

Aerodynamic Aspects of Animal Flight

SIR JAMES LIGHTHILL, FRS, Hon. FIMA
University of Cambridge



CONTENTS

Part I. Introduction to the survey

- 1.1 Scope
- 1.2 Evolution

Part II. Sustained forward flight

- 2.1 Flapping
- 2.2 Insects
- 2.3 Birds
- 2.4 Bats
- 2.5 Control
- 2.6 Migration
- 2.7 Scaling
- 2.8 Soaring

Part III. Hovering flight, take-off and landing

- 3.1 Normal
- 3.2 Exceptional

PART I. INTRODUCTION TO THE SURVEY

1.1. Scope

A LECTURE or a course of lectures on "Aircraft" would put approximately equal emphasis on aerodynamic, structural and power-plant aspects; whereas lectures on "Aerodynamics of Aircraft" would concentrate principally on aerodynamic matters while referring to just the basic elements of what limitations are imposed by structural and power-plant considerations. Similarly this paper on the "Aerodynamic Aspects of Animal Flight" will concentrate on the aerodynamic forces, and the resulting dynamic interactions, between the movements of a flying animal relative to the air and the associated air movements; and include only brief references to fundamental limitations imposed by the strength and stiffness of the skeleton of the animal and other structural considerations, or by the power-plant capabilities of the animal's musculature and metabolism. Equally it will give only a highly condensed account (section 1.2) of the biologically fundamental questions of how systems for animal flight evolved in response to environmental demands and opportunities.

In such a balance of subject matter the paper follows closely the author's previous hydromechanical surveys^{1,2,3} of aquatic animal locomotion. Evidently there are some other resemblances also between the dynamical problems of animals swimming in water and animals flying in air, and where appropriate some comparisons between them will be attempted.

1.2. Evolution

In the *evolution* of animal locomotion, the earliest developments were of course aquatic: at least 6×10^8 years of animal evolution in the marine environment can be traced through the extensive fossil record from around the beginning of the Cambrian period to the present time. By contrast, what may be called the "conquest of the air" by flying animals is a considerably more recent event than the origin of swimming.

Nevertheless, the chronology of animal flight is longer, and the epoch of the conquest of the air has to be placed earlier, than many people would imagine. Already 3×10^8 years ago, in the middle of the Carboniferous period (Fig. 1), the problems of sustained powered flight had been solved by the insects. They belong, of course, to the Arthropoda, that huge phylum of animals with articulated *external* skeletons. An excellent account of some of the processes involved in the evolution of flight has been given by Smart and Hughes,⁴ whose diagrammatic summary is reproduced as Fig. 1.

They describe the invasion of the land by both plants and animals, including primitive Arthropoda such as myriapods, as having taken place during the Silurian period a little more than 4×10^8 years ago, after which in the Devonian period arthropod evolution on land led to the six-legged form characteristic of the insects before any development of wings took place. Extensive fossil material from winged insects appears, however, by the middle of the Carboniferous period. It includes a remarkable diversity of forms: already, for example, the divergence had occurred between the palaeopterous orders such as the Odonata (dragonflies) which cannot fold their wings over the abdomen when resting and the neopterous orders, then including the Orthoptera (grasshoppers), which can.

Smart and Hughes⁴ relate this phenomenon of the development of insect flight in a wide diversity of forms during the first half of the Carboniferous period to the appearance at that time of tall terrestrial plants in great abundance in those dense "forests" whose debris were ultimately compressed to become the coal measures. Plant life in the Carboniferous period, although very different from the characteristically angiosperm (flowering-plant) life of the Tertiary era, included "trees" of the order of 30m tall: lycopods, calamites and early gymnosperms, including trees with expanded leaf-laminae and many other food sources suitable for crawling insects. These are conditions which could have favoured the evolution of aerodynamic surfaces, initially to facilitate horizontal dispersal from elevated positions through gliding. Advantages in food seeking and dispersal could then continue to accrue from a developing articulation of those surfaces through a series of stages leading to sustained winged flight.

Specialisation might then follow: for example to predatory forms such as the Odonata; and continued evolutionary development of flying in different insect groups must have resulted not only from advantages in respect of food seeking and dispersal but also from the pressures brought about by such predators, as well as by non-insect predators such as the Amphibia (who at this period became the first terrestrial vertebrates) and a different class of arthropods: the Arachnida.

After the Carboniferous period, the class Insecta continued to diversify so that structures of wide variety

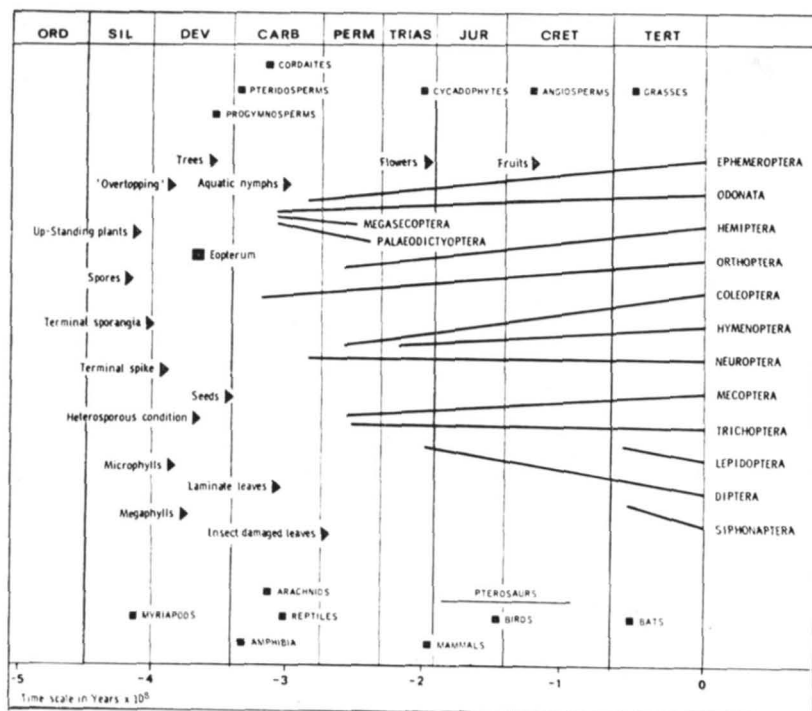


Fig. 1. Chronology of events in the development both of plants and of insects and other groups of flying animals⁴

including examples characteristic of most of the extant orders of insects were present already in the Triassic period, long before the appearance of flowering plants. Much later the development of the angiosperms led to their extraordinarily successful symbiosis with the insects, which encouraged an enormous degree of specialisation in the Insecta and made them the class including a greater number of known species than all the others put together, while also allowing certain new orders of insects to appear: especially the nectar-feeding Lepidoptera (moths and butterflies).

In the meantime the conquest of the air by the insects had been succeeded by a sequence of quite independent achievements of sustained flight by other groups of animals. The reptiles, having evolved from the Amphibia, later flourished remarkably in the Jurassic and Cretaceous periods (roughly from 2×10^8 to 1×10^8 years ago), when they included an extensive group of flying animals: the pterosaurs. A separate acquisition of the power of sustained flight was then made by the birds (again evolving from wingless forms). From yet another class of vertebrates, the mammals, there appeared still later (about 0.5×10^8 years ago) the Chiroptera or bats: a rather large order of mammals many of whom are very advanced fliers.

This paper, then, will be almost entirely about insects, birds and bats. I shall *not* try to describe the flight of extinct animals, for which the data available often exclude such details as would be of greatest aerodynamic interest. I shall make, furthermore, just a *brief* mention of various groups of vertebrates that went only part of the way towards achieving sustained flight.

These include representatives of three other orders of mammals besides the bats; among marsupials, for example (Fig. 2), there are "flying sugar squirrels" and this "flying possum" *Schoinobates volans*. The aerodynamic surfaces stretched between their limbs allow them, by unpowered gliding from tree to tree, to gain similar advantages to those that may have accrued to the insects in a primitive gliding phase of evolution of their

flight capabilities.

Fig. 3 displays a different, rather surprising, mode of evolution of aerodynamic surfaces from extensions of ribs. Long after the pterosaurs became extinct there evolved from a different reptile order (the Squamata)

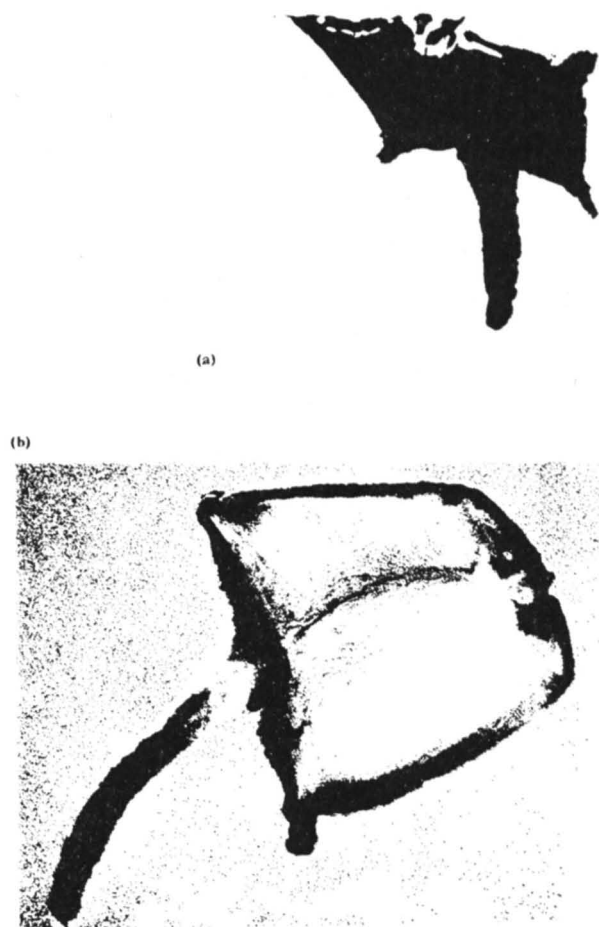


Fig. 2. Flying marsupials: (a) the sugar squirrel *Petaurus norfolcensis*; (b) the greater gliding possum *Schoinobates volans*⁵

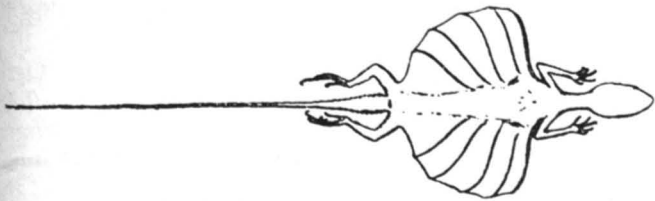


Fig. 3. The flying lizard *Draco maculatus*⁶

various animals with gliding capabilities, including "flying lizards" such as *Draco maculatus*.

A link with my surveys of aquatic locomotion is provided by the flying fishes. From various groups of fishes capable of significant aerodynamic effects (see Marshall,⁷ pp. 41-45) I choose to describe the subfamily Cypsilurinae. Fig. 4 shows how both their pectoral fins and their pelvic fins evolved into substantial aerodynamic surfaces (with the mass centre in between) enabling them to glide stably. However, they have no muscles suitable for giving forward propulsion by flapping.

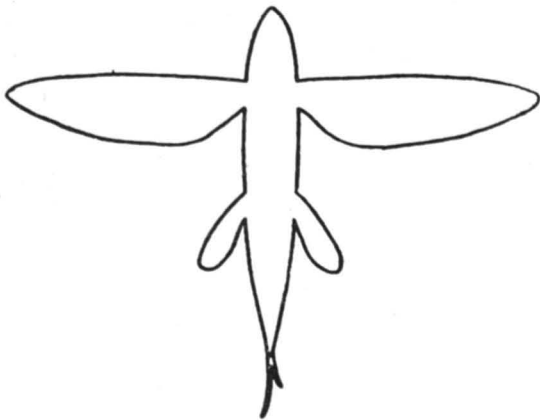


Fig. 4. Outline of a cypsilurine flying fish⁶

Fig. 5 illustrates their mode of flight. Carangiform^{1,2} propulsion from the posterior end by the beating of the caudal fin (while the pectoral and pelvic fins are folded) thrusts the fish upward and finally pushes out the anterior

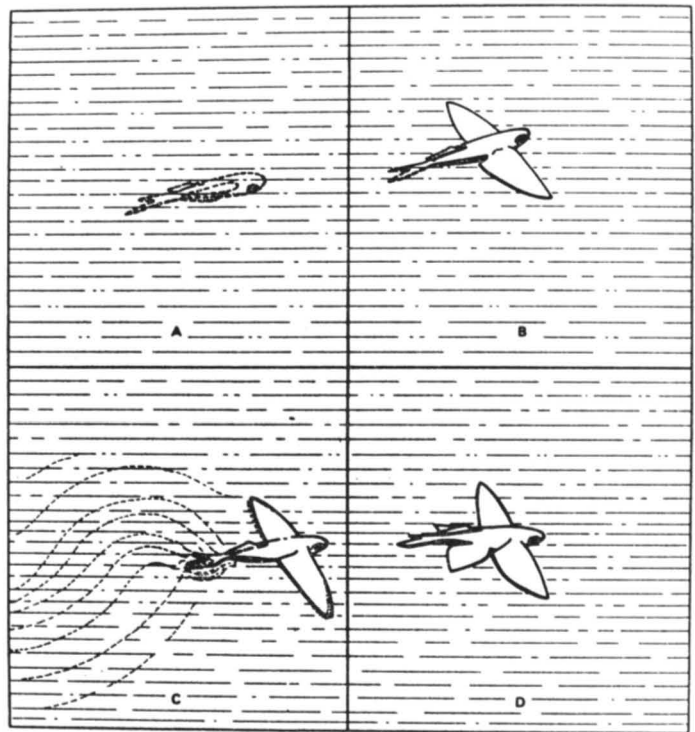


Fig. 5. Locomotion of a cypsilurine flying fish⁸: (A) fish approaches the surface; (B) pectoral fins are spread; (C) air lift on these supports anterior part of body while caudal fin continues to beat in the water; (D) gliding phase

part of the body above the water surface. The pectoral fins open to keep that part of the body airborne while the caudal fin's thrust continues to provide acceleration. Finally, when the pelvic fin breaks surface and opens up, the whole body is lifted clear out of the water for an extended glide.

After this discursive introduction, the rest of my survey concentrates on those three groups of animals that exhibit versatile capabilities of sustained forward flight: the insects, the birds and the bats.

PART II. SUSTAINED FORWARD FLIGHT

2.1. Flapping

The basic aerodynamic requirements for sustained forward flight are to generate enough lift to balance body weight and enough thrust to balance body drag. I shall discuss at length the aerodynamics of sustained forward flight in insects, birds and bats before I comment on the many other flight modes of which the same animals are capable: manoeuvres, diving, soaring, take-off, landing, hovering, etc.

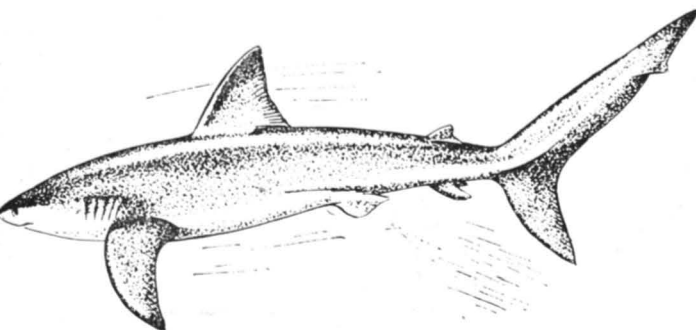


Fig. 6. The blue shark *Prionace glauca*¹

In each of these animals lift and thrust are both provided by the *same* aerodynamic surfaces: the same *flapping wings* give both, quite a different arrangement from the separation of thrust and lift noted (Fig. 5) in the cypsilurine flying fish. Of course there are numerous groups of fishes that do not leave the water but need to produce both thrust and some hydrodynamic lift because their weight exceeds their buoyancy. Some of them, like the blue shark (Fig. 6), obtain most of their lift from a substantial pectoral fin set at a fixed positive angle of incidence while the fish is propelled forward by undulations of the caudal fin and the posterior part of the body.

In contrast to that separation of thrust and lift, however, every animal capable of sustained forward flight in air uses the same surface to generate both. The flapping movements required to achieve this can be viewed as a linear combination (Fig. 7) of those carangiform movements widely used for thrust production by aquatic animals and the simple constant angle of incidence which is used for lift production by fixed-wing aircraft, or by the cypsilurine flying fish.

