

## Bird flight

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**Abstract.** Avian flight has fascinated man from ancient times but it is only in recent years that the efforts of scientists from diverse fields have been able, to some extent, to understand and explain the dynamics of animal flight. This article is based on some observations of birds in the Nellapetu and Pulicat Lake sanctuaries on the east coast of India. It essentially summarises the results of application of well-known principles of elementary incompressible aerodynamics to the flapping and gliding flight of birds. For a reader unfamiliar with the subject, brief notes on evolution of animal flight, the occurrence and classification of bird species and a description of the structure and musculature of wings and feathers and elementary theories of lift and drag are included. Observations show an incredible diversity of flight techniques and manoeuvres. A general description of the main types of bird flight and some illustrations of wing shapes and the motion of birds while taking off, landing and hovering are given. Viewing the flapping wing as a quasi-steady device imparting momentum to the air surrounding it through the expenditure of muscular energy derived from oxidation of fat, estimates of the power required to fly and that available from metabolic energy conversion can be made. Gliding and soaring flight can then be understood reasonably well. Approximate results of bird performance including range and endurance can also be obtained for steady flapping flight. However it is still not possible to calculate and predict in detail all aspects of the flight of a specific type of bird. Only a brief mention is made of the essentially nonlinear and non-steady nature of the aerodynamics of flapping bird wings which needs further research. Using dimensional analysis, the effects of bird size and weight are discussed. The intriguing question of relating the processes of natural selection for a given species in evolving a particular wing shape and flight mode that must be conducive to its continued survival remains open for much further research and study.

**Keywords.** Animal flight; aerodynamics; biophysics; bird flight; biomechanics.

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A list of symbols used is given at the end of the paper.

The top right-hand corner of all odd-numbered pages carries pictures of a pelican in flight; flicking the pages gives the reader an impression of the wing-motions involved.

## 1. Introduction

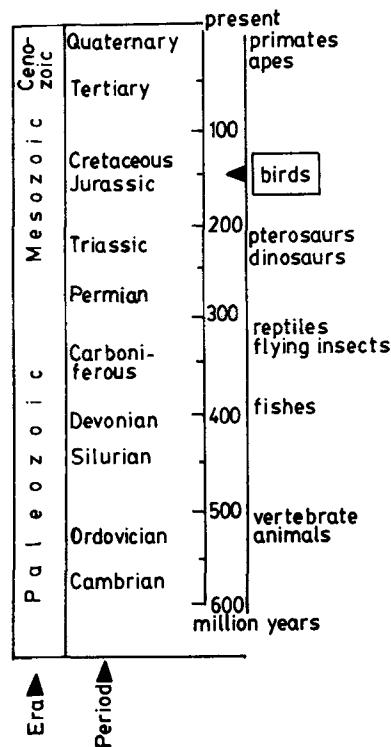
Since time immemorial man has been fascinated and intrigued by the beauty, grace and intricacies of bird flight. There is perfect harmony of form and function. It is equally exhilarating to attempt to understand how the physiology and performance of birds are related to scientific principles.

Birds (defined as feathered bipeds) evolved from reptilian stock during the Jurassic Period some 150 million years ago. Insects were the first life form to conquer the air, during the Carboniferous Period, about 300 million years ago. The pterosaurs also preceded the birds. These flying animals had evolved wings in which a membrane or skin was stretched out between elongated fingers. Until recently it was generally considered that the pteranodon, with a wing span of about 7 m and weighing 16 kg (wing area =  $4.6 \text{ m}^2$ ,  $A/R = 10.5$ ,  $W/S = 3.6 \text{ kg/m}^2$ ) was the largest flying animal that inhabited the earth. However, in 1971, the skeleton of a pterosaur – *Quetzalcoatlus northropi* (QN) – was discovered in Texas, USA. It has been deduced that QN had a wing span of 11 m and weighed about 64 kg (wing area =  $8 \text{ m}^2$ ,  $A/R = 15$ ,  $W/S = 8 \text{ kg/m}^2$ ). By the late Cretaceous Period the flying reptile experiment seems to have failed and the pterosaurs were extinct. Bird evolution overlapped that of the pterosaurs but is considered quite distinct from it; in fact, the two flying forms must have been in competition for the same ecological niche with the birds eventually proving spectacularly more successful.

### 1.1 Evolution

While there are several theories regarding the lines of bird evolution, it is generally accepted that birds evolved from reptiles and have come from the same stock as dinosaurs. Two main theses have been advanced about the route followed. One suggestion – the ‘cursorial’ theory – is that the ancestor was a bipedal ground dwelling reptile which, whilst running rapidly, derived advantage of aerodynamic lift from its forelimbs. Another view is that the first birds were arboreal in habit and had evolved from tree climbing lizard-like reptiles who used their forelimbs in gliding from tree to tree. Figure 1 depicts the evolutionary process. Evolutionary advancement must have led to the scales on the forelimbs becoming elongated, eventually developing into feathers. Very little is known about the detailed process of evolution and it is possible that during the transformation of scales into feathers there was need for body temperature control and the aerodynamic advantages which accrued were really fortuitous. Obviously a stage was eventually reached when the aerodynamic qualities increasingly gave decisive advantages. The freedom of movement, increased access to new food supplies and a more efficient means of escape from enemies and predators – these factors must have become the prime foci for evolutionary change. The oldest fossil remains discovered, which display all the essential characteristics of a bird, are those of Archaeopteryx found in limestone rocks in Bavaria, West Germany, in 1861, two years after the publication of Darwin’s *Origin of Species*. Figure 1 summarises the pre-history – the earliest known bird had feathers and was semi-reptilian in appearance. It was probably a poor flier compared to the birds of today. Its wing claws helped it to clamber about in trees and perhaps by flapping its wings it could move from tree top to tree top – often gliding part of the way. Fossils of birds since Archaeopteryx have also been found, some of which like the Ichthyornis and the Hesperornis became extinct long ago. Other more recent extinctions are the dodo and the great auk which were extant only a few hundred years ago.

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**Figure 1.** Evolution of birds. The fossil remains of Archaeopteryx, the earliest known bird, are also shown.

### 1.2 Species

Today birds inhabit every continent. There are nearly 9000 species classified into 27 orders. Some orders have only *one* species. The Order Passeriformes (*perching birds*) contains the largest number of families (70). It has generally been found that the survival rate of the primitive orders is much poorer compared to the highly evolved ones. Figure 2 (*World Book Encyclopedia*, p. 291) gives a tabulated classification of birds.

