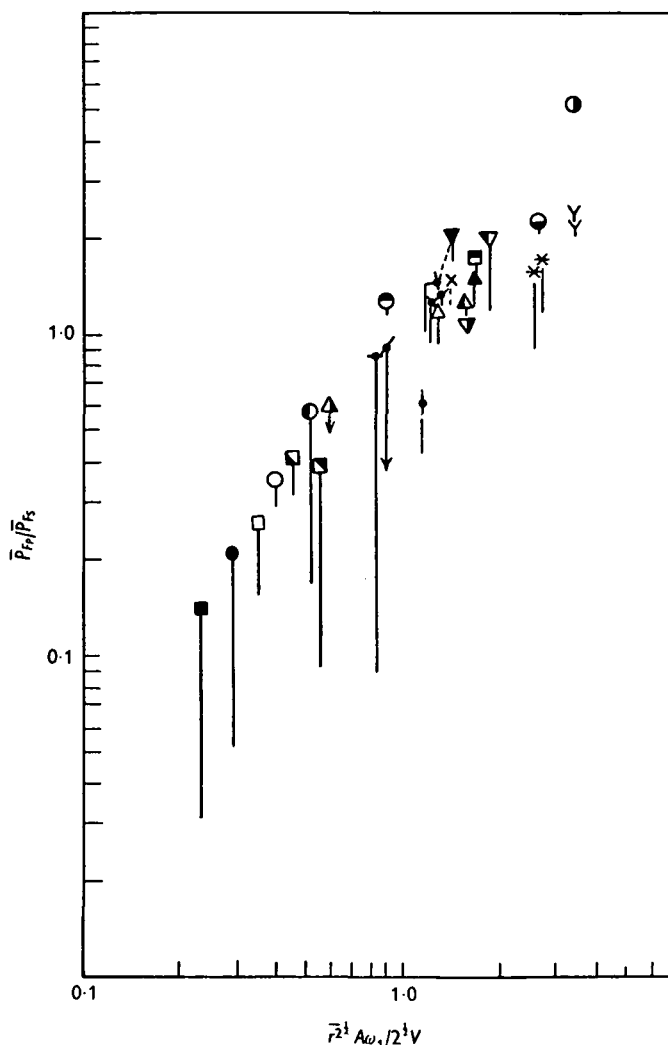

Fig. 14. Ratio of power expended against drag to power expended against lift forces v. ratio of root-mean-square flapping velocity to velocity of flight. $\xi = \zeta = 1$.

Fig. 11 gives the specific power, or power per gram, as a function of the total force coefficient. They increase together, again with surprisingly small dispersion. Fig. 11 indicates about 10^{-2} horse-power per lb.—better than a man, scarcely in a class with aircraft engines!

There is a very slight negative correlation of mass with ratio of flapping velocity to velocity of flight (Fig. 12). There is also a slight negative correlation between total

orce coefficient and mass (Fig. 13), which does not support Rashevsky's conclusion that C_L should increase with the mass (Rashevsky, 1944). In general, both lift and drag coefficients for insects are large, larger than those for birds, in the few cases where they have been evaluated (Demoll, 1919; Walker, 1925).

In Fig. 14 is plotted the ratio of the power expended against F_p (forces in C_D, second term of eq. (13)) to power expended against F_s (forces in C_L, first term of eq. (13)) as a function of the ratio of the root-mean-square wing-flapping velocity

DIPTERA		COLEOPTERA	
Tabinus bovinus	—•—	Melontha vulgaris Fabr.	✕
Sarcophaga carnaria L.	⸾	Cetonia aurata	+
Musca domestica	↘	Lucanus corvus	✳
Volucella pellucens Meig.	↗	Telephorus fuscus	Y

NEUROPTERA		HYMENOPTERA	
Brachytron pratense Mull.	◑	Xylocope violacea	△
Calopteryx splendens Harr.	◒	Bombus terrestris Fabr.	▲
Pyrosoma minium Harr.	◐	Vespa germanica	◬
Panorpa comunis L.	◓	Vespa crabro L.	◭
Orthetrum caerulescens Fabr.	○	Apis mellifica L.	▽
Aeschna mixtra Latr.	●	Amonophila sabulosa V. Del.	▼

LEPIDOPTERA	
Papilio podalirius	□
Vanessa atalanta L.	■
Pieris brassica L.	◣
Macroglossa stellatorem L.	◥
Plusia gamma L.	▭

Fig. 15. Identifications of points for all figures.

to the velocity of flight. Fig. 14 indicates that the fraction of the power expended against F_p increases with the importance of the inertia forces. This shows the increasing price in 'wasted power' paid for the use of inertia forces in flight, since C_D forces are usually in an undesirable direction, as Fig. 4 showed.