I will remind you that the tail movements in carangi-

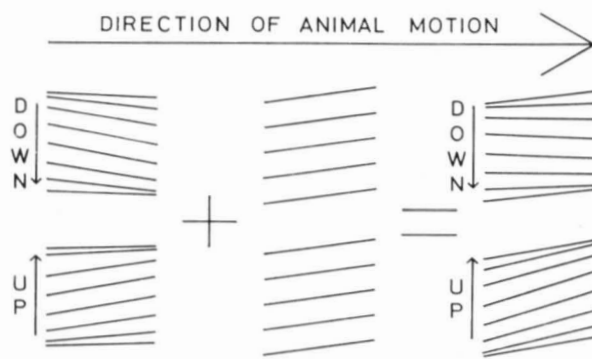


Fig. 7. Linear combination of a carangiform propulsive mode and a lift-generating mode¹

form propulsion of fishes consist of a lateral (side-to-side) oscillation with *twists* at each extreme of the oscillation so that the lateral movement has always a backward-facing component. Cetacean mammals make just the same propulsive movements with their tail-flukes, but up and down as shown in Fig. 7: again with such twists at each extreme of the oscillation. The movement on the left of Fig. 7, then, is a standard aquatic means of generating thrust without lift. Linearly combining it with the simple constant angle of incidence for lift purposes shown in the centre, we obtain on the right of the figure a fair approximation to those normal flapping movements of the wings by which insects, birds and bats generate combined thrust and lift. There are also some mid-water fishes (the aptly named "eagle rays" *Myliobatidae*) whose pectoral fins are developed to give *both* thrust *and* the lift needed to balance their excess weight in water through similar wing-like beats.⁷

In these flapping movements of powered forward flight, the wing remains approximately parallel to the direction of mean motion during the strong downstroke and then twists into a considerably "pitched-up" position for the upstroke. Note that the air forces giving thrust *oppose* the wing movements, both on the upstroke and on the downstroke. The aerodynamic lift *also* opposes the wing movements on the downstroke, which, therefore, is very heavily loaded. On the upstroke, however, the air forces giving lift work *with* the motion, in opposition to those giving thrust. The upstroke, then, is much more lightly loaded and is often described, therefore, as being in a "feathered" condition.

These ideas can help us to understand certain facts about muscles and skeletons in flying animals. The musculature responsible for the heavily loaded downstroke is characteristically very powerful indeed—much more than that for the lightly loaded upstroke, as we shall see. It can, furthermore, apply to the wing the large bending moment required in the downstroke through its attachment to rather *deep* skeletal elements: that is, in the vertebrates (with internal skeleton) to the characteristically keeled breastbone of birds and many bats, or in the insects (with external skeleton) to the deep box-like "fuselage" of the thorax.

2.2. Insects

Detailed study of the aerodynamics of forward flight, for animals just as for aircraft, can make good use of wind-tunnels. Insect forward flight was first subjected to detailed wind-tunnel observation by Weis-Fogh and

Jensen⁹: a zoologist and an aerodynamicist working in an extremely effective collaboration.

They made comprehensive investigations of the flight of the locust *Schistocerca gregaria*, from the order Orthoptera. A specimen was suspended in the wind-tunnel from a force balance, in such a way as to avoid interference with the motions of the thorax (to which the four wings are attached). A feedback control system, with the horizontal force measured by the balance controlling the speed of the wind-tunnel fan, allowed conditions representative of free sustained forward flight to be produced: the wind speed, once the insect was beating its wings regularly, was automatically adjusted so that the net horizontal force measured by the balance was zero. Thrust was then balancing drag as in free flight.

A typical specimen had wings 4 cm long and mass 2g. Experiments were carried out for a range of values of mean lift, spanning the case when it exactly balanced the insect's weight. A typical flying speed U was 4ms^{-1} , corresponding to a Reynolds number Uc/ν of around 2000 based on the forewing chord c . A typical wing-beat frequency was 20Hz, which makes the standard aerodynamic frequency parameter $\omega c/U$ take quite a low value, around $\frac{1}{4}$. (The corresponding value for the hind-wing was about $\frac{1}{2}$.)

It is generally true of the data available on sustained forward flight in insects, birds¹⁰ and bats¹¹ that frequency parameters based on radian frequency ω , wing chord c and speed through the air U lie in the range between 0 and $\frac{1}{2}$ (although admittedly data where ω and U were simultaneously measured are far too scanty). For these values $\leq \frac{1}{2}$, aerodynamic forces are changed to only a rather moderate extent from the so called *quasi-steady* values which at each moment depend only on the wing's instantaneous motion relative to the air.

Fig. 8, for example, shows how a section of the forewing of a locust (actually a section halfway towards the wing tip) moved relative to the air in Weis-Fogh and Jensen's experiments. Note in particular the extended downstroke, with the chord nearly parallel to the direction of mean motion (very much as depicted in Fig. 7). There is plenty of time during this stroke for the aerofoil to build up its steady-state force, nearly at right angles to its instantaneous path through the air, and therefore including components of both lift and thrust. After the rapid wing twist called "pronation" (becoming more "prone": in aeronautical terms, "pitch-down")

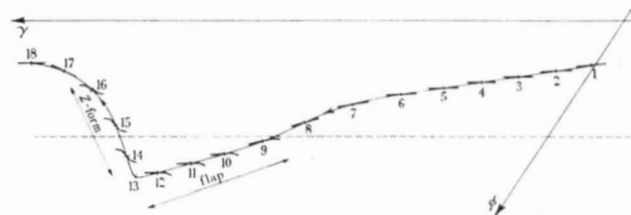


Fig. 8. Movement relative to the air of the mid-section of the forewing of *Schistocerca gregaria*⁹

immediately before the downstroke, quasi-steady values of those force components are presumably attained in a distance of only a few chord lengths.

Another twist called "supination" (a pitch-up) marks the onset of a more lightly loaded upstroke with the aerofoil at a large positive angle of pitch to the direction

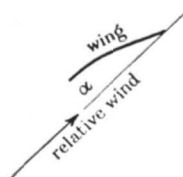
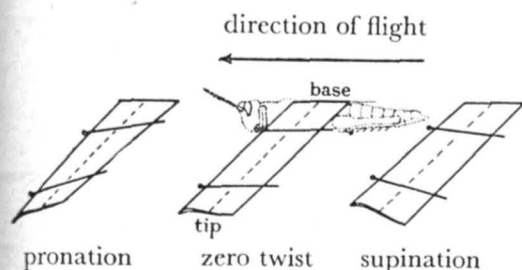


Fig. 9. Definitions⁹ of pronation, supination and angle of attack α

of mean motion (again as in Fig. 7). Fig. 9 gives a 3-dimensional view of the wing twists involved both in pronation and in supination. It shows also the definition of angle of attack used by Weis-Fogh and Jensen,⁹ in terms of the angle α between the trailing edge and the relative wind (air motion relative to wing chord).

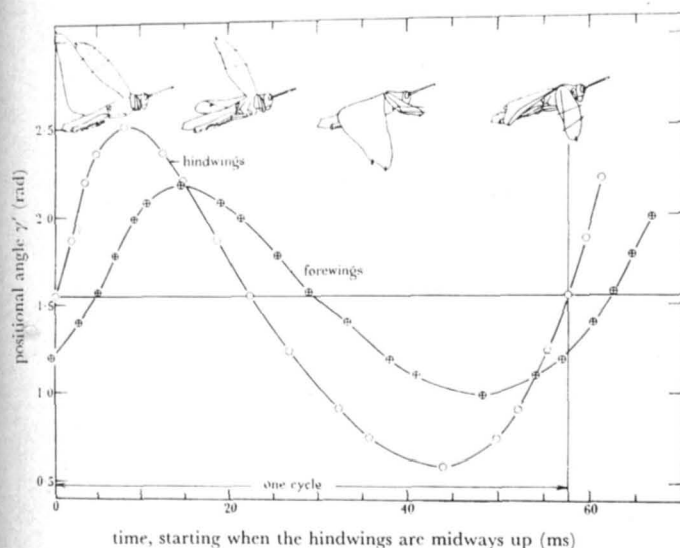


Fig. 10. The standard wing stroke of *Schistocerca gregaria*⁹

Fig. 10 shows the standard wing stroke of *Schistocerca gregaria*, indicating the variation with time of a positional angle γ' for both the hindwing and the forewing. Here γ' is the angle between a line stretching along the length of the wing and the downward vertical plane. The phase lag of the motion of the forewings behind that of the hindwings is characteristic of four-winged insects in general. Aerodynamic interference between the two wings was estimated by Weis-Fogh and Jensen⁹ as significant, but not of dominant importance: the effective angle of attack of the hindwing is reduced by about 2° through operation in the downwash from the forewing, whose own effective angle of attack is increased by about the same amount due to the upwash field ahead of the hindwing.

Weis-Fogh and Jensen⁹ made separate determinations

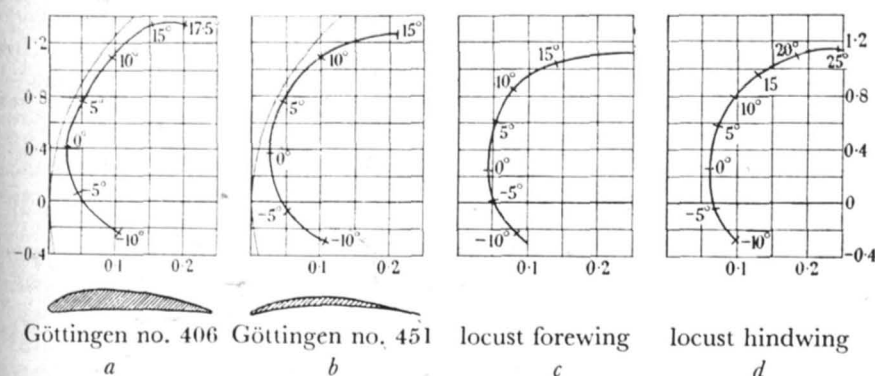


Fig. 11. Relationship between the lift coefficient (ordinate) and the drag coefficient (abscissa) in two man-made wings of aspect-ratio 5, compared with locust wings.⁹ The parameters on the curves are angles of attack

of the variation of lift coefficient and drag coefficient with angle of attack to a steady relative wind for both the forewing and the hindwing. These are shown in Fig. 11, with corresponding curves for two standard wings used in aeronautics: the main disadvantage of the insect wing is a higher minimum drag coefficient C_D , around 0.05 compared with values around 0.03 for the aeronautical shapes (which on the other hand are inherently much heavier).

They used these steady-state data together with measurements of angle of attack (corrected as noted above for mutual interference) to obtain estimates of the variation of the vertical component of force from each wing with time (Fig. 12, in which results are shown for two different experiments I and II, with mean lifts 97 and 111 per cent. of insect weight, respectively). An important check on these results was the good agreement (3 and 7 per cent. error, respectively) between the total mean lift obtained from each calculation and the values actually measured. Of that mean lift, about 70 per cent. is attributable to the hindwing and 30 per cent. to the forewing. As already suggested, the lift is developed primarily in the downstroke.

Weis-Fogh and Jensen⁹ made a similar analysis of the horizontal forces (thrusts) produced by the wings, checking the analysis this time by the fact that the mean wing thrust is required to balance body drag which was separately measured. Fig. 13 depicts as a function of time the thrust of each pair of wings as a fraction of the total mean thrust developed by both pairs (which, actually, comes to about 7 per cent. of the total mean lift). Of that total mean thrust, about three quarters comes from the hindwings.

After their very extensive wind-tunnel-based studies, which here I have just briefly summarised from an aerodynamic point of view, Jensen and Weis-Fogh¹² elucidated also certain structural features of great importance to the flight of locusts and most other insects: their capacity for making high-frequency tuned oscillations. Briefly, the insect's external skeleton, consisting of a hard cuticle of good elastic properties together with connecting tissue including a high quality elastomer,

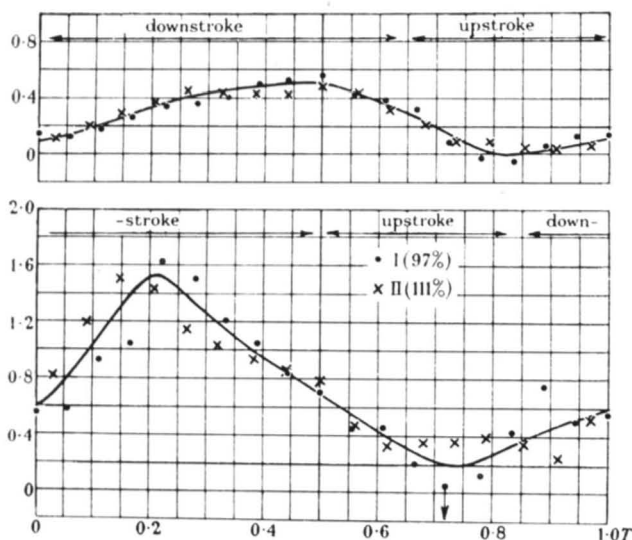


Fig. 12. Lift during a wing stroke of *Schistocerca gregaria*⁹: top, for the two forewings; below, for the two hindwings. Abscissa: time during a wing stroke beginning at the uppermost position of the forewing. Ordinate: wing lift divided by the total mean lift

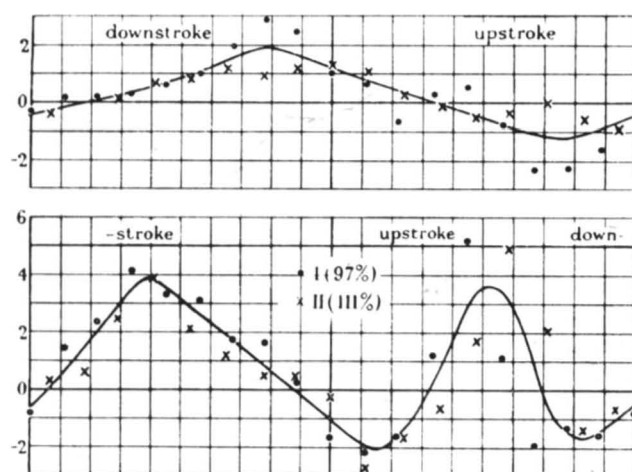


Fig. 13. Thrust during a wing stroke: top, for the two forewings; below, for the two hindwings. Abscissa as in Fig. 12. Ordinate: wing thrust divided by the total mean thrust

resilin, comparable to vulcanised rubber, responds elastically with little internal damping to complicated wing oscillations of large amplitude.

The vertebrates, for all their numerous advantages, have been seriously impeded in the development of high frequency oscillatory movements by failure to evolve a structural material or an elastomer of even approximately comparable elastic properties to those of cuticle and resilin. In every wing beat of a bird, a separate muscular effort is needed to accelerate and decelerate the wing: in other words, to overcome its inertia. The wing inertia in insects is largely balanced by elastic forces, and muscular effort only has to overcome aerodynamic damping.

Birds admittedly have their own unique advantages (section 2.3) including those of wing structures based on feathers. The impermeable insect wing is less versatile and effective aerodynamically but achieves a reasonable compromise between its structural and other needs through the well known *venation* (see, for example, reference 13, p. 115): the very thin wings are strengthened by the complicated pattern of veins, hollow conduits of thickened and hardened cuticle which contain both

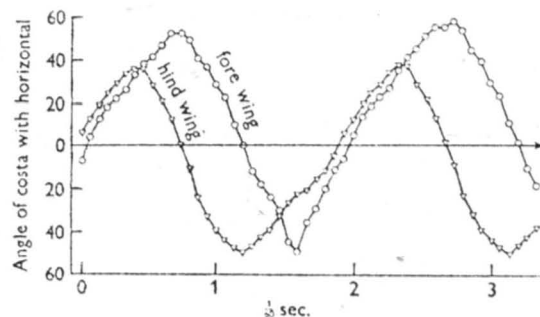


Fig. 14. The angular motion of the wings of a dragonfly *Ladona exusta* analysed by high-speed cinematography of a tethered insect¹⁴

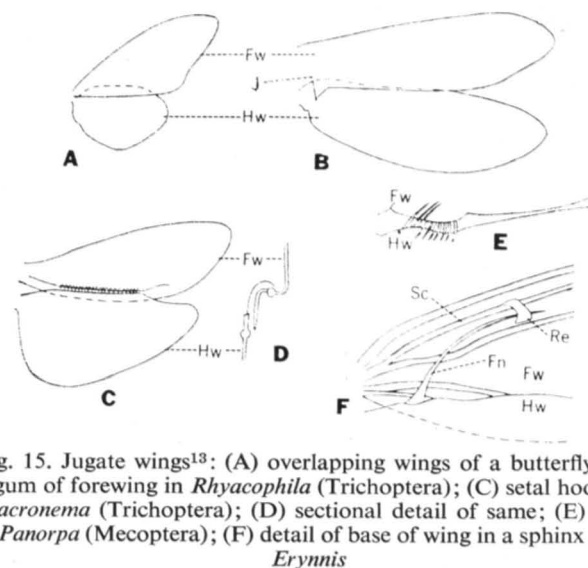


Fig. 15. Jugate wings¹³: (A) overlapping wings of a butterfly; (B) jugum of forewing in *Rhyacophila* (Trichoptera); (C) setal hooks in *Macronema* (Trichoptera); (D) sectional detail of same; (E) setae in *Panorpa* (Mecoptera); (F) detail of base of wing in a sphinx moth *Erynnis*

nerves and also separate supplies of air and of blood.

