# FLAPPING FLIGHT AND POWER IN BIRDS AND INSECTS, CONVENTIONAL AND NOVEL MECHANISMS

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## INTRODUCTION

In this general lecture I shall begin with simple observations and concepts and move towards the latest developments within the field.

During calm summer days in August one often sees small flocks of black-headed gulls gliding and circling in narrow spirals near to my cottage in Tibirke in Denmark. Suddenly, a bird will 'stop', flap briefly and catch one of the hovering beetles which, together with floating seeds of willow herb, have been carried up by a feeble and invisible dust devil. This little scene embodies the large range of performances exhibited by flying organisms, from passive floating and gliding to active flapping flight where the energy to remain airborne is provided by the rapidly contracting wing muscles. Our main problem is whether the basic aerodynamic mechanisms are the same in all kinds of flight or whether different principles are involved and to which extent. Obviously, floating seeds and aerial plankton of wingless arthropods must use the aerodynamic drag and this may apply to very small winged insects, Pterygota, in between burst of activity (cf. R. A. Norberg, (1972a)). On the other hand, gliding and soaring in bats, birds and insects of course depend on the usual aerofoil action of their wings, i. e. on the steady-state aerodynamic lift which acts perpendicular to the direction of movement through the air, while the drag acts in the direction of the movement. However, when the wings flap under the influence of muscular contractions, unsteady flow patterns must occur and we shall see that unsteady flow may become dominant features in some animals.

However, we are only beginning to understand the nature of how animals make use of unsteady flow (Weis-Fogh, (1973); Lighthill, (1973)).

The lift principle as applied to steady flow is most likely to dominate the performance when the animal is relatively large and flies at a high forward speed, i.e. during fast forward flight, as discussed by Lighthill in this Symposium. This is the situation for instance in most birds and in large insects like locusts and migrating hawk moths. However, the majority of insects are small and make use of hovering and slow flight. Under these conditions the wings sweep through a large angle and their outer parts obtain air speeds far in excess of that of the body. When an animal is gliding, its wing tips of course travel at the same speed as that of the base and of the body, but during normal forward flight of many birds the air speed at the tip is 1.3-1.4 times larger than at the base (pigeon, pheasant, rook, partridge, gull); it is two times larger in the desert locust Schistocerca gregaria (2g), three times in the horse fly Tabanus affinis (0.2g), and five times larger in the mosquito Aedes nearcticus (0.004g) (Weis-Fogh and Jensen (1956)). During true hovering on the spot, the body does not move forward at all and is exposed only to the vertical wind induced by the moving wings. As we shall see, hovering is also the type of flight during which the wings must be twisted at the highest angular velocities when they are pronated and supinated. The small forward speed and the high rate of wing twisting both tend to increase the relative importance of unsteady flow patterns. It is therefore of particular interest to analyze hovering from the point of view of aerodynamics and energetics. In addition, hovering and slow flight characterise the vast majority of flying animals, the Pterygota. Since late Devonian, about 350 million years ago, this group has been so successful in exploring the new environment created by the emergence of tall terrestrial plants that they represent three quarters, or 750,000, of all know animal species, fossil and living. This figures illustrates the extraordinary evolutionary success of active flapping flight which has been adopted as the principal mode of locomotion by birds of mass up to 10 kg, bats and by insects as small as 1 μg.

An attempt will be made to synthesize our present knowledge and to indicate future developments. The timing is fortunate partly because some important aspects of the energetics of fast forward flight have been analyzed recently (Pennycuick, (1968), (1969), 1972); Tucker (1973)) and partly because new studies of hovering flight have offered more insight and revealed novel aerodynamic mechanisms of general interest (Weis-Fogh, (1972), (1973); Lighthill, (1973)). In order to avoid technical language and mathematical expressions as far as possible, only the most essential physical relationships are described and readers with special interest must consult the original literature and the succeeding contributions to this Symposium.

## Power Supply

Lighthill (1974) emphasized that effective flapping flight has developed independently at four different times in the course of evolution, first in insects, later in reptiles and then in birds and bats. Whether the animal is large (10 kg) or tiny (1 μg), the mechanical power is derived from the same type of tissue, striated muscle. I have recently discussed the available information about the mechanical power output from birds, bats and insects and found that the power is independent of size and usually ranges between 50 and 200 $W \cdot kg^{-1}$ muscle depending on the type of flight. These are very large figures for living systems and correspond to a chemical power output (metabolic rate) of at least 250 to 1000 $W\ kg^{-1}$ (Weis-Fogh (1975)). Active sustained flight therefore always depend on aerobic metabolism while the design of the animals and the differences in their metabolic pathways are immaterial in this context. Essentially, all flying creatures are powered by an aerobic engine which can deliver up to 200 W per kg muscle irrespective of the size of the animal. The engine usually represents 0.2 of the airborne mass but this ratio varies from 0.1 to 0.3, so that the mechanical power available to the flying animal varies from 5 to 60 W per kg airborne mass or 0.5 to 6 W per Newton lifted (W/N). The design and mechanisms must comply with these limitations and no obvious exceptions are known at present.

## Drag or Lift?

Any actively flying animal must accelerate air downwards in order to counteract its own weight. This could be done either by using the drag of the wings, as the oars are used when rowing, or by means of the lift mechanism which is much less expensive in energy, at least in large and medium-sized animals. When we compare birds, bats and insects of different size, from a wing span of over 2 m to 1 mm, the flight contours are surprisingly similar. This means that small forms have smaller wing loadings than large forms; some examples are given in Table I. A natural consequence would be that below a certain size the wings may be used not as aerofoils but as 'oars' which only depend on drag. At this point another effect of size must be considered, Reynolds number (Re).

When a volume of air is accelerated its mass gives rise to inertial forces but at the same time there will be internal shearing forces caused by its viscosity. Reynolds number is the ratio between the inertial and the viscous forces in a particular flow

TABLE I

Wing loadings in flying animals (from Weis-Fogh, (1973)), expressed as the total weight of the animal divided by the sustaining wing area ($N/m^2$). One asterisk (*) indicates that most of the species hover in the normal way while two asterisks (**) imply that slow forward flight and hovering involve unusual aerodynamic mechanisms.

| | range ($N/m^2$) |
|---|---|
| *Small bats: | 10-20 |
| Birds: | |
| medium sized and large | 30-170 |
| small passarines | 20-50 |
| *hummingbirds | 20-30 |
| *swifts, swallows, bee-eaters | 13-25 |
| Insects: | |
| *large Coleoptera, Lamellicornia | 12-40 |
| *large Hymenoptera, Vespoidea & Apoidea | 8-44 |
| *large Diptera, Brachycera & Cyclorrhapha | 5-20 |
| *large Lepidoptera, Sphingidae | 4-12 |
| *medium sized Lepidoptera, Noctuidea | 3-6 |
| *many small Coleoptera | 1-6 |
| **true hover flies, Syrphinae | 3-11 |
| **Odonata, dragonflies | 1-6 |
| ***Drosophila virilis* (wing length 3 mm) | 3-4 |
| ***Encarsia formosa* (wing length 0.6 mm) | 1-2 |
| **Lepidoptera Rhopalocera, butterflies | 0.4-2 |

situation. It is proportional both to the size of the wing, as measured by a characteristic wing width or chord, and to its velocity relative to the undisturbed air. It therefore decreases with decreasing size and some examples are given in Table II. This means that the viscous forces and the drag increase relative to the inertial forces and the lift when the animal becomes small. The lift is usually the dominant force for (Re) exceeding 100 but in many tiny insects (Re) ranges between 1 and 10 (Horridge, (1956); R. A. Norberg, (1972a)), so that the drag will dominate and the usual steady-state lift becomes insignificant (Thom and Swart, (1940)). This and the decreased wing loading both indicate that small or lightly loaded insects may use a drag mechanism for flight rather than the lift principle. However, there are some arguments against this.

## TABLE II

Examples of the calculated average coefficient of lift $C_L$ during normal hovering from (Weis-Fogh, (1973)). The values in brackets refer to species or groups which turned up to make use of unusual mechanism and cannot be treated according to the simple steady-state theory. An asterisk (*) means that the insects do not perform normal hovering.

| | | airborne weight ($10^{-3}$N) | Reynolds number (Rd) | $C_L$ |
|---|---|---|---|---|
| Bats: | *Plecotus auritus* | 90 | 14000 | 1.3 |
| Hummingbird: | *Amazilia fimbriata* | 50 | 7500 | 2.0 |
| Coleptera: | *Melolontha vulgaris* | 5.9 | 4700 | 0.6 |
| | *Amphimallon solstitialis* | 2.8 | 3000 | 0.7 |
| | *Heliocopris* sp. | 125 | 23000 | 0.5 |
| Lepidoptera: | *Pieris napi* | 0.4 | 1400 | (2.2) |
| | *Sphinx ligustri* | 15.7 | 6300 | 1.2 |
| | *Manduca sexta* | 20.8 | 6700 | 1.2 |
| | *Macroglossum stellatarum* | 2.8 | 2800 | 1.1 |
| Hymenoptera: | *Vespa crabro* | 5.9 | 4200 | 0.8 |
| | *Bombus terrestris* | 8.6 | 4500 | 1.2 |
| | *Apis mellifica* | 0.98 | 1900 | 0.8 |
| | *Encarsia formosa* | $25 \times 10^{-5}$ | 15 | (5.0)† |
| Diptera: | *Tipula* sp. | 0.28 | 770 | 0.8 |
| | *Aedes aegypti* | 0.01 | 170 | 0.6 |
| | *Eristalis tenax* | 1.5 | 2000 | 0.9 |
| | *Drosophilia virilis* | 0.02 | 210 | 1.0 |
| | **Syrphus* spp. | 0.2-0.3 | 500 | (2 to 3) |
| Odonata: | **Aeshna grandis* | 8.4 | 1750 | (2 to 3) |

† Revised estimates, for more accurate figures see Ellington (1974).

First, we have never yet observed a flapping animal which uses drag rather than lift, neither the lightly loaded plume moths (Microlepidoptera; R. A. Norberg, (1972b)) nor the small chalcid wasp Encarsia formosa (wing length 0. 6 mm; see later; Weis-Fogh, (1973)) but many more cases need to be examined. Second, the drag principle is difficult to apply when the wings remain totally immersed in the fluid, as in the case with wings in air but not with rowing oars where the effective stroke is in water and the return stroke in air. (When a man is sculling a dinghy from the stern by means of a continuously submerged oar he is in fact using the lift principle.) In order to produce a net force the drag must of course be large during the effective stroke and reduced during the return stroke. This is feasible provided that there is a difference in speed between the two half strokes or if the extended wings could be folded or bent extensively during one half of the stroke. The latter mechanism is probably of limited use at low Reynolds number because the drag of a stiff extended wing of an insect tends to become independent of its actual shape and of the angle of attack of the wing and is determined mainly by its length. In general, we approach conditions in fluid dynamics where the flow tends to become reversible and many interesting problems will undoubtedly be found within the range (Re) 1 to 100 where good experimental facts are hard to come by. It represents a 'twilight' zone.

The extremely small Ptiliidae (Coleoptera), Trichogrammatidae and Myrmaridae (Hymenoptera) have wings which are only 0. 07 to 0. 2 mm long and consist of a 'stem' surrounded by a flat marginal brim of hairs (Horridge, (1956)). As pointed out by R. A. Norberg (1972a), they must operate at a (Re) of about 1 and this virtually excludes any lift action, probably even the newly discovered fling mechanism to be described later. Another possibility not hitherto suggested in the literature is an acceleration of the air caused by a twisting movement of the wing which is propagated from base to tip as a consequence of 'delayed elasticity' (Weis-Fogh, (1973), see later). If this turns out to be the case, these tiny insects 'swim' actively by means of a screw-like action reminiscent of that of an undulating membrane. However, we do not have any direct evidence for this as yet and Kuethe (1974) is suggesting another solution, also without experimental data.

