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Biology and Physics of Locust Flight. I. Basic Principles in Insect Flight. A Critical Review

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BIOLOGY AND PHYSICS OF LOCUST FLIGHT

I. BASIC PRINCIPLES IN INSECT FLIGHT. A CRITICAL REVIEW

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CONTENTS

Natural flapping flight is a complicated type of locomotion; it involves a large number of parameters and demands a higher rate of energy consumption than any other known achievement within the animal kingdom. The extensive literature provides a diffuse and sometimes misleading picture of the mechanics and energetics of flight. The purpose of this critical review is twofold; first, an attempt is made to reveal how far contemporary knowledge has advanced towards a

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quantitative understanding of the basic physical events which result in flight; secondly, the conceptual analysis and the conclusions arrived at serve as a general introduction to a detailed experimental study of the flight performance of the desert locust (*Schistocerca gregaria* Forskål). The results of this study will be published as a series of mutually dependent papers which are referred to as parts, the present being part I; their content is indicated by the general title 'Biology and physics of locust flight'.

The abstracts at the end of the major sections can be read as a continuum and independent of the remaining text.

Most qualitative principles in insect flight are fairly well understood, although some authors have claimed that the observed movements did not permit flight according to ordinary aerodynamic principles. The data upon which these calculations are based were, however, found to be inadequate. In general, if one attempts to interpret the observed performance in quantitative terms, a conceptual analysis of the necessary knowledge shows that both the conditions for observation and the measured parameters must be defined more rigorously than has hitherto been the case.

A theoretical treatment, partly based upon the experimental evidence in the succeeding parts, reveals that the energy account of a wing stroke comprises at least three *independent* terms, namely, an aerodynamic term due to the wind forces on the wings, an inertial term due to the acceleration of the wing mass, and an elastic term caused by the elastic deformations of the thorax. Finally, extra-muscular damping within the thorax *may* be involved but it does not seem to be important compared with the other quantities. The mechanical energy and the forces which the muscles must provide can be estimated by the torque about the wing hinge to which these terms give rise. However, in order to summate the torque contributions their detailed variations *during* the stroke must be known, and since all of them are extremely sensitive to alterations in the stroke cycle, no existing theory can deal with the energetics of the flight as a whole. One is therefore forced to investigate the wing stroke empirically. An experimental study must take place under rigorously controlled aerodynamic and biological conditions and must include the simultaneous variation in time and space of a considerable number of kinematic and dynamic parameters whose nature is briefly outlined.

However, an experimental approach would be much hampered if one had to take *unusual aerodynamic* (*inertial*) forces into account. Fortunately, an analysis of existing aerodynamic theories on flapping flight reveals that there is little to be said against and much in favour of considering natural flight as being based upon conventional aerodynamic principles, even in the case of small insects like mosquitoes. At least, unconventional aerodynamics need not be assumed in order quantitatively to explain observed performances, although some authors (cf. Osborne 1951) have reached the opposite conclusion. The assumptions made in the most complete theories (Holst & Küchemann 1941; Walker 1925, 1927; Osborne 1951) are discussed in detail and the basic equations have been homogenized to fit the rest of the text. Various theoretical deductions considered of general interest are tabulated (e.g. influence of distance from fulcrum, induced wind) and the theories are tested by inserting values from insect types whose performances are best known.

The calculations also gave the order of magnitude of the power necessary to overcome the aerodynamic forces (=aerodynamic power). This external power certainly claims a considerable fraction of the total metabolic rate.

A short review (§6) of the regulation of flight also emphasizes the importance of considering both aerodynamic, inertial and elastic terms as significant *simultaneous* factors in the energy account and thus in the regulation of the power output; the special mechanisms concerned with the stability in flight fall outside the scope of the paper, however, and will be discussed in part IV.

LIST OF SYMBOLS

The main physical quantities in parts I to X are listed. When symbols are used other than those given here, the reader is referred to the appropriate text. Names of independent quantities are separated by colons. Brackets indicate that the symbol is used only in a special context.

subscripts

a	aerodynamic
D	drag
d	downstroke: (damping)
e	elastic
i	inertial
L	lift
m	muscular
n	net heat produced
u	upstroke
w	heat of evaporation of water
1	forewings
2	hindwings

main symbols

A	aspect ratio: area (also S)
a	amplitude
B	body angle
b	stroke plane angle
C	coefficient or constant
C_D; $C_{D\infty}$; C_{Di}	coefficient of drag; coefficient of profile drag; coefficient of induced drag
C_L	coefficient of lift
c	chord of wing profile
D	drag: extra-to-wing drag
E	coefficient of elasticity: length of elytron
F	force: length of hind femur
I	mass moment of inertia
k	flapping ratio
L	aerodynamic lift: average vertical aerodynamic force
L_r	relative lift
l	length: length index
M, m	mass: (bending moment)
N	frequency (c/min)
n	frequency (c/s)
P	power
Q	torque
R; r	radius; distance from centre of rotation
Re	Reynolds's number
S	area (also A)
s	surface index: distance
T	thrust
t	time: period
u	velocity or speed
V	velocity or speed
v	velocity or speed: volume index
W	work
w	weight: induced wind velocity: (cross-wind)
w_f; w_b	standard flying weight; basic weight
α	angle of attack (=angle of incidence)
β	inclination of relative wind (part IV): inclination of wing axis to wind (part III)
Γ	aerodynamic circulation: positional angle of wing at elastic equilibrium (part VI)
γ	positional angle of wing
γ'	positional angle measured in stroke plane
δ	angle of plication of wing
η	efficiency
Θ	temperature difference
θ	angle of twist
Λ	aerodynamic pull
ν	kinematic viscosity: non-dimensional frequency
ρ	mass density of air ($=\text{kg m}^{-2}\text{ s}^2$)
Φ	phase difference
ϕ	stroke angle
ω	angular velocity

1. Introduction

Insects do not practice gliding or soaring comparable in extent and duration to the performances of birds though atmospheric convection may play a role in the transport of insects with small sinking speeds like aphids (Johnson & Penman 1951) and butterflies; in hot climates strong vertical wind velocities may even be essential for migrating locusts (Rainey & Waloff 1951). However, the normal and characteristic aerial locomotion of insects is that of *flapping flight*. The power output for this type of active transport is known to be very considerable and exceeds the metabolic rates found elsewhere in animals (for reference, see Weis-Fogh 1952*a*, *b*). This fact and the very rapid wing movements of some insects have aroused the interest of physiologists in the power plant of insects. Apart from the many biological problems involved, the aerodynamic principles upon which natural flight should be understood have been and are still much disputed. Swimming and flying have much in common, but flying involves an additional complication in that *lift* to overcome the *gravitational pull* must be produced as well as *thrust* to overcome the *drag* of the body moving through the fluid. Flapping flight therefore represents a complex physical and biological problem, so complex that we have found it impossible to study and understand the single parts of the process without fitting them into a coherent system which we will simply call *the flight system* and whose action results in the insect being airborne.

The purpose of our critical review is to reveal how far contemporary knowledge has advanced towards a quantitative understanding of the mechanism and energetics of the basic physical events which result in flight; in other words, to evaluate the available records on the construction, function and energy transformations of the flight system when it works under normal conditions. Many important qualitative studies have therefore been omitted as well as papers dealing mainly with problems of stability, control and regulation. For a more general presentation of the literature, the reader is referred to Chadwick (1953, insects), Brown (1951, birds), Eisentraut (1936, bats), and Slijper (1950, all flying animals). The early literature was reviewed by Erhard (1913) and Melin (1941).

Our *general conclusion* is that neither the kinematics nor the dynamics are sufficiently well known to permit a theoretical treatment of the energetics of natural flapping flight.

The *experimental approach* in parts II to IX is briefly outlined in the text. The four-winged desert locust, *Schistocerca gregaria* (Forskål; *phasis gregaria*), was used throughout, partly because it proved to be well suited for such studies and partly because of its great economic importance (cf. Uvarov 1953).

2. The problem

Flapping flight consists in oscillating the wings in such a way that the resulting wind forces upon the wings balance the resulting extra-to-wing forces acting upon the animal. In uniform horizontal flight this means that the average vertical wind force, *the average lift*, is equal and opposite to the gravitational pull, and the average horizontal force, the *average thrust* (zero during hovering), is equal and opposite to the wind resistance, i.e. to the *extra-to-wing* drag. An analysis involves a number of problems of which the following are essential in this context:

(1) The first question concerns the *functional architecture* of the wing-bearing segments (the *pterothorax*). In fact, it was found that the functional anatomy of the locust ptero-

thorax (parts V, VI, VII) could only be understood in the light of an analysis of the flight proper (parts II, III, IV). We therefore postpone the description of how the wing movements are produced until part VII and will confine the discussion mainly to the function and energy requirements of the wings.

(2) The description of the wing movements relative to the body and relative to the air constitutes the *kinematics*. It must be stressed that any attempt to understand a flying animal as an aerodynamic machine requires a detailed knowledge on the variation with time of a considerable number of parameters. This is not always appreciated, and still less that those parameters should be simultaneous and correspond to a known flight situation.

(3) The *aerodynamic* problem is to understand how the kinematically described wing movements result in the observed average forces of lift and thrust. Moreover, it should make possible an estimation of the force which the wing muscles must exert if they are to overcome the aerodynamic forces, and thus give information on the aerodynamic power involved. Studies on the average pressure distribution round the animal (cp. Magnan 1934) and of the change in momentum of the air passing the wings (Smith 1953; Hocking 1953) may of course give information on the average forces and of the kinetic energy imparted to the air respectively. But such information cannot explain how the changes are brought about. Moreover, the measurements are very intricate and must take place under rigorously controlled conditions (see p. 428).

(4) The last complex of problems concerns the *energetics* of flight, i.e. to discover the flow of energy in the essential parts of the flight system and to sum the contributions in order to estimate the work of the muscles. In locusts, and probably in most other insects, one must distinguish between at least four different terms in the energy account, namely, the *aerodynamic term*, the *inertial term* which represents the work done in accelerating the wing mass, the *elastic term* due to elastic forces in the pterothorax and, finally, the effect of extra-muscular damping. The last term seems to be of negligible importance in the locust. The sum of these contributions per unit time represents the *mechanical power* which the flight muscles must deliver. The ratio between this quantity and the *total power consumption* of the muscles is the *mechanical efficiency of the muscles*. It has no direct relationship with the efficiency of the aerodynamic machine as will appear from the discussion on p. 434.

3. Requisite conditions for observation

The dynamics of any machine or organism should first of all be studied within its normal range of operation. As will be shown on p. 426 there does not seem to be any essential difference between the aerodynamics of natural wings and of artificial airfoils. The coefficients for lift and drag C_L and C_D as well as their ratio C_L/C_D change drastically with small alterations in the *angle of attack* α, i.e. the angle between the relative wind and a reference line which is generally the chord of the profile. The total wind force upon a wing in a stationary flow is

$$F=(C_L^2+C_D^2)^{\frac{1}{2}}S\tfrac{1}{2}\rho V^2, \tag{I, 1}$$

where ρ is the mass density of the air, S the area of the wing and V the speed of the relative wind. In flapping flight the relative wind changes both in magnitude and direction with time t and with the distance r from the wing base. At the wing base, V is equal and opposite to the *flying velocity* v through the air, but at the distance r from the fulcrum the *flapping velocity* $= -\omega r$ should be added, where $\omega = \omega(t)$ is the instantaneous angular velocity about the wing base. Thus $V = V(r, v, t)$. This kinematically defined vector does not strictly correspond to the true relative wind velocity because the induced wind velocity should be added. The induced velocity depends upon the aerodynamic situation, but in this context the simpler expression will suffice (cf. p. 449). In many insects the average flapping speed of the wing tip is often of the same order of magnitude as the flying speed (cf. Vanderplank 1950). Disregarding either flapping speed or flying speed might therefore introduce serious errors in the estimation of V^2, and a tethered, flapping animal might experience wind velocities which differ significantly from those during free flight. As regards the resulting wind forces the situation is still worse because they also strongly depend upon the angle of attack. In a flapping wing there is no single value of the angle of attack; the instantaneous value of α at a given wing section is determined by the instantaneous relative wind at that section and the instantaneous twist about the long axis of the wing plane θ. In contrast to propellers the geometric pitch of the wing sections alters during the wing-stroke cycle through torsional deformations of the wing plane so that $\theta = \theta(r, t)$. These deformations are actively controlled by the animal (see parts III, IV, VII). This being so, α depends upon $V = V(v, r, t)$ and $\theta = \theta(r, t)$. Since the instantaneous as well as the average force coefficients vary with small variations of α, the product $(C_L^2 + C_D^2)^{\frac{1}{2}} V^2$ is extremely sensitive to alterations in wind speed or in twisting of the wing plane.

If, under experimental conditions, the wind field in which the flapping insect works does not fall within the limits of adjustment of the insect, the wings will stall and 'paddle' in the air rather than be carried through it in an orderly manner. Even if the insect is able to adjust its movements so that the wings do not stall, one must make sure that the aerodynamic forces come close to those experienced in natural flight.

It has been argued that the aerodynamic work of many insects is negligible compared with the inertial work (Sotavalta 1952) or that only a small part (some 2 to 5%) of the total metabolic rate is used for aerodynamic work (Chadwick 1953; Hocking 1953). If this were so, many mechanisms in flight might of course be studied with reasonable accuracy in insects 'flying' under incorrect aerodynamic conditions. But we do not consider the methods used by the above authors as conclusive for calculating the aerodynamic work (see p. 434), the results being systematically too low. In any case, a study of the mechanism and energetics of locust flight must take place under aerodynamic conditions which are capable of analysis, which approach the natural as much as possible and, finally, which do not deviate much in quality and quantity from those known to exert a profound influence on the resulting force.

The ideal would be to analyze continuous *free flight*. The average lift, thrust, flying speed, etc., should be measured while the insect possesses all translational and rotational degrees of freedom (for discussion see part II, § 3*g*; and part III, § 2*d*). However, such a detailed quantitative analysis would be very difficult to perform. Because of this most investigators of the mechanism of free flight have studied the manoeuvres during start and landing or have analyzed hovering flight (cf. Magnan 1934, insects; Knoll 1934;

Stolpe & Zimmer 1939; Brown 1948, birds). In some cases the first stages of free forward flight have been analyzed qualitatively from slow-motion films of birds (cf. Marey 1890; Brown 1953).

Another possibility is to lock those degrees of freedom which, from a quantitative point of view, are of least importance and to let the animal choose, for example, its preferred flying speed. This allows prolonged observations on *suspended flight* with restricted but controllable freedom of movement. A special compromise of this type is described in part II. Suspended flight has been studied in roundabouts with forward displacement through the air (Marey, as cited by Noguès 1933; Axenfeld 1911; Kennedy, Ainsworth & Toms 1948; Krogh & Weis-Fogh 1952; Weis-Fogh 1952*a*; Hocking 1953; Sotavalta 1954) or in wind tunnels (Hollick 1940; Krogh & Weis-Fogh 1952; Wootten & Sawyer 1954). The majority of experiments, however, have been performed with tethered insects which were stimulated to flap their wings in 'still' air. In such cases of *tethered flapping* the aerodynamic performance which the wings would yield during free flight is unknown; only if it corresponded to hovering would the 'flying' be representative of a normal performance.