For insects in general the main conclusion of Weis-Fogh and Jensen,⁹ that insect forward flight proceeds at frequency parameters small enough to make a quasi-steady type of analysis satisfactory, has been confirmed in other studies. Fig. 14 from Pringle¹⁴ gives some data on a dragonfly *Ladona*; note the same phase lag of the forewing behind the hindwing.

In many other groups of insects (see, for example, reference 13) there is no separate motion of four independent wings. In the Diptera ("flies") the hindwings have of course degenerated altogether (section 2.5); by contrast, in the Coleoptera (beetles) the forewings have changed into those protective sheaths, the elytra, which do not flap. Again, Fig. 15 shows "jugate" wings: the hindwing and the forewing linked so that they flap as one, either through simple overlap as in butterflies or by various types of hook-shaped setae keeping them hooked together in other Lepidoptera, in Hymenoptera, in Trichoptera (caddis-flies) and Mecoptera ("scorpion-flies").

Changes in muscular arrangement are found as we move away from insect orders appearing early in the fossil record like Orthoptera (grasshoppers) and Odonata (dragonflies). Instead of ordinary muscles which are activated by nerves once per wing cycle (*neurogenic* muscles), many groups developed the so called *myogenic* or fibrillar muscles which themselves can go into oscillation without each separate beat needing to be initiated by a separate motor-neurone action potential. These

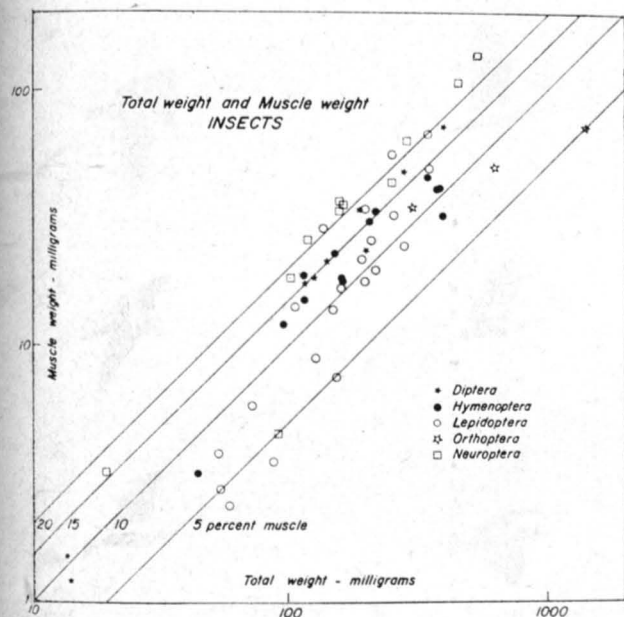


Fig. 16. Total muscle mass plotted against total mass for insects¹⁵

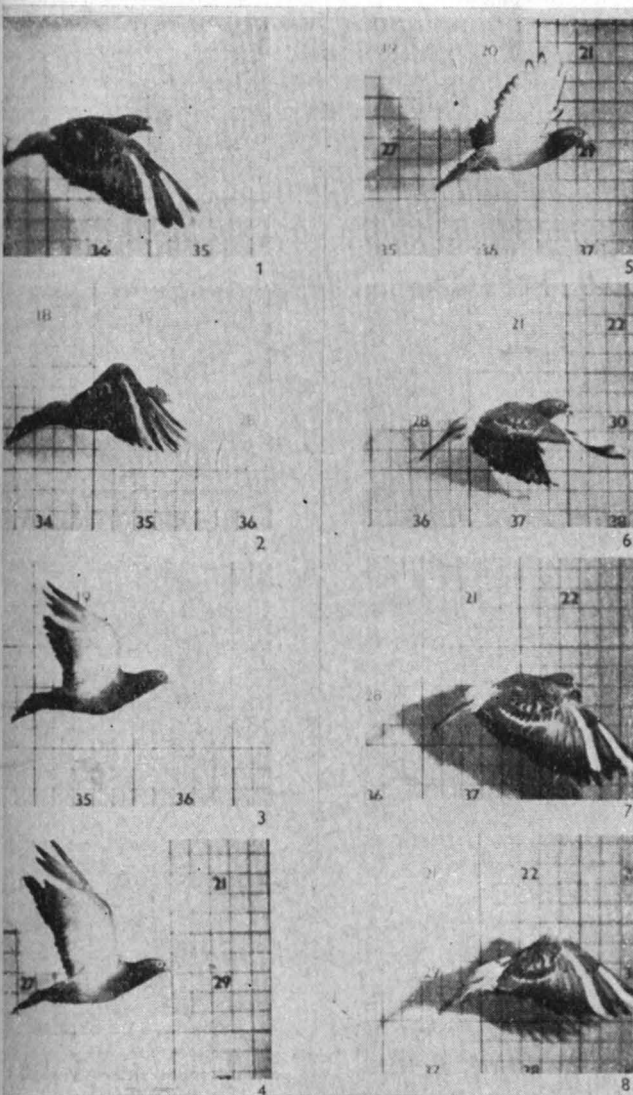


Fig. 17. Forward flight of a pigeon¹⁶

fibrillar muscles reach their highest specialisation in Coleoptera, Hymenoptera and Diptera. Both they and the elasticity properties mentioned earlier were essential for the acquisition of beat frequencies over 100 Hz, which have made possible as we shall see in Part III remarkable reductions in size for insects that are still able to hover. Wing-beat frequencies of several hundred hertz are common in small Diptera and Hymenoptera.

Finally, Fig. 16 shows that over a wide range of insects total muscle mass varies from 10 to 20 per cent. of total insect mass, which emphasises the familiar fact that the power plant is necessarily a very substantial part of the whole weight of a flying machine.

2.3. Birds

In birds we shall find generally similar muscle-mass proportions, but of course fundamental differences in muscular and skeletal arrangements; whereas there are much greater similarities, and only minor differences, between the aerodynamics of flapping flight in birds and in insects. The classic investigation, that of Brown¹⁶ on the flight of a pigeon *Columba*, established with clarity the essential aerodynamics, confidence in which has been further strengthened through subsequent work in wind-tunnels by Pennycuik,¹⁷ Tucker¹⁸ and others.

Brown trained birds to fly straight along a passage 60m long to a cage at one end. His high-speed camera system was set up halfway along the passage. Fig. 17 shows a sequence of pictures so obtained for a pigeon *Columba* flying at around 10ms⁻¹, corresponding to a Reynolds number of around 10⁵ based on the wing chord *c*. The wing-beat frequency is about 5Hz, corresponding

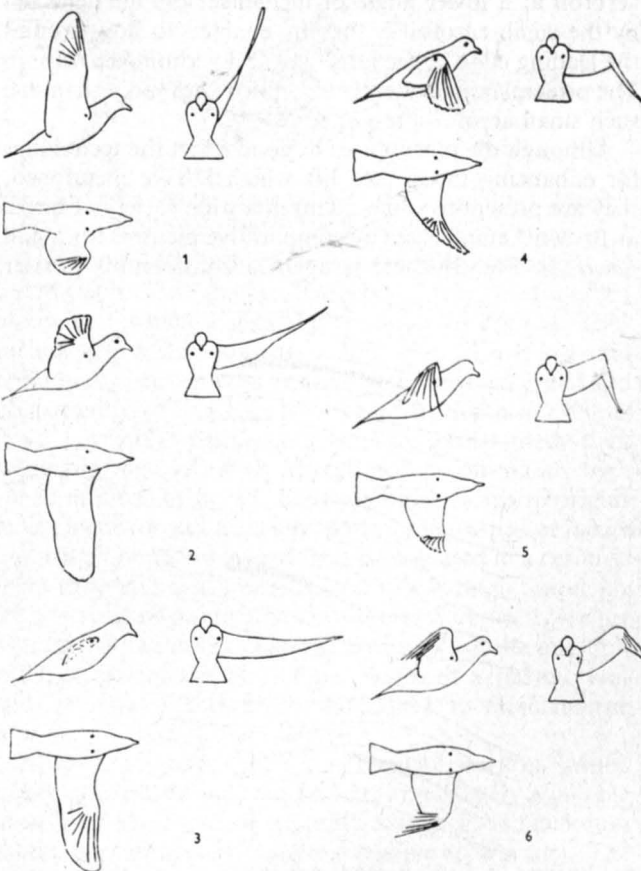


Fig. 18. Wing-movement cycle of a pigeon¹⁶: (1) beginning of downstroke; (2) middle of downstroke; (3) approaching end of downstroke; (4) beginning of upstroke; (5) middle of upstroke; (6) approaching end of upstroke

to a frequency parameter $\omega c/U$ of about $\frac{1}{2}$; within the range where aerodynamic forces depart only moderately from quasi-steady values.

Drawings of the pigeon's position from three mutually perpendicular directions are shown in six successive phases of the wing-beat cycle, beginning with the highest wing position, in Fig. 18. This emphasises the similarity of the downstroke, with the wing chord practically horizontal, to that depicted for the locust in Fig. 8 or for general flapping flight in Fig. 7. The rapid supination at the end of the downstroke, to produce a highly "feathered" upstroke (with a large positive pitch angle to the direction of mean motion) is also just as marked as in Fig. 8.

A new feature, on the other hand, is the flexure of the wrist which accompanies upward movement of the pigeon's wing. Probably this assists in the maintenance of significant wing thrust in the middle of the upstroke when the primary feathers (near the wing tip) are swung violently backwards.

Lift, on the other hand, is probably acquired mainly on the downstroke. Brown established the lift-enhancing rôle of the separation between the different primary feathers during this downstroke, seen in particular in frame 5 of Fig. 17. He made wind-tunnel experiments on various typical arrangements of feathers in an inert holder, and demonstrated a 60 per cent. improvement in maximum lift for an arrangement with such a separation of the primary feathers. Their action is similar to that of a leading edge "slot" of the type (Fig. 19) used in aeronautics, where a large aerofoil is preceded by a small aerofoil at a lower angle of incidence: the air deflected by the small aerofoil is thereby enabled to flow around the leading edge of the large aerofoil without separation. The principle can evidently be refined with more than one such small aerofoil present.

Although the pigeon uses to good effect the techniques for enhancing thrust and lift which I have mentioned, they are present to some extent in a wide variety of birds, as Brown¹⁶ emphasises by comparative pictures for a gull *Larus*. In Fig. 20 there is again a considerably greater

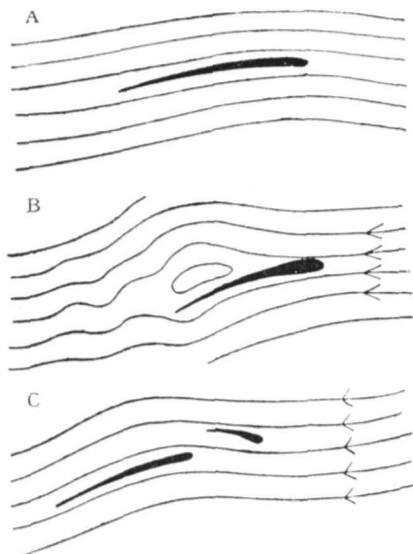


Fig. 19. Lift enhancement¹⁹: (A) flow does not separate on aerofoil at small angle of incidence; (B) flow separates on aerofoil at large angle of incidence; (C) flow does not separate on aerofoil at large angle of incidence preceded by a small aerofoil at a small angle of incidence

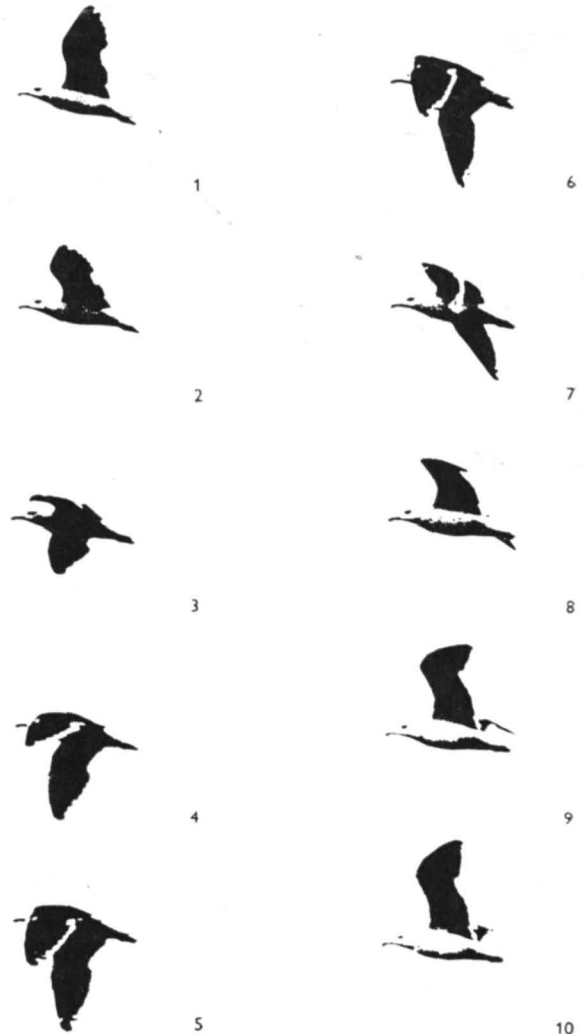


Fig. 20. Forward flight of a gull¹⁶

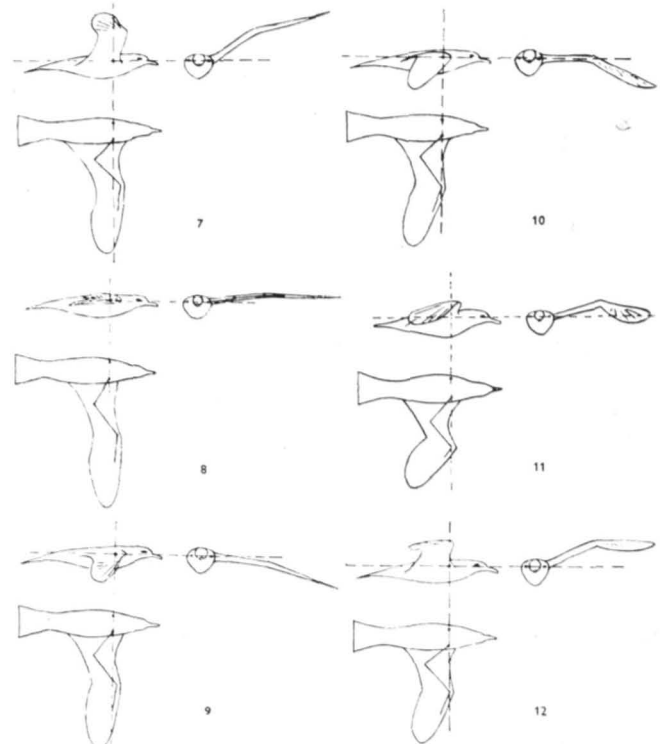


Fig. 21. Wing movements during normal flight of a gull¹⁶: (7) beginning of downstroke; (8) middle of downstroke; (9) approaching end of downstroke; (10) beginning of upstroke; (11) middle of upstroke; (12) approaching end of upstroke

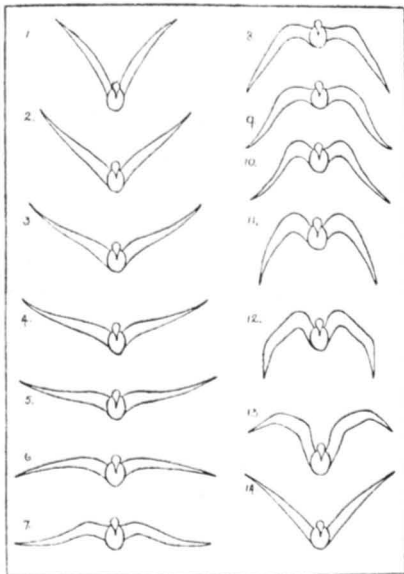


Fig. 22. Successive wing positions (1 to 14) in vigorous flapping flight of a gull¹⁹

degree of separation of the primary feathers on the downstroke (frames 1 to 5) than on the upstroke (frames 6 to 10). Fig. 21 gives diagrammatic views from three mutually perpendicular directions for comparison with Fig. 18: wrist flexure on the upstroke leading to a backward movement of the primary feathers is again very clearly present if a little less marked than before. An earlier sequence of drawings from motion picture frames by Horton-Smith¹⁹ show (Fig. 22) a gull in more vigorous flapping flight with very marked wrist flexure on the upstroke but with the wing still very straight and parallel to the direction of mean motion on the downstroke.