In Fig. 14 the dispersion is also surprisingly small, in view of the large individual departures from geometrical similarity. The small dispersion of quantities involving the power, as opposed to quantities involving the geometrical dimensions, indicates that as power plants they are essentially similar, despite their great diversity in form.

The range of solution for quantities involving the power (Figs. 10, 11 and 14) as the drag coefficients of the body C_{Db} varies between 0 and 1 is shown by the length of the vertical lines, the points being plotted for $C_{Db} = 0$. The dependence of the power on C_{Db} is considerable, a consequence of the dependence of C_D on C_{Db}.

There are four pairs of similar star-type points on the figures, connected by dotted lines. These are the Coleoptera. The upper point of each pair refers to calculations

ignoring the elytra as wings, the lower includes them as a part of the membranou●
wings. This was done since the contribution of the elytra to flight was not known,
but it was felt that these two cases were the limiting ones.

Fig. 15 identifies the points in all the figures, and Table 1 summarizes the pertinent
flight data.

SUMMARY

1. General formulae are derived giving the lift, thrust and power when the wing
motion is specified. The formulae are applied to twenty-five insects for which quan-
titative data are available. Average values for lift and drag coefficients, C_L and C_D,
are derived by equating the weight to the vertical force and the thrust to the horizontal
drag of the body.

2. The large drag and lift coefficients obtained for insect flight are attributed to
acceleration effects. There is a distinct correlation between $(C_L^2 + C_D^2)^{\frac{1}{2}}$ and the ratio
of the flapping velocity of the wings to the linear velocity of flight. When this ratio
and therefore the accelerations are small, the force coefficients do not exceed those
to be expected for flat plates. Owing to the nature of the assumptions and approxi-
mations made, the values derived for C_D, C_L and C_D/C_L are minimum values.

3. Other characteristics of insect flight are discussed. In general, insects fly in
such a way as to minimize the mechanical power required. In most, but not all cases,
the useful force is the one perpendicular rather than parallel to the relative wind.
The wing tips should move in a figure 8, the down beat should be slower than the up
beat, and the majority of the necessary force must be supplied on the down beat.

4. Figures are given using the data from the twenty-five insects considered, showing
average relations between power, specific power, mass, acceleration forces, force
coefficients and geometrical dimensions. The power per gram, the 'wasted power',
and the force coefficients all increase as the importance of the acceleration forces
increases.

5. When plotted as functions of mass, quantities involving the power show much
less dispersion than quantities involving the geometrical dimensions. This is taken
to mean that despite the diversity of insect form, as 'power plants', they are all
essentially similar.

6. A table of the observed or adopted flight parameters (frequency of beating, mass,
wing area, velocity of flight, amplitude and orientation of wing motion) is appended.

REFERENCES

BAIRSTOW, L. (1939). *Applied Aerodynamics*, p. 621. London: Longmans, Green and Co.
DEMOLL, R. (1918). *Der Flug der Insekten und der Vogel*. Jena: Gustav Fischer.
DEMOLL, R. (1919). Der Flug der Insekten. *Naturwissenschaften*, **8**, 480.
DURAND, W. (1934). *Aerodynamic Theory*, **4**, 318. Berlin: Julius Springer.
GUIDI, G. (1938). A study of the wing beats of pigeons in flight. *J. R. Aero. Soc.* **42**, 1104.
GUIDI, G. (1939). The wing beats of pigeons. *J. R. Aero. Soc.* **43**, 457.
HOFF, W. (1919). Der Flug der Insekten. *Naturwissenschaften*, **7**, 159.
HOLST, E. VON & KUCKEMANN, D. (1942). Biological and aerodynamical problems of animal flight.
    J. R. Aero. Soc. **46**, 39.
KUKENTHAL, W. & KRUMBACH, T. (1927-34). *Handbuch der Zoologie*, VII, II. Halfte. Stresemann,
    E., 'Aves', pp. 573-75. Leipzig: Walther de Gruyter.

MAGNAN, A. (1934). *La Locomotion chez les Animaux*. I. *Le Vol des Insectes*. Paris: Hermann et
        Cie.
MAREY, E. J. (1890). Le Vol des Oiseaux. Paris: Libraire de l'Academie de Medicine.
MAREY, E. J. (1895). *Movement*, p. 228. New York: D. Appleton and Co.
RASHEVSKY, N. (1944). Flight of birds and insects in relation to their form. *Bull. Math. Biophys.*
        6, 42.
RAYLEIGH, LORD (J. W. STRUTT) (1883). The soaring of birds. *Nature, Lond.*, **27**, 534.
SCHRÖDER, C. (1928). *Handbuch der Entomologie*, **1**. Jena: G. Fischer.
WALKER, G. T. (1925). The flapping flight of birds. *J. R. Aero. Soc.* **29**, 590.
WALKER, G. T. (1927). The flapping flight of birds. II. *J. R. Aero. Soc.* **31**, 337.