### 1.3 Occurrence

James Fisher, the ornithologist, has estimated that the world population of birds is approximately 100 billion. The most abundant are the oceanic birds of the large land masses. The distribution is roughly as follows:

South America	3000	species
Africa	1500	species
Indian Subcontinent	1200	species
China and Japan	1100	species
North America and Canada	750	species
USSR	700	species
Australia	650	species

The most highly evolved birds are those of the Order Passeriformes – sparrows, finches, crows, jays etc.

**Order Sphenisciformes** – Flightless swimming birds with paddle-like wings; penguin family.



**Order Struthioniformes** – Large flightless birds of Africa and Arabia; ostrich family.



**Order Rheiformes** – Large flightless birds of South America; rhea family.



**Order Casuariiformes** – Large flightless birds of Australia and New Guinea; cassowary, emu families.



**Order Apterygiformes** – Flightless birds of New Zealand; kiwi family.



**Order Tinamiformes** – Weak-billed, quaillike birds of South America; tinamou family.



**Order Gaviiformes** – Water birds with three webbed toes; loon family.



**Order Podicipediformes** – Water birds with lobed toes; grebe family.



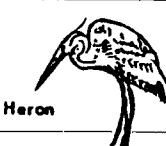
**Order Procellariiformes** – Sea birds with tube-like nostrils; albatross, diving petrel, shearwater, storm petrel families.



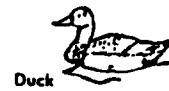
**Order Pelecaniformes** – Water birds with four webbed toes; anhinga, booby, cormorant, frigate bird, pelican, tropic bird families.



**Order Ciconiiformes** – Long-legged wading birds; flamingo, heron, ibis, stork, and other families.



**Order Anseriformes** – Water birds of marshlands; duck, screamer families.



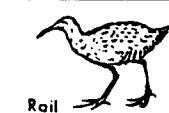
**Order Falconiformes** – Daytime birds of prey; falcon, hawk, osprey, secretary bird, vulture families.



**Order Galliformes** – Fowllike birds; curassow, grouse, guinea fowl, hoatzin, megapode, pheasant, turkey families.



**Order Gruiiformes** – Varied group of chiefly land-dwelling birds; bustard, cariama, crane, rail, and other families.



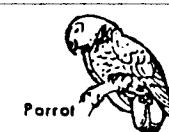
**Order Charadriiformes** – Shore birds and water-feeders; auk, gull, plover, sandpiper, and other families.



**Order Columbiformes** – Pigeon-like birds; pigeon, sand grouse families.



**Order Psittaciformes** – Seed- and fruit-eating birds with hooked bills; parrot family.



**Order Cuculiformes** – Varied group of tree- and land-dwelling birds; cuckoo, touraco families.



**Order Strigiformes** – Nighttime birds of prey; barn owl, typical owl families.



**Order Caprimulgiformes** – Owl-like birds with typically weak bills; frogmouth, nightjar, oilbird, owlet-frogmouth, potoo families.



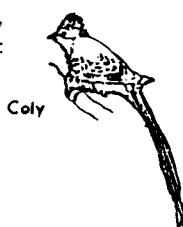
**Order Apodiformes** – Strong-winged birds that spend much time flying; crested-swift, hummingbird, swift families.



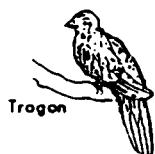
Figure 2. (Continued)

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**Order Coliiformes** – Long-tailed, fruit-eating birds of Africa: coly family.



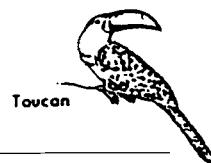
**Order Trogoniformes** – Long-tailed tropical birds with weak feet; trogon family.



**Order Coraciiformes** – Varied group of birds with large bills and metal coloured feathers; bee-eater, kingfisher, roller and other families.



**Order Piciformes** – Tree-dwelling birds, most with long, strong bills; barbet, jacamar, toucan, woodpecker, and other families.



**Order Passeriformes** – Perching birds; 70 families, including broadbill, manakin, lyrebird, and all songbird (lark, thrush, etc.) families.



**Figure 2.** Classification of birds. (Class Aves – birds; Subclass Neornithes – modern birds). Superorder Impennes – Penguins, Superorder Neognathae. (From *World Book Encyclopedia*, p. 291.)

The ability to fly – like many other biological properties of living things – came about as an adaptation to particular conditions. The variety of habitats and the varied response to them has led to an incredible diversity of flight techniques and apparatus:

- swifts spend most of their lives in the air;
- sparrows cannot glide;
- the larger vultures are champion gliders but cannot take off without a run into the wind;
- penguins and ostriches cannot fly;
- geese fly over the Himalayas (9000 m);
- the humming-bird can hover for long periods;
- Arctic terns migrate between the Arctic and Antarctic continents – 18,000 km each way.

It would therefore appear as if no two species fly exactly in the same manner!

### 1.4 Pioneers of flight

This paper examines some general features of bird flight – the flight apparatus of the bird and the modalities of flight. Man learnt to build aircraft – machines – which enable him to fly by studying birds. Pioneers like Otto Lilienthal (1849–1896) in Germany and E J Marey (1930–1904) in France and George Cayley (1773–1857) in England were among the earliest scientists who not only observed birds but analysed their flying. Marey was among the first to realise that birds in flight could be properly studied only through high speed photography. More modern work by Brown (1948, 1953, 1963), Pennycuick (1968, 1972, 1975) and Tucker (1968) has helped clarify the essential aerodynamics.

### 1.5 The scientists

The Wright brothers' first flight in a heavier than air machine in December 1903 ushered mankind into the era of the conquest of the air. The science of flight –

aerodynamics and flight mechanics – rapidly grew out of the earlier foundations laid by Newton, d'Alembert, Helmholtz, Rayleigh, Prandtl and Von Karman. The modern science of aeronautics is a very sophisticated combination of mathematical theory and physical principles supplemented by experimental measurements. Man has learnt to build aircraft which can carry 350 passengers 10,000 km non-stop across oceans, fly faster than a bullet and zoom to the outer edges of the atmosphere etc., and yet there are complexities of bird flight for which there are as yet no complete mathematical descriptions. Man-made flying machines still cannot perform the range of manoeuvres that a blackbird or a sparrow can. There is still much that science can learn from the birds.

The main text of the paper is followed by appendices A to C, which contain some data on birds including their Hindi names.