It is concluded that an understanding of flapping flight presupposes knowledge of the simultaneous variation in time and space of a considerable number of kinematic and dynamic parameters measured under normal or at least known aerodynamic conditions.

4. Review of observations and experiments

(*a*) *Kinematics*

The kinematic analysis should provide information on the three-dimensional movements of the wings in relation to the body and on the movements of the whole insect in relation to the air. Some kinematic parameters are relatively easy to measure, and much information has accumulated on, for instance, the wing-stroke frequency, but other and equally important quantities have remained obscure.

Fundamental movements

The flapping or *oscillation* of the wing can be reasonably described (cf. figure I, 1) in terms of the wing-stroke frequency n, the angle b at which the main stroke plane is inclined to a plane fixed in the animal, and by the angular movements of the long axis $\gamma = \gamma(t)$, where γ is the angular position in the stroke plane, i.e. the positional angle. If, furthermore, the angular movements of this axis perpendicular to the stroke plane are also included, the wing-tip curve can be described. The first and second derivatives of $\gamma = \gamma(t)$ give the angular velocity $\omega = \omega(t)$ and the angular acceleration $\mathrm{d}\omega/\mathrm{d}t$ respectively.

The *frequency* n has been determined in practically all studies on both free, suspended and tethered flight (for references see Sotavalta 1947; 1952; 1953; Chadwick 1953). The *stroke-plane angle* b was recorded in free (=hovering?) flight of many insects by Magnan (1934), and sometimes together with the projection of the wing-tip curve in suspended or tethered flight by Marey (1873), Magnan (1934), Hollick (1940) and Chadwick (1951). The *stroke angle* (figure I, 1), $\phi = \gamma_{\text{max.}} - \gamma_{\text{min.}}$, has also been recorded by these and other authors (Hocking 1953), whereas the variation of γ with time has been studied but rarely. Generally a sinusoidal oscillation has been assumed (Magnan & Sainte-Laguë 1933; Chadwick 1951;

1953; Sotavalta 1952), but no direct proof has been given from the published cinematographic films which refer either to tethered flight or to flight with unknown restrictions (for earlier literature see Magnan 1934; Chadwick 1940; Kennedy *et al.* 1948). The *angular movements* are therefore poorly known. On the basis of flash photographs Vanderplank (1950) has even claimed that the wings are stopped for relatively long periods at their upper and lower positions so that the angular accelerations become much greater than during a simple sine oscillation. Most authors agree with Magnan (1934), however, that, although the downstroke generally lasts longer than the upstroke, the angular velocities do not change abruptly at the extreme positions (stroboscopic observations).

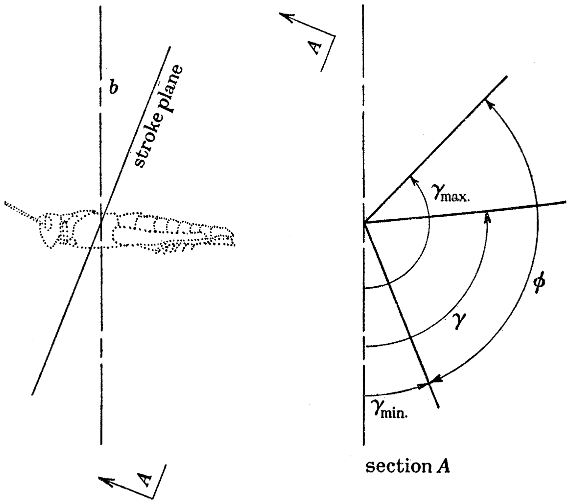


FIGURE I, 1. Wing-stroke parameters.

Since Marey's studies much attention has been devoted to the characteristics of the *wing-tip curve*, and Boel (1929) has even claimed to be able to explain the flapping flight of birds as a result of the circumduction superimposed upon the simple oscillation of the wings. Since he seems to have disregarded the fact that birds as well as insects are able to control the twisting of the wing plane, we cannot agree with his conclusions. In locusts we found that the wind velocities due to the *deviations* from a simple oscillation were very small compared with the flying velocity and the flapping velocity so that they would only influence the velocity of the relative wind V by an insignificant amount. They can therefore be neglected. This might also apply to other insects; but alterations of the wing-tip curve can, of course, alter the position of the resulting wind forces in relation to the body and so be of importance for manoeuvres and stability (Hollick 1940).

Twisting of the wing

The variation of the *twist* $\theta = \theta(t)$ of the wing plane has been observed and described qualitatively several times. Students of insect and avian flight agree on the following main principles (see Snodgrass 1930; Brown 1951; Chadwick 1953; Slijper 1950): during the downstroke the wing is *pronated*, i.e. the leading wing edge of the horizontally orientated animal is twisted downwards; during the upstroke it is twisted upwards or supinated (figure I, 2). No quantitative measurements exist, however, from which $\theta(r, t)$ can be deduced. From his films Magnan (1934) made models of the stroke phases of *Volucella*, but the wing was treated as a plane plate which could be moved only at the base and the 'twisting' was determined by visual estimation of coincidence between photo and model.

The wings of birds and bats are often moved in a much more complex way for which the simple scheme adopted here is inadequate (cf. Marey 1890; Lorenz 1933; Eisentraut 1936; Brown 1948; 1953). The hovering of humming-birds might be an exception as judged from the studies by Knoll (1934), Stolpe (1938), and Stolpe & Zimmer (1939), but the twisting of the wings was not analyzed quantitatively by these authors.

Movements relative to the air

The movements through the air depend upon the oscillation, the twisting, and on the air speed or *flying speed v* of the whole insect through the air. *v* has been estimated by many authors under different conditions: free flight of insects (Demoll 1918; Frisch 1927; Rainey & Waloff 1951); flight with a thread attached and wound on a pulley (Magnan 1934); flight in a roundabout (Krogh & Weis-Fogh 1952; Hocking 1953) or in a wind tunnel (Krogh & Weis-Fogh 1952; Wootten & Sawyer 1954). In no case, however, was the air speed measured at the same time as the other wing-beat parameters necessary for a kinematic description. It is highly probable that Magnan's (1934) failure to explain the flight of the fly *Volucella* in ordinary aerodynamic terms was to a considerable extent due to his neglecting the air speed, and also to the roughness of his calculations. In any case, his method does not give a reliable determination of the angles of attack. This failing in a paper describing the results of a large number of observations exerted an unfortunate influence on later work because it revived the ideas of Demoll (1918) and Oehmichen (1920) who concluded that ordinary aerodynamics was insufficient to explain the observed performances. Recently Osborne (1951) has used Magnan's data for theoretical estimations of the force coefficients. Apart from inherent restrictions of his theory, the highest coefficients of lift which he has calculated are inconsistent with normal steady-state aerodynamics.

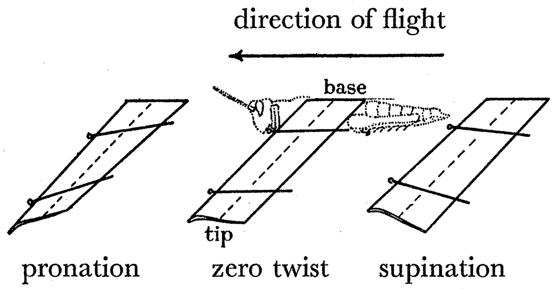


Figure I, 2. Wing twisting.

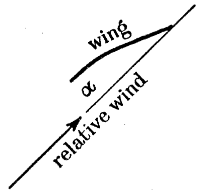


Figure I, 3. Angle of attack of a wing element.

Angle of attack

In no instance do we have an analysis of the simultaneous variation in space and time of the air velocity and of the twisting of a wing from which $\alpha = \alpha(v, r, t)$ can be calculated (figure I, 3). The fundamental kinematic basis for analysing the aerodynamics is therefore still lacking although some progress has been obtained with birds (Brown 1953).

Conclusion

There is general agreement on the qualitative principles, but some authors (Demoll, Oehmichen, Magnan, Osborne) have concluded that the observed movements do not permit an understanding of the flight performance in ordinary aerodynamic terms. Their statements have not been adequately challenged, and one must remember that simultaneous data of the most important parameters in natural flight have hitherto been lacking.

A detailed study of the kinematics of the desert locust was therefore performed during steady-state suspended flight in a wind tunnel, the wind speed being continuously adjusted to the preferred flying speed (parts II to IV).

(*b*) *Aerodynamics*

The aerodynamic problems peculiar to insect flight are best presented by a comparison with similar problems in the action of airscrews like propellers and helicopter rotors. The main characteristic of an airscrew is the production of aerodynamic transverse forces, the lift. Therefore, as a starting point, the essentials of circulation theory are outlined. A comparison of rotating airscrews with oscillating wings is complicated by four features. The dynamic law of flow similarity states that Reynolds's number Re should be the same in comparable experiments, $Re = ul/\nu$, where u = the velocity of the immersed object in relation to the fluid, l = a characteristic length, and ν = the kinematic viscosity. Practically all airfoil investigations have been performed at much higher values of Re ($0{\cdot}2\times10^5$ to 5×10^6) than are found in insects (10^2 to 3×10^3; Holst & Küchemann 1941). This does not necessarily mean that the aerodynamic problems differ greatly, but a rigid comparison with ordinary airfoil data may be misleading. Secondly, the velocity changes periodically at all wing elements beyond the wing base. Thirdly, the wings, in contrast to airscrew blades, not only alter their pitch periodically (like most helicopter rotors) but also their profile, due both to active twisting and to their flexibility. Finally, the rapid acceleration of the wing at its extreme position may be so great that the acceleration of the air adjacent to the wing can give rise to forces which do not play any role in ordinary aerodynamics with established circulation. These forces will be referred to as *aerodynamic inertial forces* in contrast to the forces due to acceleration of the wing mass and responsible for the inertial term in the energy account. The latter is of no direct aerodynamic importance, but it can sometimes be converted into aerodynamic work (part IX). For a thorough, general treatment of the airfoil theory and the propeller theories the reader is referred to the monographs by Prandtl (1935), Betz (1935) and by Glauert (1935) in Durand's handbook, vols. 3 and 4, respectively.

(i) *Lift and circulation*

Consider an airfoil which is either of infinite span or enclosed between plane rigid walls perpendicular to the leading edge and parallel to the wind velocity v. All wind velocities are then parallel to the walls and the flow is two-dimensional. The general circulation theory states that the lift per unit length of the wing span is

$$L = \rho v \Gamma \qquad \text{(I, 2)}$$

or

$$\Gamma = \tfrac{1}{2} C_L v c,$$

where ρ = the mass density of air, v = the uniform linear velocity, c = the chord of the profile, and Γ = the cirulation round the airfoil $\left(=\oint (v\cos\alpha)\,\mathrm{d}s\right)$. In the case of two-dimensional flow, no drag other than the profile drag D_∞ is experienced as long as the flow does not separate; the power P_a for moving the airfoil through the air becomes

$$P_a = \tfrac{1}{2}\rho v^3 S C_{D\infty}, \tag{I, 3}$$

where S = the wing area, $C_{D\infty}$ = the profile drag coefficient (drag at infinite span). Both in ordinary airfoils and in flat or slightly cambered profiles $C_{D\infty}$ varies but little with angles of attack between 0° and 10°. The work necessary for aerial transport of a given weight over a given distance has therefore no fixed lower value. As far as lift is concerned we cannot define an aerodynamic efficiency analogous to the efficiency of propellers because, in the ideal case, no work is performed, the lift being perpendicular to the direction of movement. The small amount of energy given to the air is soon dissipated as heat and no downwash occurs.

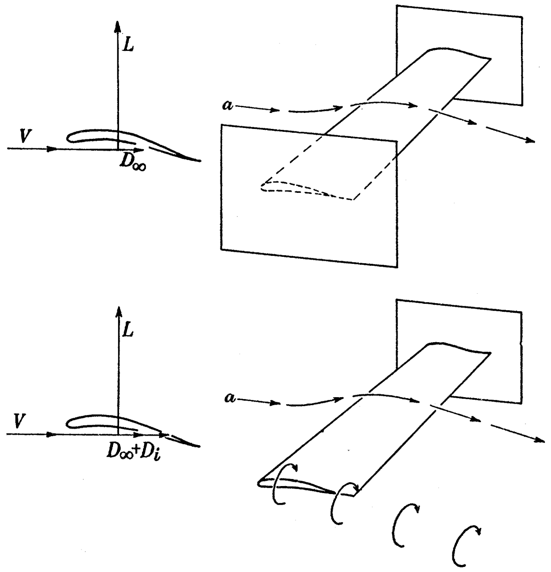


FIGURE I, 4. Tip vortex and induced drag.

However, when the span is finite (figure I, 4), as in all airplanes and natural wings, tip vortices are continuously formed which both reduce the lift and produce a downwash of the wake so that kinetic energy is imparted to the air. The result is a lift-dependent increase of the drag of the wing, the *induced drag* D_i, and a change of the wind velocity adjacent to the profile, the *induced wind*.

Thus the finite span as well as the finite wing area both set a lower limit to the flying speed necessary for the production of a given lift without separation of the flow (stalling) and imply an extra drag. If the ratio between span and wing width is A (= aspect ratio), an elliptical distribution of lift along the span results in the following expression for the final drag coefficient:

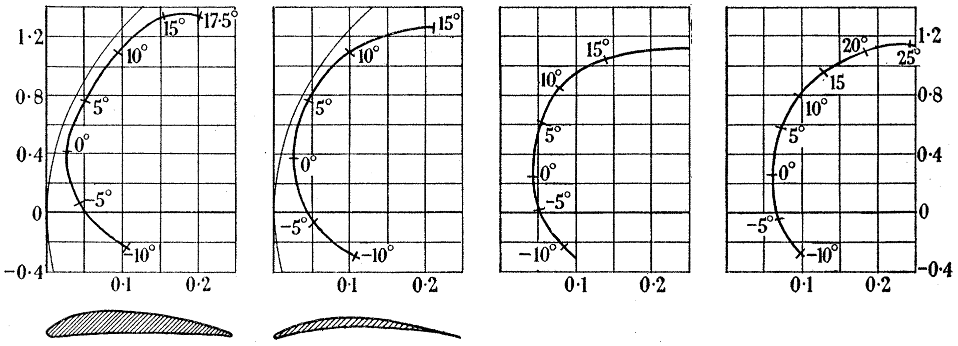
$$C_D = C_{D\infty} + \frac{C_L^2}{\pi A}, \tag{I, 4}$$

where the induced drag coefficient $C_{Di} = C_L^2/(\pi A)$.

The power becomes
$$P_a = \tfrac{1}{2}\rho v^3 S(C_{D\infty} + C_{Di}). \qquad \text{(I, 5)}$$

Thus C_{Di} increases with the second power of the lift. Although the elliptic distribution of lift is an approximation, the general nature of the expression is valid for most wing types.