Fig. 23. An American robin in slow flight²²

Gulls are among the many groups of birds that often use a mode of sustained forward flight through *alternate* periods of flapping and gliding, any height lost in a glide being regained during the immediately following period of flapping flight. It would be interesting to analyse the

energetics of this type of sustained forward flight, as Weihs²⁰ did for the corresponding method of locomotion of fishes heavier than water. His work suggests that the method may have substantially lower metabolic cost than continuous thrusting in any circumstances when the animal's extra power requirement for thrusting, divided by the resulting forward speed, greatly exceeds its drag in the gliding condition. Lack²¹ (p. 113) made a similar suggestion on the flight of swifts.

Fig. 23 shows an extreme case of the use of feather separation to enhance lift. The American robin *Turdus migratorius* is here photographed in slow flight; the condition when it needs a particularly high lift coefficient.

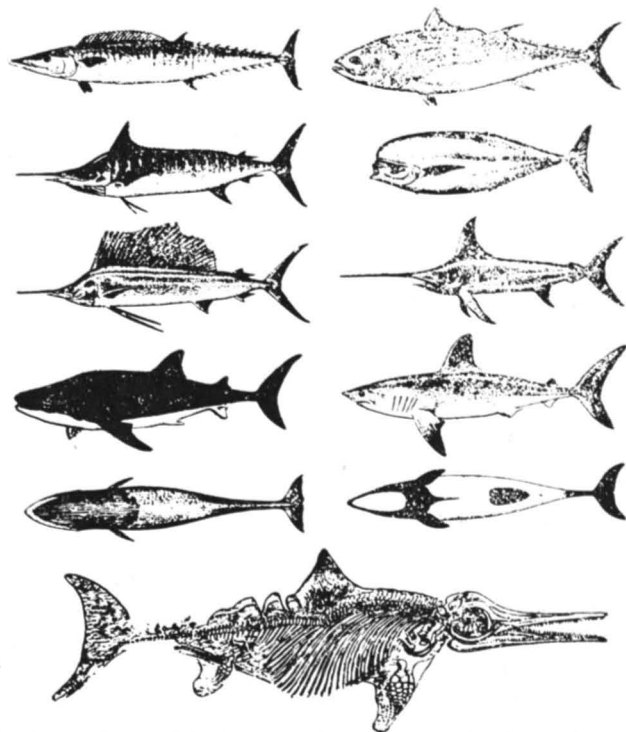


Fig. 24. Variants of the lunate tail in 6 percomorph fishes, 2 sharks, 2 cetacean mammals and 1 extinct reptile¹

I have emphasised in my surveys of aquatic animal locomotion the special features of the lunate-tailed animals of which a selection is shown in Fig. 24. They include the fastest animals in the sea; all are fast and continually active swimmers, living in the open ocean and able rapidly to make large changes in depth as well as large horizontal displacements. The special method of achieving high efficiency thrusting for continuous high speed motion, on which these animals of diverse origins have all converged, is the crescent-moon-shaped or *lunate* tail, which remains rigid while it is oscillated in a carangiform thrusting mode at an exceptionally high frequency for the sizes of animals involved (for example, 12Hz for a tunnyfish 2m long). It is interesting to ask the question whether any of the birds have modes of aerial motion, and of aerial life generally, analogous to these marine modes.

If we try to answer the rather simpler question "which are the fastest birds?" we find no immediately available answer in the form of accurate statistics of maximum attainable "airspeeds" (speeds relative to the air). The difficulty is that emphasised by Meinertzhagen¹⁰ in his extensive critique of the available observational data on bird speeds: the conditions under which birds are likely to fly at their maximum speeds are not those which

permit *either* really reliable measurements of speed relative to the ground, *or* those simultaneous measurements of the wind speed *where the bird is flying* that are necessary to infer its speed relative to the air. The highest airspeeds which can be regarded as well attested, if we take into account Meinertzhagen's reservations about much of the data he quotes, are in the range 25 to 30ms^{-1} , recorded for racing pigeons, golden plovers, mallards, peregrine falcons (with gravity assistance in a "stoop" or dive), hummingbirds and swifts; but this statement in no way rules out the possibility that higher airspeeds *are* achievable by certain species, or the possibility of some



Fig. 25. Showing the lunate wing-pair of the common swift *Apus apus*²⁵

more definite ordering of species (or of groups of species) in terms of their maximum attainable airspeed.

Almost all the ornithological evidence beyond these quantitative statistics suggests, indeed, a more precise answer to both our questions. Eminent ornithologists in every generation from Gilbert White onwards have agreed in the view that the fastest birds are the swifts; that is, the family Apodidae, characterised by "the extreme rapidity of their flight and their unwearied activity" (McGillivray²³ p. 607). Horton-Smith¹⁹ emphasises (p. 143) that expert falconers are repositories of large amounts of practical knowledge on relative speeds of birds, and goes on to adduce extensive evidence from such sources that among British birds the fastest is the common swift *Apus*: the only one that the peregrine falcon cannot catch! On p. 307 of Landsborough Thomson²⁴ the Apodidae are singled out as "the ultimate in high speed types" of birds. A brilliant special study by the great ornithologist Lack²¹ describes the swift (p. 110) as the bird which supremely excels "where birds as a group excel: in flight."

All writers on swifts have emphasised their continuous aerial activity: they feed exclusively in the air, off that "aeroplankton" of insects which is found (see section 2.6) up to remarkably high altitudes. There have been many observations of swifts at altitudes of 2km and more, and they change altitude readily and quickly (Lack²¹ p. 163). That swifts normally spend all day flying is well known but Lack²¹ (pp. 129–136) brings together clear evidence that they often fly all night as well.

It is intriguing, in view of the parallels between the swift's extreme mastery of the aerial medium in 3 dimensions through continued unwearied high-speed horizontal and vertical activity and the similar mastery of

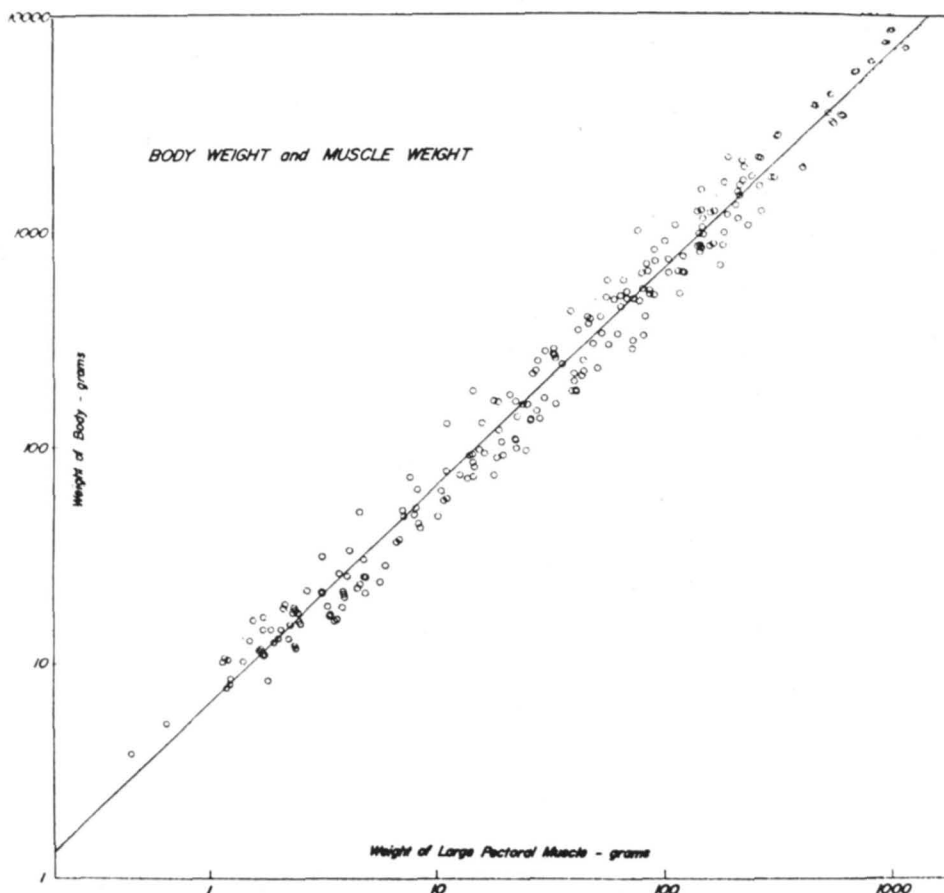


Fig. 26. Mass of pectoralis-major muscle (abscissa) plotted against total mass (ordinate) for birds¹⁵

the marine medium exhibited by the animals of Fig. 24, that the swift's thrusting surface is also lunate or crescent-moon-shaped (Fig. 25). Furthermore, this lunate wing-pair, like aquatic lunate tails, is observed to generate its thrust by rigid-body movements (that is, without any wrist bending) at exceptionally high frequency (Lack,²¹ p. 115).

This attribution of an exceptionally high wing-beat frequency to swifts is supported by the fact that systematic collection of frequency data by direct timing in the field was made for a wide range of birds in their general range of sizes¹⁰ but not for swifts whose wing-beat frequency was too great for visual estimation by a considerable margin. It is possible that the swifts are exceptional among flying animals, and similar to the lunate-tailed marine animals, in generating thrust by oscillations at a frequency parameter $\omega c/U$ of order 1 or more: the conditions under which Lighthill² argued that the lunate shape would improve thrusting efficiency. It would be most interesting if accurate motion pictures of swifts' wings in fast forward flight could be obtained for possible analysis from this point of view.

Not only do swifts spend most of their time in flight, but when they do land they avoid doing so on a horizontal surface. Indeed, their wings, specialised for fast flight, lack the freedom of shoulder rotation that facilitates the type of take-off movements to be described in section 3.1. In addition, any kind of "hop" off the ground as part of the take-off procedure is prevented by the extreme shortness of the swift's legs, which on the other hand are well adapted for clinging to nearly vertical surfaces by the "suction-cap" properties of the feet. They leave those surfaces by an initial motion under gravity followed by flapping forward flight as soon as they have got up speed. Frequently swifts nest in *towers*: a swift from Tournai church tower in Belgium was taken in a box to London Airport and released, and performed the return journey of 240km in 4 hours (Lack,²¹ p. 118); a remarkably short time considering that it included the time needed for navigation!

In Fig. 26 the mass of the pectoralis major muscle, which powers the downstroke in birds, is plotted against total bird mass for a large number of species. The straight

line represents a mean ratio 15 per cent. of pectoralis-major mass to total mass, like the corresponding result for insects (Fig. 16). For swifts, on the other hand, the ratio is well above this average (Lack,²¹ p. 116). Fig. 27 gives comparable results for the muscle that powers the upstroke: the mean ratio is here 1.5 per cent., only one tenth of that for the downstroke. The ratio is still lower for birds specialising in lift rather than in thrust, like the soaring birds of section 2.8; for swifts, specialising in thrust rather than in lift, the ratio of the mass of the muscle powering the upstroke to that powering the downstroke has risen exceptionally to one fifth. These trends are accentuated still further in the swifts' close relatives, the hummingbirds (Trochilidae, belonging to the same order Apodiformes), with their remarkable hovering capabilities (section 3.1).

Earlier I mentioned some advantages over the birds which the insects possess. On the other side of the balance, birds possess feathers, with the aerodynamic advantages already mentioned as well as great structural suitability for transmitting the air pressure load at low weight cost to the bones of the wing. Various further features are of great structural benefit to birds in general: especially their hollow bones, and the distribution of air sacs that reduces the mean density of the body without much loss of stiffness while also making possible a unique respiration system where continuous flow of air through a *constant-volume* lung, promoting highly efficient exchange of oxygen and carbon dioxide with the blood stream, is maintained by the expansions and contractions of the air sacs.

2.4. Bats

The outer part of the bird's wing, commonly called the hand (section 2.3), corresponds to the hands of other vertebrates, but the four finger bones are fused into a single strong skeletal member, only the small thumb ("alula") being separately identifiable. A great contrast is presented by the flying mammals of the order Chiroptera (bats), which possess wing membranes each primarily spanning (as the order's name implies) the bones of an extensive five-fingered hand, and secondarily spanning also the hind limb and tail (Figs. 28, 31, 32 and 33). The

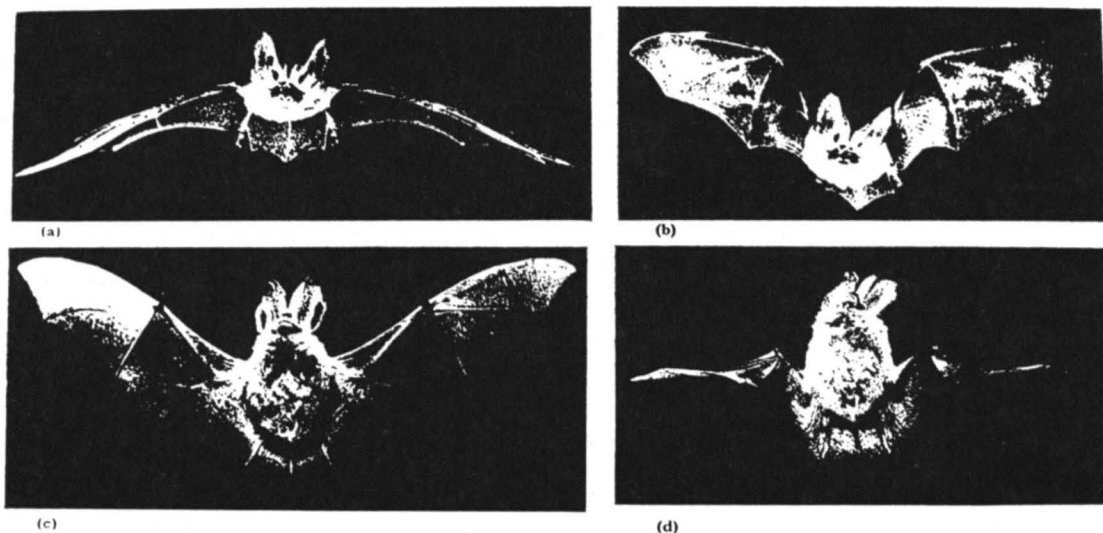


Fig. 28. A long-eared bat *Plecotus auritus*⁵ (mass 9g, wing span 26cm) flying horizontally at 3.5ms^{-1} (a) downstroke photographed from directly ahead; (b) upstroke photographed from directly

ahead; (c) downstroke photographed from below; (d) upstroke photographed from below. Photographs by Dr. Ulla Norberg

order, which includes (Wimsatt,²⁷ p. 10) 875 known species and is the second largest of mammalian orders (after Rodentia), is divided in two suborders: the Megachiroptera (or "megabats!") with picturesque names like "flying foxes" (Figs. 32 and 33) and the Microchiroptera or "microbats" including the vast majority of the species. Highly developed "echolocation" or "sonar" and good aerodynamic properties make many of them marvellous exponents of the art of night flying.

The family Vespertilionidae (containing most of the well known small British bats) has this combination of qualities to a marked degree. They can fly quite fast, and with superb control (and insect-catching performance), through forest-like environments of numerous branches and other obstacles. Fig. 28 shows the flight of *Plecotus auritus*: in the upper two pictures, the bat is flying towards us, with the wing parallel to the direction of mean motion in the downstroke (on the left) but given a large positive angle of pitch in the lightly loaded upstroke (on the right) as in the basic flapping-flight mode of Fig. 7. The same motions are seen from beneath the bat in the lower two pictures.

Evidently the wing deployed on five fingers is readily modified in shape for control purposes. For example, it can be given additional camber to improve maximum lift coefficient by depression of the fifth finger (as when an aircraft pilot lowers a trailing-edge flap) and bats are observed to do this at precisely those low airspeeds when the lift coefficient they need is high (Wimsatt,²⁷ p. 200).

A keeled breastbone (sternum), although present in many bats, is not the only skeletal element facilitating the application of a large bending moment to the wing in the downstroke (by means of a pectoralis muscle). The shoulder-blade (scapula) is also the origin of important muscles involved in the downstroke so that the depth of the whole rib cage from sternum to scapula is effective in applying the moment (Wimsatt,²⁷ pp. 114, 128). The mass of the pectoralis muscle is around 8 per cent. of the total mass but consideration of the many other muscles involved in chiropteran flight nearly doubles the proportion (p. 192) to make it comparable to that in insects or in birds.

It is interesting to ask whether any bats have developed wings of a much higher aspect-ratio than in Fig. 28, presumably for prolonged fast flight. Two such groups may be mentioned. The one with a mode of life closest to that of the swifts is the family Molossidae of free-tailed American bats. Wimsatt²⁷ (p. 212) emphasises this similarity (see also Allen,²⁶ p. 122): they forage for insects in the open air, flying high and fast for long periods. Specialisations for high speed include not only a high aspect-ratio but forearms with streamlined cross sections replacing the nearly circular cross sections of most other bats. Like the swifts, they avoid landing on a level surface from which they would have difficulty in taking off (Wimsatt,²⁷ p. 212). I have chosen to show a member of this family, *Eumops californicus*, in a somnolent mood (Fig. 29), to make the point that bats are flying machines that fold their wings like naval aircraft when at rest! Another group of bats became ferociously carnivorous: *Phyllostomus hastatus* with its spear nose (Fig. 30) and wing of high aspect-ratio (Fig. 31) is a notably active and fast predatory flier.