## Nature of the Aerodynamic Lift

If a solid cylinder is placed horizontally in still air and spins round its axis in the direction indicated in Figure 1A, the surrounding air is set in uniform motion due to viscous effects. At the surface itself the air rotates with the same speed and direction as the solid surface and the speed decreases linearly with the distance from the cylinder. The result is a steady cylindrical vortex of air 'bound' to the cylinder but this does not in itself imply any other forces than a small drag against its rotation. If, however, a horizontal wind blows from left to right, the resulting air velocities on the upper side will become increased and become decreased on the lower side. This causes the pressure to decrease above the cylinder and to increase beneath it due to the usual Bernoulli effect. The cylinder will now experience an aerodynamic force in the transverse vertical direction which we call the lift. The phenomenon observed with the spinning cylinder is known as the Magnus effect. Figure 1A shows the resulting streamlines when the horizontal wind is superimposed upon the vortex. Note that the air behind the cylinder has been accelerated downwards.

Lift and circulation. The magnitude of the lift L is determined only by the translational wind velocity $v_t$ and a property of the vortex called its circulation $\Gamma$. The circulation is the same at all distances from the cylinder surface and can easily be calculated as the product of the surface speed $\omega r$ and the circumference $2\pi r$, $\Gamma = 2\pi \omega r^2 (cm^2/s)$, where $\omega$ is the angular velocity of rotation and r is the radius of the cylinder.

In other cases it may be difficult to estimate $\Gamma$ but whether we are dealing with a cylinder or any other long body like a wing, the fundamental relationship holds:

$$L/\text{unit length} = \rho v_t \Gamma , \qquad (1)$$

where L is lift, $\rho$ the mass density of the air and $v_t$ the translational wind velocity. This applies to an infinitely long wing and has to be modified due to the formation of tip vortices in a real wing because air will move from the high-pressure region below into the low-pressure region above the wing at the tip region. This gives rise to a loss in usable flow and energy which manifests itself in less lift, higher drag and the so-called induced power loss (see later). Because the loss is related to the pressure differential, i. e. to the actual lift produced, it can sometimes be calculated with fair precision, as first done by Prandtl for a wing with elliptical pressure distribution along its span. Provided a circulation is established in some way or other, the wing will experience a lift when exposed to a wind, in accordance with equation (1). But how is the circulation set up in the first place? The answer is essential for an understanding of several aspects of animal flight.

Bound and starting vortex. We return to the infinitely long aerofoil seen in transverse section in Figure 1, i. e. to the simplified case of two-dimensional flow. Let us first assume that the aerofoil is immersed in a fluid which has mass but no viscosity, i. e. in an ideal fluid. It is then possible to calculate the flow pattern but since a wing cannot generate (or destroy) vorticity and circulation in an inviscid fluid, the calculated ideal flow in Figure 1B (irrotational or potential flow) results in zero lift and drag. This was one of the dilemmas in classical fluid dynamics. It is seen both that the fluid is not directed downwards behind the wing and also that there are some discontinuities near to the trailing edge, leading to large shearing forces in a real fluid like air or water. If, however, the pure rotational flow in Figure 1C is superimposed on the irrotational flow in Figure 1B, the result is the orderly 'streamlined' flow in Figure 1D which corresponds to the observed flow round an aerofoil after it has been in uniform motion relative to the fluid for some time, i. e. after it has reached a steady state. The streamlines are now directed downwards behind the profile and lift is produced.

The problem of creating the bound vortex with the circulation round the aerofoil was solved by Prandtl in 1912, the main point being that in a real fluid of even very small viscosity like air, the flow in the boundary layer near the solid surface must be influenced by viscous forces, particularly near to the trailing edge in Figure 1B. When an aerofoil starts from rest or when its angle of attack is so small that no lift is produced and the angle is then suddenly increased, these viscous forces will induce a vortex behind the profile, the starting vortex, which has the opposite sense of that seen in Figure 1C. Now, it is a fundamental rule in fluid dynamics that no vortex can be created unless a vortex of the opposite sense and strength is set up simultaneously. In our case this is the bound vortex in Figure 1C which causes the lift.

At the start of movement or when the lift changes we now have to consider two opposite vortices close to each other, the starting and the bound vortex, and they interact destructively in proportion to their distance apart. At the start of the streaming the net circulation round the aerofoil will therefore only be about half as large as later on when the starting vortex has been left well behind. This interaction and delay in building up of lift is called the Wagner effect and represents an unavoidable unsteady phase in the action of an ordinary aerofoil. Conversely, when a flapping wing stops and the lift is reduced at the end of one half-stroke, the bound vortex must be shed and become a 'free' vortex which will interact with the new starting and bound vortices which initiate the return stroke (Weis-Fogh, (1972)). Some of these phenomena will be discussed by Ellington (1974) in relation to a small insect.

Ordinary aerofoil action. An ordinary wing or aerofoil is then a solid body which is shaped and placed relative to the streaming air in such a manner that viscous forces create a starting vortex near to its trailing edge and therefore a bound vortex of the opposite sense round its profile. The starting vortex is left behind and the

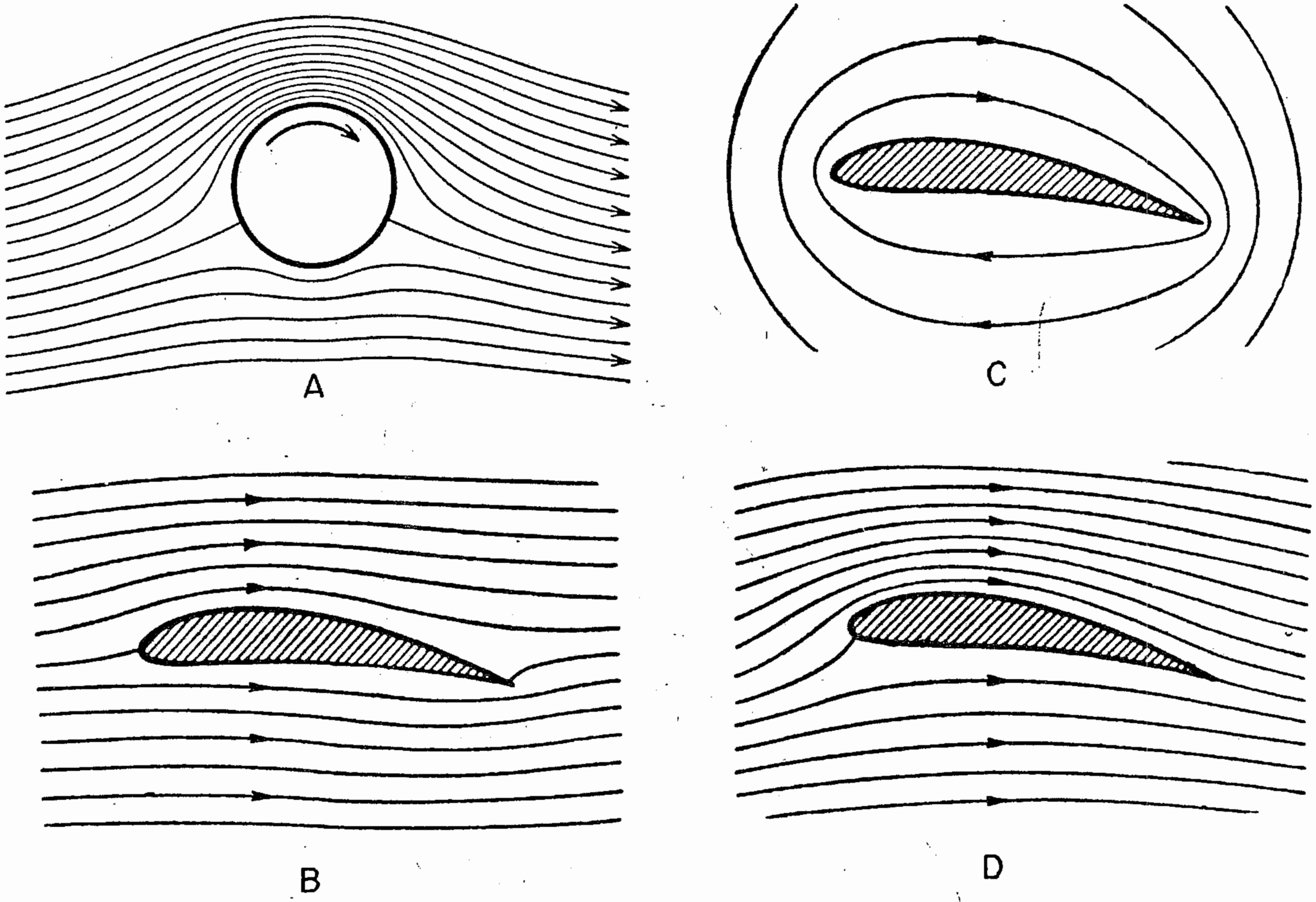


Figure 1. Two-dimensional flow and circulation. (A) a spinning cylinder placed in horizontally streaming air or water, the Magnus effect. (B) the flow round an aerofoil in an ideal fluid (irrotational or potential flow). (C) pure rotational flow, and (D) the real steady-state flow in a real fluid where (B) and (C) are combined.

steady-state bound vortex is maintained by the continuous shedding of small vortices; this gives rise to a small drag component. In addition, friction in the boundary layer close to the surface represents a skin drag; together the two are called the profile drag. Furthermore, a wing of limited span also experiences an induced drag caused by the tip vortices, as already explained.

After the flow has become steady it is customary to express the lift in terms of the coefficient of lift $C_L$ rather than in terms of circulation. The two are related as follows,

$$L/\text{unit length} = \rho v_t \Gamma = \frac{1}{2} \rho v_t^2 c C_L, \tag{2}$$

where $c$ is the width or chord of the wing section in question. Because of the increased importance of viscous over inertial forces at low Reynolds numbers it is understood intuitively that both the creation of a starting vortex and the maintenance of a bound vortex become expensive in energy and difficult to achieve. The result is that the lift decreases relative to the drag. The maximum $C_L$ for a Drosophila wing at (Re) = 200 is about 0.9 (Vogel, (1967)), for the forewing of a locust at 2000 it is 1.3 (Jensen, (1956), while it may reach 2.0 or even more in bird wings operating at 5000 or above. We may therefore use the calculated value of $C_L$ as an indicator of whether ordinary steady flow is sufficient to explain a given flight performance or not (Osborne, (1951); Weis-Fogh and Jensen, (1956); Bennett, (1970); Weis-Fogh, (1972)), but more detailed investigations are needed in order to estimate the true role of steady versus unsteady flow. This is particularly relevant to flapping flight where the lift changes rhythmically throughout the wingstroke. The extreme is reached when the animal hovers because the lift then drops to zero at each end of the wing path. In the case of ordinary aerofoil action, a hovering animal must experience the Wagner effect during an appreciable part of the wingstroke. This need not be as serious a problem as one may think at a first glance because stalling is also delayed and $C_L$ can be increased above the usual stalling limit for brief periods of time so that the two effects tend to cancel each other, but extra power is of course needed (Hertel, (1966); Weis-Fogh, (1972)).

We shall now discuss active flapping flight in the light of these elementary considerations, starting with the simplest and best known cases.

## Fast Forward Flight

Although the majority of insects and some small birds and bats use hovering and slow flight when feeding and courting, all birds and bats and some insects make extensive use of fast forward flight. The air speed $\underline{V}$ of the body then corresponds to 50-300 body lengths per second. This is a complicated mode of forward transport because the wind forces acting on the individual wing segments vary from base to tip as the square of the vector sum of the horizontal velocity $\underline{V}$ and the flapping velocity relative to the body. It is therefore not surprising that there is no exact theory for this type of flight but only approximations relating to certain aspects, including the generalized equations of Osborne (1951) and the approximate expressions for the aerodynamic power components in birds derived by Pennycuick (1968), (1969) and recently revised by Tucker (1973). All theories applied so far rest on the assumption that the principles of steady flow dominate the pattern and this is indeed likely to be the case during forward flight, as discussed elsewhere (Weis-Fogh and Jensen (1956); Lighthill (1974)). However, we have only one complete experimental study of fast forward flight, namely Martin Jensen's analysis (1956) of the desert locust which offers direct and details insight into the aerodynamic processes. This and the recent studies of bird flight make it possible to extend his results and compare them with the power requirements of other animals in relation to the speed and cost of transport. The latter is particularly relevant to an understanding of migrating insects.