## **2. What it takes to fly**

Among the living animal species, true flight is confined to insects, birds and bats. Man has to use machines to be able to fly. Before we examine 'how' a bird flies we first look at the essential elements necessary for flight. These are:

- a lightweight high-strength structure;
- wings and feathers for generating lift and forward thrust;
- flight muscles to provide the power;
- a fast response flight control and navigation system.

We briefly discuss each of these.

### *2.1 The structure – adapted for flight*

The skeletal structure of the birds has evolved into an efficient lightweight structure consisting of the body box – the rigid ribcage – with the many-vertebraed neck and tail remaining flexible. The skeleton is essentially a frame for the attachment of the movable wings and the powerful flight muscles to the deeply keeled breast bone, and has evolved to suit the demands of walking and flying. Most of the larger bones are hollow and criss-crossed with supporting struts inside (see figure 3).

Compared to reptiles or mammals, whose main mode of locomotion is on all fours, the birds' body evolution/adaptation has caused a shift in the centre of gravity by a shortened body. The demands of flight have produced a relatively rigid, but a much lighter, skeleton.

### *2.2 Wings and feathers*

The most remarkable features of the bird's flight structure are the wing and feathers. Figures 3 and 6 show the details. In the long evolutionary process, the forelimbs were transformed into wings. The bone structure of the bird wing (figure 4) is analogous to the human arm, wrist and fingers with obvious differences. The upper arm, 'humerus', is proportionately shorter, the 'wrist' and 'palm' bones are fused together for greater strength in supporting the primary flight feathers. Of the three digits, 'fingers', two support feathers. The third, 'alula' supports a small auxiliary wing extendable at will. This controls the airflow over the wing during landing and take-off manoeuvres – somewhat akin to a leading edge slot or flap on aircraft.

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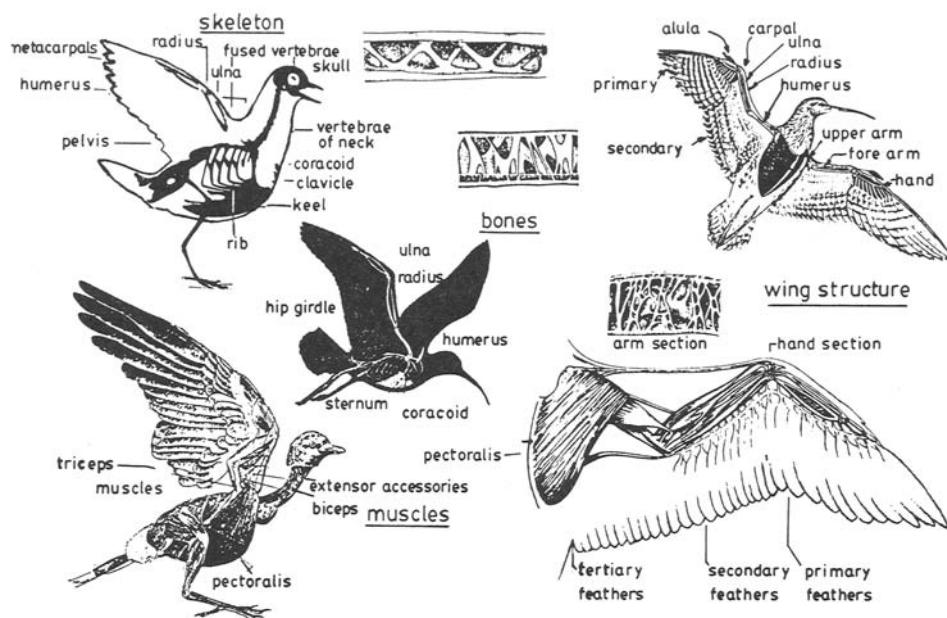


Figure 3. Framework for flying. This figure is compiled from figures taken from Dalton (1977, pp. 74, 75 & 79), Ward-Smith (1984, p. 69) and Ardley (1984, pp. 4 & 6).

The bird wing is a complex flexible airfoil – cambered and adjustable for control. It tapers from root to tip and generally has a characteristic shape but the planform varies with the type of bird. Figure 5 shows some wing profiles as well as some airfoils used in aircraft. The feathers of a bird are perhaps its most unique possession and are a marvel of engineering. A feather is both extremely light and structurally strong – but still very flexible. Feathers have greater strength/weight ratio than any man-made structure. The structure of a feather can be seen in figure 6. Essentially a flexible structure, it is designed to be stiffer along the length than fore and aft. The shaft carries branches called *barbs* which in turn have offshoots called *barbules* with *barbicels* or hooklets which interlock like a zipper. The shaft or stem is hollow and

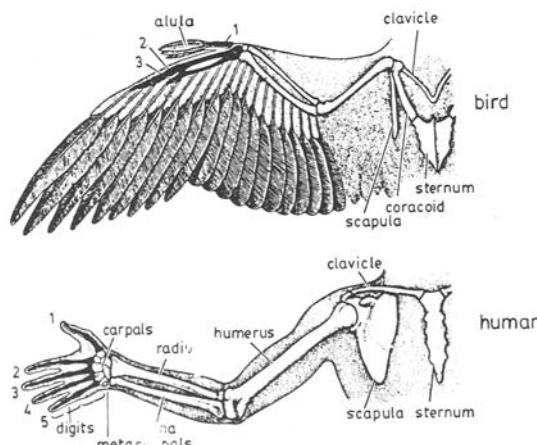
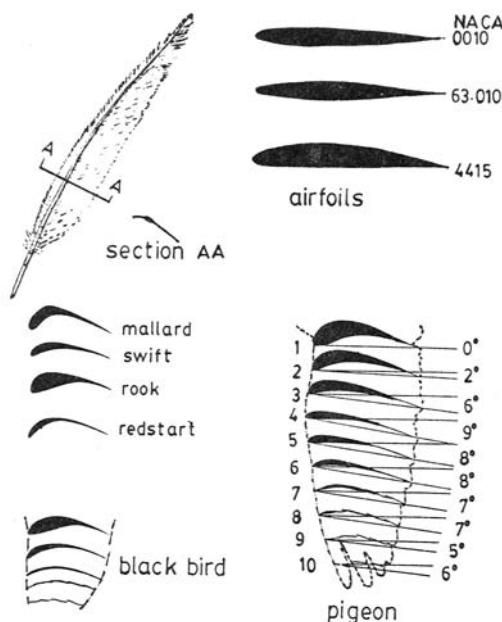
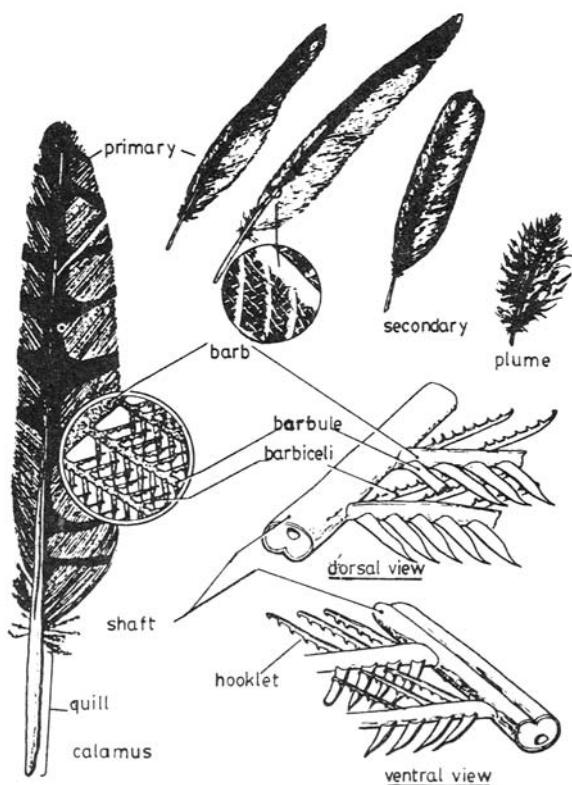