Among the Megachiroptera, the large fruit-eating "flying foxes" of the genus *Pteropus* were investigated



Fig. 29. California mastiff bat *Eumops californicus*, showing its wide gape for insect catching²⁶



Fig. 30. The spear-nosed bat *Phyllostomus hastatus*²⁶



Fig. 31. The 43cm wing span of a specimen of *Phyllostomus hastatus*²⁶

very carefully in flight by E. H. Hankin,⁶ an exceptionally gifted observer working in India. He demonstrated that they use *leading-edge flaps*. Fig. 32 shows that part of the wing (shaded area) which they can depress by a voluntary movement of the thumb and index finger; Hankin made prolonged studies of this movement which he found was made when the airspeed was low—just when a consequent increase of lift coefficient would be advantageous.

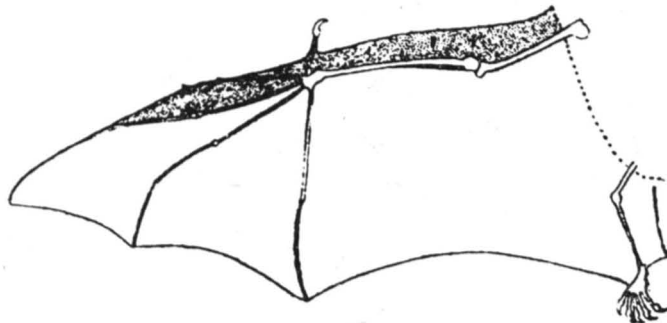


Fig. 32. Wing of flying fox *Pteropus medius* showing bones supporting the wing membrane: the "leading-edge flap" is shaded⁶

Other species of *Pteropus* are shown in flight in Fig. 33. Note in particular the specimen with dropped feet and arched wings: a common arrangement (see Hankin,⁶ p. 218) when a flying animal needs a high drag from balanced resistive forces below and above its mass centre. It is used either to slow the animal down or to facilitate (in a manner discussed in section 2.8) a steep dive.



Fig. 33. Flying foxes in flight.²⁶ Upper photograph: *Pteropus poliocephalus*. Lower photograph: *Pteropus natalis*

2.5. Control

But I have begun to consider control; this leads me into a general discussion of aerodynamic aspects of control and stability in flying animals. It is worth

beginning this by asking if flying animals normally achieve longitudinal stability by the typical aeronautical method: an aircraft derives inherent aerodynamic stability in pitch from its lift being supported by a main aerodynamic surface forward of the centre of gravity and another aerodynamic surface behind it: the stabilising tailplane. It would be a mistake, however, to postulate a general tendency in flying animals to achieve longitudinal stability in this way.

To be sure, such inherent aerodynamic stability was probably essential in the earliest developments of animal flight: both in any primitive gliding insects and in early flying insects that may have developed wing articulation before they developed sophisticated systems for controlling it. In fact, the wing arrangements in flying insects of the Carboniferous period were aerodynamically of the general type represented today by the dragonflies (Fig. 34), and the two pairs of wings, one anterior and one posterior to the centre of gravity, must have been important for their stability.



Fig. 34. The typical wing configuration in dragonflies proper (suborder Anisoptera of the Odonata)²⁸

Existing four-winged insects may benefit from the aerodynamic *damping in pitch* (an aerodynamic moment resisting rate of pitch) conferred by their wing arrangements. Even in Coleoptera the inert elytra (modified forewings) may play a stabilising rôle of this kind. Insects' need for aerodynamic stabilisation must not be overemphasised, however. Existing flying insects possess in general automatic control systems of a very advanced and rapidly acting nature (Pringle,¹⁴ p. 103). Weis-Fogh and Jensen⁹ already showed that one of their locusts responded to a change in pitch attitude by a change in pronation (degree of twist before the downstroke) *in the very next beat*; and similar rapidity of response to maintain a required angle of incidence is characteristic of insect control systems in general.

In the dragonflies, Mittelstaedt²⁹ showed that the relatively massive head (Fig. 34) acts as an attitude sensor for control purposes. When the attitude of the body

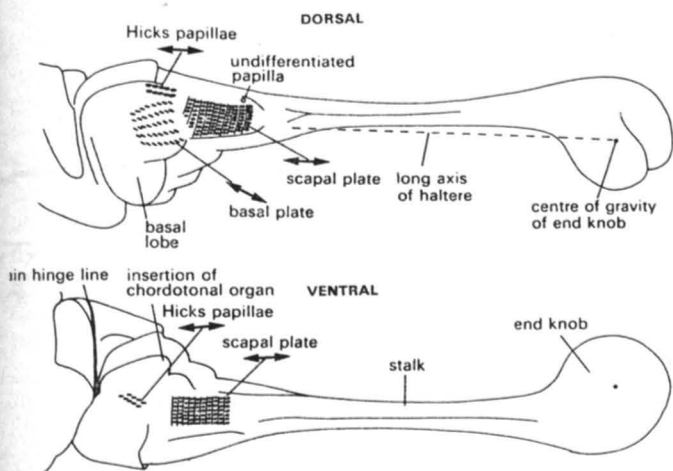


Fig. 35. Dorsal and ventral views of the halteres of the fly *Lucilia*³⁰

changes, that of the head lags behind and "there are strain gauges in the neck" (speaking anthropomorphically of the stretch receptors between head and thorax) which generate signals controlling pronation so as to produce compensatory attitude changes bringing the body into line with the head.

In the Diptera, those organs into which the hindwings degenerated are even more sensitive organs of balance, the halteres (Fig. 35), each with a "knob" at the end of a flexible "stalk" with a complex system of receptors at its base. Pringle³¹ and Faust³² worked out the mechanisms for sensing attitude changes through the resulting gyroscopic couples acting on the vibrating halteres which give the Diptera an exceptionally effective flight control system.

The above systems make the Odonata and Diptera in general able to maintain fully stable flight in the dark. Other orders of insects, on the other hand, need visual indications of attitude changes for their flight control systems.

By contrast, the birds and the bats, like vertebrates in general, sense their attitude changes by means of the semi-circular canal system of the vertebrate inner ear, and their flight control systems depend on that sensory information. For bats in particular, it is integrated with information from the echolocation system to produce superb nightflying capability.

It can of course be argued that birds with their tail feathers spread approximate to the typical aircraft configuration, with main lifting surface (wing) and stabilising tail surface. Certainly, birds make extensive use of their ability to spread these tail feathers to a markedly variable extent. In slow flight they are usually extended, and used for both stability and control. They are fully retracted, however, in normal fast flight which proceeds successfully without any tail contribution to stability and control; although for any sharp manoeuvre required in fast flight a bird often extends its tail feathers rapidly to produce a large pitching moment. Birds with amputated tail feathers, on the other hand, are capable of stable flight.

In this connection, it must be recognised that a rather different form of longitudinal stability is present in most birds and bats, and even in many insects. This is the element of longitudinal stabilisation referred to in aeronautics as "the pendulum effect" and characteristic of a high-wing monoplane. With a wing situated well

above the centre of gravity as in many flying animals, stability rather like that of a ship is derived from the fact that the centre of pressure lies above the centre of gravity. An attitude change is then resisted by a couple due to the displacement of the line of action of the animal's weight from that of the aerodynamic forces.

With aircraft pilots, this type of additional longitudinal stability derived from the pendulum effect is not always popular, because it can make the aircraft slow in responding to control movements. However, this is partly because the pilot cannot use the pendulum effect to generate extra pitching moments, which must be produced by the elevator attached to the tailplane which is his other source of longitudinal stability. Flying animals, on the other hand, can produce fore-and-aft displacements of the wings to derive controlling moments from the stabilising pendulum effect itself. Note that for acceleration a displacement of the wing's centre of pressure towards the tail will cause the centre of gravity to swing round beneath it producing a reduced angle of incidence such as is required at higher speeds.

Hankin⁶ (p. 110) made careful observations of the longitudinal control system used by a certain species of parrot with good flying capabilities. Fig. 36 shows his drawings of the parrot's configuration in slow, medium and fast flight. The tail feathers are fully retracted at both medium speeds and high speeds; the pendulum effect, however, is then used both for stability and control, displacements of the wings towards the tail being made progressively with increasing speed. By contrast, in slow flight they are displaced towards the head, while the tail feathers are spread; note that these then enhance stability not only in the ordinary way but also by providing an extra element of drag *below* the mass centre to offset the wing drag above it (which is enhanced at a high angle of incidence).

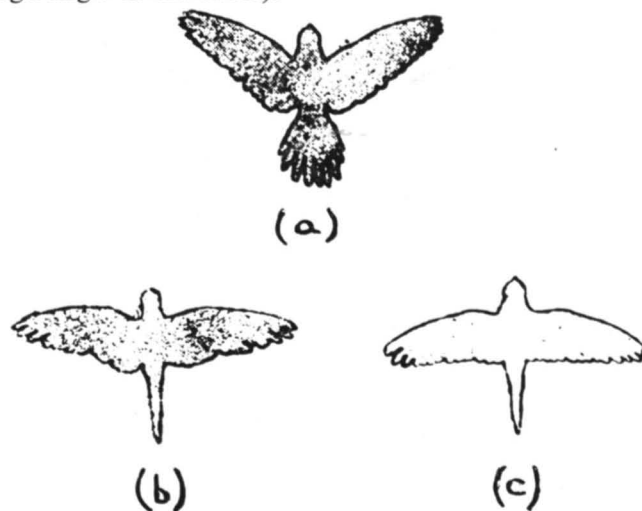


Fig. 36. Drawings of a parrot in (a) slow, (b) medium and (c) fast flight⁶

Directional control is provided entirely by the principle of the banked turn in all flying animals; see, for example, Fig. 37 showing the small brown bat *Myotis* in a steeply banked turn. Control action broadly similar to that of an aileron is used to produce the banking, but Hankin⁶ (pp. 68 and 114) describes detailed observations establishing that the antisymmetrical movements of ailerons on aircraft (those on opposite wings being moved in opposite directions) are absent. A bird



Fig. 37. The small brown bat *Myotis* in a steeply banked turn²⁶

typically initiates a turn to the right by a wrist rotation in the right wing only, reducing its angle of incidence near the tip so that it falls, producing the banked condition. A quicker change of attitude in roll is sometimes made by rotating the whole wing from the shoulder. In either case the new attitude would be maintained stably once the twist is annulled owing to any wing's normal strong *damping in roll*, angles of incidence being enhanced on a falling wing and reduced on a rising one.

2.6. Migration

The above brief discussion of systems for "tactical" control of animal flight may be supplemented by an even briefer discussion of "strategic" control as exhibited particularly in the migration of flying animals. The birds are especially noted for their precise strategic control of flight between closely defined summering and wintering grounds, or breeding and feeding grounds; Dorst³³ gives an excellent general account of bird migrations.

They typically migrate at speeds *above* their normal cruising speed (Dorst,³³ p. 213). Birds are not deterred by head winds in their choice of direction, and partly compensate for them by a certain increase in airspeed. When flying over land they periodically alight for food and rest. Many birds unable to forage at sea, however, have demonstrated "unrefuelled ranges" of 1000 km and more.

Many species of geese, ducks, pelicans, cranes and plovers commonly migrate in a V-formation (Dorst,³³ p. 260). They almost certainly gain aerodynamic advantages thereby as well as visual convenience for purposes of keeping the flock together. The idea that every bird except the foremost one (at the apex of the V) exerts reduced power, because it flies in the upwash field diagonally behind the bird in front, is supported by the observed fact that the rôle of leader is changed over on a rota system during the flight.

In the accurate navigation of which birds have shown themselves capable, it is well established that (as might be expected) landmarks of all kinds are extensively used. Nevertheless, birds prove able to exercise significant navigational powers without any landmarks at all. The perplexing question of how they do it has been extensively studied for many years: the accumulated evidence from many different lines of research (Dorst,³³ p. 282) has more and more forced ornithologists to conclude that birds possess adequate internal biological clocks to be able to make use of astronomical indications (particularly the bearing and elevation of the sun) for navigational purposes; by contrast, the existence or otherwise of methods of indication using any other physical effects, although still being very actively investigated, remains unproved.

Migration of insects differs in many ways³⁴ especially because the airspeeds of which they are capable are usually much lower. Consequently, they are more at the mercy of the winds and much less likely to be able to make a voluntary choice of the direction of flight.

Actually, entomologists use a specialised definition of the aerodynamic term "boundary layer"—and one different for each species of insect. The boundary layer in their parlance means that region which is near enough to the ground for the wind speed to be less than the speed of the insect. A few species, including the American Monarch butterfly *Danaus plexippus*, have been proved to migrate within their boundary layer: not between accurately predetermined summering and wintering sites but on a *broad* north-south pattern such as could be explained by a general tendency to follow the sun in the autumn and to fly away from the sun in the spring (Chapman,³⁰ p. 243).

A much wider range of insects, while possessing a well defined instinct to migrate at particular periods in their life cycle, lack any tendency to migrate in a particular direction. Their tendency is, rather, just to start actively flying, normally right out of their boundary layers into the region where the wind can blow them "where it chooses." Such tendencies have definite advantages in securing the dispersal of the species.

In practice the displacements so produced are not exclusively horizontal. The atmosphere contains substantial regions of updraught, both coherent and random. As a result insects are commonly found at substantial altitudes; indeed, the average density of insects at 1 km altitude is reduced only to 10 per cent. of the density at 60m (Johnson,³⁴ p. 296). These form the extensive aeroplankton of insects upon which the swifts feed (section 2.3).

It should not be assumed that insects being carried to such great heights make no statistical contribution to the future of their species. It must be remembered that the typical flying endurance of an insect is from 5 to 10 hours

(see, for example, reference 35) and that downdraughts are statistically just as common as updraughts; so many of the insects carried up to substantial altitudes subsequently start a successful life again in some new clime!

In the Intertropical Convergence Zones, meteorological tendencies (mathematically speaking, a negative horizontal divergence of the wind vector) act to produce dense concentrations of insects. The locusts in a swarm are all flying vigorously but headed in different directions (Chapman,³⁰ p. 246) but the wind's convergence concentrates them more and more, with of course potentially devastating effects.

2.7. Scaling

In the discussion in section 2.6, I have commented that larger flying animals such as birds achieve much greater airspeeds than do small flying animals such as insects. In sections 2.2 and 2.3 we encountered figures for cruising speeds (4 ms^{-1} for a 2 g locust; 10 ms^{-1} for a 500 g pigeon) along similar lines. Within the insects themselves, Fig. 38 shows a general trend of observed airspeeds (ordinate) increasing with a measure of insect size (abscissa).

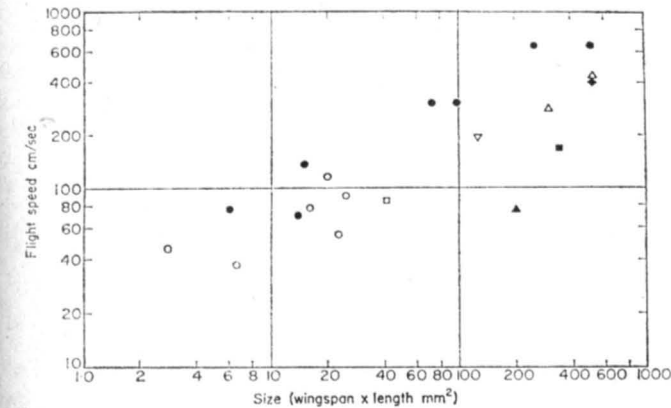


Fig. 38. Mean airspeed plotted against a measure of size for various insects³⁴

The general result is by no means unexpected to those familiar with the aeronautical concept that the *larger* flying machine requires a *higher* wing loading, and therefore higher characteristic speeds. Fig. 39 is a famous diagram due to Karman³⁶ showing the wing loading of birds (in pounds per square foot) plotted against their weight (in pounds) with an early aircraft plotted on the same diagram. As a linear scale l varies the weight should vary as l^3 but the wing area as l^2 , making the wing loading vary as l , and therefore as the *cube root* of the weight. Accordingly, the straight line on Fig. 39 represents a cube root law.