Horizontal flight of the desert locust. An average *Schistocerca gregaria* has a mass of 2g and the ratio between flapping and forward speed is about 1, i. e. appreciably larger than in most birds. In a detailed wind-tunnel study we first established the normal range of variation of the flight parameters (Weis-Fogh (1956)) and then Martin Jensen (1956) analyzed the kinematics, aerodynamics and energetics of a few selected examples on the basis of our stroboscopic slow motion films. Figure 2 shows the wing movements during the downstroke (A) and upstroke (B) when the insect flew horizontally (vertical force equals weight) at a forward speed of 3. 5 m/s. During the downstroke the leading edge of both wings is twisted downwards, i. e. pronated and, in addition, a flap at the trailing edge of the forewing is tilted downwards when it passes the horizontal position. During the upstroke, the leading edge is supinated (cf. frames 12 and 13) and the flap is bent upwards (frame 14), creating the so-called Z-profile. The exact movements of the wings relative to the air were computed and Figure 3 is an approximate visual image of the forewing. In both cases and in both wings, the individual wing profiles meet the air under small positive angles of attack during the downstroke and almost edgewise during the shorter upstroke. This is consistent with an ordinary and orderly aerofoil action whereby an aerodynamic lift is produced perpendicular to the tangent of the path through the air. The resulting force points upwards and provides thrust and a large vertical force during the downstroke and a small vertical force and some negative thrust during the upstroke.

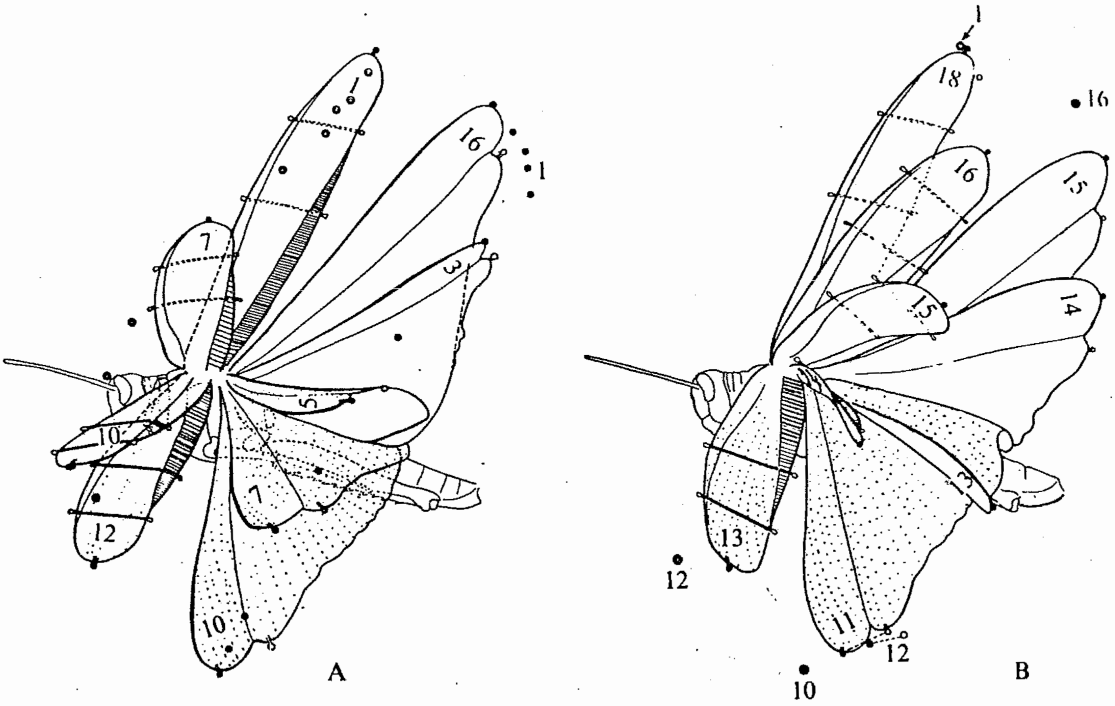


Figure 2. The wing movements of a desert locust (Schistocerca gregaria) flying horizontally at a speed of 3.5 m/s (from Weis-Fogh, (1973)). (A) downstroke and (B) upstroke.

Indeed, this was the mechanism proposed by Otto Lilienthal (1889) and illustrated in Figure 4, redrawn from his famous monograph on flying storks which heralded the era of modern aeronautics (and his own death in a crash).

Martin Jensen then measured the lift and drag of the actual locust wings in a special wind tunnel in which he established a smooth velocity gradient from base to tip almost similar to that observed during real flight but, of course, under steady conditions of flow. On the assumptions that steady principles apply he could compute the fluctuating vertical and horizontal forces which the wings impart upon the body and compare them with the average forces measured in the aerodynamic balance when we exposed the film. Within a few per cent the two sets of results agree and it is therefore justified to conclude that fast forward flight of locusts depends on a succession of steady flow situations. He also took into account the mutual effect of the circulation round the two pairs of wings; it is small but significant. Another point was the effect of the new starting vortex which must be created between frames 18 and 1 in Figure 2. Under the worst conceivable

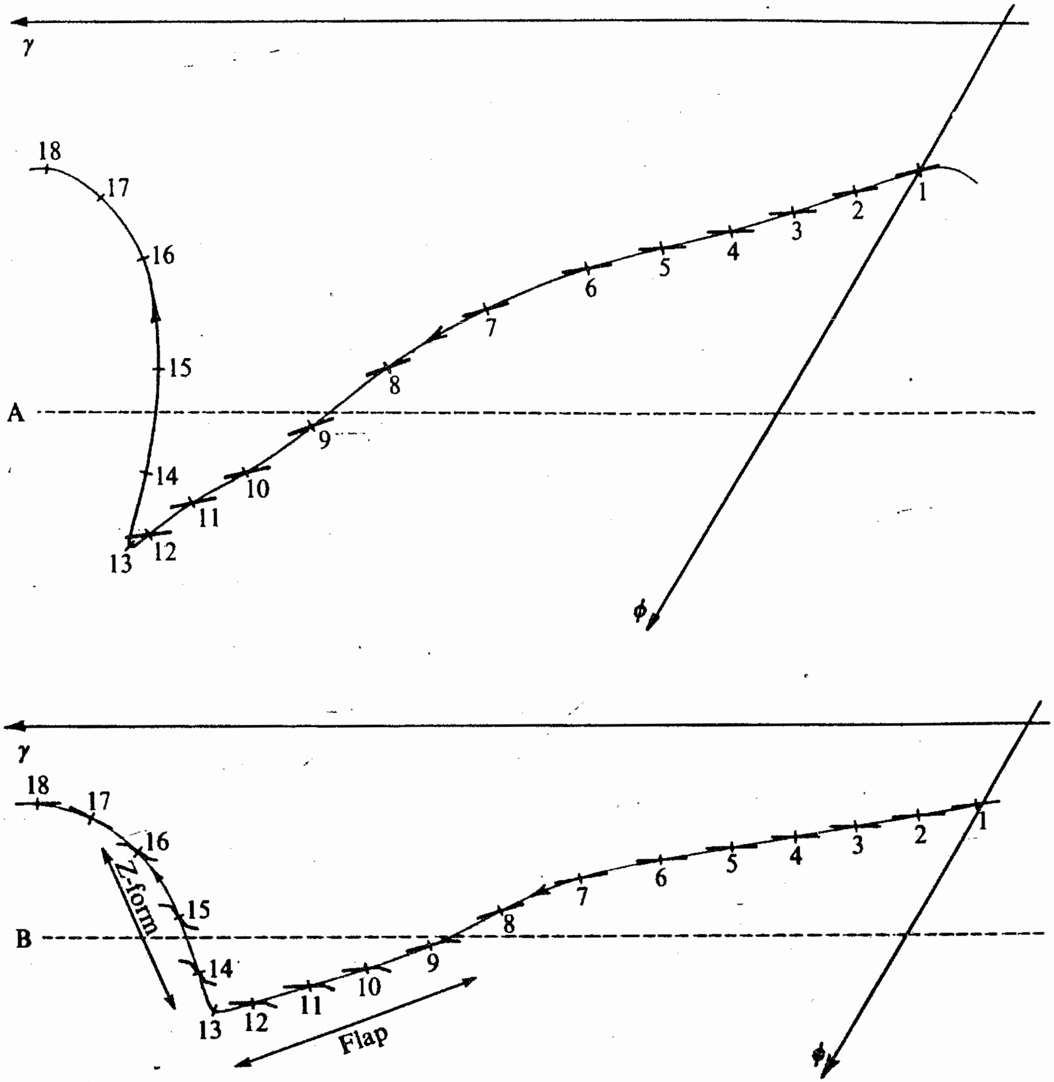


Figure 3. The movements of the wing chord near to the tip (A) and at the middle of a locust forewing (B) in relation to the air. The two-dimensional diagram is in fact the unfolded surface of the elliptical cylinder upon which the mid-points of the two chords travel, disregarding small forwards and backwards movements. (Redrawn from Jensen, (1956)).

conditions the effect would amount to less than 10% of the total, probably to 5% reduction in lift, and this also applies to fast flying hover flies and mosquitoes.

We are therefore able to proceed with the anlysis of power requirements both in this and in other insects provided that the

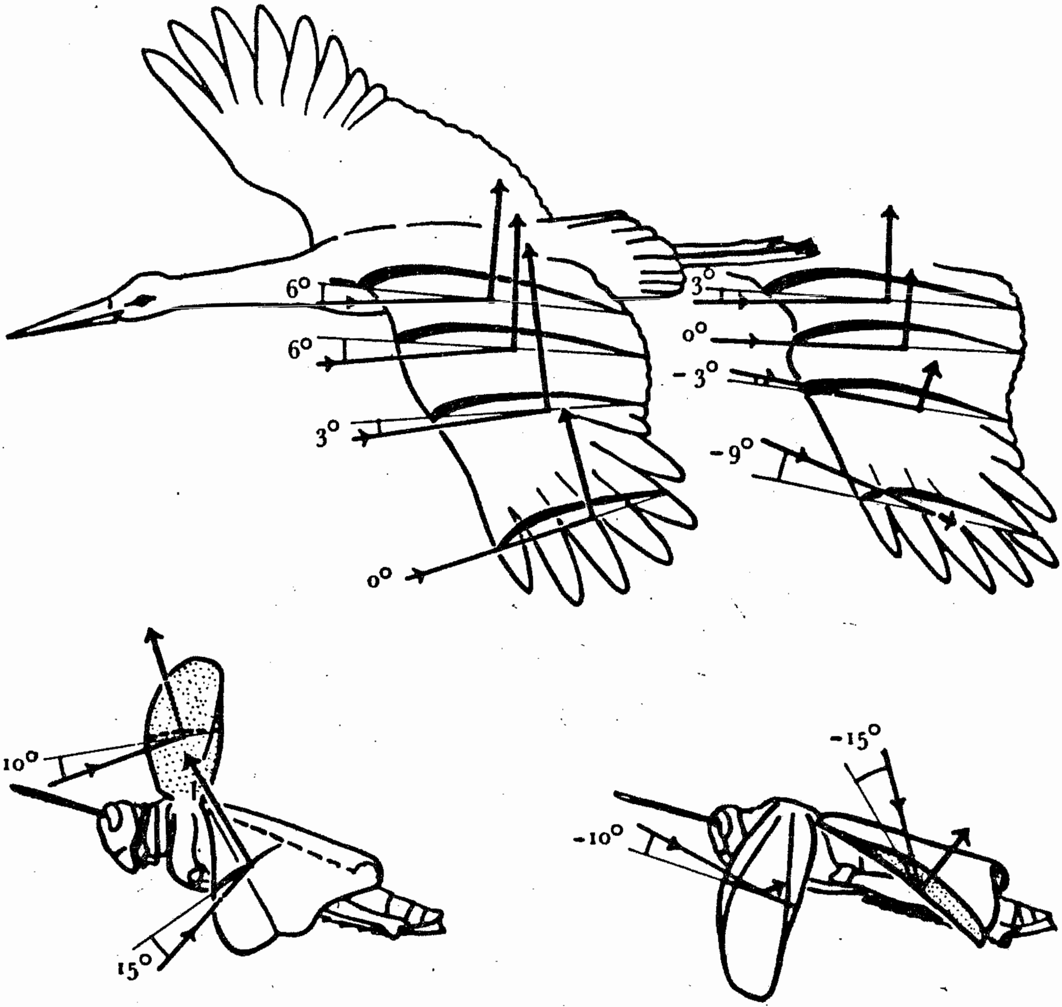


Figure 4. The main force component during fast forward flight in the stork (from Lilienthal, (1889)), and the desert locust (from Weis-Fogh, (1961)). The downstroke is shown to the left-hand side and the upstroke to the right.

wings are in fact moved in such an orderly fashion. During the major part of the wingstroke, Nachtigall (1966) found a similar type of movement in the blow fly Phormia regina but with an apparently disturbing difference at the top and at the bottom of the stroke. Here the rate of change in wing twist is large and the angles of attack are very high (Figure 5). This may indicate important unsteady periods to be discussed later.