The thick curves in figure I, 5 show the relationship between the lift (C_L, ordinate) and the drag (C_D, abscissa) of various airfoils as obtained by experiment. The angles of attack are indicated on these so-called 'polar curves'. Curves *a* and *b* derive from artificial airfoils of aspect ratio 5 placed in a uniform wind. Curves *c* and *d* are natural wings of locusts exposed to a wind the speed of which is graded from base to tip in nearly the same way as during flight (part III). The similarity between the curves is obvious, but the insect wings are less efficient than the 'good' profile *a*, the slightly cambered profile *b* being intermediate between *a* and *c*. The maximum lift is reached when α is about 15° (25° in the hindwing), i.e. just before the flow stalls. The optimum lift/drag ratio corresponds to values of α between 5° and 10°. Hence the importance of an accurate estimate of α. The thin curve in *a* and *b* is the 'parabola' of the induced drag (cf. second term in equation (I, 4)). The induced drag C_{Di} can be read as the horizontal intercept between the ordinate and the parabola, while the intercept between the latter and the thick curve is $C_{D\infty}$. At normal aspect ratios C_{Di} may be 3 to 4 times larger than $C_{D\infty}$.



Göttingen no. 406 *a* Göttingen no. 451 *b* locust forewing *c* locust hindwing *d*

FIGURE I, 5. Relationship between the lift coefficient (ordinate) and the drag coefficient (abscissa) in two artificial wings (aspect ratio 5) compared with locust wings (see Martin Jensen, part III). The parameters on the curves are the angle of attack.

The circulation Γ is the strength of a vortex line bound to the wing and parallel to the wind velocity. The polar diagrams refer to steady-state three-dimensional flow in which the circulation has been increased from zero to its uniform magnitude before the experiment. When the air is at rest Γ is of course zero; and when the flow begins no circulation exists until a starting vortex has been formed near the trailing edge on account of the viscosity of the air. During the initial phase the circulation about the wing at any instant is equal and opposite to the strength of the starting vortex. Once formed Γ and thus the lift is established, but alterations cannot occur unless a new trailing vortex is formed of opposite sense and of the same strength as the alterations in Γ. The bound vortex continues at the wing tips as a system of tip vortices. The tip vortices cause the downwash and are responsible for the induced drag. They are of the same strength as Γ, but ultimately they disappear due to viscosity. In an oscillating wing L and Γ change periodically and, therefore, new trailing vortices must be formed and the strength of the tip vortices must also change cyclically. One important problem of insect flight is whether the continuous cyclic variation of the relative wind is too rapid to allow building up a circulation corresponding to the strength it would attain provided the instantaneous velocity was maintained, in short, whether flapping flight can be considered consistent with the aerodynamics of steady-state flow.

(ii) *Airscrews*

Some elementary points in airscrew theory may throw light upon the action of flapping wings and therefore fall within the scope of this paper. The dynamics of propellers have been analyzed from three different points of view which have their parallel in the study of natural flight.

The change in momentum of the air passing the propeller disk is treated by the momentum theory. In its general form it accounts both for the axial and the rotational changes in velocity at the propeller disk and in the wake. The momentum theory does not explain how the changes are brought about. However, it can give information on the maximum obtainable thrust efficiency η_1 when the thrust T, the flying speed v, and the propeller radius R are known

$$\frac{2(1-\eta_1)}{\eta_3}=\frac{T}{S\rho v^2}=\frac{T}{2\pi R^2\rho v^2}.$$

The ideal efficiency is unity when the right-hand term is zero, i.e. when T is zero and the propeller is not loaded at all. η_1 decreases to 0·5 when the right-hand term has increased to 4. Thus η_1 depends upon the conditions of working and decreases with increasing loading. When v has become zero, as during hovering of a helicopter, the expression is of no value. The actual efficiency $\eta=\eta_1\eta_2\eta_3$, where η_2 and η_3 in properly designed propellers are less than but fairly near to unity. They allow for losses due to rotational movements in the slipstream and to frictional drag respectively. These expressions are based upon the assumptions that the distribution of thrust is uniform over the propeller disk. In the flight system of insects, at least of locusts (part III), conditions are very different partly because the circulation changes during the stroke and partly because it differs from base to tip. For these reasons it is not possible to assess the risk of applying the above efficiency concept. It can certainly not be rigorously applied as has been proposed by Hocking (1953). In model experiments v. Holst (1943*a*) in some cases found values of η of the same magnitude as in propellers (p. 452). It is also probable that the rotational velocities of the flight system are greater than in propellers. Moreover, Hocking's figure 5, which is reproduced on p. 428 as figure I, 6, shows that the wake spreads out conically in his experiments, making any direct comparisons with actual propeller equations highly dubious. Hocking (1953), for instance, argued that the efficiency was probably as high as in propellers *inter alia*, because Williams & Galambos (1950) concluded that there was a 'polarized' flow of air (i.e. there was an increase in momentum) during 85 % of the wing-stroke cycle of *Drosophila*. The design of the experiment would hardly permit such conclusions, however, because the flow pattern was estimated from measurements with a condenser microphone of very large dimensions compared with the insect and at an average distance ensuring that the dynamic wind pressure ($\frac{1}{2}\rho v^2$) upon the microphone would derive from several wing beats. What was actually measured was the *average* dynamic wind pressure in the wake and, superimposed upon it, the sound disturbances propagated with the velocity of sound.

It is of course justified to apply the general momentum conception to flying insects. According to this, the average change in momentum of the air which passes the animal per unit time ($=mu$, where m is the mass per unit time and u is the increase in velocity) must equal the average resulting lift and propulsion $(\bar{L}^2+\bar{T}^2)^{\frac{1}{2}}$ of the flight system. Magnan (1934) measured the pressure distribution in the neighbourhood of the wings and found that the average decrease in pressure over the insect could account for the observed average lifting force. This is nothing but a reflexion of the decrease in pressure due to the increased air velocity plus the possible rarefaction caused by aerodynamic inertial forces. The observation does not explain anything and can be considered trivial, in spite of the great technical skill involved. Hocking (1953) measured the distribution of velocities in the wake of *Tabanus affinis* and of *Apis mellifica* performing tethered flapping in still air. Similar experiments were briefly reported by Smith (1953). Hocking's figures are reproduced in figure I, 6. They clearly show that, under these experimental conditions, the velocities have both vertical and horizontal components, the latter being the largest in his experiments. Since Hocking draws extensive conclusions from his measurements of the aerodynamic power necessary for flying they will be treated in some detail. Our criticism has concentrated upon the following points. If a tethered insect is stimulated to flap its wings in still air it might happen that both the wing movements and the air flow did correspond to free hovering flight of which both species are capable. If so, there should be no propulsion and the resulting average force should be vertical. This was not the case.

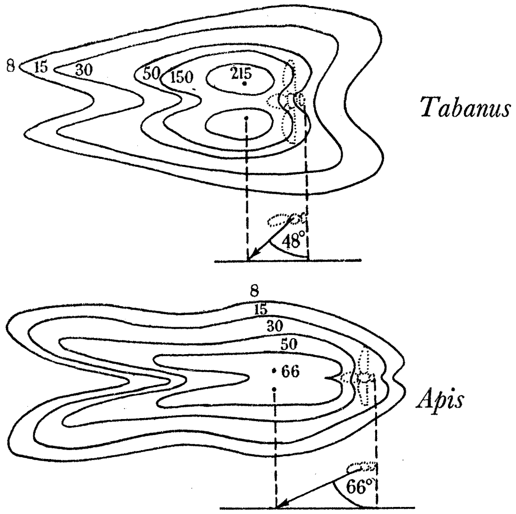


FIGURE I, 6. The distribution of wind speeds in the wake of two insects performing tethered flapping (the horse-fly *Tabanus affinis* and the honeybee *Apis mellifica*). Redrawn after Hocking (1953). The wind speeds are given in cm/s and the average inclination of the wind is indicated below each diagram.

Consequently, the insects were moving the wings in such a way that they would fly forwards if released; the flow would then be altered as they gained speed, but it is impossible to say just how. The flow situation must therefore be considered as artificial in the sense that it would certainly be completely different during free flight both as regards direction and speed. It must also be doubted whether the closeness of the table would not alter the wind field. The method did not allow an estimate of the rotational energy of the wake. From the resulting wind speeds was calculated the average kinetic energy produced per unit time. It is not clear exactly how this was done, but it should be summed for all three co-ordinates as $\frac{1}{2}\Sigma(m_n v_n^2)$ x, y, z, which is the total kinetic 'axial' power. Hocking only used the vertical components for calculating the 'power to remain airborne'. Moreover, he corrected for the flying speed. It is dubious how this correction can be made. In helicopters it is most complicated and presupposes a rigid theory (cf. Nikolsky 1945). The distinction drawn between 'power to remain airborne' and the total kinetic power ($=\frac{1}{2}mv^3$) therefore seems arbitrary and unjustified. The power for propulsion was estimated from the flying speeds and the drag of the body. Their sum was considered as the aerodynamic power necessary for flight. Thus the 'power to remain airborne' per unit weight was found to be constant and of the order of magnitude of 2 kcal kg^{-1} h^{-1} (*Tabanus* and *Apis*). We also disagree with Hocking's use and definition of the 'wing action constant' for calculating the power necessary for other insects, since it is based upon a somewhat mysterious concept related to the 'stroke volume' (Chadwick 1953). The power to overcome the drag of the body was much larger. These figures and conclusions differ considerably from our findings with locusts. To sum up our criticism: the insects worked under unknown conditions; the 'power to remain airborne' constituted a small and undefinable fraction of the total 'axial' kinetic power both under the experimental conditions and especially during forward flight; other losses due to friction and rotation were neglected; the 'wing-action constant' is of dubious nature. The 'overall efficiency' of flight defined as the ratio between the theoretically necessary aerodynamic power to the metabolic rate cannot, therefore, contribute to our understanding of the energetics of insect flight.

Although the flight system in many respects resembles an airscrew system homologous momentum considerations should be treated with caution. The experiments hitherto performed to determine the aerodynamic power in flight (Hocking 1953) are still too incomplete and have given values too low; the mechanical efficiency of the wing muscles has therefore been underestimated.

The simple blade element theory attempts to determine the thrust and torque of an element of a propeller at the distance r from the hub by means of the flying speed v, the speed of rotation ωr, the blade angle θ, and the polar diagram of the profile in question. The integration (often graphical) over the radius should then give the total thrust and torque of the blade. Although the elements can be treated as nearly independent the theory is, however, unsatisfactory; it turns out to be in contradiction to the momentum theory in that an optimum disk diameter could be deduced at which the efficiency was highest, the momentum theory implying increasing efficiency with increasing diameter. Furthermore, the effect of the aspect ratio cannot be ruled out. The discrepancies are due to neglect of the axial and rotational induced velocities which alter the geometrically estimated velocities and the angle of attack ($V_r^2 = v^2 + \Omega^2 r^2$; $\alpha = \theta - \phi r$, where $\tan \phi r = v/(\Omega r)$) by unknown quantities. When designing propellers, the theory can of course give an approximate solution, especially at low loadings and flying speeds. During hovering when $v=0$ (helicopter rotor; insects) the induced velocities are more important (see p. 449). Even if the mechanical principles upon which Magnan & Sainte-Laguë (1933) based their theoretical analysis of hovering flight of insects were valid, these authors would possibly still have found force coefficients that were too high because they neglected the induced velocities. Walker's theory (1925, 1927) is analogous to the simple blade element theory; it is discussed in detail on p. 444.

The vortex theory was developed by combining the two foregoing theories with the circulation theory, operating with the vorticity of the wake which is considered as composed of annular elements of uniform vorticity. Thereby, the thrust and torque can be calculated from the aforementioned quantities and C_L and C_D of the airfoil exposed to two-dimensional flow. The efficiency is determined for each annular element of the disk and presupposes assumptions on the distribution of thrust. The success of the theory shows that it is justifiable to consider the flow over the elements of a uniformly rotating propeller as steady. Osborne (1951) has made a theoretical analysis of insect flight along somewhat similar lines, the induced velocities being calculated according to Glauert's helicopter theory for forward motion (cf. Glauert 1935). But he could not confirm the application of steady-state principles to the flapping flight of insects and postulated the existence of aerodynamic inertial forces, in conformity with Oehmichen (1920). The latter author made experiments with accelerating plates in water, but his conclusions are invalidated because of the formation of gravitational waves and the proximity of rigid walls. The same seems to have been the case in Moineau's experiments (1939). Osborne's theory is discussed in detail on p. 448.

(iii) *Conclusion*

Bearing in mind the data necessary for an understanding of natural flight, our present knowledge is extremely scanty. It is obvious from the lack of kinematic data that a theoretical analysis analogous to the vortex theory of propellers cannot yet be undertaken. Moreover, the flexibility of many natural wings would prevent the use of two-dimensional polar diagrams.

(iv) *Experimental approach*

A theoretical treatment being highly speculative, the most promising procedure appears to be a compromise which refrains from an analysis of the aerodynamics of the wing elements and confines itself to a study of the force system of the whole wing exposed to graduated velocity fields similar to the velocity field existing during the different phases of the stroke. If the aerodynamics is consistent with steady-state flow, the induced velocities are then automatically established. The integration of the forces over the stroke period should give the average lift and thrust acting upon the body which can be measured directly as a control. Moreover, the variation with time of the torque as well as the aerodynamic work could be estimated. Such an analysis has been performed in the case of locusts (part III).

(*c*) *Torque, work and power*

Consider a wing of length R which oscillates about the fulcrum f through the arc ϕ (=stroke arc) in the stroke plane. If the wing mass is M, or per unit of R is $m(x)$ and the radius of gyration is r (figure I, 7), the mass moment of inertia becomes

$$I=\int_0^R m(x)x^2\,\mathrm{d}x=Mr^2.$$

Suppose that we know the change of the positional angle γ with time, i.e. $\gamma=\gamma(t)$ as seen in the figure.

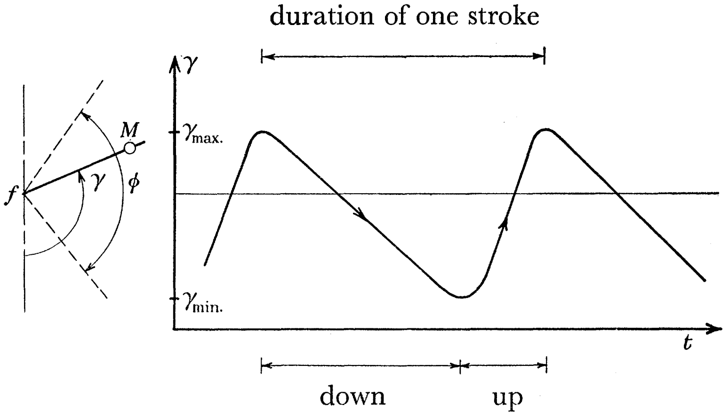


Figure I, 7. Angular movements of an oscillating wing.