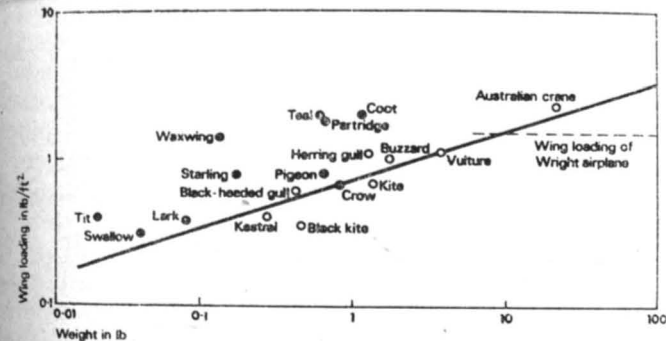


Fig. 39. Wing loading plotted against weight³⁶

The band of data on this diagram is thick, but is oriented at an angle approximately parallel to the line. We may note, furthermore, one excellent reason for the thickness of the band: all the birds towards its lower margin are birds of prey able to seize prey and fly off with it. Their wing loadings have to be relatively lower therefore so that they are able to fly away successfully carrying that *additional* payload. . . . The earlier, low-speed part of that flight is especially facilitated by the low wing loading, and by the tendency of many of these birds to possess a highly cambered wing (with large maximum lift coefficient).

Fig. 40 from the invaluable survey of Greenewalt¹⁵ gives considerably more data for birds. As wing area is there plotted against total mass, the straight lines used for comparison purposes have a slope corresponding to a *two thirds* power law. The total band of data is again very wide but splits up into three thinner bands each parallel to those lines, indicated by colour codes on Greenewalt's original; those, which are not reproduced here, show that the wing area (in cm^2) divided by the two thirds power of the mass (in g) lies in the middle range 10 to 20 for birds outside two exceptional groups: *birds of prey* with values from 15 to 30, and various birds that *avoid low-speed flight* in the range below 10. These latter are birds with high wing loading, including fast birds such as swifts, and also various aquatic and other birds that will be seen in section 3.1 to fly only after an extended runway-type take-off.

The scaling arguments are set out more formally in Fig. 41. After wing loading has been defined, its relationship to characteristic speeds U is formulated in an equation that is little more than a *definition* of the lift coefficient C_L : this equation specifies the *stalling* speed when C_L is given its maximum value, and the *cruising* speed when C_L takes a lower value corresponding to maximum lift-drag ratio. In either case the arguments making the wing loading vary as l or as $m^{1/3}$ make the characteristic speed U vary as $l^{1/2}$ or as $m^{1/6}$. That conclusion is consistent with animals like a pigeon and a locust whose masses are in the ratio 250 having cruising speeds in a ratio 2.5 close to the sixth root of 250.

For sustained forward flight through the air, the minimum thrust T that must be exerted is equal to the minimum drag, which is equal to the weight mg divided by the maximum lift-drag ratio. Thus the *thrust per unit mass* of animal needed to sustain it in forward flight tends to be approximately independent of size. To deduce from this quantity the *power per unit mass*, however, we must multiply by the velocity of flight U which has already been seen to vary roughly as $m^{1/6}$. Thus, the minimum power per unit mass required to sustain an animal of mass m in forward flight tends to increase in proportion to $m^{1/6}$.

Recently, Weis-Fogh³⁷ discussed the maximum power output per unit mass of muscle found in actively flying animals. He concluded that a maximum of order 200W per kg of muscle is reached in insects, birds and bats. It is interesting that this is about 10 times the power output per kg of human muscle. On the other hand, it represents according to his calculations something like an upper limit on power output subject to the fundamental biophysical and biochemical features common to all known animal muscles.

If we accept both Weis-Fogh's conclusion that there is

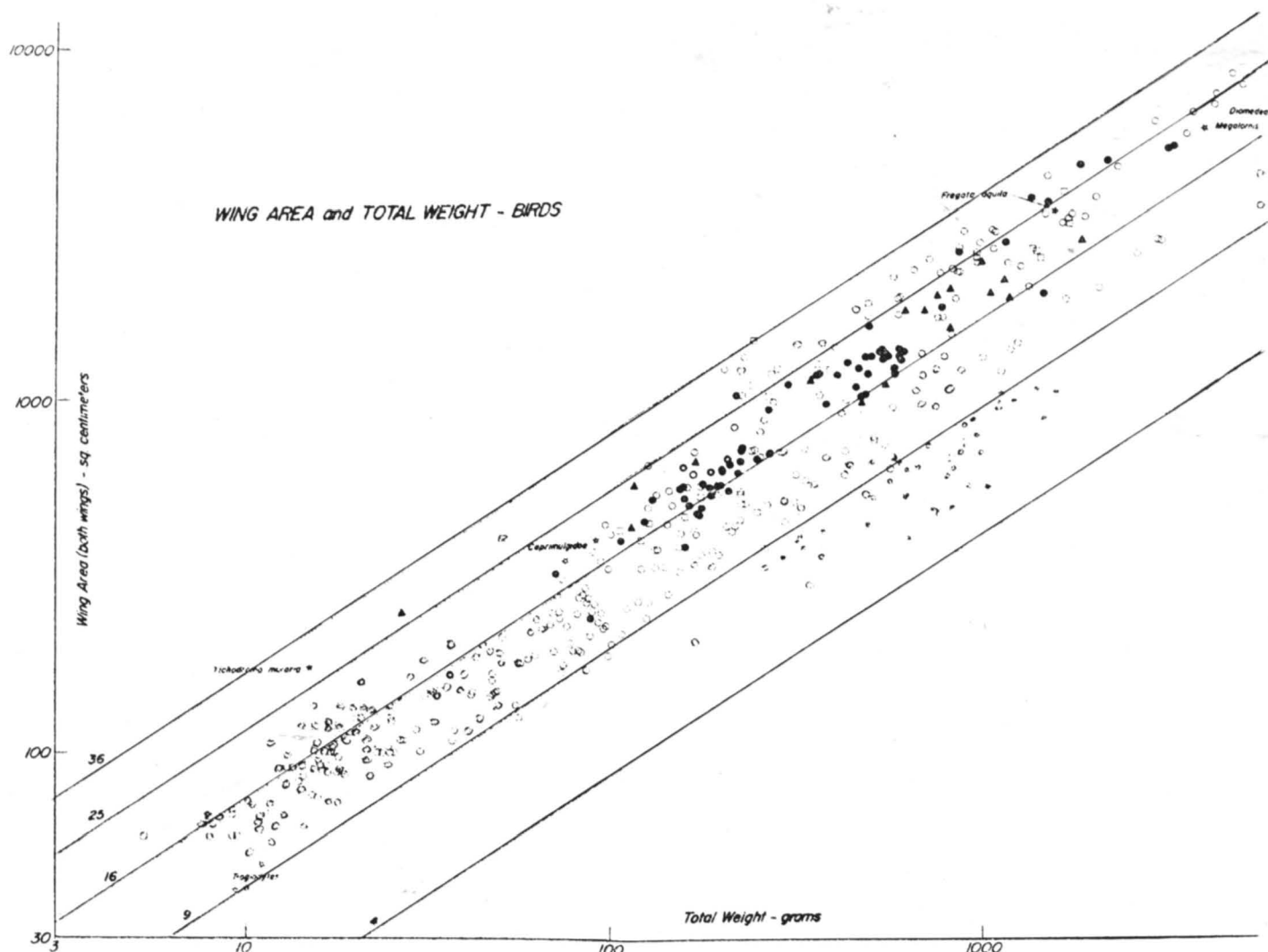


Fig. 40. Wing area plotted against total mass for birds¹⁵

The wing-loading $\left(\frac{\text{all-up weight}}{\text{wing area}} = \frac{mg}{S}\right)$ fixes characteristic speeds U according to equation

$$\frac{mg}{S} = \frac{1}{2} \rho U^2 C_L,$$

where $\begin{cases} U = \text{stalling speed when value of } C_L \text{ is maximum;} \\ U = \text{cruising speed when value of } C_L \text{ gives max lift/drag ratio } L/D \end{cases}$

In terms of linear scale l , $S \propto l^2$; $m \propto l^3$. Thus $mg/S \propto l$ and so $U \propto l^{1/2} \propto m^{1/6}$.

For sustained forward flight,

$$\text{thrust } T = \text{drag } D \geq \frac{mg}{\max L/D} \propto m.$$

$$\frac{\text{power}}{\text{mass}} = \frac{TU}{m} \text{ goes up like } U \propto m^{1/6}.$$

Fig. 41. Scaling arguments

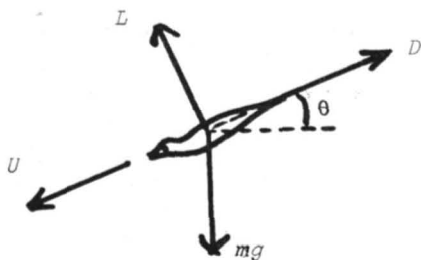
an upper limit of the order of 200W output per kg of muscle, and also the limits recorded in Figs. 16 and 26 of the order of 20 per cent. on the proportion of a flying animal's total mass devoted to muscle, we may infer that an animal's power output per unit mass cannot significantly exceed 40W per kg. Note that in smaller animals, such as insects and hummingbirds, the *hovering* motions to be discussed in section 3.1 are those requiring rates of

power expenditure near a maximum. For certain fast fliers, however, such as swifts or the powerful carnivorous bat of Figs. 30 and 31, the maximum power must be achieved in forward flight. Observed maximum flight speeds U of around 30 ms^{-1} in level flight through still air are consistent with equating a power output per unit mass of 40W per kg to a value suggested by Fig. 41 of gU divided by the product of a lift-drag ratio and some sort of mechanical efficiency.

Even for groups of animals which have a low wing loading for their size, the wing loading must increase with mass m ; ultimately, then, the minimum power per unit mass required for their flight, increasing (Fig. 41) as $m^{1/6}$, must exceed the maximum available power per unit mass. It is not surprising, therefore, that there is an overall *maximum mass* observed in flying animals. This is approximately 12kg, and the idea that a rather fundamental upper limit is involved here is supported by the fact that the same upper limit is found in four quite different *orders* of birds (Pennycuik,⁵ p. 39): Falconiformes, Anseriformes, Gruiformes and Pelecaniformes.

2.8. Soaring

The above discussion makes it clear that large birds, that is, birds of sizes comparable to the maximum for sustained forward *flapping* flight, use that method for maintaining themselves in the air only at a formidable



At angle of glide θ relative to the air, $mg \cos \theta = L$, $mg \sin \theta = D$, $\theta = \tan^{-1}(D/L)$.

$$\text{drag } D = \frac{1}{2} \rho U^2 S C_{Df} + \frac{KL^2}{\frac{1}{2} \rho U^2 b^2}$$

(b = wing semi-span) frictional induced

For given L , D is minimum for $U = U_{md}$ (e.g., when two terms equal if C_{Df} , K constant). Stable gliding needs $U > U_{md}$; e.g.,

$$b > \left(\frac{KS}{C_{Df}} \right)^{1/2} \left(\frac{L}{\frac{1}{2} \rho U^2 S} \right)$$

(Note that last bracket cannot exceed C_{Lmax} .)

Bird must spread wings at lower U .

Fig. 42. Motion relative to the air of a bird in a fixed wing configuration

cost in energy expenditure relative to their size. Such a cost is fully appropriate to emergency conditions of various kinds. Since, however, large birds in general benefit from being able to remain for *extended* periods in the air at convenient heights for surveying predatory opportunities, it is not surprising that they have evolved some less costly methods for achieving this. In these, the bird does not flap its wings, but sustains itself in forward flight through the air by extracting energy from natural winds: in a word, by *soaring*.

I shall give the theory of soaring in that frame of reference in which the air around the bird is *at rest*. In such a frame, as Fig. 42 reminds us, the bird simply glides downward at an angle θ whose tangent is equal to the ratio of the drag D to the lift L (these are the aerodynamic forces opposite to, and perpendicular to, the direction of motion). The drag is made up of a *frictional* component proportional to U^2 and specified by a frictional drag coefficient C_{Df} , and an *induced* drag proportional to U^{-2} representing effort needed to generate the trailing-vortex-pair wake. The lift L is generated as an inertial reaction from this vortex-pair wake, with its *momentum* L/U per unit length at right angles to the flight path. The *mass* of the wake per unit length is of order ρb^2 where b is the semi-span of the wing. The induced drag is the kinetic energy per unit length of wake, proportional to momentum squared divided by mass. This gives the expression in Fig. 42, where K is found to take values around 0.10.

For analysing gliding at a fixed angle θ , we may take the lift L as fixed since it must balance the weight component $mg \cos \theta$. Then for given wing span b , the total drag D takes a minimum value for a particular speed U . For example, when any variations of C_{Df} and K are neglected, this is the speed U_{md} (Fig. 42) for which the frictional and induced drags are equal. Birds could not glide stably at speeds much below their minimum drag speed, since a further decrease in speed would produce an *increase* in drag, leading to still more deceleration until stalling would occur; similarly, an increase in speed would produce a decrease in drag, leading to acceleration towards the minimum drag speed.

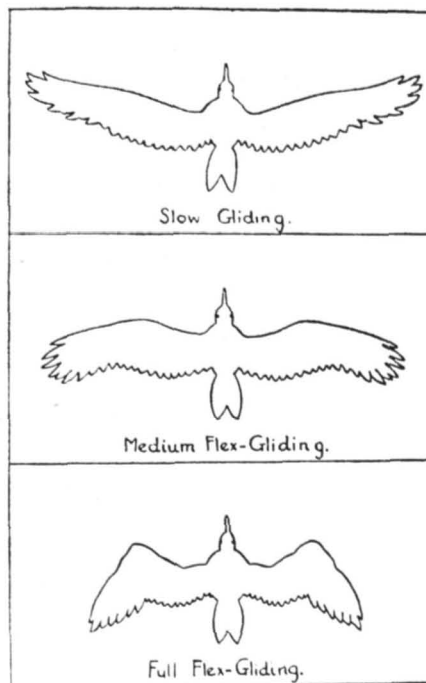


Fig. 43. Gliding at slow, medium and fast speeds¹⁹

With variations in C_{Df} and K neglected, the condition $U \geq U_{md}$ for stable gliding is that the induced drag does not exceed the frictional drag. As Fig. 42 shows, this is a condition on the wing semi-span b . It means that for gliding at lower and lower velocities a bird must increasingly *spread its wings*, as is observed. Fig. 43 reproduces a classical ornithological picture of this,¹⁹ showing the wings at maximum span in a slow glide, at a somewhat reduced span in a medium speed glide, and "flex-gliding" with greatly reduced span at high speeds.

Experiments on gliding can be carried out in a wind-tunnel with the airstream *inclined upwards* so that the bird can remain at rest in the laboratory frame of reference (just as in nature the same bird can be motionless relative to the ground by gliding downwards through an airstream with an equal and opposite velocity vector). Fig. 44 shows changes in span similar to those of Fig. 43 at three different speeds of gliding in such an inclined wind tunnel.¹⁷

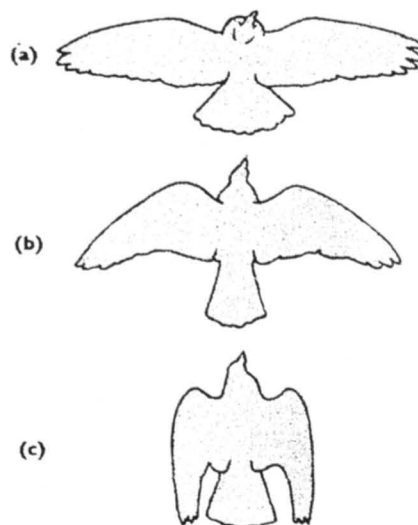


Fig. 44. Pigeon gliding in a wind-tunnel¹⁷ at speeds of (a) 8.6ms⁻¹, (b) 12.4ms⁻¹ and (c) 22.1ms⁻¹

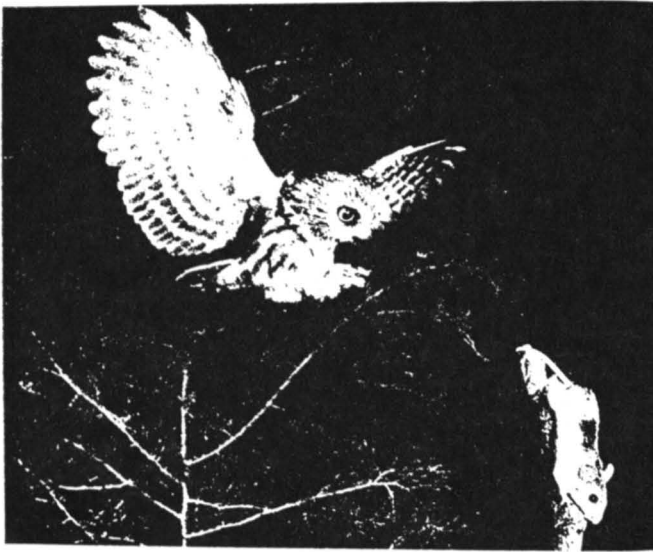


Fig. 45. Quiet slow glide of an owl²²

Fig. 45 shows a slowly gliding owl, whose *quietness* helps to take its prey by surprise. Note that vortex shedding, which generates aerodynamic noise, is minimised by the “softness” of the owl’s feathers (that is, by the fineness of the barbules), by rigid-teethed comb-like leading edges to the first (and sometimes the second) primary feathers, and by a flexible fringe on the wing trailing edge (Horton-Smith,¹⁹ p. 82).