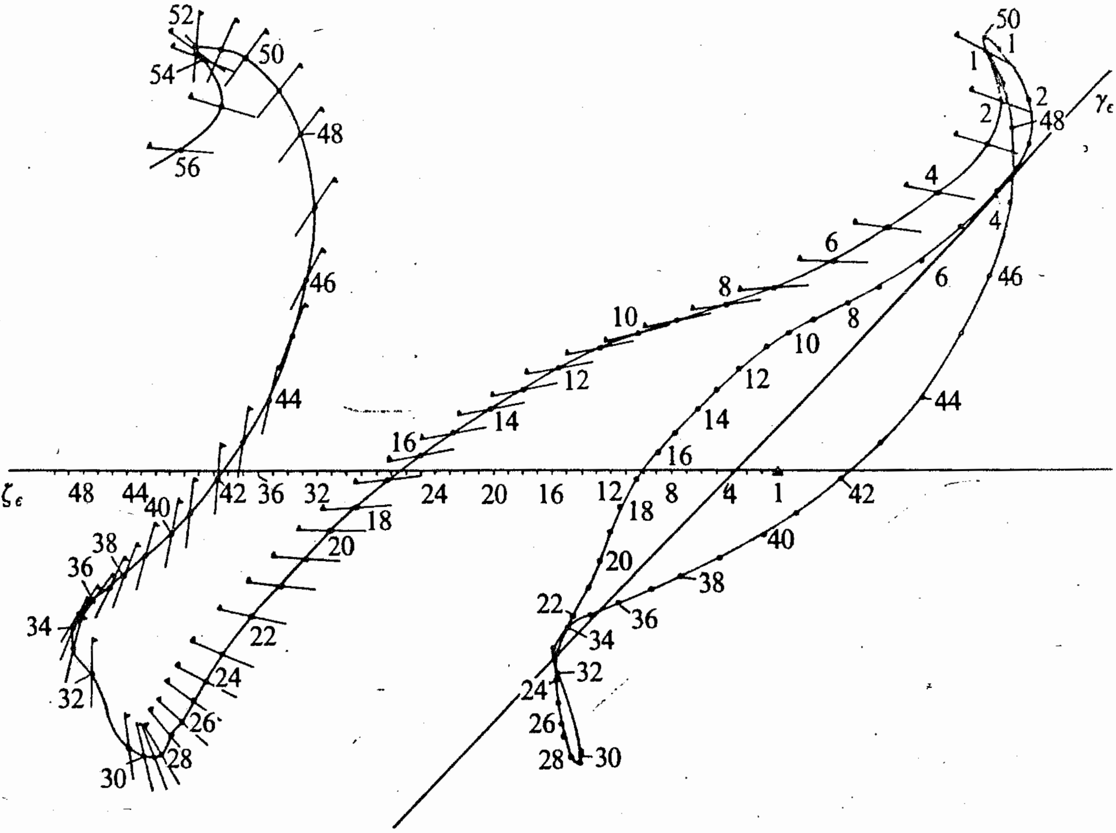


Figure 5. A diagram similar to that of Figure 3 but for the large Dipteran fly Phormia regina, flying at 2. 8 m/s in a wind tunnel. (Redrawn from Nachtigall, (1966)).

Aerodynamic power and speed in locusts. In the example just mentioned (Jensen, (1956)) the power expended against wind forces (energy per unit time) as determined directly from the movements amounted to 0. 86 W/N at the speed of 3. 5 m/s; this is the aerodynamic power per unit vertical force produced, or the specific aerodynamic power $P_a^*$. In another locust flying at 3. 2 m/s and lifting 162% of its body weight, the specific power was 0. 82 W/N, the average being 0. 84 W/N at these speeds.

It is of more than trivial interest to compare these results with the power calculated according to the procedure of Pennycuick (1969) and Tucker (1973), partly because it enables us to make predictions about migrating locusts and partly because the strength and shortcomings of the theory become obvious. In insects, we need not incorporate the increased work done by the circulatory and respiratory systems during flight (Tucker, (1973)) because these components are negligible (Weis-Fogh, (1967)) compared with the work done against the air and against inertial forces due to the oscillating wing mass. As to the inertial power needed to oscillate the wings without doing any aerodynamic work, it is probably true that fast flying birds make use of the kinetic energy of the wings for aerodynamic work, as assumed implicitly in the theory (Pennycuick, (1969); Tucker, (1973)) although this apparently does not apply to hovering hummingbirds (Weis-Fogh, (1972)). In insects, the fast flying locust also uses the kinetic energy to some extent (Jensen, (1956)) but the major part is stored in an elastic system in its thorax and paid back with high efficiency later during the wingstroke (Weis-Fogh, (1961), (1972), (1973)). We may therefore confine ourselves to the specific aerodynamic power $P_a^*$ which in insects can be compared directly with the metabolic rate during flight. The ratio between the two is a measure of the mechanical efficiency of the flight system.

Since power equals drag times velocity, the method of Pennycuick (1968, 1969) is to split up the components into three independent parts which are then summed. Let the air speed of the animal be $V$. The drag $D$ of the body plus the appendages is the parasite drag and is proportional to $V^2$, similar to the lift in equation (2). This means that the parasite power is $DV^3$. This is the uniformly increasing curve in Figure 6. As already mentioned, the flapping wings exert a drag whether they produce any lift or not. It is not a simple function of $V$ and depends on the wingstroke frequency and the stroke angle. However, detailed computations on the actual wing movements of a pigeon flying horizontally at different speeds showed that the profile power was almost constant and independent of the speed (Pennycuick, (1968)) and this we shall assume to be the case also in locusts, as seen by the horizontal straight line in Figure 6. In the present treatment, there is no need to introduce the modifications caused by Reynolds number (Tucker, (1973)) because we are dealing with a first-order approximation and the drag components were measured at an intermediate value of Reynolds number.

The third major power component is caused by the tip vortices which are shed continuously and give rise to the induced drag already mentioned. During moderate to high forward speeds the induced power caused by this component has the form

$$\text{induced power} = 2G^2/(\pi\rho b^2 R' V), \qquad (3)$$

where $G$ is the weight of the horizontally flying animal and equals the average vertical force, $b$ is the wing span, and $R'$ is a correction factor for the wing disc area, $\pi b^2/4$, through which air is accelerated downwards. Note that the power decreases when the speed increases. The expression applies not to a flapping animal but to a convertional fixed-winged monoplane with elliptical

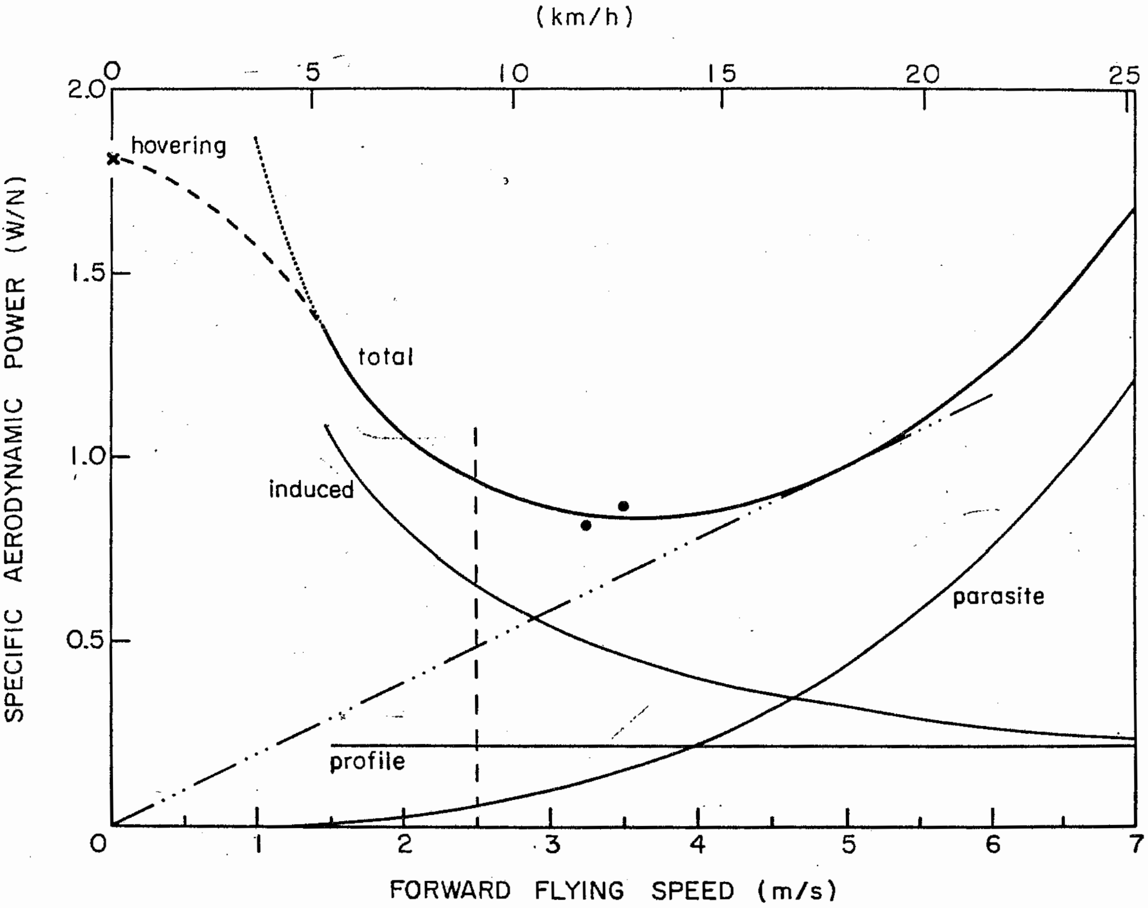


Figure 6. The relationship between specific aerodynamic power (W/N, ordinate) and horizontal flying speed (m/s, Abscissa) in a desert locust. The three curves for parasite power, profile power and induced power are estimated either from measured parasite and profile drag (Jensen, (1956)) or calculated according to Pennycuick (1969) but with correction factors based upon true flapping flight, as explained in the text. The tangent from the origin to the upper thick curve indicates the speed for minimum cost of transport. The two filled circles are values found independently by experiment (Jensen, (1956)).

pressure distribution, or to a helicopter; in practice the correction factor for well-designed aircrafts varies from 0.90 to 0.95. Tucker (1973) reduced it to 0.7 in birds because of the width of the body relative to the total span. However, the authors on bird flight did not take into account (a) that the actual speed of the flapping wings is larger than $\underline{V}$ and tends to reduce the power, (b) that lift is produced mainly during the downstroke in real birds and insects so that the effective $G^2$ is higher and tends to increase

R', (c) that the downstroke usually lasts longer than the upstroke and, most important, (d) that the aerodynamic lift is not vertical except when the wings happen to pass the horizontal position; the vortex sheet created by the tip vortices is therefore not horizontal. The last point is particularly important when the stroke angles are as large as in locusts and other insects. Without giving the details here, I have calculated the correction factor for a desert locust on the basis of all the known details of the wingstroke as analyzed in the wind tunnel, (Jensen, (1956); Weis-Fogh, (1956)). The result was R' = 0. 47, or 0. 5, and this is the value used for the steadily decreasing curve in Figure 6. It should be noted that a real locust cannot lift its body weight at speeds lower than 2. 5 m/s indicated by a vertical line (Weis-Fogh, (1956)) because its wings then begin to stall (Weis-Fogh and Jensen, (1956)). Finally, the theoretical power needed for true hovering, if this were possible for the insect, would be too small if estimated according to Pennycuick (1969) who estimated it directly from the momentum theorem applied to an actuator disc of 100% efficiency, and both the profile power and the induced power are therefore not included. In the hummingbird this increases the figure by a factor of 2 and in Drosophila by 4 (Weis-Fogh, (1972). In Figure 6, I have therefore multiplied the calculated value by 2.