Figure 4. Bird wing and human arm.



**Figure 5.** Wing profiles. (Adapted from Ward-Smith 1984, p. 74.)



**Figure 6.** Structures of feathers. (Adapted from Freethy 1982, p. 69.)

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filled with *keratin* – a horny substance of which the feather is made. Feathers are classified according to function:

- primaries – usually 10 in the ‘hand’ – are unsymmetric, pointed and strongly arched;
- secondaries attached to the arm. Their number varies from bird to bird;
- scapulars (shoulder feathers);
- contour (external; determine outer aerodynamic shape);
- down (insulation).

How many feathers does a bird have? There are approximately 1000 feathers on a small bird! Typical examples are:

gull	~	6000
duck	~	12000
swan	~	25000

A pigeon’s primary feather would have approximately 1000 barbs and 500 barbules on each barb. A complete feather may have about  $10^6$  barbules.

Feathers overlap, interweave and present a smooth, but not quite impervious, surface to the air. Each feather has an approximately streamlined profile. Along with the whole wing a cross-section is generated which is aerodynamically similar to an airfoil section. Figure 5 shows typical cross-sectional shapes of feathers as well as profile variations along the wing span. The profiles resemble, in a general way, those used for aircraft. An important point to note is that bird feathers and wings are very flexible; their shapes take on a range of variations depending on the conditions of flight.

### *2.3 The muscles*

The power for flight, through movement of the wings, is provided by two massive ‘pectoralis’ muscles anchored to the deep keel of the sternum as shown in figures 3 and 7. In the main power stroke (downwards), the large pectoral muscles contract to pull the wings down. Since muscles can work only through contraction, the return (or upstroke) is effected by a ‘rope and pulley’ system; as the pectoralis muscles relax the two ‘supracoracoideus’ muscles contract raising the wing by means of a tendon running over the shoulder joint to the top of the upper arm (see figure 7). Since, during the upstroke, wing movement is assisted by the air pressure, the secondary muscles are much smaller than the primary ones. The flight muscles may account for between 15 and 20% of the total body weight. Considering the large variety of birds ranging in size from a few centimetres to several metres, and weighing from a few grams to several kilograms, the musculature can be expected to show significant variations in detail. Greenewalt (1962, 1975) has collected extensive data, some of which is shown in figure 8. Depending upon the dominant flight characteristics – fast flapping, slow flapping, soaring and gliding with occasional flapping etc., the depressor (and elevating muscles) vary in size. Thus small passerines have elevators much smaller than the depressors – so also large slow flapping birds. The structure varies depending on whether the muscles are to supply the necessary power continuously or intermittently. Humming-birds have large elevators. So do medium large birds which produce propulsion as well as lift on both down- and upstroke. They have elevators not much smaller than the depressors. On the average the small or secondary pectoral muscles are about 10% in weight of the large pectoralis.

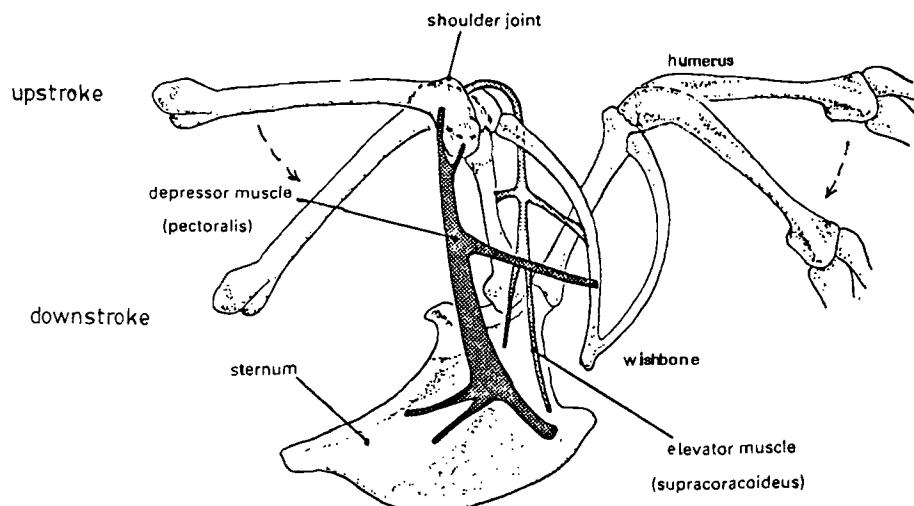


Figure 7. Muscle action. (From Freethy 1982, p. 68.)