At any instant the sum of the torque contributions about the fulcrum must be zero according to

$$Q_m+(Q_a+Q_i+Q_e+Q_d)=0, \tag{I, 6}$$

where Q_m is the torque produced by the flight muscles, Q_a is the aerodynamic torque, Q_i is the inertial torque, Q_e is the elastic torque, and Q_d is the damping torque. If the term in brackets is $-Q$, the muscular torque can be determined by

$$Q_m=Q.$$

The extra-muscular work $\mathrm{d}W$ done during an arbitrary instant of time can therefore be estimated from $\mathrm{d}W=Q_m\,\mathrm{d}\gamma$. Obviously, it is necessary to know both the variation of Q and of γ with time in order to find W, i.e. $Q=Q(t)$ and $\gamma=\gamma(t)$. In locusts we found that all components except Q_d were significant so that none of them could be neglected (part IX), and it is reasonable to assume that this applies to many other insects. If, from a simple set of kinematic data, we wish to calculate W we must assume simple functions of Q_a, Q_i, Q_e and γ with time. From a biological point of view the problem is still more complicated, because phases of negative extra-muscular work must be distinguished from phases of positive work. The only *a priori* approximation which might be possible concerns the inertial torque and γ.

The aerodynamic torque, whether it involves aerodynamic inertial forces or not, has not been studied quantitatively although some qualitative principles are understood. It must be studied by observation; even the best theory is inadequate because the variations *during* the cycle must be known and not only the average resulting forces.

The inertial torque can be expressed as

$$Q_i = I\frac{\mathrm{d}^2\gamma}{\mathrm{d}t^2}, \tag{I, 7a}$$

and

$$W_i = I\int_{t_1}^{t_2} \frac{\mathrm{d}^2\gamma}{\mathrm{d}t^2}\frac{\mathrm{d}\gamma}{\mathrm{d}t}\,\mathrm{d}t. \tag{I, 7b}$$

It is possible to calculate the torque at any moment and W_i provided I and $\gamma = \gamma(t)$ are known. Sotavalta (1947, 1952) has already stressed the importance of the wing inertia. His figures were based upon the stroke frequencies and the moments of inertia found in loading and mutilation experiments with a large number of insects. Sotavalta (1952) and Chadwick (1951) both assumed a simple sinusoidal oscillation where the inertial work done during one-quarter of a stroke (from $t=0$ to $t=1/4n$) per wing can easily be calculated as

$$W_i = \tfrac{1}{2}I\pi^2\phi^2n^2. \tag{I, 8}$$

Sotavalta postulated that the positive contributions (positive angular acceleration) must be wasted, whereas the negative terms (negative accelerations or braking) did not involve any cost. The total inertial power necessary to oscillate the mass of a single wing would then be

$$P_i = I\pi^2\phi^2n^3. \tag{I, 9}$$

When P_i was calculated in this way and compared with the total metabolic rate P, it appeared that some insects, for instance, the honeybee, used practically all the available mechanical power for oscillation work, leaving only a small fraction for aerodynamic work.

Sotavalta checked the general result indirectly by altering I and observing the corresponding change of n. Since the found relationship corresponded reasonably well to the above assumption $\mathrm{I} \propto n^{-3}$, provided P_i and ϕ were assumed constant, the inertial work was considered as the dominating type of work in many Hymenoptera and Diptera. There are, however, some debatable points in this argument. First, the movement need not be a simple sine oscillation; in nearly all insects the downstroke lasts longer than the upstroke (Magnan 1934), increasing the values of P_i by a factor $F = \frac{1}{8}\left(\frac{1}{a^2} + \frac{1}{(1-a)^2}\right)$, where a is the duration of the upstroke in relation to the total stroke period (see part II). Secondly, if γ varies with time in a different way, P should be calculated from the observed maximum angular velocity

$$\omega_{\text{max.}} = \left(\frac{\mathrm{d}\gamma}{\mathrm{d}t}\right)_{\text{max.}}$$

as

$$P_i = 2\frac{n}{2}\,\omega^2_{\text{max.}}. \tag{I, 10}$$

Small deviations from a sine function thus severely influence the result. Thirdly, the most important objection to Sotavalta's conclusions on the energetics (*not* on the regulation of the stroke frequency) is that in locusts an elastic torque has been observed which, to some extent, counterbalances the inertial torque.

The elastic torque has never been subjected to a quantitative analysis, but some suggestions and important observations should be mentioned. Chabrier (1822) concluded that the elastic deformations of the air sacs caused by the wing movements played a mechanical role in flight. These changes in pressure are insignificant in locusts (Weis-Fogh 1953, and unpublished). In the male cicada Pringle (1954) recently found that the tympanum is clicked in by the pull of a muscle while the natural elasticity of the structure serves to click it back to its original position. The integrity of the elastic cuticle was found to be indispensable for the establishment of the myogenic rhythm of this muscle. Similarly, Boettiger & Furshpan (1950, 1952) found that the pterothorax of CCl_4-anaesthetized flies exhibits elastic resistance against passive movements of the wings (the so-called click mechanism), whereas this was not the case with dead or non-flying insects. They interpreted their results as a consequence of elastic deformations which were modified by the action of some special muscles. The elastic torque would then depend both on the cuticular architecture and on the active contraction of the pleuro-sternal muscles. A quantitative analysis therefore seems to be extremely difficult in flies. But in locusts muscular contractions outside the wing muscles proper could not exert any profound influence on Q_e, as will be shown in part VI. In these insects the elastic torque could be analyzed under static or semi-dynamic conditions (parts VI and VII).

Extra-muscular thoracic damping. The extra-muscular energy losses caused by damping have never been studied. They may be of three types. In the first air or haemolymph is subjected to pressure and squeezed through narrow passages. The abundance of air sacs open to the exterior (part VII) and the small pressure changes measured during flight (Weis-Fogh 1953, and unpublished) makes air damping and blood transport of little quantitative significance. The second type consists in losses due to sliding friction between adjacent flight muscles. The interspaces are to a great extent filled with thin-walled air sacs. This, together with the relatively small degree of deformation, the speed of contraction (Buchthal, Weis-Fogh & Rosenfalck, unpublished) and the lubrication by means of blood, tends to minimize these frictional losses. The third type of loss derives from internal friction of the cuticle undergoing deformations and from the wing hinges. The relatively small internal damping of the cuticle (part V) and the small size of the wing hinge compared with the mechanical power passing it (part VII) indicate also that internal friction plays but an insignificant role. The extra-muscular damping has therefore not been subjected to further studies.

Conclusion. To understand the energetics of flight a knowledge of the variations during a complete wing-beat cycle of the following torques about the fulcrum will be essential: the aerodynamic torque, the inertial torque, the elastic torque, and the torque due to extra-muscular damping. The last seems to be negligible in insects. The intra-muscular damping is part of the contractile mechanism and has been left out of the problem by choosing to solve the equilibrium equation (I, 6) with respect to the muscular torque Q_m necessary to produce the observed forces and movements.

The summation of the different torque contributions is complicated by the fact that phases of positive muscular work must be distinguished from those of negative muscular work. None of the contributions seems to have been determined in any animal, although many estimates have been put forward.

(*d*) *Total power output and 'efficiency'*

Power

The metabolic rate of insects performing wing movements under many different external conditions has been extensively studied by physiologists (for references see Krogh & Weis-Fogh 1951; Chadwick 1953; Hocking 1953). All authors agree in finding a very high total power output as estimated from the oxygen consumption (10 to 100 l. O_2 taken up per kg body weight per hour) or from the disappearance of carbohydrates and fats (Williams, Barness & Sawyer 1943; Wigglesworth 1949; Weis-Fogh 1952*a*; Hocking 1953). Only three studies derived from animals which flew 'freely' in a container (Kalmus 1929, with *Deilephila elpenor*; Zebe 1953, 1954 with various butterflies and moths; Pearson 1950, with hovering humming birds). Weis-Fogh (1952*a*), Hocking (1953) and Sotavalta (1954) suspended the insects to a roundabout and could relate the metabolic rate to the flying speed obtained under these special conditions. This, of course, could provide a basis for estimating a reasonable average power output, but it did not give reliable information on the relationship between flight performance and energy requirements, as is discussed in part VIII. The remaining results were derived mainly from situations of tethered flapping and cannot provide such information. An *experimental investigation* was therefore undertaken on the power output during various known flight performances in the wind tunnel (part VIII).

Efficiency

The term 'efficiency of flight' has been extensively used, often with little consistency. In physiology the term *muscular efficiency* means the ratio between the external mechanical work of groups of muscles to their total energy consumption. As applied to flying insects, the muscular efficiency of the flight muscles is the ratio *total extra-muscular work/total energy consumption*. The previous section showed how complex the work outside the muscle is and, since it has never been estimated, we are ignorant of the order of magnitude of the mechanical efficiency of flight muscles, i.e. of the efficiency of muscles which convert energy at higher rates than any other known biological system (cf. Weis-Fogh 1952*a*). We therefore attempted to correlate the mechanical power with the total power output of locusts (part IX).

In some cases, the 'efficiency' of flight means the ratio aerodynamic power/total power output (Smith 1953; Hocking 1953). This might express the fitness of the aerodynamic machine as such and could be used as an empirical figure of comparison between various machines of the same general plan. It implies, however, a determination of the total aerodynamic power output of the given insect in the given situation. If only the 'useful' power is determined (Hocking 1953) the term has been deprived of meaning because most of the aerodynamic power is 'useless' (except for that due to profile drag), the ideal machine using no power for sustainment. In aeronautics the power used per km per kg transported weight during ordinary cruising conditions provides a figure of comparison between different aeroplanes. Similar figures have been calculated for insects (Weis-Fogh 1952*b*) and were shown to vary only from 1 kcal kg^{-1} km^{-1} in the biggest airplanes to 7 kcal kg^{-1} km^{-1} in the smallest insects; jet fighters, helicopters and locusts give nearly identical values of 5, 4 and 5 kcal $\mathrm{kg}^{-1}\,\mathrm{km}^{-1}$ respectively. The flight of the honeybee was more expensive. Such comparisons are of no theoretical significance. A non-dimensional figure of merit analogous to that used in helicopter theory (see Glauert 1935; Nikolsky 1945) might prove useful when adapted to the special flight system of insects. Holst & Küchemann (1941) calculated the efficiency of propulsion, but this only refers to a small part of the power for flying (see p. 442).

In some cases the 'efficiency' has been determined as the ratio between the *extra-to-flying* work which suspended insects could produce and the total energy consumption (Chadwick 1953, on the basis of figures from Magnan & Planiol (1933), and unpublished data by Williams). Such a procedure would only be justified if the ratio between *small* and known increases in external work could be related to the corresponding small *changes* in total power output, the insects otherwise flying under natural conditions. This was not the case.

From time to time it has been argued that the aerodynamic 'efficiency of flight' may be higher than can be understood from ordinary aerodynamics (Oehmichen 1920; Magnan 1934; Brown 1951) *because* of the relatively low mechanical power of mammalian muscles (*ca.* 0·01 h.p. per lb. of muscle). The argument is invalidated after it has been demonstrated that insect flight muscles convert energy 20 times faster than the muscles of man (cf. Weis-Fogh 1952*a*; Hocking 1953), and that the same rates are found in humming birds (from Pearson's figures 1950). Hill (1950) and Buchthal, Kaiser & Rosenfalck (1951) have discussed the dependence of mechanical power upon the bodily dimensions from a theoretical point of view. Their deductions are consistent with the experimental results cited.

Conclusion

The literature does not provide the necessary data for calculating the energy changes in insect flight so that neither the individual contributions nor their sum can be estimated. The mechanical efficiency of the high-powered flight muscles is therefore unknown. The term 'efficiency of flight' needs to be defined on a much more rigorous basis than has hitherto been the case or to be abandoned altogether.

5. Review of models and theories

The validity of theoretical conclusions and of model experiments ultimately depends upon the simplifying assumptions which characterize the conceptual systems. We have mainly attempted to discuss the basic presuppositions of some theoretical studies in relation to the results which have been or could be deduced from them. The following classification is designed only to help perspicuity, and some rather misleading theories are included because until recently they have been used to interpret experimental data.

(*a*) *Highly simplified systems*

Some theories more or less disregard the most essential element, namely, the flapping velocity itself. Demoll (1918, 1919) calculated the average lift coefficient of various insect wings from the flying speed, the body weight and the wing area. He found (1919) that most good flyers had C_L values between 1 and 2, or about 10 to 20 times higher than his figures for birds calculated in a similar way. He therefore concluded that insect flight ('Hubflug') differed in principle from avian or artificial flight ('Drachenflug'). Hoff (1919) argued that the C_L values were not so high compared with artificial airfoils that he could support Demoll's ideas. Since none of them took the flapping velocity into account, the true C_L remains unknown and can hardly have failed to be lower than estimated.

As to the flight of birds, Fullerton (1925) calculated the aerodynamic power necessary, but his procedure for calculating velocities and forces was too rough and has been criticized by Gnosspelius (1925) and Walker (1925). Gnosspelius tried, as a first approximation, to calculate the necessary aerodynamic power of flying birds on the assumption that birds could be compared with airplanes with the same weight, flying speed and span. At a speed of 70 ft./s (=77 km/h), the necessary power was nearly the same for small birds (swift and pigeon) and large (stork and swan), namely, about 100 lb./h.p., or, in the units adopted here, about 14 kcal kg^{-1} h^{-1}.

(*b*) *Dimensional considerations*

It is of course possible to use highly simplified systems for dimensional considerations. In the papers cited below the insects were considered as similarly shaped and similar with respect to the stroke angles. The relationship between stroke frequency n and a linear dimension l could then be deduced from the theories. The type of approach is indicated in brackets:

$n \propto l^{-\frac{1}{2}}$ (Lippisch 1940, wind forces),
$n \propto l^{-\frac{1}{2}}$ (Attila 1947, wind forces),
$n \propto l^{-\frac{2}{3}}$ (Sotavalta 1952, wing inertia),
$n \propto l^{-1}$ (Reed, Williams & Chadwick 1942, wind forces),
$n \propto l^{-1}$ (Rashevsky 1944, wind forces and wing inertia).

It appears that opinion differs as to the power of l. This is understandable when we consider the very crude methods of estimation, which do not allow of any greater accuracy than is shown by the range of powers. As a whole, dimensional considerations have provided some general information on the types of relationship to be expected between a few conspicuous wing-beat parameters (linear dimensions, frequency, stroke angle) and therefore on the regulation of the oscillation (see §6). However, this type of approach cannot provide any deeper understanding, especially as far as the complex energetics is concerned.

(*c*) *Systems with major limitations*

A few theories essentially deal with flapping flight, but one or more significant factors are lacking.

Magnan & Sainte-Laguë (1933) analyzed *hovering* flight of insects and humming birds. The wing was considered as a rigid plate whose plane was normal to the *vertical* stroke plane. The resulting instantaneous wind force was calculated according to the assumption that $\frac{1}{2}\rho C_D = \frac{1}{15}$, i.e. that C_D was nearly unity (namely $\frac{16}{15}$). The authors assumed that the wings acted as paddles during the downstroke ($C_L = 0$; $C_D^d = 1{\cdot}07$), but that they did no aerodynamic work during the upstroke ($C_D^u = 0$). Assuming a sine oscillation, they could now integrate the energy per stroke which was required to keep the insect airborne. This procedure automatically results in much higher power outputs per unit weight than are necessary in systems taking advantage of the aerodynamic transverse force (=lift) realized by the periodical twistings of the wing plane. The improbability of the theory also becomes obvious when we calculate the 'useful' aerodynamic power necessary for a small insect of 0·1 g, with wing length 1 cm, a frequency of 100/s, and a stroke angle of 120°. It would amount to 85 kcal $\mathrm{kg^{-1}\,h^{-1}}$. And the 'total' aerodynamic power should be much larger according to the formulas. In fact, the overall power output estimated as the metabolic rate seldom exceeds 100 kcal $\mathrm{kg^{-1}\,h^{-1}}$ (cf. table I, 10), only a fraction of which is available for external work.