The summed thick curve in Figure 6 serves to bring the transport performance of fast-flying insects into a form comparable to that of birds and aeroplanes. The two values found by Martin Jensen from the direct anlysis (1956; solid circles) are seen to be in remarkably good agreement with the indirect approach by Pennycuick provided that the correction factors are introduced as explained. This justifies the extrapolation to higher speeds. A number of interesting features then emerge. As pointed out by Pennycuick (1969), the U-shaped curve is a consequence of the induced power being inversely proportional to the speed and the fact that the parasite power increases as $V^3$ so that it is negligible at small speeds. The minimum specific aerodynamic power for steady horizontal flight in locusts (0. 84 W/N) occurs exactly at the speed for steady long-range flights in the laboratory, about 3. 5 m/s (Weis-Fogh, (1956)); this is also likely to be true of locusts flying freely in nature during long continuous migrations. In contrast, the speed for minimum cost of transport is higher and range from 4. 5 to 5. 5 m/s, as seen from the tangent drawn from the origin of the graph. This might explain why direct measurements of migrating Schistocerca gregaria in nature have resulted in values ranging mainly between 4 and 6 m/s (Waloff, (1972)) because most observations were obtained during intermittent flight when the locusts were disturbed and probably tried to escape quickly. However, from an aerodynamic and energetic point of view there is no reason why locusts should not exceed 7 m/s for short periods since they can double the metabolic rate relative to the rate needed for sustained flying at 3.5 m/s (Weis-Fogh, (1964). At the latter speed the metabolic rate is 7.7 W/N so that the overall metabolic efficiency during long migrations is 0.84/7.7 = 0.11.

If suitable methods for correcting the 'disc area' are introduced, there is therefore good reason to believe that Pennycuick's procedure can be applied to other migrating insects with advantage, for instance to the moths of army worms in East Africa, dragonflies, etc. It is also of interest to compare the minimum aerodynamic power $P_a^*$ in insects and birds. According to Tucker (1973) it varies from 1.9 W/N in the budgerigar (mass 35 g) to 1.0 W/N in the laughing gull (322 g), 1.4 W/N being the average value calculated from non-passarine birds ranging in mass from 3 to 10000 g. This is the same order of magnitude as found in locusts. It reflects what appears to be a general rule, namely that the aerodynamic power expenditure of flying animals tends to be proportional to the body weight throughout the Animal Kingdom. This also applies to hovering species (Table III) and of course reflects the properties of the wing muscles already discussed.

## Normal Hovering

A different approach based upon an analytical model of the moving wings has recently been proposed by Weis-Fogh (1973) and has resulted in a reasonably complete theory for hovering flight. Essentially it consists of estimating the lift and drag forces at each instant, using steady-state lift/drag diagrams of known wings, and integrating the results over a complete wingstroke. In this way the induced and the profile drag are incorporated simultaneously. One can then quickly calculate the average lift coefficient $C_L$ needed to hover on the spot and compare it with the maximum values to be expected from the type of wings and the Reynolds number involved. At present, this can only be done in a few cases because we lack information about the lift/drag relationship, particularly at low (Re). Only reliable flight data from freely flying animals were applied but one had to assume that the animal performed normal hovering with wings beating sinusoidally and in an almost horizontal plane. This is in fact true for the majority of animals, and is illustrated in Figure 7.

Coefficient of lift. With the exception of the true hover flies (Syrphinae) and the dragonflies (Aeshnidae) in Table II, all the animals listed perform normal hovering. The general result is that the average coefficient of lift is sufficiently small for the flight to be explained on the basis of steady-state aerodynamics. This is true also of the heavily loaded lamellicorn beetles hitherto considered exceptions (Osborne, (1951); Bennett, (1966), (1970))

TABLE III

The calculated aerodynamic power output per unit body weight lifted during normal hovering (the specific power $P_a^*$, in W/N), the dynamic efficiency $\eta$, and the measured metabolic rate if known (M, in W/N). Same examples as in Table II with the exclusion of the unusual cases. (From Weis-Fogh, (1973)).

| | | $P_a^*$ (W/N) | $\eta$ | M (W/N) |
|---|---|---|---|---|
| Hummingbird: | *Amazilia fimbriata* | 2.6 | 0.51 | 24 |
| Coleoptera: | *Melolontha vulgaris* | 2.7 | 0.41 | — |
| | *Amphimallon solstitialis* | 2.3 | 0.47 | — |
| | *Heliocopris* sp. | 4.7 | — | — |
| Lepidoptera: | *Sphinx ligustri* | 1.8 | 0.49 | — |
| | *Manduca sexta* | 1.4 | 0.47 | — |
| | *Macroglossum stellatarum* | 1.7 | 0.33 | — |
| Hymenoptera: | *Vespa crabro* | 2.1 | 0.31 | 12 |
| | *Bombus terrestris* | 3.9 | 0.51 | — |
| | *Apis mellifica* | 2.1 | 0.30 | 35 |
| Diptera: | *Tipula* sp. | 2.1 | 0.39 | — |
| | *Aedes aegypti* | 3.3 | 0.70 | 12 |
| | *Eristalis tenax* | 2.3 | 0.34 | 14 |
| | *Drosophila virilis* | 2.3 | 0.95 | 14 |

and of bees and wasps. However, there are some notable exceptions for which the results are shown in brackets, namely butterflies (Rhopalocerca), the tiny chalcid wasp *Encarsia formosa*, *Syrphus* and *Aeshna* species. We shall return to them later.

From these results it would be wrong to conclude that steady flow principles are the *only* ones of importance during normal hovering but with some confidence we may assume that they represent the major mechanism in most animals, even quite small ones.

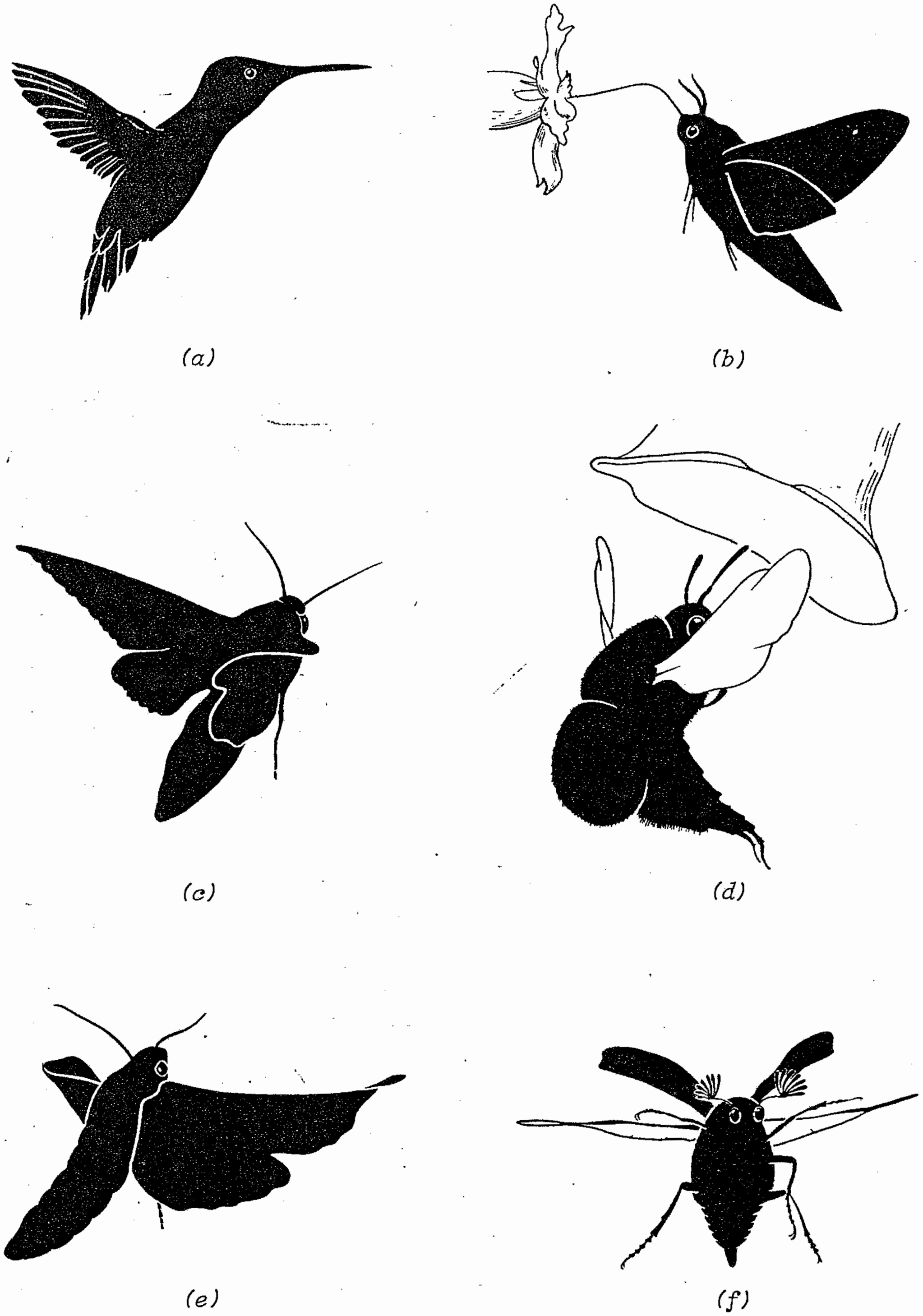


Figure 7. Examples of normal hovering as indicated from flash photographs; (A) hummingbird, (B) sphingid moth Deilephila, (C) hawk moth Manduca, (D) bumble bee Bombus, (E) Manduca during quick escape, and (F) cockchafer Melolontha. (From Weis-Fogh, (1973)).

Aerodynamic power $P_a^*$. If we exclude the exceptional cases in this context, the theory makes it possible realistically to calculate the cost of hovering, as seen in Table III. It ranges from 1.4 to 4.7 W/N with an average of 2.5. Again, there is no obvious variation with size and the general conclusion must be that flying animals have adjusted their shape and performance to the mechanical power output available from the contracting wing muscles. This output depends mainly on muscle volume, i.e. on the cross-sectional area times the length of the muscles, because the contractile force F is determined by the area and the shortening velocity U by the length. The power, F x U, is then proportional to the weight of the wing muscles so that in similarly built animals the specific power is independent of size, as found empirically (although details may modify the relationship to some extent; Pennycuick, (1969); Weis-Fogh, (1961)). Some animals may in fact not need as much power because of small wing loadings, gliding or soaring; they may then reduce the relative amount of muscle or fly in a more 'expensive' way in accordance to whatever selective advantage they may gain. It is in this light we should view the variations in shape and performance of flying animals.