Brown (1963) gives the following ratios of elevator to depressor muscles:

Chaffinch	0.104	Wagtail	0.10
Goldfinch	0.068	Blue tit	0.116
Sparrow	0.106	Blackbird	0.113
Magpie	0.09	Linnet	0.12
Pigeon	0.25	Osprey	0.047
Stork	0.086	Crows	0.075–0.085
Partridge	0.33	and Jays	

#### 2.4 Flight control and navigation

All birds, to search for food and to avoid predators, have to manoeuvre in flight, i.e. change the direction of motion in a controlled manner. As flying machines, birds are

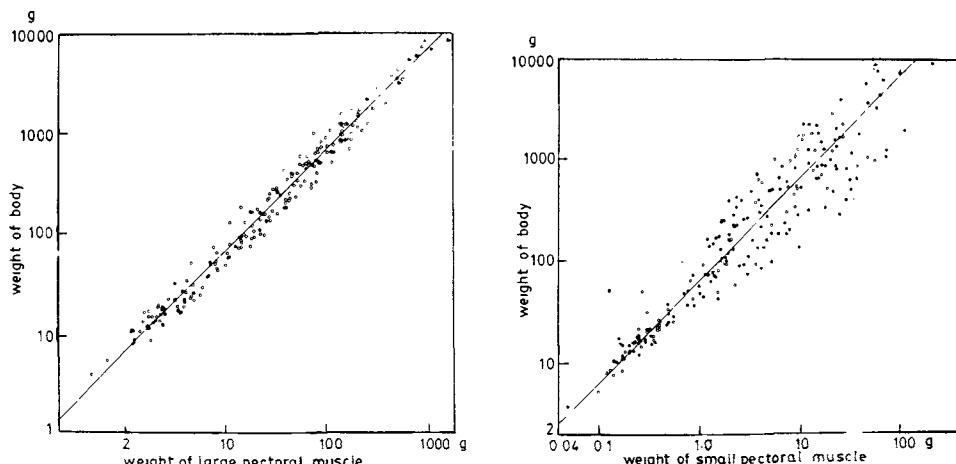


Figure 8. Weight of muscle as function of body weight. (From Greenewalt 1962.)

inherently unstable and their flight is actively controlled and maintained by the neuro-muscular control of shape and position of the wings and tail. This instability appears to be a general feature of all animal mechanisms. Stability and manoeuvrability are inherently antagonistic qualities. A highly stable system is little affected by external disturbances or forces and would require relatively large forces to change its direction. An unstable system is easily upset but requires small control forces to correct the deviations and change the direction.

Birds are equipped with excellent eyesight – no other living being can match their visual acuity. Most birds are equipped with both monocular and binocular vision. Coupled with the sense of hearing, the birds' awareness of the external environment is accurate and fast. The fast sensory system is able to detect deviations during flight such as gusts, turbulence etc., and also provide the assessment for avoiding obstacles etc. Control of pitching, rolling and yawing are accomplished by movements of the tail and wings – sometimes differential changes, some times coordinated – as also through changes in the flapping modes of the wings i.e. unequal beat frequencies and amplitudes.

Birds migrate over long distances. The question of navigation is still not resolved. It is known that some birds use sun orientation; others use the earth's magnetic field. However the question is still not fully understood and will not be discussed in detail here.

### **3. Types of bird flight**

Before we take up a discussion of the way in which a bird's wings produce the required forces for flight, it would be useful to take a general look at the main types into which bird flight may be classified. Although practically every species seems to have some specific features, it is easily observed that, broadly speaking, there are two main types:

- flapping flight, and
- gliding flight.

Figure 9 depicts these types in summary form. Figure 10 shows a sample of wing shapes (adapted from Ali & Ripley 1983). Every bird flaps its wings in (what generally appears to be) an up-and-down repetitive fashion. Some birds flap continuously throughout their flight. Others may, after attaining adequate speed and altitude, stop the flapping motion and glide like sail planes on their outstretched wings – flapping again when required. Yet others may alternate between flapping and gliding – “bounding” like some kingfishers and small birds.

#### **3.1 Flapping flight – “power-on”**

This can be regarded as “power-on” flight since the bird continuously expends energy in flapping its wings and generates the thrust and lift forces to propel it and overcome gravity. Careful observation shows that, while the general manner of wing flapping motions may appear similar in all birds, there are many subtle differences between these motions in small and large birds. The motion of the flexible wings is not only in the up-and-down direction but there are also forward and backward components, and parts of the wings twist during the flapping cycle. The details of wing motion, attitude and configuration change during take off, slow climbing flight, fast forward

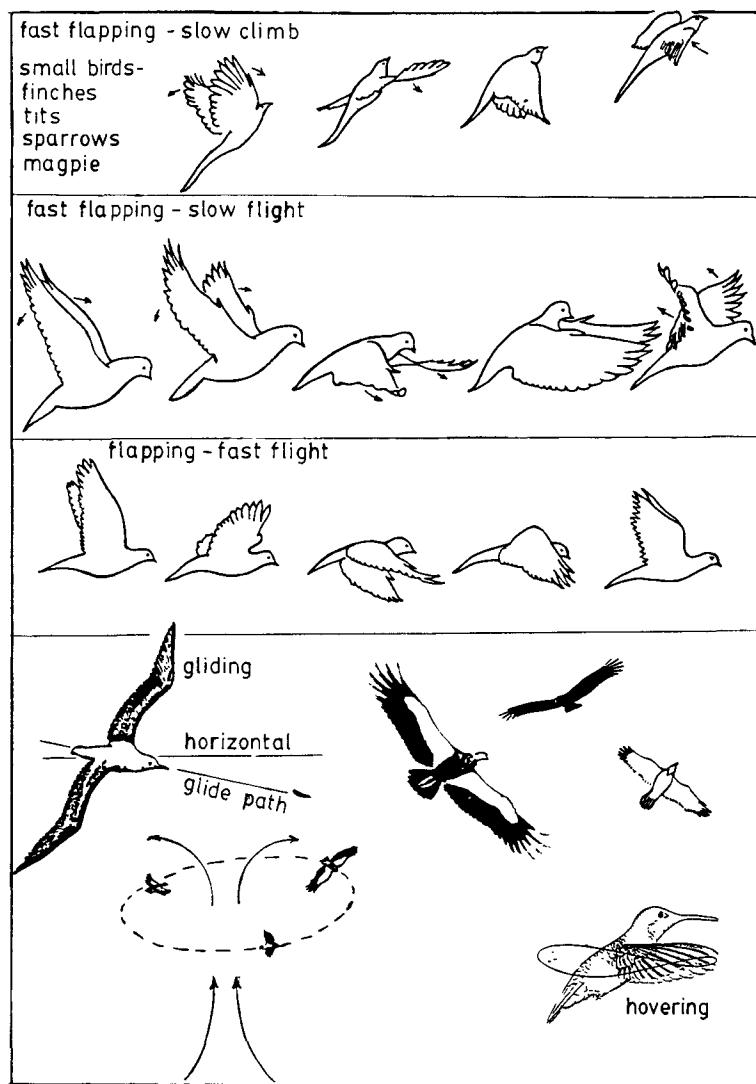


Figure 9. Types of bird flight. (From Brown 1963.)