Attila (1947) has generalized Magnan & Sainte-Laguë's theory by introducing arbitrary functions for the oscillation, $\phi=\phi_0 f(\omega t)$, and for the drag coefficient, $C_D=C_D(\omega t)$. Apart from the unrealistic physical simplifications already mentioned as well as some generalizations of dubious validity, Attila equated the calculated expression for the aerodynamic work done per downstroke A_1 with the sum $A_2=mg^2/4n^2$, i.e. equal to the loss in potential energy + the increased kinetic energy due to free falling during the passive upstroke. (m is the mass of the insect.) The rhythmical changes in altitude of a hovering insect of course represent work, but this is only a small amount compared with the aerodynamic work necessary for creating lift by means of wings of small span. Moreover, as in humming birds (Stolpe & Zimmer 1939), Chadwick (1953) has stressed that the wings of hovering insects move to and fro in a nearly horizontal plane, and that the wings are twisted so as to ensure lifting forces during both halves of the stroke. Attila's theory is therefore not supported by fact and must not be used for estimating the aerodynamic work, as has been done by Sotavalta (1952).

The many studies by Chadwick, Williams and co-workers have been interpreted according to a 'stroke-volume' theory (see Chadwick 1953). Since the basic purpose of the theory was to explain the mutual variations in metabolic rate, frequency, stroke angle, air density, etc., rather than to provide a physical understanding of the flying as such, it will be discussed in relation to the regulation of flight (§6). Magnan's (1934) 'rarefaction' hypothesis has already been mentioned (p. 428) as well as the theoretical basis for Hocking's (1953) calculations (p. 429).

Boel (1929) developed a qualitative theory for the flight of birds, emphasizing the circumduction of the wing tip as the means by which the angle of attack is altered. Since he did not take the twisting into account and otherwise considered the avian wing as a very simple structure (cf. Brown 1951), the theory has but little interest. The same applies to the quantitative theory of Lippisch (1940).

(*d*) *The most complete systems*

Three different theories (Holst & Küchemann 1941 (in German), 1942 (in English); Walker 1925, 1927; Osborne 1951) contain essential elements for a quantitative understanding of flapping flight. The first presupposes a rather low flapping ratio (equation I, 11) and only Osborne's theory was applied to insects. Nevertheless, the three treatises will be reviewed in some detail, each having its special advantages and limitations. The original notations and in some cases the structure of the formulae have been homogenized

Table I, 1. Dimensions and flight data of the insect types in figure I, 8

The figures marked (*) are actual quantities measured in the species listed below the table. The flight data derive from observations on prolonged steady-state performances.

	(1) 'locust type'	(2) 'horse-fly type'	(3) 'mosquito type'
*weight (g)	2·00	0·18	0·0035
*length of one wing (cm)	6·00	1·43	0·38
*area of one wing (cm^2)	13·3	0·574	0·036
maximum wing width (cm)	2·5	0·52	0·121
*extra-to-wing drag at flying speed (g)	85×10^{-3}	10^{-2}	$1{\cdot}6\times10^{-4}$
*flying speed, v (cm/s)	350	250	100
*frequency, n (c/s)	20	120	320
*stroke angle, ϕ (rad)	1·75	2·00	2·00
adopted aspect ratio, A	4 to 6	4 to 6	4 to 5
flapping ratio at $\frac{2}{3}$ point, k	0·8	1·8	3·2
*total metabolic rate during flight, P (kcal kg^{-1} h^{-1})	75	100	100

(1) 'Locust type', data from *Schistocerca gregaria* (present study), adapted to a functionally two-winged type.
(2) 'Horse-fly type', data from *Tabanus affinis* (Hocking 1953).
(3) 'Mosquito type', data from *Aëdes nearcticus* (Hocking 1953).

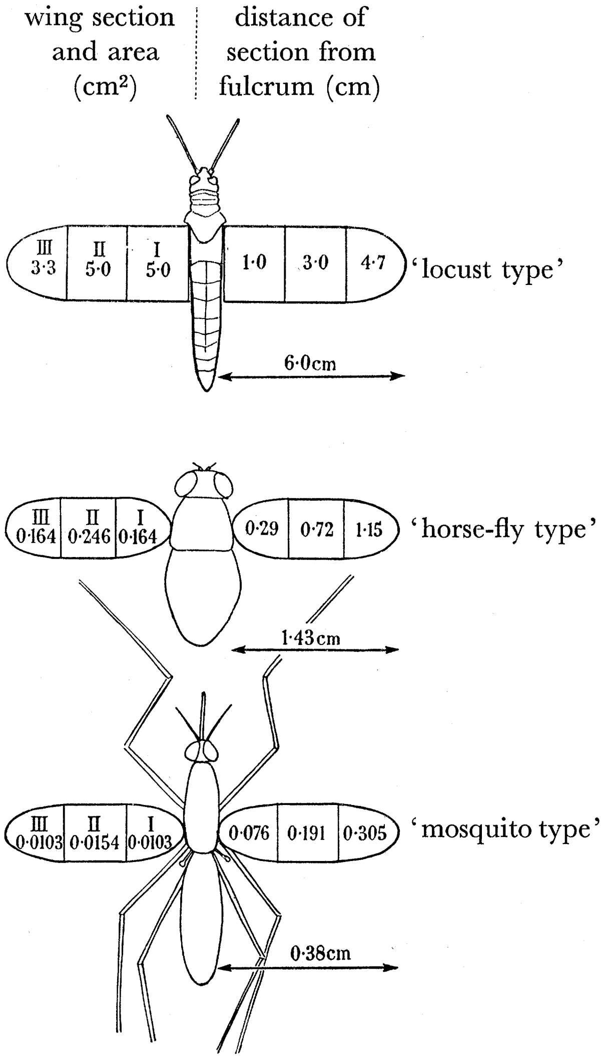


Figure I, 8. Geometry and dimensions of the three insect types described in the text and in table I, 1. Wing sections I to III are explained on p. 445 (Walker's theory).

to fit the present account; but deductions and applications which differ in principle from those of the authors have always been mentioned. They were all based upon the principles of steady-state aerodynamics. Otherwise, by mere inspection they look rather different as to the type of approach. However, the fundamental formulae could be solved with respect to the average coefficients of lift and drag, C_L and C_D, or, alternatively, with respect to the average angle of attack α.

In order to compare the three theories when applied to insects and to estimate their limitations, the same flight data from the three insect types in table I, 1 and figure I, 8 were inserted in the expressions. The 'locust type' differed most from its ideal *Schistocerca gregaria*, because a functionally two-winged insect had to be used in the theories; the total wing area was 26·6 cm^2 against 29·9 cm^2 in a standard locust (Weis-Fogh 1952*a*). The other two insect types were very close to *Tabanus affinis* and to *Aëdes nearcticus* respectively. All functional data are derived from prolonged flight experiments (Hocking 1953, and the present study). The total metabolic rates during prolonged average performances were of the same order of magnitude in spite of the 'locust' being 110 times heavier than the 'horsefly' and 570 times heavier than the 'mosquito'. The outline of the wing was adjusted to straight lines or parabolic sections, but the length and surface area was the same as in the insect; the distribution of area was also close to that of the natural wing.

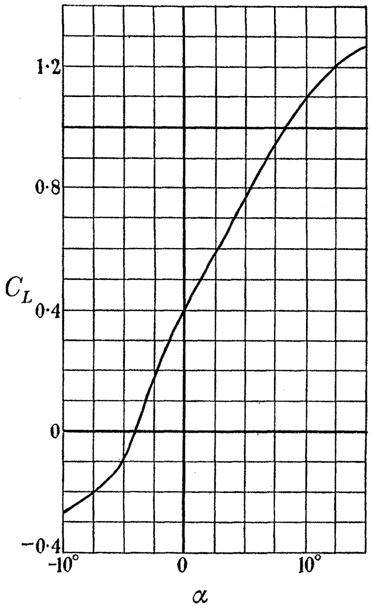


FIGURE I, 9. Relationship between lift coefficient (ordinate) and angle of attack (abscissa) in the artificial, slightly cambered airfoil Göttingen 451 (aspect ratio 5).

The flapping ratio k, i.e. the ratio of the flapping speed of a wing element to its forward speed, is of great significance:

$$k = \frac{2n\phi}{v} r, \qquad \text{(I, 11)}$$

where r is the distance of the element from the fulcrum. In Walker's theory, the wing was divided into three parts of equal length as seen in figure I, 8, where r is shown for each segment. k is only an approximation since the actual difference in duration of upbeat and downbeat is disregarded, the stroke-plane angle is considered as constant at 0° (wings move merely up and down), and the angular velocity is also constant. However, the flapping ratio is suited for comparisons and is given in table I, 1 for a section situated two-thirds of the wing length from the fulcrum. In many birds k thus calculated amounts to about 0·3 (Walker 1925). The aspect ratio A is difficult to evaluate but must be near to 4 or 6. The lower value was used here because the velocity gradient along the flapping wing is likely to increase the induced drag somewhat compared with a wing of similar dimensions but exposed to a uniform wind. The selected airfoil was Göttingen no. 451 (see also Durand 1935, vol. 4, p. 42, fig. 44), the characteristics of which for $A=5\simeq 4$ are given in figure I, 9 and in figure I, 5. It has a thin, slightly cambered profile comparable to an insect wing although aerodynamically better than the locust wings (figure I, 5), provided α is less than 12°.

(i) *Holst & Küchemann's theory* (1941)

These authors first discussed the influence which small values of Reynolds's number *Re* might have upon the establishment of circulation about the wings of insects. In birds *Re* often exceeds 3×10^5, so that the same type of flow is realized as in the case of ordinary airfoils. In insects where *Re* can drop to a few hundreds it might be difficult to have a circulation established so that C_L might be lower than expected by comparisons with ordinary airfoils. However, our knowledge on this point is at present too scanty. The authors also discussed the *reduced* or *dimensionless* frequency

$$\nu = nl/v,$$

where n is the frequency, l the wing length, and v the flying speed; ν was originally introduced by Küssner (1936; Küssner & Schwarz 1940) for characterizing the ratio between forward velocity and vibrating velocity of airplane wings where the stroke angle ϕ is always small. When, under such conditions, ν did not exceed 0·2, there should be no quantitative reason for taking non-stationary flow situations into account. Similar non-dimensional figures are used when considering the influence of wind upon the oscillation of suspension bridges and other rigid structures; the idea is to express the ratio between the non-stationary streaming (oscillation) and the stationary streaming (wind speed, forward speed, etc.). In the case of insects the speed of the wing tip of course depends both upon n, l and ϕ, so that it seems more reasonable to use the length of the stroke arc than that of the wing, i.e. to use k. The problem is further discussed in part III where a new point of view is also suggested. In any case ν calculated as nl/v does not permit direct comparisons between Holst & Küchemann's figures for birds (about 0·1) and Küssner's for airplane structures. However, ν is of no decisive importance in the mathematical treatment of Holst & Küchemann's theory and could be eliminated from all calculations by substituting

$$\nu\xi\left(=\frac{nlx}{lv}\right) \quad \text{by} \quad \frac{nx}{v},$$

as has been done in the following account.

Figure I, 10 shows the essential kinematic assumptions: the *entire* wing of double span $2l$, area S, and aspect ratio $A=2l/c$ experiences a forward uniform movement of velocity v

along the x-axis and superimposed upon it a vertical sine oscillation of amplitude a. The entire wing is turned in such a way that there is a resulting mean angle of attack α_0 about which the instantaneous angle $\alpha(x)$ oscillates according to another sine function the amplitude of which is α_a. The fundamental equations become

$$Z(x) = a \cos \frac{2\pi n x}{v}, \tag{I, 12}$$

$$\alpha(x) = \alpha_0 + \alpha_a \cos\left(\frac{2\pi n x}{v} - \Phi\right), \tag{I, 13}$$

where Φ is the phase difference between (I, 12) and (I, 13).

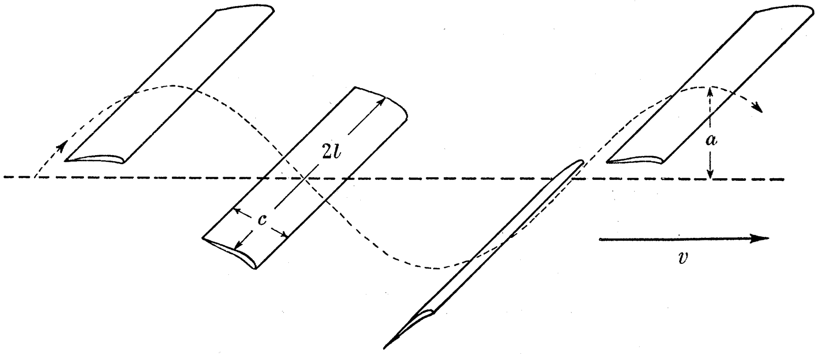


FIGURE I, 10. Kinematic assumptions in Holst & Küchemann's theory.