Dynamic efficiency. A problem common to all hovering animals is that a major loss in energy must occur if the kinetic energy of the oscillating wings cannot be converted into stored elastic energy (Weis-Fogh, (1972), (1973)). How much this loss could amount to is expressed by the ratio $\eta$ in Table III between the aerodynamic work and the aerodynamic + inertial work, as integrated over one complete wing stroke. The results show that a hovering hummingbird pays the penalty of lacking an elastic system and must combust fuel at a much higher rate than needed for flight alone whereas the potential loss in some insects like Drosophila is insignificant (Weis-Fogh, (1972)). Although hampered by lack of material, I have tried to find an elastic system in recently dead hummingbirds but without luck. Vertebrate muscles are not elastic when inactive in contrast to insect wing muscles. One should be open to the possibility that somehow activated breast muscles of some small birds may have suitable elastic properties but it is not known. The majority of insects have low dynamic efficiencies and could not fly at the relatively small metabolic rates shown in the Table III unless they possess an elastic storage system which decreases the loss and increases the true efficiency. Such a system is known in locusts and some other insects. The morphology of the insect pterothorax must then be understood not only in terms of wing movements and muscle contractions but, equally important, in terms of the capacity to store elastic energy and release it effectively at high rates. This represents a large but difficult field of investigation for functional morphologists. It has been suggested (Pennycuick, personal communication) that some birds may store useful energy when the primaries are bent towards the end of each half stroke but a similar mechanism has not been reported from insects and hummingbirds.

## Novel Aerodynamic Mechanisms

The four exceptions in Table II are characterized by unusually large lift coefficients and fall into two distinct categories. The first consists of the butterfly *Pieris* and the small wasp *Encarsia* which appear to hover normally but at very high lift coefficients of 3 or more. They 'clap' their wings together and 'fling' them open at the one extreme wing position (*Encarsia*) or at both ends of the stroke (*Pieris*) (Weis-Fogh, (1973), and unpublished). Such a clap may also be present in a slowly flying *Drosophila* (Vogel, (1965)). The other category consists of the true hover flies, (*Syrphinae*) and the large dragonflies (*Aeshnidae*) which hover with horizontal body and nonhorizontal, obliquely beating wings which never touch each other. In addition, the stroke angles in the latter groups are so small that the average steady-state lift coefficients range between 2 and 3 as an *absolute* minimum. As will be discussed by R. A. Norberg (1974) the lift coefficient for a hovering *Aeshnae* species is in fact as high as between 4 and 6. All these forms must make use of unsteady principles. What are their nature?

The best understood case is the Hymenopteran wasp *Encarsia formosa* Gahan (Figure 8) which is used for biological control of the greenhouse white-fly *Trialeurodes vaporariorum* Westwood which, incidentally, also uses the clap-fling mechanism (Weis-Fogh, unpublished).

*Flight of a tiny wasp and the fling mechanism.* By means of high-speed cinematography of freely flying *Encarsia* the following picture was obtained recently by Weis-Fogh (1973). Like many insects *Encarsia* can jump but the wing movements seen in Figure 9 relates to free unaided hovering with a slow climb. It is seen that the wings are moved essentially in a horizontal plane both during the morphological downstroke (frames 0 to 7) and during the upstroke (frames 7 to 14). This strongly indicates that the flight depends on a true lift mechanism. It is also seen that the sequence of movements contains three phases which are unusual in the sense that nobody seems to have noticed them before nor their significance: (a) the *clap* preceeding the downstroke where the two pairs of wings are brought together as a single vertical plate (frames 14 to 17); (b) a very rapid pronation where the wings are flung open in a manner reminiscent of the 'flinging open' of a book and *before* the two pairs of wings start the horizontal downstroke; this I shall refer to simply as the *fling* (frame 1 at the beginning and frame 0 at the end); and (c) a

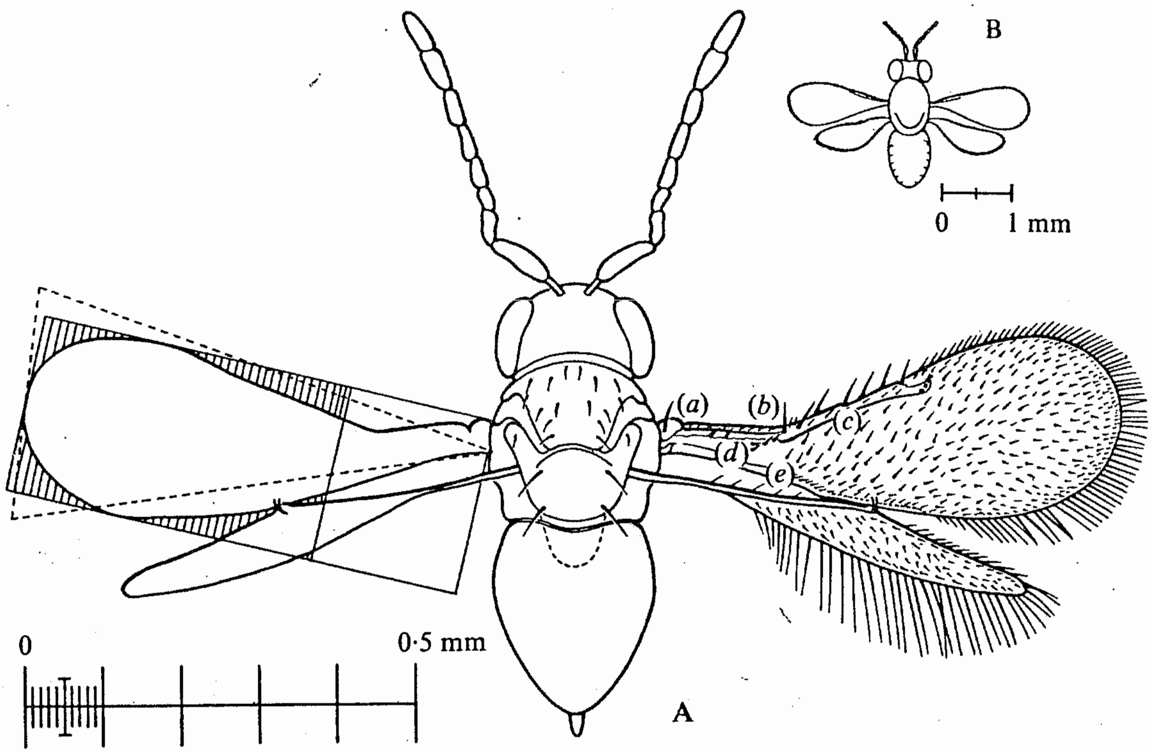
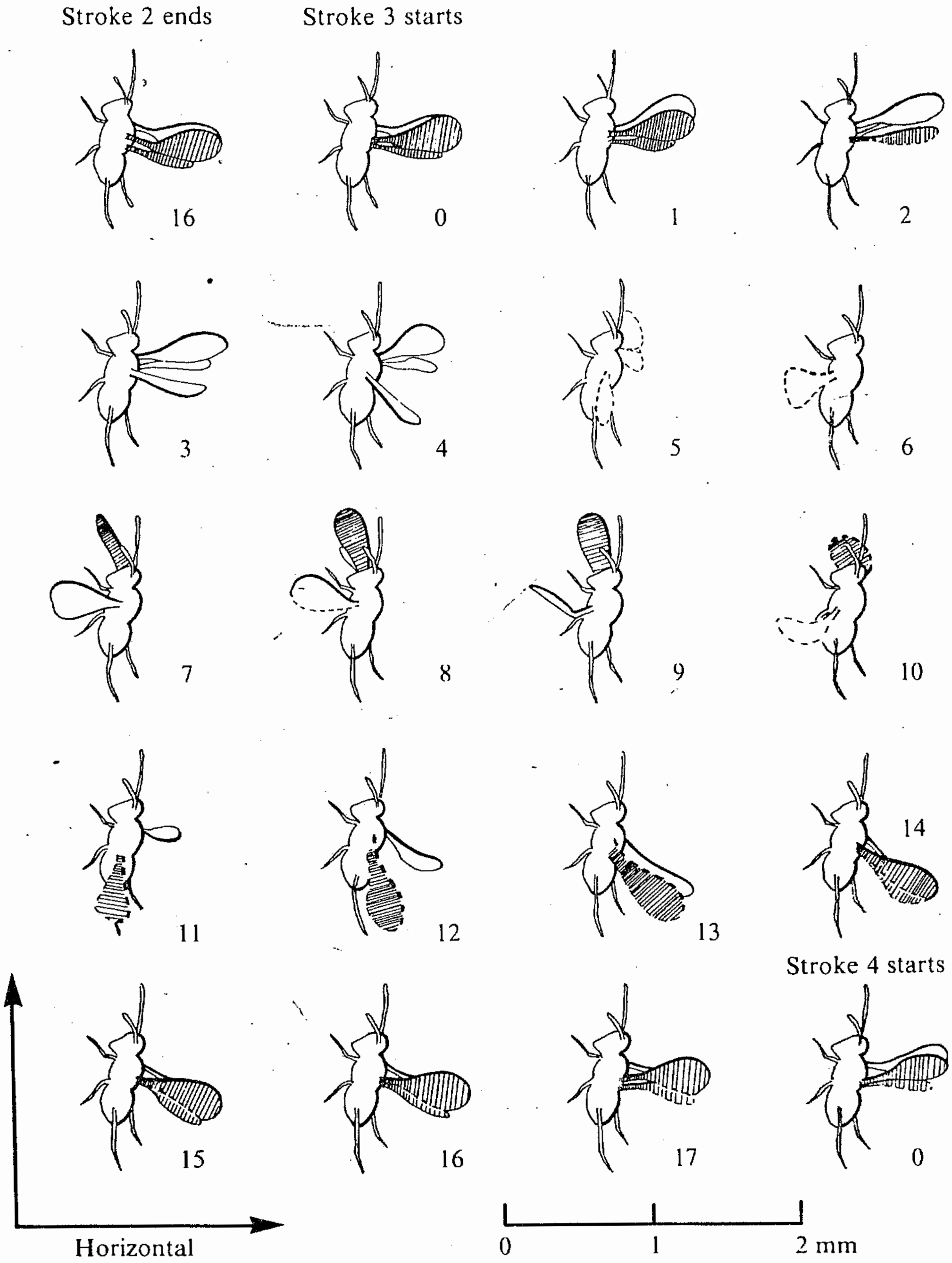


Figure 8. The small chalcid wasp Encarsia formosa (A) as compared with a larger related species Coccophagus spectabilis. (From Weis-Fogh, (1973)).

very rapid supination before the upstroke which I shall call the flip (between frame 7 and 9). According to the direct analysis of the films these phases are always present in Encarsia during all kinds of flight. Moreover, the lift equalled the body weight long before the wings in Figure 9 reached maximum angular velocity, namely between frames 3 and 4, as if circulation had been built up prior to the wing sweep itself and during the fling. This led to the idea illustrated in Figure 10A. Towards the end of the clap, the wings are essentially at rest relative to the air. During the fling it remains at rest along the 'hinge' represented by the hind margins of the hindwings but a potential flow is induced so as to fill the triangular void created between the two upper wing surfaces, giving rise to two bound vortices of equal strength and opposite sign. When the wings break apart along the 'hinge' and start the horizontal downstroke in Figure 10C, they already have circulation and can produce lift in accordance with equation (1) and independently of a starting vortex, the two vortices being both bound vortices so that there is no delay and no Wagner effect. Also, the creation of the two bound vortices of opposite sign and



igure 9. Tracings from a high-speed film of a freely hovering *ncarsia formosa*, at 7150 frames per second. (From Weis-Fogh, 1973)).