flight as well as landing, turning and other manoeuvres which the bird performs are illustrated in figures 11a-c. Actual wing configuration during the process of flapping can be studied in detail only with the help of high speed photography. Figures 11-13 are a collection of drawings made from high speed photographs reproduced from various sources, including those photographed at Sriharikota, and they serve to illustrate the complexities of wing form and attitude during flapping flight. Detailed studies show that the wings perform a dual function, working both as airfoils and propellers. Lift and propulsion are effected by a complex combination of vertical and horizontal motions along with bending and twisting of the wings during the flapping cycle. Broadly speaking, the inner and outer parts of the wing perform distinct functions. The inner part, closer to the shoulder and with a lower amplitude of motion, also undergoes relatively smaller changes in attitude and mainly carries the lift during normal cruise flight. The outer wing - the hand section with the primary flight

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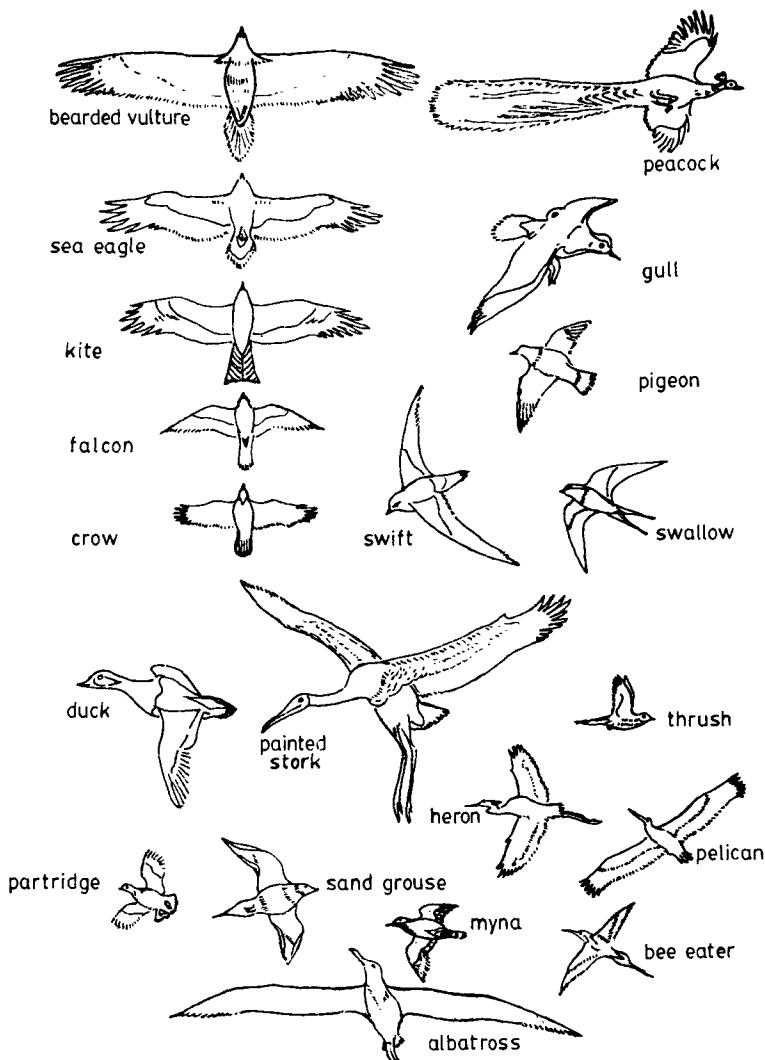
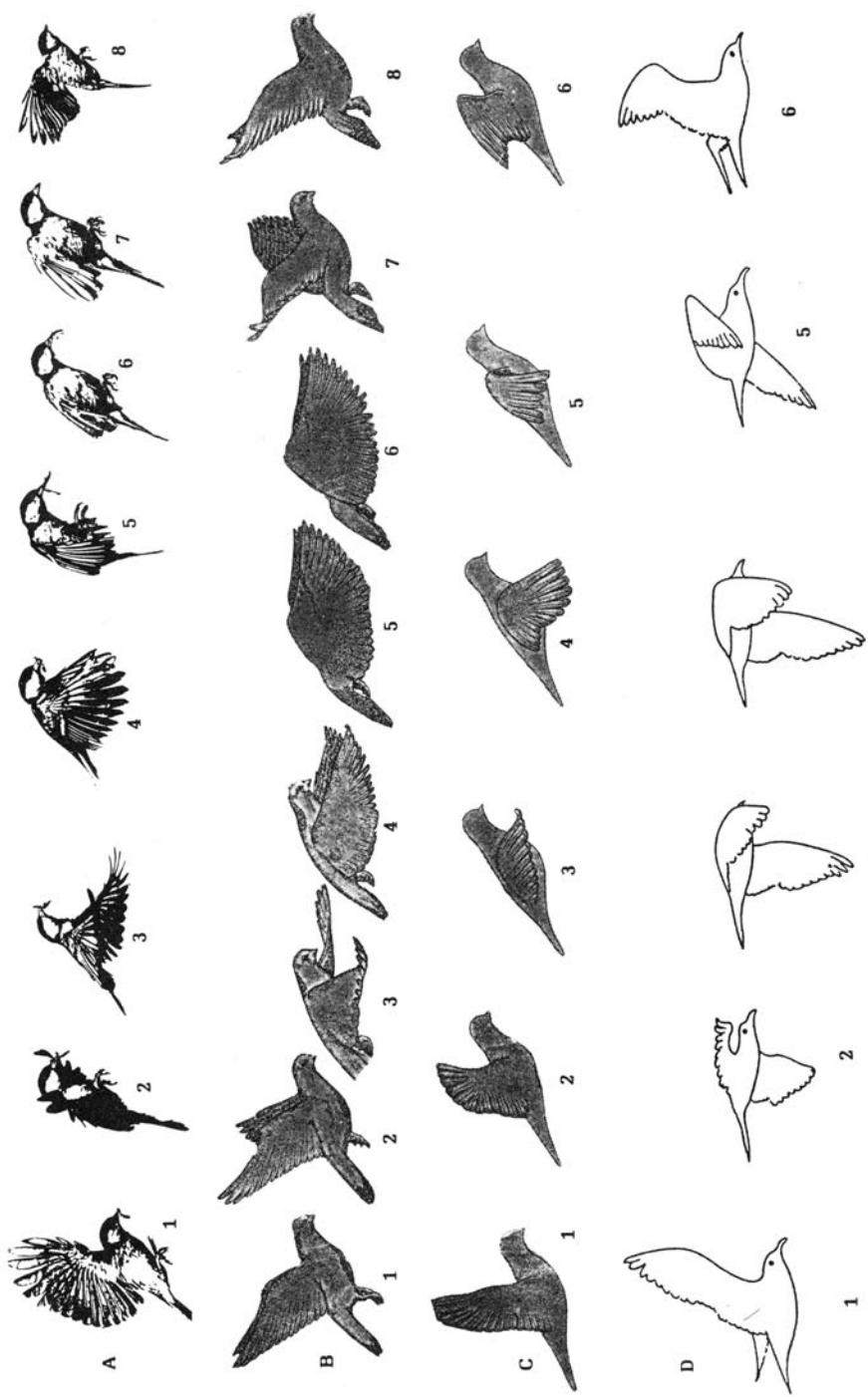
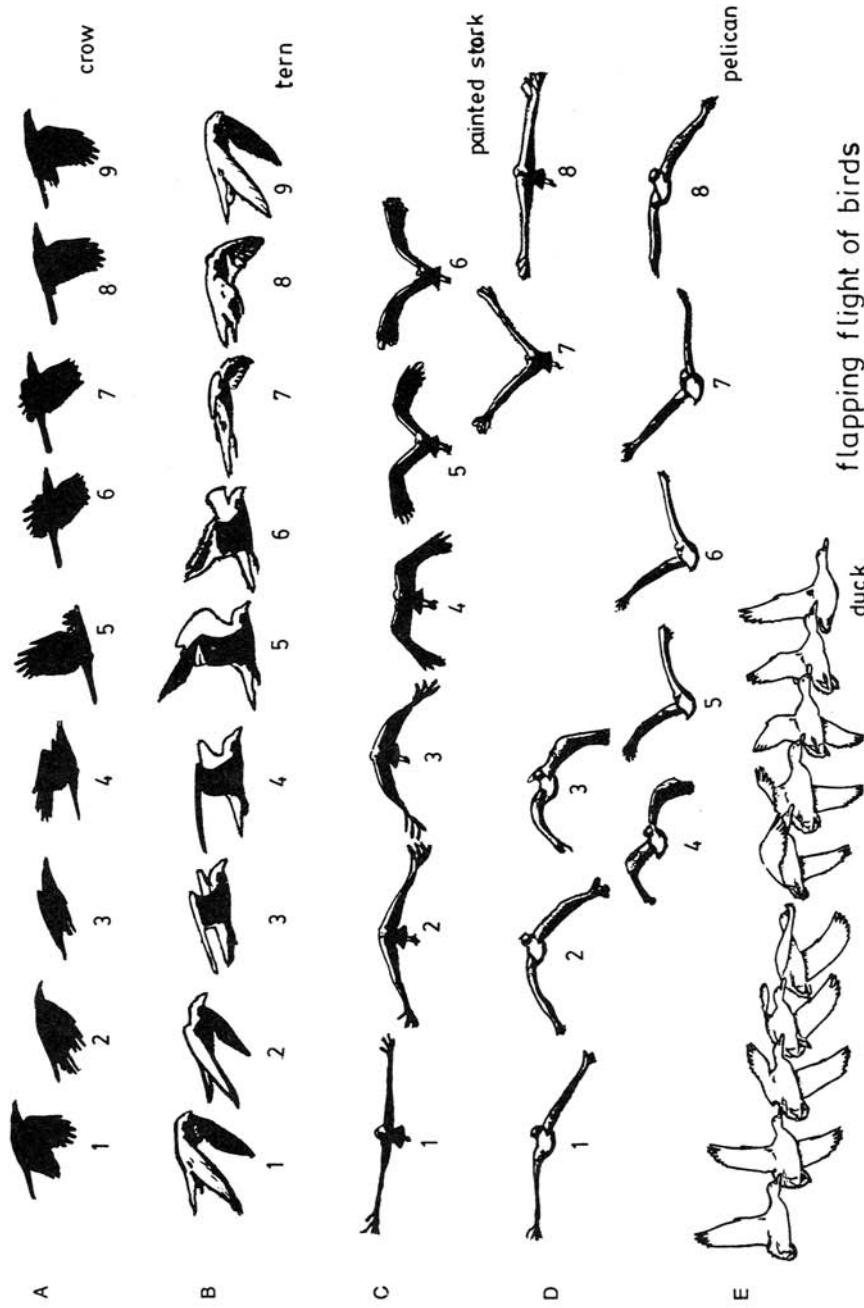