Apart from these assumptions (i.e. uniform oscillation of whole wing instead of flapping about the fulcrum, sine functions for $z = z(t)$ and $\alpha = \alpha(t)$), the authors assume that the wing resembles an ordinary airplane wing with approximately elliptical lift distribution where, according to Prandtl, for small values of α (cf. figure I, 9)

$$C_L(x) = \frac{\mathrm{d}C_L}{\mathrm{d}\alpha}\alpha(x) \tag{I, 14}$$

and

$$C_L(x) = \frac{2\pi}{1+\dfrac{2}{A}}\alpha(x). \tag{I, 15}$$

Furthermore, ν should be small, i.e. the forward speed should be large compared with the product nl (k should be small) so that the vertical force coefficient C_z and the horizontal coefficient C_x could be calculated from the simplified expression for $\sin\gamma(x)$, where $\gamma(x)$ is the inclination to the horizontal of the tangent of the curve $z(x)$. Thus

$$\gamma(x) = -\frac{\mathrm{d}z}{\mathrm{d}x} = \frac{2\pi n a}{v}\sin\frac{2\pi n x}{v}. \tag{I, 16}$$

When v is large compared with $2\pi n a$, $\sin\gamma \simeq \gamma$ and is small. Thus

$$C_z(x) = C_L(x) + C_D(x)\gamma(x) \simeq C_L(x), \tag{I, 17}$$

$$C_x(x) = -C_L(x)\gamma(x) + C_D(x). \tag{I, 18}$$

The average force coefficients in the upward and forward directions were found by integrating (I, 17) and (I, 18) from $x = 0$ to $x = v/n$, i.e. during a complete stroke. Multiplication by $\frac{1}{2}\rho v^2 S$ gives the average vertical force, i.e. the lift L, and the average horizontal force, the thrust T. $\mathrm{d}C_L/\mathrm{d}\alpha$ was considered as constant (cf. eq. (I, 15)). Thus

$$L=(\tfrac{1}{2}\rho v^2 S)\frac{\mathrm{d}C_L}{\mathrm{d}\alpha}\alpha_0, \tag{I, 19}$$

$$T=(\tfrac{1}{2}\rho v^2 S)\left\{\pi\frac{\mathrm{d}C_L}{\mathrm{d}\alpha}\sin\Phi\frac{na}{v}\alpha_a-\left[\frac{\left(\frac{\mathrm{d}C_L}{\mathrm{d}\alpha}\alpha_0\right)^2}{\pi A}+C_{D\infty}\right]-\frac{\left(\frac{\mathrm{d}C_L}{\mathrm{d}\alpha}\alpha_a\right)^2}{2\pi\alpha}\right\}. \tag{I, 20}$$

Results. Equation (I, 19) is the simpler of the two but also the least satisfactory. According to it the *lift* depends on the flying speed v, the aspect ratio A (see equation (I, 15)) and the average angle of attack α_0, whereas neither the amplitude (=half-stroke angle), the frequency or α_a should have any influence. In other words, the oscillation as such was disregarded because of the low ν or k. Partly because of this limitation and partly because the induced wind is neglected, the theory cannot explain the production of lift at low or zero flying speed. In actual flapping flight the lift will also be reduced by a factor depending on ϕ (see Walker's theory p. 444). In *rapid forward* flight of birds with cambered wings it provided a reasonable approximation (cp. Gnosspelius 1925).

Equation (I, 20) for the thrust T, on the other hand, contains all the essentials of flapping propulsion; but one must remember that it applies to a uniform oscillation of the total wing rather than to a true flapping about the fulcrum. It has been used by Parry (1949) for calculating the thrust of whales and, in this case, L and α_0 should be zero. Moreover, ν was small, and since the oscillation of the tail corresponds essentially to figure (I, 10) its application to swimming is well justified. When applied to flight, the various terms in equation (I, 20) demand comment. The first term within the brace is the average coefficient of *propulsion*; it depends upon $\sin\Phi$. The phase difference should be $\Phi=90°$ in order to give maximum thrust. The angle α_a should be as big as possible provided $\alpha_0\pm\alpha_a$ does not reach the stalling value; and the flapping ratio should be as big as is consistent with the assumptions for deducing the formulae. The term in squared brackets is the sum of the coefficients of the ordinary lift-dependent *induced drag* C_{Di} and of the *profile drag* $C_{D\infty}$ (see equation (I, 4) on p. 425). The third term is the coefficient of the special drag connected with oscillatory propulsion, the *oscillation drag*. Like the propulsion it depends upon the wing characteristics and upon α_a^2. The efficiency of propulsion η could be calculated as

$$\eta=1-\frac{\text{oscillation drag}}{\text{propulsion}}.$$

When $\Phi=\frac{1}{2}\pi$ and (I, 15) was inserted in (I, 20),

$$\eta=1-\frac{1}{\pi(A+2)}\frac{\alpha_a v}{na}.$$

The expression leads to the same general conclusion as in propellers, namely, that the theoretical efficiency of propulsion approaches unity when the loading approaches zero. It must be stressed that η has nothing to do with the efficiency of the flying as such (cf. p. 434) and that $C_{D\infty}$ should enter any expression for the total efficiency of propulsion.

Equation (I, 20) therefore contains the most essential factors in producing thrust by oscillating wings. Since the thrust runs parallel to the x-axis, it does not depend on the stroke angle as does the lift. By assuming $\Phi=\frac{1}{2}\pi$ and 'normal' wing characteristics (equation (I, 15)), Holst & Küchemann could show that positive lift and thrust would result in a number of theoretical examples.

The most favourable conditions for *both* large lift and large thrust were those where $\alpha_0=\alpha_a=c$, i.e. the angle of attack was c at the beginning of a downstroke, $2c$ when the wing passes the middle position, c at the bottom and zero during the middle of the upstroke. In this case the lift will be positive during the entire stroke and the main thrust be produced during the downstroke; during the upstroke the wing drag is only insignificantly bigger than the thrust. This state of affairs resembles that which was actually found to be the case in locusts (part III). Holst & Küchemann's theory therefore provides an approximate quantitative understanding of how oscillating flight *can* be understood. It cannot be directly applied to insects with a high flapping ratio. It has not actually been tested on animals, although Holst (1943 *b*) has constructed and flown an ornithopter model designed according to the main features of their theory.

Numerical examples. In spite of these limitations it is instructive to insert the values from the three insect types in order to estimate the order of magnitude of the different terms involved. Concerning the *locust type* the results will be considered in detail.

When equation (I, 19) was used directly for estimating α_0, the result was $\alpha_0=0{\cdot}17$ rad $=9{\cdot}8^\circ$. In other words, α_0 was of a reasonable order of magnitude. The extra-to-wing drag was 85×10^{-6} kg and when $\Phi=\frac{1}{2}\pi$, equation (I, 20) could be solved with respect to α_a, giving $\alpha_a=0{\cdot}058$ rad $=3{\cdot}3^\circ$. The profile drag $C_{D\infty}$ at $\alpha_0=10^\circ$ is in fact bigger than the average from figure I, 5 *b* (0·037), but the lower value was decided upon because of the flexibility of the insect wing. When $\alpha_0=0{\cdot}17$ rad, $\alpha_a=0{\cdot}058$ rad and $C_{D\infty}=0{\cdot}037$ were inserted in (I, 20) the result was

$$T=\tfrac{1}{2}\rho v^2S\{0{\cdot}211-[0{\cdot}078+0{\cdot}037]-0{\cdot}0065\}$$

$$=\tfrac{1}{2}\rho v^2S\times0{\cdot}089\simeq90\times10^{-6}\text{ kg}=90\text{ mg}.$$

The necessary average thrust should be 85 mg according to our experimental results (table I, 1).

If we consider the terms within the brace, 0·211 is the coefficient of propulsion; 0·078 is the coefficient of induced drag and is seen to be the biggest drag component of the wings; in actual flight, it will hardly be smaller on account of the velocity gradient along the wing. Next in magnitude comes the profile drag coefficient of 0·037. This is also likely to be bigger in natural insect wings. The oscillation drag coefficient is insignificant (0·0065) at such low flying speeds and thrusts. The value of η was as high as 0·985. According to this theory, *the induced drag is therefore a most important factor in locust flight.* In this calculation the extra-to-wing drag amounted to about 40 % of the total drag (equivalent coefficient 0·089).

Power. From Holst & Küchemann's theory it should now be possible to estimate the power which the wings must deliver, i.e. *the aerodynamic power* P_a:

$$P_a=\tfrac{1}{2}\rho v^3S0{\cdot}211\text{ kg m s}^{-1},$$

In this example $P_a=0{\cdot}750\times10^{-3}$ kg m s^{-1} per wing. Since each wing should lift 1 g on average, the power became 6·4 kcal kg^{-1} h^{-1}. This estimate tends to be too low (*a*) because the selected wing profile had a higher lift/drag ratio than the locust wings and (*b*) because positive and negative power contributions were directly summed; as has already been pointed out by Walker (1927) this is hardly justified, and recent studies on positive and negative muscular work have shown that direct summation must not be performed (see discussion in part IX).

In spite of these limitations the calculated figure clearly shows that *flapping flight of larger insects is expensive and that it must require a total metabolic rate of* 25 *to* 30 kcal $\text{kg}^{-1}\,\text{h}^{-1}$ *as a minimum*, other than aerodynamic expenses being neglected. Since the thinnest possible wing profiles must be used on account of the big inertial losses (Sotavalta 1952; and parts III, VI, IX), the actual figure is likely to be somewhat higher.

General result. As far as locusts are concerned ($k<1$), Holst & Küchemann's theory thus offers reasonable values of α_0 and α_a and might give an idea of some important factors. The principles for estimating the average vertical force (equations (I, 16), (I, 17) and (I, 19)) reduce its applicability when $k>1$. In the 'horse-fly' and the 'mosquito' the calculated α_0 was 0·69 rad (=39·5°) and 1·35 rad (=77°) respectively, i.e. deprived of aerodynamic meaning.

(ii) *Walker's theory* (1925, 1927)

Walker developed a theory for flapping forward flight of birds. The simplifying assumptions were: (*a*) a positive forward velocity v exists; (*b*) the angular velocity is numerically constant and equal during upstroke and downstroke $|\mathrm{d}\gamma/\mathrm{d}t| = 2\phi n$; (*c*) the plane of oscillation is vertical, i.e. the stroke plane angle $b=0$; (*d*) the angle of attack α is constant during one half-cycle but differs during upstroke and downstroke; (*e*) as in the former theory, the induced wind as well as the vertical migration of the centre of gravity are disregarded.

The downstroke (superscript d) was separated from the upstroke (superscript u). The vertical, average force L, the horizontal average force T, the aerodynamic work during the downstroke W_a^d, and the aerodynamic work during the upstroke W_a^u can now be calculated by integrating from $t=0$ to $t=\frac{1}{2}n$. The equations refer to a *unit wing area* in the *distance* r from the fulcrum.

$$L=\tfrac{1}{2}\rho v^2\surd(1+k^2)\{(C_L^d+C_L^u)+k(C_D^d-C_D^u)\}\frac{\sin\frac{1}{2}\phi}{\frac{1}{2}\phi}\,\tfrac{1}{2}, \tag{I, 21}$$

$$T=\tfrac{1}{2}\rho v^2\surd(1+k^2)\{k(C_L^d-C_L^u)-(C_D^d+C_D^u)\}\,\tfrac{1}{2}, \tag{I, 22}$$

$$W_a^d=\tfrac{1}{2}\rho v^3k\surd(1+k^2)\{C_L^d+kC_D^d\}\,\tfrac{1}{2}\quad\text{(downstroke)}, \tag{I, 23}$$

$$W_a^u=\tfrac{1}{2}\rho v^3k\surd(1+k^2)\{-C_L^u+kC_D^u\}\,\tfrac{1}{2}\quad\text{(upstroke)}. \tag{I, 24}$$

In (I, 21) to (I, 24) k is the flapping ratio (equation (I, 11)) at distance r from the fulcrum. At the wing tip of birds performing typical flapping flight Walker estimated k to be about 0·3 to 0·4 (pigeon, pheasant, rook, partridge, herring gull). In *Schistocerca* it would be about 1·1. In a later paper (1927) the theory was refined by taking the different duration of upstroke and downstroke into account, without other essential alterations.

Results. Although based upon rather rigorous assumptions as to the form of the oscillation and the variation of α, Walker's theory has the advantage of being easy to follow and of being deduced from a true flapping movement about the shoulder joint. Its applicability is of course influenced by the choice of wing profile as well as of aspect ratio which has to be estimated for each value of r. One important limitation was found to be that the wings were assumed to oscillate in a vertical plane and that the induced wind was disregarded (see p. 449).

Some essential deductions can be made from equations (I, 21) and (I, 22). Concerning the *lift*, the flapping velocity will contribute by more than 20% only if $\sqrt{(1+k^2)} > 1{\cdot}2$. Table I, 2 shows the limiting distance $r_{\text{lim.}}$ beyond which the flapping will be of essential importance for the production of lift in the rook and in the three insect types.

Table I, 2. The importance of flapping for production of lift according to Walker's theory

The limiting distance $r_{\text{lim.}}$, as compared with the wing length, beyond which the flapping speed contributes by more than 20% of the total aerodynamic force in different flying animals.

animal:	v flying speed (cm/s)	n frequency (c/s)	ϕ stroke angle (rad)	l wing length (cm)	$r_{\text{lim.}}$ (cm)	$\frac{r_{\text{lim.}}}{l}$
rook	1100	4	1·75	43	52	> 1
'locust type'	350	20	1·75	6	3·3	0·55
'horse-fly type'	200	120	2·00	1·43	0·27	0·19
'mosquito type'	150	320	2·00	0·38	0·07	0·18

Table I, 3. The angles of attack α in Walker's example (rook)

	α (degrees)	
part of wing	downstroke	upstroke
inner third (I)	12	12
middle third (II)	12	6
outer third (III)	12	0

In the rook the forward speed is by far the most important velocity component, but when k increases the extra wind pressure from flapping rapidly becomes important. This fact must be considered as the essential reason for the failure of Holst & Küchemann's theory to explain the flying of small insects.

In the rook (weight 0·5 kg) Walker concluded that the flapping was insignificant for lift production so that the aim of flapping of larger birds was mainly to create propulsion during forward flight. In insects both tasks are essential. In hovering animals, the production of lift is of course the only energy-consuming aerodynamic task. Walker's formulae cannot then be used because the induced wind becomes increasingly important (p. 449).

The *lift* depends upon $(C_L^d + C_L^u)$ and to a lesser degree $(C_D < C_L)$ upon $k(C_D^d - C_D^u)$. Under optimum conditions for flight both quantities should be as big as possible. The *thrust*, however, depends upon $k(C_L^d - C_L^u)$, and the lift coefficient during the upstroke should therefore be as small as possible, as should also be $(C_D^d + C_D^u)$. The opposing optimum conditions for lift and thrust production therefore led Walker to assume different working conditions for the different parts of the wings of birds. He divided the wing of the rook into three regions, I, II, III (see figure I, 8), and used the polar diagram for an ordinary aeroplane wing. This procedure resulted in the following assumption in table I, 3 concerning α which could explain the flying of the rook. These values were somewhat altered when the relative duration of upstroke and downstroke was taken into account, but the order of magnitude was the same (Walker 1927).

In a simple way, Walker's theory therefore makes possible a rough estimate of the aerodynamic function of different parts of the wing in a flapping animal. The resulting aerodynamic forces could be found by numerical integration. The main principles are analogous to those of the simple blade element theory of propellers (p. 429). In the rook, Walker concluded that the inner part of the wing (I) could produce lift during the entire stroke but contributed by a negative amount to the thrust; the outer part (III) could produce lift and thrust during the downstroke only, the aerodynamic effect being small during the upstroke. The middle part (II) came in between. These conclusions (1925, 1927) were obtained by applying flight data from the 'Bird Construction' Committee's report and from slow-motion films (1927). They are consistent with the later observations on flying birds by Lorenz (1933) and by Brown (1953).