In gliding birds, with the induced drag not exceeding the frictional drag, the total drag must lie between 1 and 2 times the frictional drag. This leads (Fig. 46) to conditions that must be satisfied by the airspeed U for steady gliding at an angle θ . For large θ (that is, in a dive) these limits on U may be brought down by measures to increase C_{Df} like feet dropping (Fig. 33). Whenever the conditions of Fig. 46 are satisfied, the bird can adjust its wing semi-span b to meet the requirements of Fig. 42.

We see now how large birds can remain continuously airborne “without doing work” (in the engineer’s sense): they can indeed remain poised motionless, relative to the ground, wherever they can find an airstream *upwardly*

Requirement that $D = mg \sin \theta$ is between 1 and 2 times the frictional drag $\frac{1}{2} \rho U^2 SC_{Df}$ fixes the gliding speed U between

$$\left(\frac{mg \sin \theta}{\rho SC_{Df}} \right)^{\frac{1}{2}} \quad \text{and} \quad \left(\frac{2mg \sin \theta}{\rho SC_{Df}} \right)^{\frac{1}{2}}.$$



On inclined wind at such speed (if greater than stalling speed) bird can be *motionless*. In an updraught v , bird can soar *horizontally* at speed U

$$\text{between} \quad \left(\frac{mgv}{\rho SC_{Df}} \right)^{\frac{1}{2}} \quad \text{and} \quad \left(\frac{2mgv}{\rho SC_{Df}} \right)^{\frac{1}{2}}.$$

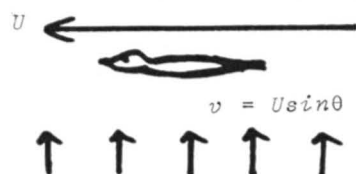


Fig. 46. Conditions on the airspeed U in gliding and soaring

inclined at an angle θ and with a wind speed U satisfying the conditions of Fig. 46. Large birds often make such use of the upwardly inclined airstreams that they can readily find on the windward sides of cliffs, hills and tall vegetation.

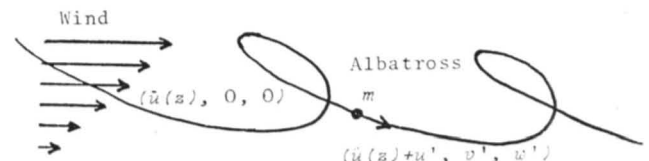
In hot climates large birds also make extensive use of “thermals”: regions of convective updraught with velocity, say, v . In such an updraught a bird can sustain continuous *horizontal* motion (often making horizontal *circles*) without doing work. At airspeed U the sine of its angle of glide θ relative to the air is equal to v/U ; hence, circling is possible at an airspeed between the limits shown at the bottom of Fig. 46 if that airspeed exceeds the stalling speed. In the morning, as the ground warms up and the updraught velocities v increase, this condition becomes satisfied first for the birds with lowest wing loading mg/S (e.g., in the meticulous observations of Hankin,⁶ a certain species of kite), and later for the birds of higher wing loading (e.g., vultures).

At sea, thermals are not found but *sheared winds* commonly blow (Fig. 47). The albatross *Diomedea* is famous for its ability to sustain itself in flight for long periods “without doing work” by extracting energy from a sheared wind. Although the essence of the explanation was sketched already by Rayleigh,³⁸ I give here an account in modern terms suggested to me by Professor S. Corrsin.

Wherever the albatross is, we use as before a frame of reference in which the local air is at rest (Fig. 47). In such a frame of reference, *accelerating* horizontally at a rate $w' d\bar{u}/dz$ (positive when the albatross is climbing), the equations of its motion take their usual form except for the presence of an additional “inertial force” equal to minus the mass times this acceleration of the frame of reference. As usual they lead to an energy equation, written in Fig. 47 in a form *averaged* over a long period.

The left hand side is the mean rate of change of the total energy of the bird’s motions relative to the air: kinetic and potential. Evidently the potential energy has its ups and downs (as the bird does) but cannot change on the average, so the left hand side is effectively the mean rate of change of kinetic energy relative to the air. If this were consistently negative, the bird’s airspeed would show a general tendency to become less, until its wings finally stalled.

On the right hand side of this equation the last term is indeed negative: aerodynamic drag D reduces the bird’s energy relative to the air at all times (note that the perpendicular force L does no work, however). But the first term (mean rate of working by the inertial force) can



Equations for albatross velocity (u' , v' , w') in frame of reference moving at wind speed $(\bar{u}(z), 0, 0)$ include an extra inertial force $-mw' (d\bar{u}/dz)$.

Mean rate of change of total energy $\frac{1}{2} m(u'^2 + v'^2 + w'^2) + mgz$ in this frame
= (mean rate of working by this force) — (mean rate of loss by air resistance).

First term, $-m \overline{u'w'} \frac{d\bar{u}}{dz}$ is positive if $\overline{u'w'}$ is negative.

Fig. 47. Theory of albatross soaring

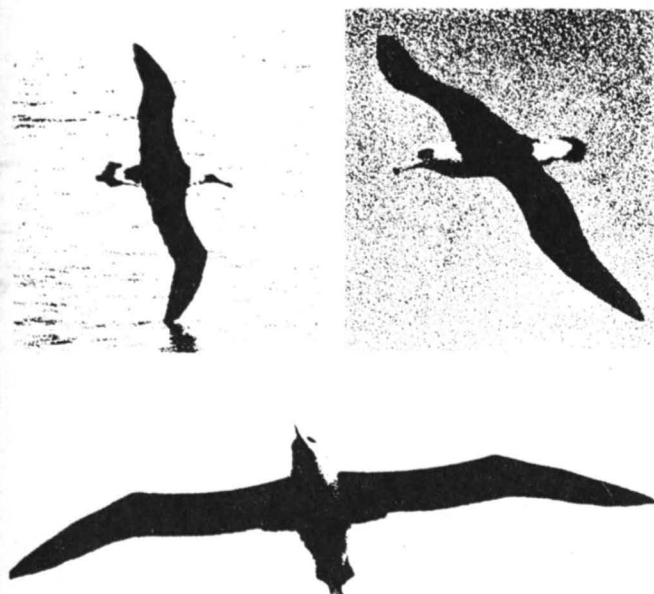


Fig. 48. The albatross *Diomedea immutabilis*³⁹

be positive, allowing a steady mean state to be achieved, if the mean value of $u'w'$ is negative, as is achieved by the type of motion illustrated (with the bird's motion relative to the air typically at angles around 45°). In aerodynamics, this is just the well known condition for a turbulent eddy to extract energy from a sheared airstream. The albatross has evolved an efficient technique for doing just this by means of such long accelerating glides leeward and downward, alternating with shorter decelerating climbs windward and upward.

Fig. 48 shows how one species of albatross (*Diomedea immutabilis*) appears when it is doing it. The high aspect-ratio wing minimises the rate of loss of energy by aero-



Fig. 49. Vultures "leelooping" in a strong wind (directed along large arrow)⁶; successive positions of each bird are marked at intervals of 0.5s

dynamic drag. The albatross can continue for very long periods indeed this motion (alternated sometimes with motions using updraughts associated with ocean wave propagation).

Fig. 49 makes the point that vultures can do it too! When a strong wind blows away their thermals, they go over to such a mode of motion which Hankin⁶ called "leelooping." His accurate records of a vulture's position at equally spaced intervals of time establish that their motion is what has just been described.

PART III. HOVERING FLIGHT, TAKE-OFF AND LANDING

3.1. Normal

From seeking to discuss many different aspects of sustained forward flight in Part II, I have now but little space for describing hovering flight: movements of wings through which the *body* of an animal remains effectively motionless *in still air*. This fascinating subject must not be neglected altogether, however, in a paper on "Aerodynamic Aspects of Animal Flight."

A capacity for sustained hovering flight is characteristic above all of the flying *insects*. We may observe that many of their modes of life, and especially their very successful symbiosis with the flowering plants noted in section 1.2, make great use of this capacity. It is facilitated furthermore, by their range of *sizes*, since the upper limit on size for animals capable of sustained flight, noted in section 2.7, is reduced enormously if the animal's weight must be supported *without* the aid of any horizontal relative wind. Indeed, among birds and bats sustained hovering in this sense is possible only in certain animals at the low end of the size range, outstanding examples being the hummingbirds (Trochilidae) with masses at *most* 20g (found in *Patagona gigas*), or small bats like that of Fig. 28 with masses around 10g. The largest hovering insects like the elephant-dung beetle *Heliocopr* are in the same size range 10 to 20g.

There is obviously great interest both in observing the

wing motions whereby flying animals with masses around 10 to 20g or less can hover in still air for extended periods, and in studying how aerodynamic, skeletal and muscular limitations may have combined to set this upper limit to the mass of such animals. Yet another excellent reason for studying the *same* wing motions is that much larger flying animals are commonly capable of making them *for short periods*, using the characteristic ability of muscle to generate anaerobically, for such short periods, much greater powers than can be sustained continuously under limitations imposed by oxygen supply.

Those larger flying animals, which can briefly make the motions of hovering flight to support their weight in still air, use that ability especially in take-off and landing. In aeronautical terms they are "V.T.O.L."; for example, they take off vertically by making "hovering" movements, followed as quickly as possible by a transition to ordinary forward flight (see below). These, indeed, are the commonest take-off arrangements in birds, the principal exceptions having been noted in section 2.3 (take-off under gravity from elevated positions) and section 2.7 (runway-type take-off, especially found in aquatic birds).

In his general review of sustained hovering flight, Weis-Fogh⁴⁰ has identified an essentially common pattern of what he has named "normal hovering" in the hummingbirds generally (Trochilidae) and in insects from

eleven different orders. These motions of "normal hovering" may be recognised as an adaptation of those flapping motions that are used for forward flight. Lift for weight support requires horizontal movements of wings relative to the air: therefore, in the absence of any horizontal movement of the animal as a whole relative to the air, the wings must themselves beat *horizontally* back and forth. Evidently wings, that for forward-flight purposes beat in a plane perpendicular to the horizontal body axis, are readily adapted to this requirement if the body axis becomes erect (that is, practically vertical) in hovering flight.

Fig. 50 depicts normal hovering flight in the sphingid moth *Manduca sexta* viewed from above. As just suggested, the body axis is practically vertical, which facilitates beating of the wings in an approximately horizontal plane. In order to ensure that the wing leading edge

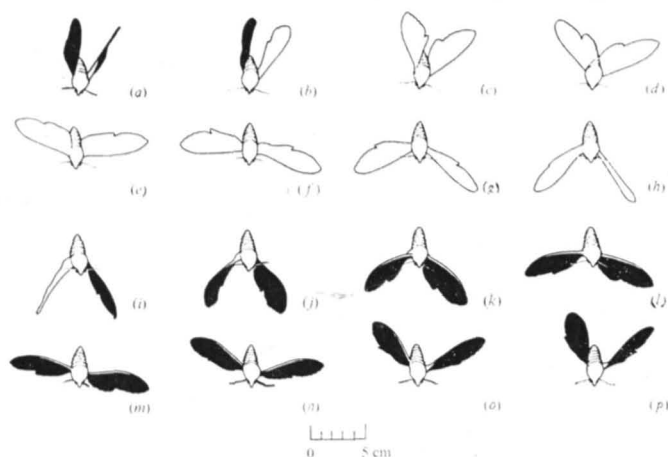


Fig. 50. Normal hovering of *Manduca sexta* as traced from a slow-motion film, with the undersides of the wings shaded black⁴⁰

moves forward always at an effective angle of attack within the range for good lift-drag ratio, the twisting movements depicted for flapping flight in Fig. 3 are necessarily much enhanced: the usual pronation at the start of the downstroke is greatly intensified (frames (a) and (b)), leading to a horizontal wing movement (frames (c) to (g)) with the upper surface uppermost at a geometrical angle of attack of less than 30° . (The effective angle of attack is still smaller because the wings move in the general downdraught produced by the animal's hovering activity.) Next, the usual supination at the start of the upstroke is greatly intensified (frames (h) and (i)), so that the wing with its *underside* uppermost (and thus with the *same* leading edge leading!) follows in reverse the previous horizontal path at approximately the same angle of

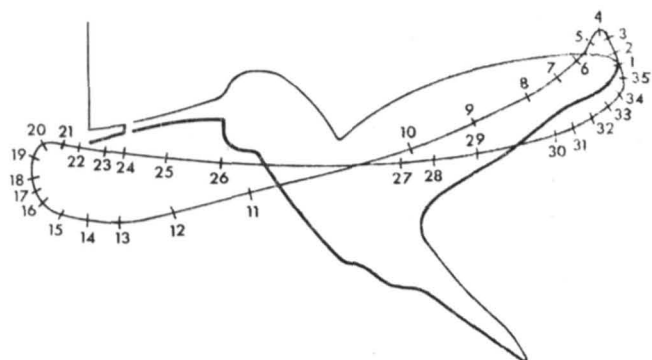


Fig. 51. Path of the wing tip of a hovering hummingbird⁴¹

attack. Both strokes generate the lift needed to support the animal's weight.

Fig. 51, depicting the path of the wing tip during the sustained hovering of a hummingbird,⁴¹ demonstrates that essentially the same motions, which Weis-Fogh calls those of "normal hovering flight," are used. Fig. 52 reminds us that many hummingbirds have "converged" with insects not only in their flying motions but also in their ways of life; the lower photograph, indeed, shows one not much larger than a bumblebee. Compared with the insects, they have the advantage of high lift coefficients C_L (about 2.0 according to Weis-Fogh's estimates) resulting from the properties of wings with feathers which in flash photographs like Fig. 52 are shown to be spread in a lift-enhancing manner. On the

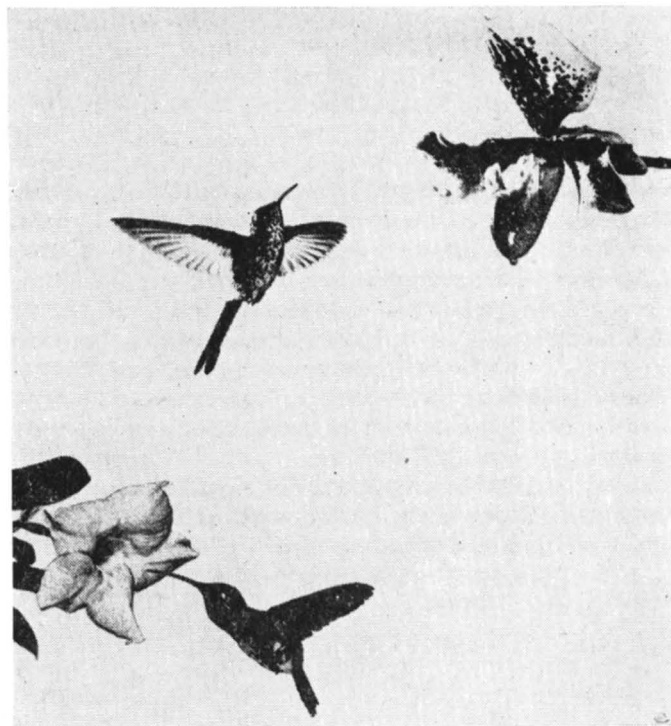


Fig. 52. Flash photographs of hummingbirds hovering near flowers⁴²
Above: *Lesbia victoriae*. Below: *Calothorax lucifer*

other hand, they lack the insects' elastic systems. Even with their high C_L , they need to beat their wings at high frequencies (15 to 50 Hz) to support their weight, and the associated power requirements⁴³ are not far below the maximum values indicated in section 2.7 (although an elastic system would have reduced them by 40 per cent.).

We have observed that "normal hovering" is a rather logical adaptation to hovering requirements of the wing capabilities needed in flapping forward flight. An actual *transition* between the two modes is interesting to watch in large birds as they come in to land. Fig. 53 is from an old film record of a gull alighting¹⁹ which makes the sequence clear enough. First the tail feathers are spread, feet dropped and wings arched to provide braking while the body becomes more erect, the stroke plane of the wing-beat turns from vertical to horizontal and the twistings of the wing are intensified; finally, as the bird alights, its weight is being supported by the lift on horizontally moving wings.

In take-off, again, a few strong strokes of "normal hovering" with the body almost erect are followed by a



Fig. 53. Phases in the landing of a gull¹⁹

transitional "slow forward flight" mode of motion⁴⁴ which is an interesting blend of the motions of normal hovering and of fast forward flight, with an intermediate degree of wing twisting at the extremes of the stroke (Fig. 54). The stroke plane is diagonal so that even at a low forward speed the wings can develop both thrust and lift without stalling. By comparison with *pure* hovering, however, the power needed for weight support is much *reduced*, because the wing's component of forward motion relative to the body in the heavily loaded down-stroke can effectively be lessened by about the speed of the body's forward motion through the air.