Figure 10. Wing shapes (from Ali & Ripley 1983).

feathers – performs two roles. The first is as a propeller providing thrust and the second in providing lift and control. The first function is common to all birds but the details of the second take on different forms depending upon the size of the bird. During flapping flight one can distinguish two distinct movements of the wing. The first is the “downstroke”, or the power stroke, during which the wing generally moves downwards with the outer and faster moving part also moving forward, especially towards the end of the stroke. The second movement – the “upstroke” – essentially restores the wing to the fully up position from which the next downstroke starts (see figure 14). However, in the upstroke, so as not to produce unnecessary resistance (drag) and lose the lift, the wing goes through a complex bending and twisting motion. At the end of the downstroke, the wing first rotates upwards from the shoulder while the elbow is relaxed so that the outer wing bends down as well as rotates to present the least resistance to forward motion. Approximately half way through the upstroke the outer wing is moved up and back at a very rapid rate with outer feathers separated.



**Figure 11a.** Illustration of flapping flight of small (A), medium (B & C) and large (D) bird. (A) Great tit climbing (downstroke 1-3; upstroke 4-8); (B) pigeon in slow flight (downstroke 1-4; upstroke 4-8); (C) pigeon in fast flight (downstroke 1-4, upstroke 5-6); (D) fast flight of a gull (downstroke 1-3; upstroke 4-6). Note the forward bending of primary feathers in A3, B3 & C3 indicating lift + thrust; B7 shows propulsive flick on upstroke. (From Brown 1963 and Ruppell 1977, p. 87)



**Figure 11b.** Flapping flights of the crow (A), tern (B), painted stork (C), painted stork (D) and duck (E). (A) Crow with  $f = 4$  cycles/s. (upstroke 1–5; downstroke 6–9); (B) tern with  $f = 3.5$ /s. (upstroke 1–5; downstroke 6–9); (C) painted stork with  $f = 3$ /s. (downstroke 1–3; inner wing moving up, outer wing down 4; upstroke 5–7; downstroke 8); (D) pelican with  $f = 2.5$ /s. (downstroke 1–2; upstroke 3–6; downstroke 7–8); (E) downstroke and upstroke of the duck (taken from Petersen 1968, pp. 44 & 45).