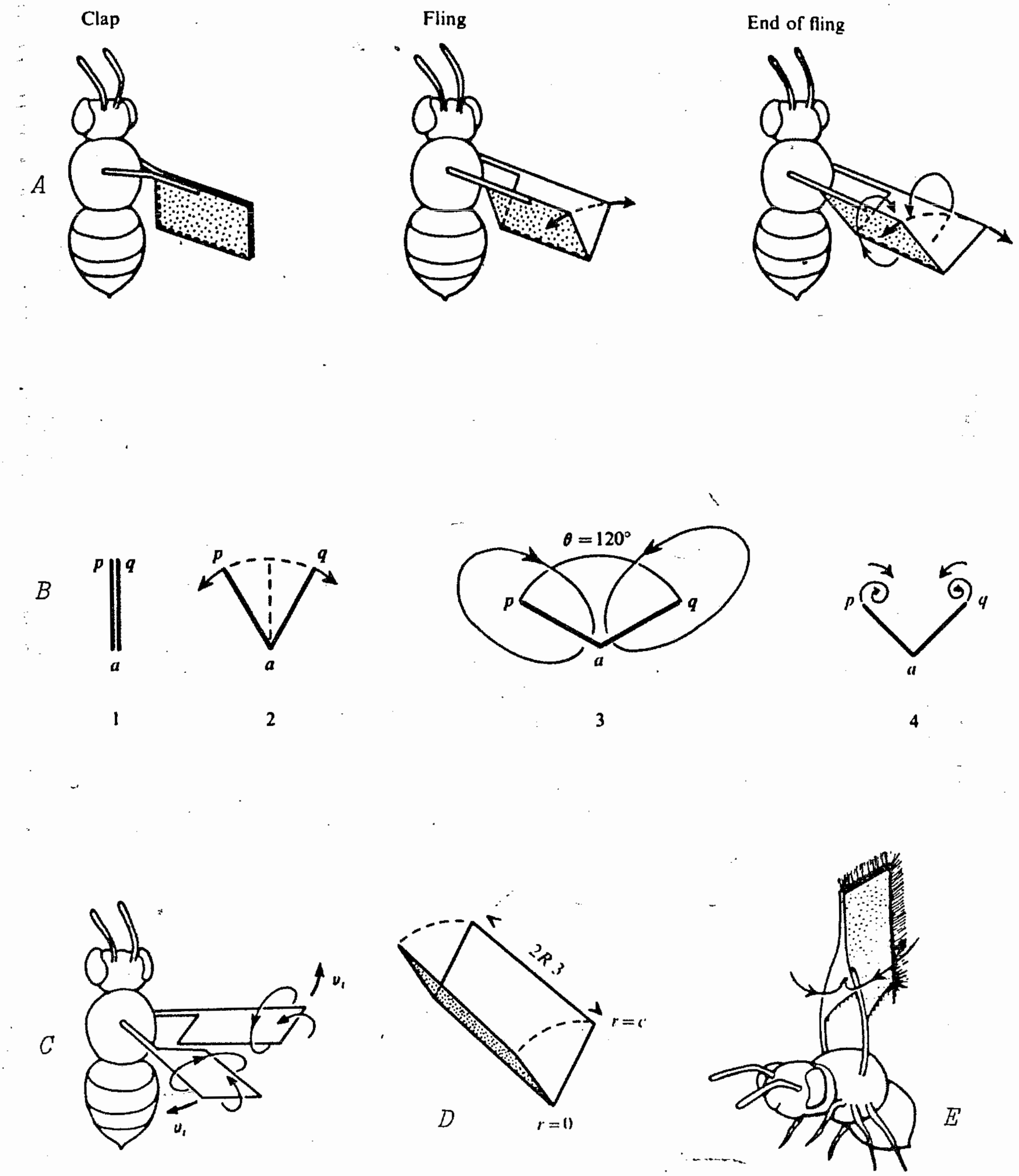


Figure 10. The fling mechanism for creating circulation prior to the separation of the wings after the 'clap' (A). (B) details of the flow, (C) the bound and tip vortices after the wings have separated. ((D) and (E) indicate additional details: from Weis-Fogh, (1973)).

equal strength does not depend on viscous forces but can be understood in terms of irrotational flow applicable also to an ideal inviscid fluid. Moreover, the energy needed to start the vortices is higher in the beginning (between Figure 10B, 1 and 2) than later (3), and the major cost occurs before viscous forces create serious problems (Weis-Fogh, (1973)).

These results are surprising at a first glance because they appear to violate established principles of flight but, in fact, they do not. They have been analyzed and amplified in an important theoretical study by Lighthill (1973) who was able to derive an expression for the circulation $\Gamma$ round each wing as calculated on the basis of two-dimensional potential flow. Combined with the general expression in equation (1) the unsteady lift caused by the fling takes the form

$$\text{L/unit length} = \rho v_t \Omega c^2 g(\alpha) \qquad (3)$$

Where $\rho$ is the mass density of air (as before), $v_t$ is the flapping velocity indicated by the arrow in Figure 10C, $\Omega$ is the angular velocity with which the two sets of wings open during the fling (cf. Figure 10B, 1 and 2), c is the wing chord, and $g(\alpha)$ is a function the numerical value of which depends on the angle $\alpha$ which is the angle through which each wing has rotated from the vertical (Figure 10B, 2) and until they split apart before the downstroke. The function $g(\alpha)$ can be computed exactly and is analogous to the coefficient of lift for the case of steady flow (Figure 11). It has the interesting property that its value changes only slowly from 0.90 to 0.64 when $\alpha$ varies from 30° to 90°. For a small angle of 10° the coefficient shoots up to 1.7, in conformity with the previous remarks about the energy needed.

In the case of Encarsia, $\Gamma = 0.69\,\Omega c^2$ and this is equal to a circulation of 2.7 $\text{cm}^2$/sec. Using this value in equation (1), the flapping speed at which lift equals body weight is reached about frame 3 in Figure 9, i.e. when direct film observations showed that parity between lift and body weight was in fact achieved. Lighthill (1973) also analyzed some aspects of the boundary layer (cf. Figure 10B, 4) and the three-dimensional flow; the reader should consult his paper on these important points and also Ellington's (1974) more detailed calculation of $C_L$ and the time course.

The novel principle which I call the fling mechanism is therefore that during the rapid opening phase after a clap useful circulation is created round each wing profile independently of the Prandtl mechanism and prior to the translation of the wing as a whole through the air. The clap-fling situation is particularly simple and amenable to theoretical (and experimental) analyses

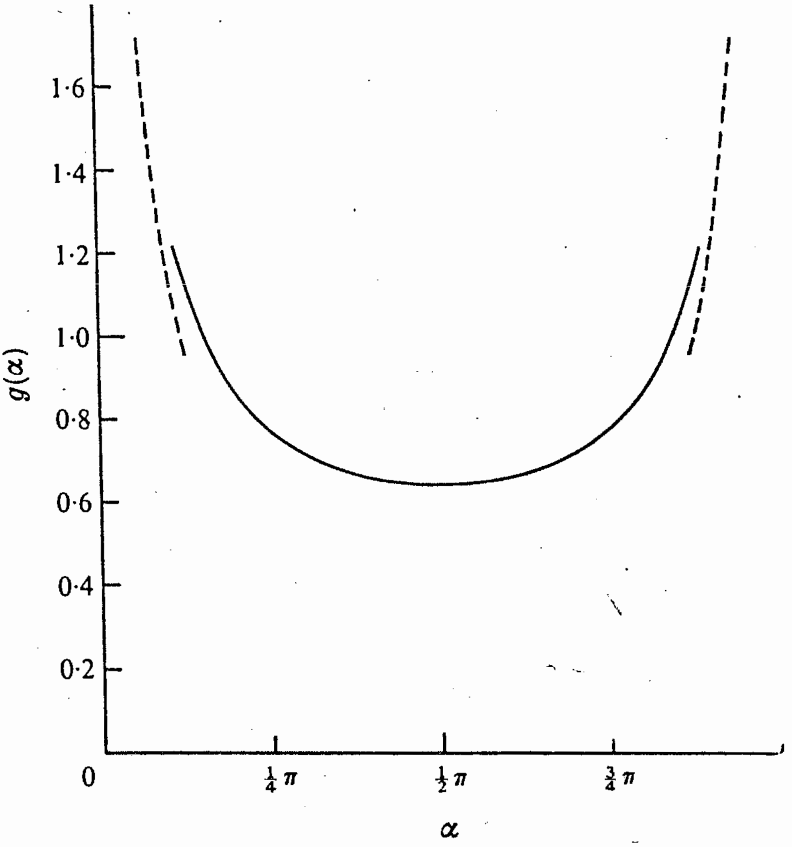


Figure 11. The coefficient g(α) in equation (3) for the unsteady fling mechanism. α is the half-angle between the two wing chords just before the wings from the two sides separate and begin to swing 'downwards' or 'upwards' (reproduced after Lighthill, (1973)).

but it need only represent one extreme possibility out of many. As already mentioned, the clap appears to be present in Drosophila and I have recently observed it in Trialeurodes as well as during vigorous hovering flight of the cabbage white Pieris brassicae, in the latter case both at the top and bottom of the horizontal stroke. It also appears present in a moth Euoxa ochrogaster, according to smoke trail observations by Chance (1974).

Flight of Syrphinae and Aeshnidae. The flip phase in Encarsia (Figure 9, frames 8-9) cannot be resolved for detailed analysis on the basis of existing material but the results indicate that the building up of circulation at the extreme wing positions prior to the succeeding wing movement through the air is possible also without a clap followed by a fling. The hover flies and dragonflies also hover without any clap and so that the wings on the two sides remain far apart and independent of each other (Weis-Fogh, (1973)), and still they attain lift coefficients which are far too high for steady aerodynamics. The suggested explanation is the *flip* mechanism illustrated in Figure 12. It rests partly on Nachtigall's (1966) measurements of the twisting speeds during pronation and supination in *Phormia*, a fly of the same size and wingstroke frequency as a large hover fly, partly on the observation that the wings of Syrphinae and Aeshnidae are stiff and reinforced at their anterior leading edge and very soft and pliable at the trailing edge, and finally, on rough calculations of the speeds with which a torsional deformation during pronation and supination can travel from the base of the wing to the tip in the stiff anterior region as compared with the soft posterior part. The main result is that the deformations cannot reach the trailing edge before they are completed at the anterior part ('delayed elasticity'). The trailing edge