TABLE I, 4. AVERAGE AERODYNAMIC FORCES ACCORDING TO WALKER'S THEORY ON WING SECTIONS I TO III IN THE 'LOCUST TYPE' (TABLE I, 1 AND FIGURE I, 8)

Examples (*a*) and (*b*) refer to the artificial airfoil seen in figures I, 5*b* and I, 9, whereas (*c*) was based upon the average polar diagram of the locust wings (figure I, 5*c* and *d*). In all examples a constant angle of attack α_d was assumed during the downstroke; during the upstroke α_u varied as follows:

	α_u		
wing section	I	II	III
example (*a*) and (*c*)	x	$\frac{1}{2}x$	0
example (*b*)	x	$\frac{2}{3}x$	0

In the left column (*c*) the figures within the brackets are the lift contribution when the stroke plane angle *b* was 30° (normal) instead of 0°.

	average vertical force, i.e. lift (mg)					average forward force, i.e. thrust (mg)		
	example					example		
wing section	(*a*)	(*b*)	(*c*)			(*a*)	(*b*)	(*c*)
I	838	806	670	(690)		−138	−134	−109
II	737	788	670	(1050)		50	−21	−5
III	425	406	410	(670)		336	326	206
total force	2000	2000	1750	(2410)	force	248	171	92
	body weight 2000 mg					extra-to-wing-drag 85 mg		
max. C_L	1·21	1·18	1·00	(0·8)	max. C_D	0·17	0·17	0·14

Numerical examples. If we insert the data from the 'locust type' given in table I, 1, the resulting average *forces* are seen in table I, 4 when calculated on the assumption that the wing twisting took place according to either of the two possibilities shown in the legend. It is seen that the artificial profile assumed in (*a*) and (*b*) would enable the 'locust' to fly although the thrust was bigger than necessary; $\alpha_{\text{max.}}$ was about 12° and $C_{L\text{max.}}$ was 1·21 and 1·18. Without using the flap mechanism described in parts III and VII, the locust wing (figure I, 5*c*, *d*) does not, in fact, give C_L values above 1·0 ($\alpha = 15°$); if a combination of the true locust polar diagrams from forewings and hindwings was used the results in column (*c*) were found. In this case the lift would hardly be adequate (1750 mg against 2000 mg body weight). However, Walker presupposed that the wings beat up and down in a vertical plane ($b=0°$). In the locust the stroke plane is inclined about 30° to the vertical, i.e. $b=30°$. This implies that the relative wind increases during the downstroke (d) and decreases during the upstroke (u) compared with the velocities for $b=0°$. The figures in brackets indicate the lifts obtained when making an approximate correction for $b=30°$. There should now be no problem in getting sufficient lift. The real locust wing would also produce thrust of the same order of magnitude as required by the locust.

Table I, 5. The aerodynamic power in the 'locust type' according to Walker's theory

P_a was calculated for each wing section. For further explanation, see legend to table I, 4. Superscripts d and u denote downstroke and upstroke respectively.

	aerodynamic power (kcal kg^{-1} h^{-1})					
	downstroke: P_a^d			upstroke: P_a^u		
wing section	(a)	(b)	(c)	(a)	(b)	(c)
I	1·43	1·39	1·19	−1·35	−1·31	−1·10
II	5·18	5·02	4·27	−2·26	−2·38	−2·70
III	6·55	6·35	5·40	0·17	0·17	0·29
total	13·2	12·8	10·9	−3·4	−3·5	−3·5

Table I, 6. Resulting aerodynamic forces in the 'horse-fly type' and in the 'mosquito type' according to Walker's theory.

The artificial airfoil in figure I, 5b and I, 9 was used; α varied as in example (a), table I, 4. The results for $b \neq 0$ are shown in brackets.

	average vertical force (mg)					average forward force (mg)	
	'horse-fly'		'mosquito'			'horse-fly'	'mosquito'
wing section	$b=0°$	($b=30°$)	$b=0°$	($b=45°$)			
I	15	(18)	0·16	(0·31)		−2·1	0·025
II	35	(69)	0·41	(0·60)		3·5	0·053
III	25	(122)	0·33	(0·64)		24·7	0·410
total	75	(209)	0·9	(1·6)	total	26	0·44
weight (mg)	180		3·5		drag (mg)	10	0·16
max. C_L	1·2		1·2		max. C_D	0·17	0·17

The conclusion was that three-quarters of the lift is produced by the inner two-thirds of the wing, II being the most important part in the natural wing. The thrust, on the other hand, entirely depends upon the outer third of the wing (III), the remaining sections giving no (II) or a negative average forward force (I).

Power. Unfortunately, exact calculations of the aerodynamic *power* $P_a=nW_a$ become much complicated when $b \neq 0°$, so that the figures in table I, 5 refer to situations when $b=0°$ (equations (I, 23) and (I, 24)). During the downstroke P_a^d ranges from 13 to 11 kcal kg^{-1} h^{-1}, and the outer third consumes nearly half of it. The upstroke as a whole gave negative values of P_a^u ($=-3·5$ kcal kg^{-1} h^{-1}), so that, except for III, energy is transferred from the air to the wing. If the flight system were an ideal mechanical construction the total power for flight of the 'locust type' would range from 9·8 in (a) to

7·4 kcal kg^{-1} h^{-1} in (c), i.e. expenditures of the same order of magnitude as found according to the deductions from Holst & Küchemann's theory (p. 443). Simple summation is not justified, however (Walker 1927; part IX) and, according to Walker's theory the power would not be less than 11 kcal kg^{-1} h^{-1}. Introduction of $b=30°$ would reduce the necessary maximum C_L by about 20 % and probably also the power by a comparable amount. The necessary power could therefore be roughly estimated to be between 6 and 10 kcal kg^{-1} h^{-1}.

General result. Walker's theory not only offers a fairly reasonable quantitative explanation of the flight of a 'locust' in ordinary aerodynamic terms; it also makes possible an estimate of the function and power expenditure of the different parts of the wings which is not in contradiction to experiments (part III).

According to table I, 6 the theory can also explain the flight of the 'horse-fly' type provided that correction is made for the stroke plane angle. In the 'mosquito type' even this is not sufficient.

(iii) *Osborne's theory* (1951)

Both Demoll (1918, 1919) and Magnan (1934) concluded that the lift coefficient required to explain the flight of some insects was inordinately high. Osborne (1951) attacked the problem from a theoretical point of view. He has developed general expressions for the force acting on a wing-surface element which is moved in an arbitrary manner under the assumption that the force is proportional to the square of the relative wind. The force is resolved normal and parallel to the relative wind, integrated over the surface of the wing and averaged over the total wing beat. The resulting horizontal component should equal the average thrust (known from the extra-to-wing drag) and the vertical component should equal the average lift (= the body weight). The average values of the force coefficients, $\overline{C}_L$, and $\overline{C}_D$, can then be determined, i.e. the above problem could be solved without any knowledge of the variation of α which was necessary in the former theories.

The induced average wind velocity $\overline{w}$ was calculated approximately from the general momentum theory as applied to helicopter rotors (Glauert 1935). The expression then became

$$\overline{w}^2=\frac{1}{2}\left\{\sqrt{\left(v^4+\left(\frac{L}{\pi\rho l^2}\right)^2\right)}-v^2\right\}. \tag{I, 25}$$

As was mentioned on p. 427 it is of course questionable whether the average value for propellers with uniform disk loading will be representative, but, in any case, introduction of the induced velocity in the theory greatly facilitates an understanding of the performances, especially at low forward speeds. The second term within the square root, $[L/(\pi\rho l^2)]^2$, becomes relatively large when v is small; it increases when L increases and decreases when the wing length is increased at a given L (i.e. decreasing propeller load). The induced wind is particularly important for an understanding of hovering flight, where $v=0$. In equation (I, 25) Osborne has considered the oscillating wings as a circular actuator disk. At small forward speeds we therefore propose to use the smaller area actually covered by the wings instead of the total disk area. Equation (I, 25) should then be multiplied by π/ϕ. When $v=0$, the induced wind speed becomes

$$\overline{w}=\frac{0{\cdot}71L}{\phi\rho l^2}, \quad v=0. \tag{I, 26}$$

The average relative wind velocity of a hovering insect is the resultant of the average flapping velocity $\bar{v}$, and the vertical average induced velocity $\bar{w}$. In table I, 7 these quantities have been calculated for three types; it appears that $\bar{w}$ approaches the order of magnitude of the normal forward flying speed.

Osborne's method implies that some of the integrations must be replaced by suitably chosen average values; the integration of the relative wind over wing length and time thus rests upon an expansion whose principles are given but with no details. The integrations leading to the expressions for $\bar{C}_L$, $\bar{C}_D$ and P_a contain terms in which various shrewdly chosen average values are introduced and they are therefore not exact. The equations upon which $(\bar{C}_L^2+\bar{C}_D^2)^{\frac{1}{2}}_{\text{min.}}$ is based can be integrated exactly, however, so that the estimates of the minimum average force coefficients are open to control. This is not the case as far as the other quantities are concerned.

TABLE I, 7. AVERAGE INDUCED WIND SPEED $\bar{w}$ AND AVERAGE FLAPPING VELOCITY $\bar{v}$ IN HOVERING INSECTS (m/s)

hovering of	$\bar{w}$	$\bar{v}$
'locust type'	1·8	2·8
'horse-fly type'	2·5	4·5
'mosquito type'	0·7	3·2

Besides body weight, wing dimensions, extra-to-wing drag, n, ϕ and v, the following parameters are taken into consideration: (*a*) the positional angle γ varies sinusoidally $\gamma=\gamma_0+\frac{1}{2}\phi \sin \omega t$; (*b*) allowance is made for different duration of downstroke (superscript d) and upstroke (superscript u); (*c*) b is introduced and allowance made for it being different during the two phases of the stroke; (*d*) finally, the introduction of ξ and ζ in the following equations makes possible a distinction between the lift and thrust during the stroke:

$$\bar{C}_L^d=\bar{C}_L(1+\xi), \quad \bar{C}_L^u=\pm\bar{C}_L(1-\xi),$$
$$\bar{C}_D^d=\bar{C}_D(1+\zeta), \quad \bar{C}_D^u=\bar{C}_D(1-\zeta).$$

For instance, $\xi=\zeta=1$ implies that lift and thrust are only produced during the downstroke. $\xi=\zeta=0$ means that both phases contribute by similar amounts.

The necessary aerodynamic power P_a is calculated along similar principles. There can be no doubt, therefore, that Osborne's theory is by far the most complete of the three; it seems to have taken a reasonable number of parameters into account. The final expressions for $\bar{C}_L$ and $\bar{C}_D$, $(\bar{C}_L^2+\bar{C}_D^2)^{\frac{1}{2}}_{\text{min.}}$, and for P_a are somewhat lengthy and laborious to use. The reader should consult the original paper, taking care to check every expression as to dimensions, since misprints concerning powers and factors occur in many formulae.

Results. Osborne used his theory for calculating the average force coefficients and the aerodynamic power of twenty-five insects the flight data of which were taken from Magnan (1934). When $\xi=\zeta=0$ he found highly aberrant values. He therefore decided to use $\xi=\zeta=1$ as a more plausible condition. In the following results, quoted from his paper, it has been assumed that lift and thrust are only generated during the downstroke; the coefficients therefore have the superscript d. Other combinations of ξ and ζ were not used; in *Schistocerca*, for instance, some lift is actually produced during the upstroke (see part III), so that a slightly different choice would give a better fit for this insect.

Table I, 8 shows the values of $\overline{C}^d_L$ in twenty-five insects arranged in order of decreasing lift coefficients (from Osborne's fig. 3). The very large range of $\overline{C}^d_L$ from nearly 5 to 0·1 is most striking. Most of the insects (nos. 11 to 25), however, had coefficients below 1·5, so that their flight performances *can* be understood from ordinary aerodynamics. If we consider the first group where $\overline{C}^d_L \geqq 2$ (nos. 1 to 7) it ranges from very large (*Lucanus*, 2600 mg) through medium-sized (*Vespa germanica*, 187 mg) to fairly small insects (*Sarcophaga*, 45 mg; *Panorpa*, 30 mg). This and the following group of three animals (nos. 8 to 10) are the most interesting because $\overline{C}^d_L > 1{\cdot}5$, i.e. larger than consistent with ordinary aerodynamics of slightly cambered wings. This result forced Osborne to suggest that aerodynamic inertial forces were responsible for the high lift coefficients. Before accepting his deduction it is worth while to consider the flight data from which the calculations were made. The square of the speed of the relative wind is the backbone of the calculations; v, n and ϕ, all entering in the second power, might therefore influence the result by a factor 2 to 4 if they deviate in the same direction by 15 to 25 % from the true values. Now the flight data given by Magnan (1934) were *not* of one set. The flying speed v was estimated very approximately as the maximum speed obtained when the insect unrolled a thread wound round a pulley; the wing-beat frequency n was determined from films taken under

TABLE I, 8. THE AVERAGE COEFFICIENTS OF LIFT $\overline{C}^d_L$ GIVEN BY OSBORNE (1951, FIG. 3)

These results were based upon Magnan's data (1934) and are arranged according to decreasing lift coefficients. Superscript d denotes downstroke, the aerodynamic work being assumed negligible during the upstroke, i.e. $\xi = \zeta = 1$.

no.	species	$\overline{C}^d_L$	adopted flying speed (m/s)	frequency (c/s) according to		'wing loading' (mg/mm²)
				Magnan	Sotavalta	
1	*Lucanus cervus*	4 to 5	1·5	33	—	3·25
2	*Ammophila sabulosa*	3	1·5	120	140	1·07
3	*Sarcophaga carnaria*	2·5	2	160	200	1·25
4	*Melolontha vulgaris*	2·5	2·5	46	62	2·39
5	*Telephorus fuscus*	2·5	0·8	72	—	0·94
6	*Vespa germanica*	2	2·5	110	139	1·90
7	*Panorpa communis*	2	0·5	28	50	0·17
8	*Xylocope violacea*	1·8	4	130	—	3·58
9	*Bombus terrestris*	1·6	3	130	158	2·73
10	*Cetonia aurata*	1·6	3	86	100	2·23
11	*Apis mellifica*	1·3	2·5	250	240	1·86
12	*Tabanus bovinus*	1·1	4	96	130	1·50
13	*Musca domestica*	1·1	2	190	200	0·60
14	*Plusia gamma*	0·9	1·5	48	48	0·33
15	*Volucella pellucens*	0·9	3·5	120	150	0·94
16	*Calopteryx splendens*	0·8	1·5	16	—	0·14
17	*Vespa crabro*	0·7	6	100	105*	2·18
18	*Macroglossum stellatarum*	0·6	5	85	73	0·86
19	*Pyrosoma minimum*	0·5	0·6	27	—	0·11
20	*Vanessa atalanta*	0·3	4	10	—	0·12
21	*Orthethrum coerulescens*	0·3	4	20	—	0·23
22	*Brachytron pratense*	0·2	5	33	—	0·46
23	*Pieris brassicae*	0·2	2·5	12	10	0·08
24	*Papilio podalirius*	0·15	3·5	10	—	0·08
25	*Aeschna mixta*	0·1	7	38	30 to 40*	0·38

* Estimated by Weis-Fogh during typical continuous flying at normal speed and lift.

non-specified conditions (hovering, tethered flight, or start); the stroke angle ϕ was assumed from the projection on the yz-plane and derived from the same films. There are, therefore, ample possibilities for error. If Sotavalta's (1947, 1952) values for n of freely flying insects are compared with those applied by Osborne, they are seen to be systematically higher in the first group (nos. 1 to 7). This group is furthermore characterized by low flying speeds. The possible lift which is generated during the entire stroke of the spread-out passive forewings (elytra) of *Lucanus* and *Melolontha* were not taken into consideration. Moreover, it does not seem reasonable that $\overline{C}_L^d$ of *Vespa germanica* (no. 6) was 2 while that of the very closely related *V. crabro* (no. 17), which has a higher wing loading, was only 0·7. There are therefore several indications that the high lift coefficients in nos. 1 to 7 are incorrect.