Fig. 54. Eight successive positions (A to H) in the slow forward flight of a pigeon⁴⁴

There are those who assert that the kestrel *Falco tinnunculus* is capable of sustained hovering motions in still air. Aerodynamically, it would be surprising if this bird with typical mass 200g, an order of magnitude greater than the largest hummingbird, could support its weight in still air for long periods by motions compatible with its muscular and skeletal limitations. Furthermore, it is not always recognised that, in those open places where kestrels are seen motionless in the air, there is normally a significant horizontal wind component. Ornithologists of great experience have stated that the kestrel remains motionless *only* under those conditions, facing into the wind (see for example Witherby,⁴⁵ p. 26); and the wing motions they describe are precisely those of slow forward flight (Fig. 54), which could presumably maintain the bird stationary in a modest wind without impossible metabolic or structural demands.

3.2. Exceptional

Weis-Fogh,⁴⁰ while establishing that the hovering motions described in section 3.1 are found so very widely that they can properly be designated as those of "normal" hovering flight, identified also certain groups of animals exceptional in the types of motion used. These all raise aerodynamic questions of very considerable interest.

We have implied that the size range for hovering animals is limited at its upper end by a conflict between the maximum lift coefficient that can be achieved (which defines the speeds of horizontal wing motions required for weight support) and the animal's muscular and skeletal limitations. On the other hand, these latter limitations conflict with a *different* aerodynamic requirement at the lower end of the size range. Lift generation by classical horizontal motion of an aerofoil at an appropriate angle of incidence becomes less and less effective as the Reynolds number Uc/ν based on aerofoil velocity U and chord c falls to very low values: say,⁴⁶ below 50. Then, thick boundary layers bring about poor lift-drag ratios, as well as severe difficulties in generating

adequate circulation for lift purposes by the usual processes of trailing-edge vortex shedding. "Normal" hovering requires two reversals of circulation per wing beat, and lags in achieving these can be expected to be enhanced at very low Reynolds numbers.

At the lower end of the range of sizes of insects capable of hovering, there are major problems in achieving Reynolds number high enough to avoid these difficulties. A lower limit on Reynolds number defines a lower limit on the wing speed U which *increases* (as l^{-1}) as an animal's linear dimension decreases. This means a lower limit on frequency increasing very fast (as l^{-2}), which for small enough insects again conflicts with upper limits imposed by structural and metabolic requirements.

To be sure, the evolutionary opportunities for insects that could remain functionally effective at greatly reduced sizes gave rise, as has long been recognised (section 2.2), to remarkable muscular developments allowing the beating of wings at extraordinarily high frequencies. Now Weis-Fogh⁴⁰ has shown that the same evolutionary opportunities gave rise to aerodynamically novel modes of flight, permitting weight support at *lower Reynolds numbers* than would be possible with "normal" hovering.

Fig. 55 shows *Encarsia formosa*, an insect of size around 1mm from the suborder Chalcidoidea of the Hymenoptera, on which Weis-Fogh did all the initial work of identifying these aerodynamically novel motions and demonstrating their significance. The two pairs of wings, being "jugate" (compare Fig. 15), move effectively as a

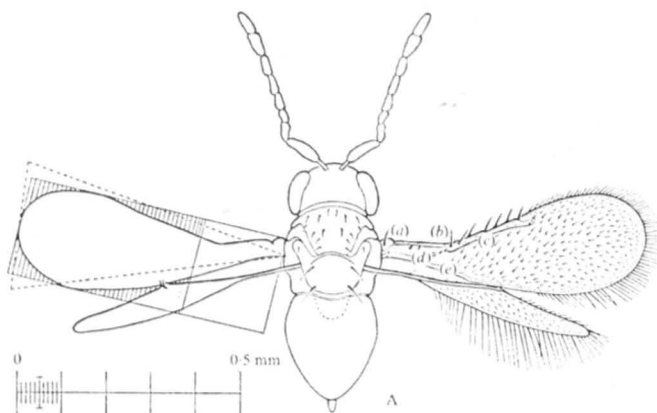


Fig. 55. Morphology of *Encarsia formosa*⁴⁴

single pair. The wing-beat frequency, although as high as 400Hz, yields a Reynolds number of only 20 in such a small animal: a value seemingly too low for generation of the lift needed for weight support. Indeed, Weis-Fogh showed from his observations that *Encarsia* requires a mean lift coefficient around 3, more than twice the maximum found at that Reynolds number in steady-state aerodynamics⁴⁶; while the usual unsteady effects such as the "Wagner effect" are known to imply a reduction from the steady-state figure.

Weis-Fogh went on to prove experimentally and theoretically, however, that the animal uses special unsteady effects, previously unknown to aerodynamicists: the "clap and fling" mechanism of lift generation. He explained clearly how the "clap and fling" manoeuvre, performed once per wing beat, generates immediately the circulation required for achieving a high lift coefficient without the need to wait for the classical processes of trailing-vortex shedding. Lighthill⁴⁷ analysed from an aerodynamical standpoint various features contributing

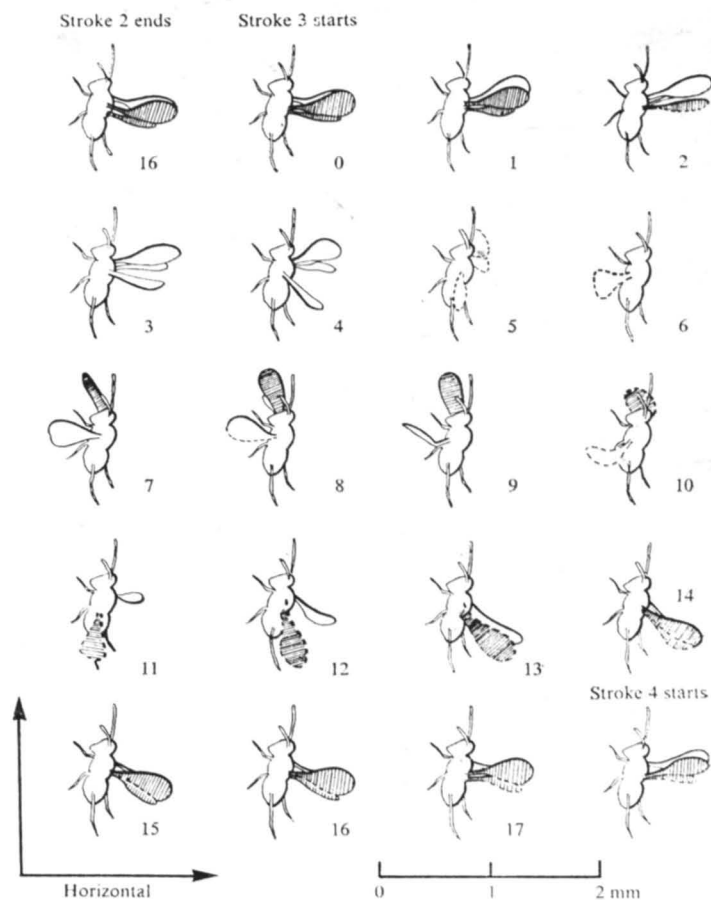


Fig. 56. Tracings from a slow-motion film, at 7150 frames per second, of a hovering specimen of *Encarsia formosa*⁴⁰

to make this Weis-Fogh mechanism of lift generation so effective.

Professor Weis-Fogh's remarkable slow-motion pictures of the hovering motion of *Encarsia formosa*, taken at over 7000 frames per second, show what a considerably more complicated wing-beat cycle even than that of Fig. 49 this insect succeeds in performing 400 times a second. Fig. 56 shows tracings from successive frames of that film. Note again the erect body of the insect during hovering; note also the positions of the legs which indicate that in these pictures the right hand side, where the insect claps its wings, is the *dorsal* side of the insect's erect body.

The sequence begins (frames 16 and 0) with wings temporarily at rest in the clapped together position. The "fling" then occurs (frames 1 and 2): a rapid rotation of the *effectively single pair of wings* (see above) *about a common axis along their trailing edges*. The rest of the motion (frames 3 to 13) is as in "normal hovering" (Fig. 12) until the next "clap" occurs (frames 14 to 16).

For a detailed analysis of these motions, see the papers cited. Briefly, the mechanism depends on the inrush of air into the opening gap between the wings during the "fling" motion generating immediately about each wing a circulation of the right magnitude and sign to produce a high lift coefficient during the immediately ensuing stroke (without *any* conflict with Kelvin's theorem, since the total circulation round a contour enclosing *both* wings remains zero!).

There is immense scope for research in this field, based on further exploration of the use of the "clap and fling"

mechanism and other specialised unsteady aerodynamic effects by flying animals. It will be of interest to determine how widespread is the use of the mechanism by insects so small that they encounter low Reynolds number problems. A quite different question is whether the mechanism has been used at all by much larger animals, operating at substantial Reynolds numbers. For example, butterflies (suborder Papilionoidea of the Lepidoptera) hold their wings "clapped together" behind their back when resting, and appear to use a "fling" mechanism, followed by a second "fling" from a position with the wings clapped together ventrally, to facilitate rapid generation of the lift needed for take-off. This and many other exceptional features of the flight of butterflies would repay aerodynamic analysis.

I shall conclude by mentioning just two other orders of insects whose hovering flight would be especially worth studying in detail. The Odonata exhibit quite exceptional modes of hovering flight, with the body horizontal. It would be of great interest to analyse the complicated combinations of wing motions involved.

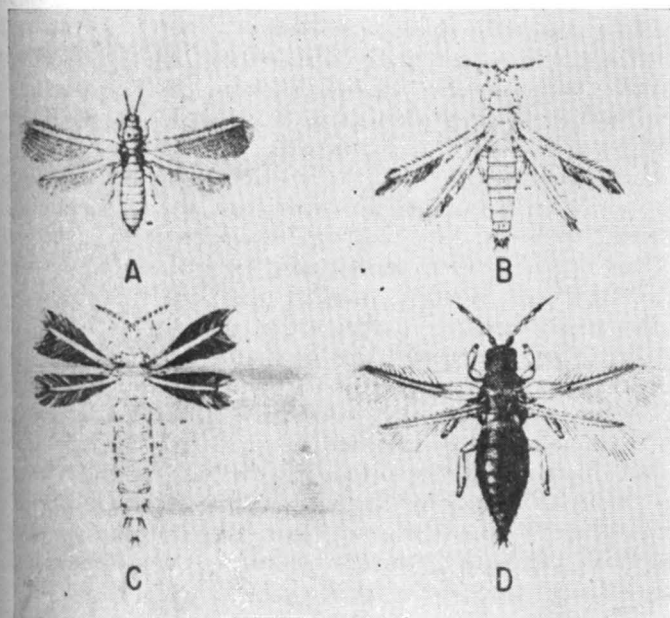


Fig. 57. Selected species of Thysanoptera²⁸

Finally, the Thysanoptera appear to have penetrated into regions of still lower Reynolds number (<10) than those discussed above, in association with a quite exceptional wing morphology (Fig. 57), almost suggestive of ciliary arrangements for aquatic motions at low Reynolds number. It will be a challenging problem to study by experiment and analysis what are the special movements by which these "thrips" or "fringe-winged" insects are enabled, at such very low Reynolds numbers, to support their bodies in the air.

Acknowledgment

It is a pleasure to thank Professor Torkel Weis-Fogh for his generous help given at many stages in the preparation of this paper. I also thank Dr. Ulla Norberg for her permission to reproduce the outstanding photographs of *Plecotus auritus* as Fig. 28; and also A. Root, Tierbilder Okapia, Frankfurt for Fig. 2; English Universities Press,

Fig. 35; W. B. Saunders, Figs. 23 and 45; South Illinois University Press, Fig. 48; Holt, Rinehart and Winston, Figs. 34 and 57.

References

1. Lighthill, M. J., *Ann. Rev. Fluid Mech.*, 1969, **1**, 413-446.
2. Lighthill, M. J., *J. Fluid Mech.*, 1970, **44**, 265-301.
3. Lighthill, M. J., "Aquatic animal locomotion," in Becker, E., and Mikhailov, G. K., *Editors*, "Proc. 13th Int. Cong. Theor. Appl. Mech.," Springer, Berlin, 1973, 29-46.
4. Smart, J., and Hughes, N. F., "The insect and the plant: progressive paleoecological integration," *Insect/Plant Relationships*, Symp. Roy. Entomol. Soc., London, no. 1972, **6**, 143-155.
5. Pennycuik, C. J., "Animal Flight," Edward Arnold, London, 1972.
6. Hankin, E. H., "Animal Flight," Iliffe & Sons, London, 1913.
7. Marshall, N. B., "The life of fishes," Weidenfeld & Nicolson, London, 1965.
8. Gray, J., "Animal Locomotion," Weidenfeld & Nicolson, London, 1968.
9. Weis-Fogh, T., and Jensen, M., *Phil. Trans. Roy. Soc. B.*, 1956, **239**, 415-584.
10. Meinertzhagen, R., *Ibis*, 1955, **97**, 81-117.
11. Eisentraut, M., *Zeit. wissen. Zool.*, 1936, **148**, 159-188.
12. Jensen, M., and Weis-Fogh, T., *Phil. Trans. Roy. Soc. B.*, 1962, **245**, 137-169.
13. Fox, R. M., and Fox, J. W., "Introduction to comparative entomology," Reinhold, New York, 1964.
14. Pringle, J. W. S., "Insect Flight," Cambridge University Press, 1957.
15. Greenewalt, C. H., "Dimensional relationships for flying animals," *Smithsonian Misc. Coll.*, 1962, **144**, no. 2, 46 pp.
16. Brown, R. H. J., *J. exp. Biol.*, 1953, **30**, 90-103.
17. Pennycuik, C. J., *J. exp. Biol.*, 1968, **49**, 509-526.
18. Tucker, V. A., *J. exp. Biol.*, 1968, **48**, 67-87.
19. Horton-Smith, C., "The flight of birds," H. F. & G. Witherby Ltd., London, 1938.
20. Weihs, D., *J. Marine Res.*, 1973, **31**, 194-209.
21. Lack, D., "Swifts in a tower," Methuen, London, 1956.
22. Welty, J. C., "The life of birds," W. B. Saunders, London, 1962.
23. McGillivray, W., "British Birds, vol. 3," Scott, Webster & Geary, 1840.
24. Landsborough Thomson, A., "A New Dictionary of Birds," Nelson, London, 1964.
25. Hanzák, J., "Pictorial Encyclopedia of Birds," Paul Hamlyn, London, 1967.
26. Allen, G. M., "Bats," Harvard University Press, 1940.
27. Wimsatt, W. A., *Editor*, "Biology of bats, vol. 1," Academic Press, London, 1970.
28. Borror, D. J., and De Long, D. M., "Introduction to the study of insects," Holt, Rinehart & Winston, New York, 1964.
29. Mittelstaedt, H., *Z. Vergl. Physiol.*, 1950, **32**, 422-463.
30. Chapman, R. F., "The insects: structure and function," English Universities Press, London, 1969.
31. Pringle, J. W. S., *Phil. Trans. Roy. Soc. B*, 1948, **233**, 347-384.
32. Faust, R., *Zool. Jahrb., Allg. Zool. Physiol.*, 1952, **63**, 325-366.
33. Dorst, J., "The migrations of birds," Heinemann, London, 1962.
34. Johnson, C. G., "Migration and dispersal of insects by flight," Methuen, London, 1969.
35. Hocking, B., *Trans. Roy. Entomol. Soc. London*, 1951, **104**, 223-345.
36. Karman, T., "Aerodynamics," Cornell University Press, 1954.
37. Weis-Fogh, T., "Scale, dimensions and design principles in actively flying animals," *Biol. Rev.*, in the press.
38. Rayleigh, Lord, *Nature*, 1883, **27**, 534-535.
39. Fisher, M. L., "The Albatross of Midway Island," Southern Illinois University Press, 1950.
40. Weis-Fogh, T., *J. exp. Biol.*, 1973, **59**, 169-230.
41. Stolpe, M., and Zimmer, K., "Der Vogelflug," Akademische Verlagsgesellschaft, Leipzig, 1939.
42. Scheithauer, W., "Hummingbirds," Arthur Barker, London, 1967.
43. Weis-Fogh, T., *J. exp. Biol.*, 1972, **56**, 79-104.
44. Brown, E. H. J., *J. exp. Biol.*, 1948, **25**, 322-333.
45. Witherby, H. F., *Editor*, "Handbook of British Birds, vol. 3," H. F. & G. Witherby Ltd., 1939.
46. Thom, A., and Swart, P., *J. Roy. Aero. Soc.*, 1940, **44**, 761-770.
47. Lighthill, M. J., *J. Fluid Mech.*, 1973, **60**, 1-17.