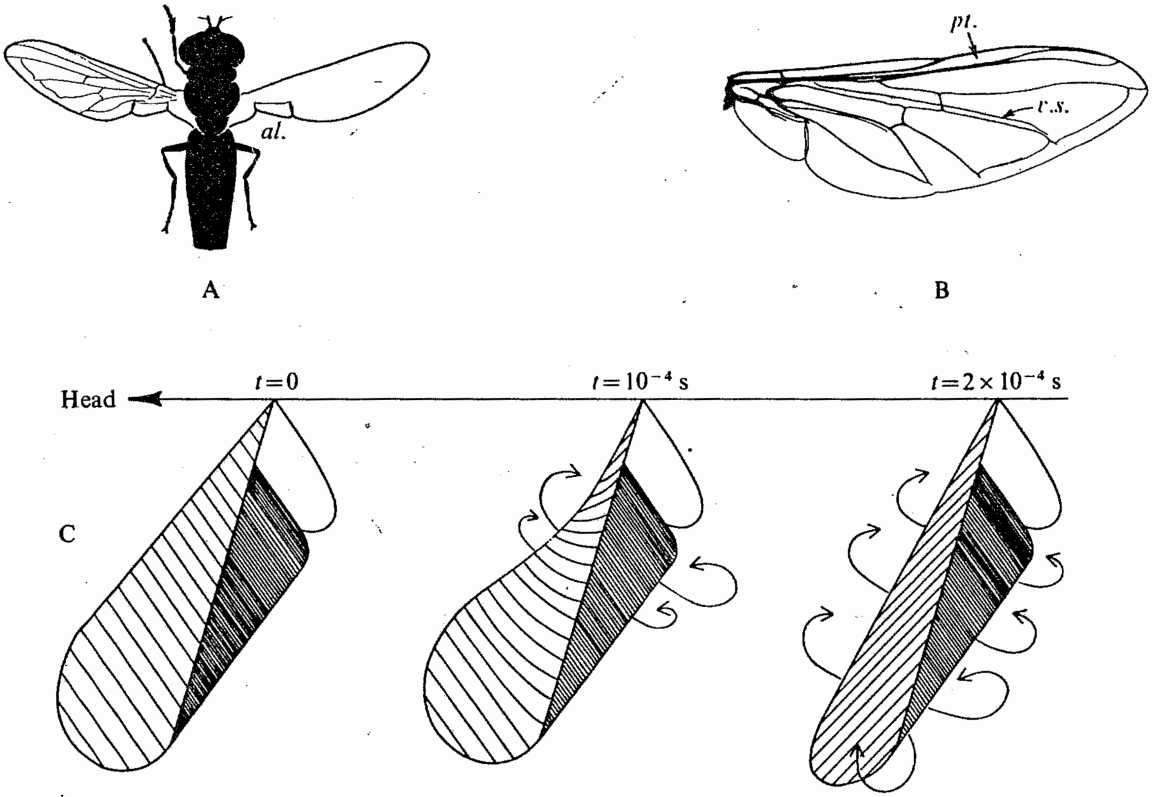


Figure 12. (A) A hover fly *Platychirus peltatus*. (B) A wing of *Syrphus balteatus* with a stiff anterior part, a large pterostigma (pt.) and a soft almost rubber-like posterior membrane. (C) The suggested propagation of a twisting wave resulting in two opposite vortices, the trailing edge being a stagnation line. (From Weis-Fogh, (1973)).

may therefore represent a stagnation line relative to the air so that the pronation in Figure 11 (or a similar supination) should result in two opposite vortices, an anterior one bound to the wing and a posterior one which is free and situated mainly behind the hind margin. When the actual translation starts during the downstroke or the upstroke, the bound vortex gives rise to lift from the very beginning of the stroke, although the resulting lift is somewhat reduced to begin with because of the Wagner effect which is unavoidable in this case. Further analysis showed that such a system renders supreme manoevrability based mainly upon alterations of the wing-tip path (Weis-Fogh (1973)), but much more direct and detailed evidence is needed before it is profitable to discuss this and other possible effects in detail. There is undoubtedly a rich field for discovery here and other solutions than those outlined may come to light. Also, the flip mechanism has not been subject to any theoretical analysis as yet.

## General Aspects of Flapping Flight

There must be non-steady periods in any type of active flapping flight but the quantitative importance of non-steady aerodynamics is small during fast forward flight of birds, bats and most insects, and even when the majority of them hover on the spot. However, in very small insects and in some insect groups which have small wing loadings (cf. Table I), novel but definable non-steady principles based upon the creation of circulation, and thereby aerodynamic lift rather than drag, dominate the flow pattern. It is also significant that lift caused by the fling mechanism is independent of size and can operate at both small and high Reynolds numbers so that it could be used to good effect during hovering and vertical takeoff and in emergencies, also in birds. It is highly interesting that U. M. Norberg (1974) has found that a flycatcher Ficedula hypoleuca obtains a $C_L$ of about 4 when hovering (wing loading 13 $Nm^{-2}$). The wood pigeon (Columba palumbus), the rock dove (Columba livia) and its domestic descendants often start flight with one or two audible claps when disturbed, as already described by Virgil (Vergilius (19 B.C.)) in the Aeneid (5th book, Vs. 213-17) and shown by Marey (1890) to be caused by the two fully stretched wings meeting dorsally in a real clap-fling. It should also be mentioned that the relatively small wing loadings of terns and kestrels may make it possible for these birds to hover according to the flip principle although Lighthill has some justified misgivings about this being true hovering (1974). Only future studies can tell.

One point needs emphasis. As is the case with the revolving cylinder used to illustrate the Magnus effect, the creation of circulation of the air round the wing is the essential prerequisite for lift production and the actual shape of the wing is of less significance during the non-steady period. This may explain the otherwise abnormally high geometrical angles of attack found in Phormia regina towards each end of the stroke (Nachtigall (1966); see Figure 5) and one should not use these observations to draw conclusions about forces based upon steady-state considerations alone. It may also explain some of the bizarre wing shapes seen particularly in many Neuroptera, Lepidoptera and perhaps Thysanoptera. Application of non-steady principles makes possible innumerable modifications of flight mechanisms and wing shapes and one must take this into account when discussing the function and evolution of winged insects.

A figure of merit. In order to estimate the relative importance of the unsteady fling mechanism as compared with the usual steady flow, I have recently derived a ratio between the circulation immediately after the fling and the circulation caused by the normal lift mechanism at the middle of the half-stroke. If we disregard the dying-off of the unsteady flow in the course of the half-stroke, this figure of merit $\mu$ is unity when the two circulations are equal. It has the form

$$\mu = \frac{4\alpha c}{\pi \epsilon R} \times \frac{g(\alpha)}{\phi C_L}$$

where $2\alpha$ is the angle between the wing chords $c$ just before the wings split apart in Figure 10b3 (usually about 2 rad), $\epsilon$ is the fraction of the stroke period occupied by pronation and supination (about 0.05 to 0.1), $R$ is the wing length and $\phi$ the stroke angle. The interesting observation is that $\mu$ is independent of the absolute size and of the wingstroke frequency. We also observe some interesting correlations between this expression and the morphology and flight of the animals now known to utilize unusual aerodynamics. For instance, animals with a small aspect ratio ($2R/c$) should benefit most from unsteady flow, butterflies and moths being a good example. A small stroke angle also increases $\mu$ in accordance with our observations on hoverflies and dragonflies. Finally, since $g(\alpha)$ does not vary much, it is seen that the animals with small wing loadings and therefore small values of $C_L$ should be able to take most advantage of the unsteady flow situations, exactly as observed and indicated by the double asterisks in Table I.

For Encarsia and hovering butterflies, $\mu$ is larger than 5 and they are likely to depend almost entirely on unsteady flow, a general result substantiated by the more detailed calculations of Ellington (1974). If there is a true effective clap in Drosophila, $\mu$ is about 3. In these and similar cases one must take into consideration that the fling circulation is likely to have become reduced when the wings reach their full angular velocity. In hovering hummingbirds the figure would be 1.5 if they did use a clap (which they do not) but in a pigeon starting vertically from a perch with a real clap the figure of merit is 1 so that unsteady flow could contribute significantly during take-off. Virgil's observation that the rock dove starts from its nest on the cliff with a few loud claps before it glides silently through the peaceful air probably indicates a real transition from unsteady to steady-state aerodynamics. We may find the answer two millenia after the observation was first recorded.

## ACKNOWLEDGMENTS

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## REFERENCES

Bennett, L. 1966 Insect aerodynamics: vertical sustaining force in near-hovering flight. Science, N. Y. 152, 1263-6.

Bennett, L. 1970 Insect flight: lift and rate of change of incidence. Science, N. Y. 167, 177-9.

Chance, M. A. C. 1974 Air flow and the flight of a Noctuid moth. Proc. Symposium Swimming & Flying in Nature, Pasadena, California, July 8-12.

Ellington, C. P. 1974 Non-steady state aerodynamics of insect flight. Proc. Symposium Swimming & Flying in Nature, Pasadena, California, July 8-12.

Hertel, H. 1966 Structure, Form, Movement. Reinholt, New York.

Horridge, G. A. 1956 The flight of very small insects. Nature, London, 178, 1334-5.

Jensen, M. 1956 Biology and physics of locust flight. III. The aerodynamics of locust flight. Phil. Trans. R. Soc., London, B, 239, 511-52.

Kuethe, A. M. 1974 On the mechanics of flight of small insects. Proc. Symposium Swimming & Flying in Nature, Pasadena, California, July 8-12.

Lighthill, M. J. 1973 On the Weis-Fogh mechanism of lift generation. J. Fl. Mech. 60, 1-17.

Lighthill, M. J. 1974 Aerodynamic aspects of animal flight. Proc. Symposium Swimming & Flying in Nature, Pasadena, California, July 8-12.

Lilienthal, O. 1889 Der Vogelflug als Grundlage der Fliegekunst. R. Oldenbourg, Berlin.

Marey, E.-J. 1890 Le vol des Oisoaux. G. Masson, Paris.

Nachtigall, W. 1966 Die Kinematik der Schlagflugelbewegungen von Dipteren. Methodische und analytische Grundlagen zur Biophysik des Insektenflugs. Z. vergl. Physiol. 52, 155-211.

Norberg, R. A. 1972a Evolution of flight of insects. Zoologica Scripta, 1, 247-50.

Norberg, R. A. 1972b Flight characteristics of two plume moths. Alucita pentadactyla L. and Orneodes hexadactyla L. (Microlepidoptera). Zoologiza Scripta, 1, 241-46.

Norberg, R. A. 1974 Hovering flight of the dragonfly, Aeschna juncea L. Proc. Symposium Swimming & Flying in Nature, Pasadena, California, July 8-12.

Norberg, U. M. 1974 Hovering flight in the pied flycatcher (Ficedula hypoleuca). Proc. Symposium Swimming & Flying in Nature, Pasadena, California, July 8-12.

Osborne, M. F. M. 1951 Aerodynamics of flapping flight with application to insects. J. exp. Biol. 28, 221-45.

Pennycuick, C. J. 1968 Power requirements for horizontal flight in the pigeon Columba livia. J. exp. Biol. 49, 527-55.

Pennycuick, C. J. 1969 The mechanism of bird migration. Ibis, 111, 525-56.

Pennycuick, C. J. 1972 Animal Flight, E. Arnold, London.

Thom, A. and Swart, P. 1940 The forces on an aerofoil at very low speeds. J. R. aeronaut. Soc. 44, 761-70.

Tucker, V. A. 1973 Bird metabolism during flight: evaluation of a theory. J. exp. Biol. 58, 689-709.

Vergilius, P. V. M. 19 B. C. The Aeneid.

Vogel, S. 1965 Studies on the flight performance and aerodynamics of Drosophila. Thesis, Harvard University.

Vogel, S. 1967 Flight in Drosophila. III. Aerodynamic characteristics of fly wings and wing models. J. exp. Biol. 46, 431-43.

Waloff, A. 1972 Observations on the airspeeds of freely flying locusts. Anim. Behav. 20, 367-72.

Weis-Fogh, T. 1956 Biology and physics of locust flight. II. Flight performance of the desert locust (Schistocerca gregaria). Phil. Trans. R. Soc. Lond. B, 239, 459-510.

Weis-Fogh, T. 1961 Power in flapping flight. In Ramsay, J. A. and Wigglesworth, V. B., eds., The Cell and the Organism, Cambridge University Press, 283-300.

Weis-Fogh, T. 1964 Biology and physics of locust flight. VIII. Lift and metabolic rate of flying locusts. J. exp. Biol. 41, 257-71.

Weis-Fogh, T. 1967 Energetics of hovering flight in hummingbirds and in Drosophila. J. exp. Biol. 56, 79-104.

Weis-Fogh, T. 1973 Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. J. exp. Biol. 59, 169-230.

Weis-Fogh, T. 1975 Scale, dimensions and design principles in actively flying animals. (Biol. Rev., in manuscript).

Weis-Fogh, T. and Jensen, M. 1956 Biology and physics of locust flight. I. Basic principles in insect flight. A critical review. Phil. Trans. R. Soc. London, B, 239, 415-58.