Numerical examples. In order to check the method of calculation, $(\overline{C}_L^{d^2}+\overline{C}_D^{d^2})^{\frac{1}{2}}_{\text{min.}}$ was estimated for some insects from table I, 8 (*Lucanus* (no. 1), *Musca* (no. 13), and *Aeschna* (no. 25)), for both forewings and hindwings of *Schistocerca gregaria* (data from parts II and III), and, finally, for the 'horse-fly type' and the 'mosquito type' seen in table I, 1. The results are given in table I, 9 together with the values of the induced wind, according to equation (I, 25). The minimum coefficient of the first group was of the same order of magnitude as stated by Osborne, although the very low coefficient was doubled by reducing the flying speed of the dragonfly (*Aeschna*) to the more common value of 3·5 m/s. In *Schistocerca gregaria* flying would be impossible at 2·0 m/s, the coefficients being 1·7 and 2·0. In the laboratory, the desert locust never lifted its own weight at speeds below 2·5 m/s and at 100 to 110% of lift the average speed was 3·6 ± 0·5 m/s (s.d.) (part II). However, at 3·5 and 4·5 m/s, the calculated coefficients corresponded closely to what should be expected from experiments (part III). The last figures in table I, 9 show that both the 'horse-fly' and the small 'mosquito' with the high wing-beat frequency of 320 c/s could

TABLE I, 9. MINIMUM AVERAGE FORCE COEFFICIENT $(\overline{C}_L^{d^2}+\overline{C}_D^{d^2})^{\frac{1}{2}}_{\text{min.}}$ CALCULATED ACCORDING TO OSBORNE (1951)

The figures refer to three insects from table I, 8 and to the forewings and hindwings of the desert locust *Schistocerca gregaria* flying at different supposed speeds, 3·5 m/s being the normal speed and 17·3/s being the normal frequency. At the bottom are seen the calculated coefficients during forward flight of the 'horse-fly' and the 'mosquito' (table I, 1). The vertical induced wind speed $\overline{w}$ should be compared with the flying speed v. The approximate angle of attack α is seen in brackets. $\xi = \zeta = 1$.

no. in table I, 8	insect:	v flying speed (m/s)		$\overline{w}$ induced vertical wind speed (m/s)	$(C_L^{d^2}+C_D^{d^2})^{\frac{1}{2}}_{\text{min.}}$	(α)
1	*Lucanus cervus*	1·5		1·29	2·9	—
13	*Musca domestica*	2		0·25	0·92	—
25	*Aeschna mixta*	7		0·07	0·16	—
		3·5		0·39	0·32	—
	Schistocerca gregaria	2·0	forewings	0·12	1·7	(above stalling)
			hindwings	0·28	2·0	(above stalling)
		3·6	forewings	0·06	0·55	(5°)
			hindwings	0·16	0·94	(15°)
		4·5	forewings	0·06	0·41	(2° 5)
			hindwings	0·13	0·65	(7°)
	'horse-fly type'	2·5		0·44	1·0	—
	'mosquito type'	1·0		0·30	0·8	—

fly in a manner which is consistent with steady-state aerodynamics. According to this estimate the flight of even small insects would hardly necessitate the assumption of unknown aerodynamic inertial forces.

One should furthermore remember that all useful aerodynamic work was assumed to take place during the downstroke. This is nearly true in *Schistocerca* (part III) but hardly in insects flying at low speeds and with the wing plane almost horizontal (*Lucanus*, *Melolontha*, and others in the high lift groups). Such insects, like hovering humming birds, can generate lift during both phases, so that the true force coefficient would be considerably smaller than the calculated. We cannot as yet explain the very peculiar results which Osborne got by assuming $\xi=\zeta=0$, but in insects with zero or small forward speed it seems obvious that a general lowering of the coefficients should result as compared with the values for $\xi=\zeta=1$. In hovering or slow forward flight the upstroke and downstroke often last equally long (cf. *Lucanus*) and the stroke plane is nearly horizontal ($b=90°$); thus $\xi=\zeta=0$ instead of unity implies that the lift coefficient should be halved.

Osborne's analysis therefore indicates that under the given assumptions, most insects would be able to fly without making use of unusual aerodynamic principles. The very high coefficients found in some of the insects considered do not prove that aerodynamic inertial forces are involved, partly because the accuracy of the analyses was too small and partly because the empirical flight data as well as some of the assumptions were especially misleading in these insects, tending to increase the high values of the calculated force coefficients.

Power. The aerodynamic power P_a^d was also estimated *inter alia* by applying the calculated values of $\bar{C}_L^d$ and $\bar{C}_D^d$. In table I, 10 the results have been recalculated from Osborne's figure 10; they are compared with the total metabolic rate determined from experiments with the same or closely related species. The asterisk means that $\bar{C}_L^d$ as estimated was greater than unity. This was the case in all species where P_a^d exceeded 34 kcal kg^{-1} h^{-1}. In most cases (apart from *Tabanus* spp.) the metabolic rate was at least five times bigger than P_a^d, so that there is no *a priori* reason for considering Osborne's figures unlikely. They range from 8·6 to nearly 50 kcal kg^{-1} h^{-1}, the average being 34 kcal kg^{-1} h^{-1}. However, since increased force coefficients for a given oscillation will increase the power consumption, the above discussion renders the highest values of doubtful validity (compare, for instance, *Vespa crabro* and *V. germanica*). 30 kcal kg^{-1} h^{-1} is a more probable *maximum* which was reached by *Macroglossum* (345 mg; $\bar{C}_L^d=0{\cdot}6$) and by *Volucella* (73 mg; $\bar{C}_L^d=0{\cdot}9$). The theory demonstrates the order of magnitude. It is unlikely that the *minimum* value will turn out to be lower than about 8 kcal kg^{-1} h^{-1} in animals of insect size.

Holst (1943*a*) has measured the average lift, drag and power of a flapping, artificial wing of the same size as the forewing of a locust. In many points the ingenious technique corresponded to Osborne's theoretical model. The results were analyzed in the light of current propeller theory, however, so that the two studies cannot be directly compared. In some instances η (p. 427) was as high as in propellers, but this does not give any information on natural flight.

General result. Osborne's theory, the essential point of which is an estimation of the minimum average force coefficient, results in sufficiently small values of $(\bar{C}_L^{d^2}+\bar{C}_D^{d^2})^{\frac{1}{2}}_{\text{min.}}$ to make the flying of the three insect types in table I, 1 understandable without the intro-

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duction of unusual aerodynamics. Moreover, the calculated values for *Schistocerca gregaria* come close to those determined experimentally. Evidence is put forward suggesting that the abnormally high (and low?) lift coefficients calculated by Osborne were due to the application of unsuitable flight data.

TABLE I, 10. THE AERODYNAMIC POWER AS CALCULATED BY OSBORNE (1951) COMPARED WITH THE METABOLIC RATE.

An asterisk (*) indicates that $\overline{C}_L^d > 1$ in table I, 8. Arranged according to increasing aerodynamic power.

aerodynamic power as calculated by Osborne (kcal kg^{-1} h^{-1}), P_a^d		metabolic rate as measured during continuous flight of the same or closely related species, P (kcal kg^{-1} h^{-1})		
genus or species		species		authors
Calopteryx, *Vanessa*, *Pieris*, *Panorpa**, *Sarcophaga**, *Brachytron*, *Papilio*	8·6 to 17	*Lucilia sericata*	400	(Davis & Fraenkel 1940)
		Vanessa io	200	(Zebe 1954)
Aeschna, *Orthetrum*, *Pyrosoma*, *Vespa crabro*, *Plusia*, *Musca**	17 to 26	*Aeschna grandis*	110	(Weis-Fogh†)
		Vespa crabro	125	(Weis-Fogh†)
		Plusia gamma	150	(Zebe 1954)
Macroglossum, *Volucella*	26 to 34	*Metopsilus porcellus*	300	(Zebe 1954)
*Melolontha**, *Bombus**, *Xylocope**, *Apis**, *Vespa germanica**, *Telephorus**, *Tabanus**	34 to 43	*Apis mellifica*	400	(Jongbloed & Wiersma 1935)
		A. mellifica	300	(Hocking 1953)
		Tabanus affinis	100	(Hocking 1953)
*Lucanus**	above 43	—		—

† Unpublished, estimated at normal lift and flying speed.

(*e*) *Conclusion*

Three theories of increasing complexity have provided quantitative information on the aerodynamic principles upon which the flapping flight of birds and insects *might* be understood.

Holst & Küchemann's theory (1941, 1942) could explain the flying of birds and of large insects like locusts on the basis of conventional aerodynamics and a highly simplified kinematic system. It has the advantage of giving information on the average induced drag, the profile drag and on the oscillation drag. It could not be used for insects with a high ratio of flapping speed to forward speed ($k > 1$, equation (I, 11)).

Walker's theory (1925, 1927) is based upon a true flapping movement and could be successfully applied both to large birds and to insects as small as a horse-fly (*Tabanus* sp.). In such small insects, however, correction must be made for the inclination of the stroke plane to the vertical. The flight of the mosquito falls beyond its applicability *inter alia* because the induced wind is disregarded.

Osborne's theory (1951) includes a reasonably large number of parameters and takes into consideration both the complex kinematics and the induced wind. In *Schistocerca gregaria* his equations give aerodynamic force coefficients which are consistent with the actual experimental findings in part III. It could also explain the aerodynamic performance of the 'horse-fly' type and of the 'mosquito type' according to ordinary aerodynamic principles. The very high force coefficients which Osborne calculated for some insects are critically discussed; most probably they are incorrect owing partly to their derivation from misleading flight data and partly from wrong assumptions about the aerodynamic action of the wings during the upstroke.

It is therefore concluded that neither birds nor insects make use of unusual aerodynamic forces; at least, such forces need not be postulated to explain the observed *average* performances.

According to Walker's theory, the 'locust type' resembling *S. gregaria* should use from 6 to 10 kcal $\text{kg}^{-1}\,\text{h}^{-1}$ in order to overcome the aerodynamic forces. In other insects, Osborne's estimates indicate 8 kcal $\text{kg}^{-1}\,\text{h}^{-1}$ as the lowest probable aerodynamic power output and about 30 kcal $\text{kg}^{-1}\,\text{h}^{-1}$ as the highest. Holst & Küchemann's theory indicates that the average induced drag of the wings is large compared with the profile drag and the oscillation drag.

6. REGULATION OF FLIGHT

The detail of the regulatory mechanisms in insect flight is outside the main scope of this paper. Moreover, Chadwick (1953) has recently reviewed the extensive literature to which he himself has contributed so much. The problem of regulation involves consideration of (*a*) the kinematics, (*b*) the power output and (*c*) stability and control during flight.

The previous discussion has made it clear that an understanding of the variation of the kinematic parameters (n, ϕ, θ, etc.) under different experimental conditions will demand a knowledge of the interaction of all the force systems into which these parameters enter by significant amounts. Mainly based upon extensive studies on the flight of *Drosophila* spp. (Chadwick 1939, 1947, 1951; Chadwick & Gilmour 1940; Chadwick & Williams 1949; Reed *et al.* 1942), an attempt has been made formally to correlate the experimental findings in the following expression (Chadwick 1953):

$$P_a \propto \rho \phi^3 n^3 \sin \alpha, \tag{I, 27}$$

where '$\sin \alpha$' was the 'sine of the angle of attack'; the other terms have already been defined (see list of symbols). Since P was found to be almost constant during short tethered flights, P_a was also considered as constant. When ρ was altered, n and ϕ varied less than would be expected from (I, 27) so that the remaining compensation should be realized by varying '$\sin \alpha$'. The deductions rested upon the assumption that the aerodynamic work was the only significant quantity. Furthermore, in the 'stroke-volume' theory of Chadwick '$\sin \alpha$' bears no true relationship to the angle of attack; it represents the collective variation of a number of unknown parameters rather than of $\alpha = \alpha(v, r, t, \theta)$ (cf. p. 423). Chadwick (1951, 1953) did not think the inertial power P_i of importance and concluded (1953, p. 630): 'Viewed in this way, the flight mechanism exhibits homeostatic characteristics in that, when stress is applied, large changes in any one element are ordinarily avoided by spreading the strain over several components. The situation therefore suggests the existence of regulatory mechanisms, previously unsuspected, which operate in such a way as to resist deformation in the proportion which each of the several factors normally contributes to the process as a whole. The identification and characterization of these regulatory systems remain problems for future study.' In locusts, at least, some special parts of this general statement on homoeostasis have been confirmed; it could simply be considered as the consequence of the action of a special sensory system which serves to keep the lift constant during a given flight performance (part IV). In general, however, it hardly applies to normal, free flight where the metabolic rate P seldom would be maximal, as will be discussed in parts II and VIII.

While Chadwick stressed the importance of the aerodynamic forces as regulators of frequency and stroke angle, Sotavalta (1947, 1952, 1954) has, along similar lines, put emphasis to the inertial power according to the relationship (see p. 432)

$$P_i \propto \phi^2 n^3. \qquad (I, 28)$$

In fact, the close similarity between (I, 27) and (I, 28) and the large forces which *both* systems involve make an explicit solution of the problem meaningless, especially if the elastic torque has also to be taken into account. Sotavalta has undoubtedly shown that the mass moment of inertia of the wing is an important factor in this complex, and the American physiologists have shown that aerodynamic forces can also be of great significance. A common point of view is obviously needed and will be provided in part IX.

The individual control mechanisms as represented by specific sensory organs (for example, Hollick 1940; Pringle 1948; Weis-Fogh 1949, 1950) can of course be studied without detailed knowledge of the flight system as a whole. This is hardly advisable when problems of stability are discussed. Stability problems in man-made aircraft are extremely complex and are unlikely to be simpler in animals where practically no essential quantity need be constant during the stroke.

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References

References to other Parts of this study are given as part II, part III, etc. The following Parts are printed in this issue:

Part II. Weis-Fogh, T. 1956 Flight performance of the desert locust (*Schistocerca gregaria*).

Part III. Jensen, Martin 1956 The aerodynamics of locust flight.

Part IV. Weis-Fogh, T. 1956 Notes on sensory mechanisms in locust flight.

The following Parts are being prepared:

Part V. Jensen, Martin Strength and elasticity of locust cuticle.

Part VI. Weis-Fogh, T. Wing movements and elastic deformations in flying locusts.

Part VII. Weis-Fogh, T. Functional anatomy of the wing system of the desert locust (*Schistocerca gregaria*), including the tracheal system.

Part VIII. Weis-Fogh, T. Lift and metabolic rate of flying locusts.

Part IX. Jensen, Martin & Weis-Fogh, T. The energetics of locust flight.

Part X. Jensen, Martin & Weis-Fogh, T. General discussion of locust flight.

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