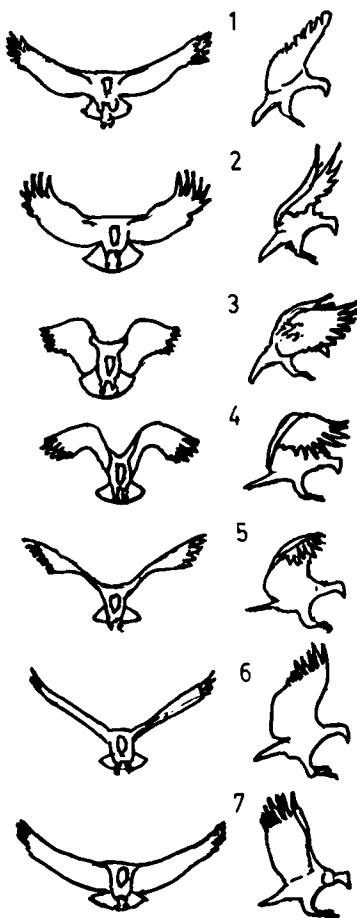


Figure 11c. Landing of Andean condor (downstroke 1–4; upstroke 5–7). (From McGahan 1973.)

This action not only reduces the drag but, in some birds, actually provides extra lift and forward thrust. During the power (down) stroke, the primary feathers are held close together to produce a near perfect airfoil for producing the maximum lift and thrust with minimum drag. In smaller birds like sparrows, tits etc., the outer part of the primary feathers get separated on the upstroke and function like slots, allowing air to pass through, thereby reducing drag. This does not occur in many of the larger birds like gulls or on birds with slender wings like swallows. These birds partially close the outer tips while flinging them back, thereby producing some thrust.

### 3.2 Detailed observations of wing motion

The most detailed studies have been in the case of the pigeon, *Columba livia* (Brown 1948, 1953; Pennycuick 1968). Figure 11a (B & C) illustrates these and figure 15 shows the wing motions during normal flight.

The changes in wing beat kinematics occur in response to flight needs. Immediately after take-off the requirement of adequate thrust and lift causes the birds to use a "tip reversal" upstroke (figure 11a – A6, 7, 8 & B6, 7, 8) during which the primary feathers generate both weight support (lift) as well as propulsion (thrust). The downstroke in this phase of flight primarily generates lift except towards its end (see

## Bird flight

figure 11a – B3). When flying very slowly the secondary feather region (inner wing) is not moving fast enough to generate much useful aerodynamic forces. At higher speeds the pigeon modifies its upstroke (figure 11a – C4, 5, 6), bringing the wing close to the body with the primary feathers rotated and separated so that they present the “Venetian blind” appearance similar to small birds (figure 11a – A4). As the pigeon’s flight approaches the normal cruise speeds, the wing kinematics change again. Now the wings remain partially extended during the upstroke and force is generated throughout the stroke. Other birds like the kestrel (*Falco tinnunculus*) also use this type of “reduced span” upstroke in fast flight.

### 3.3 Take-off and landing

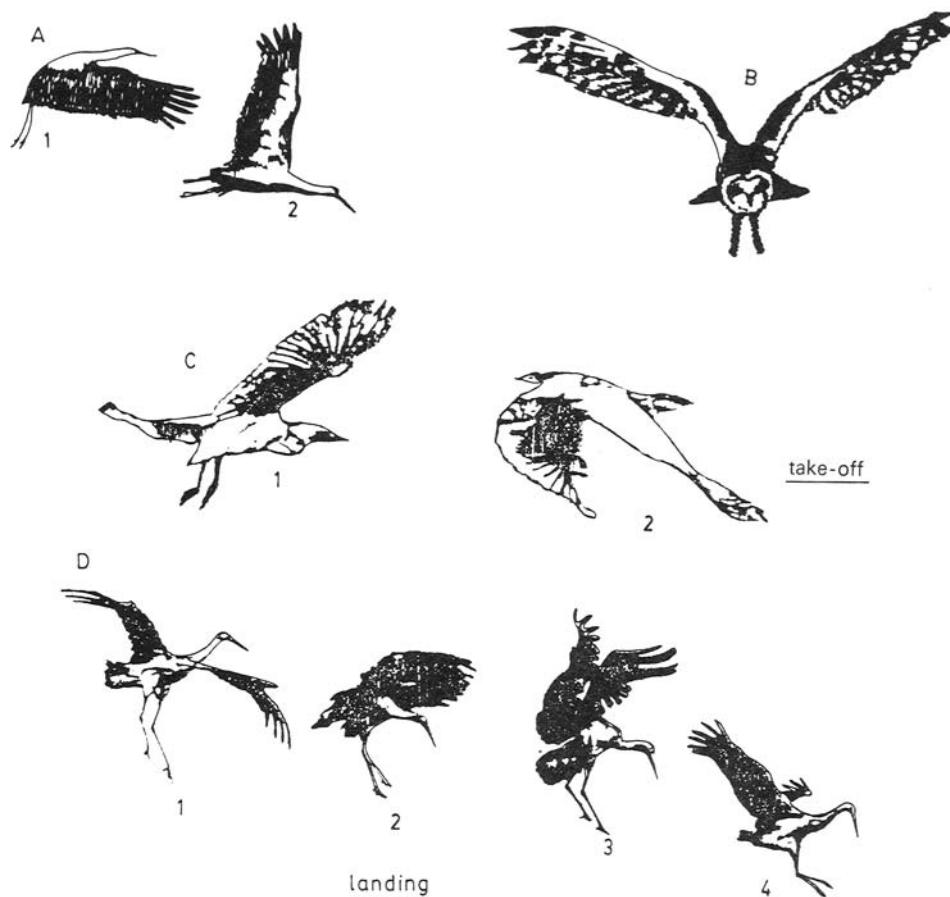
During take-off, the forward speed of the bird being low, the primary requirement of lift to overcome gravity is essentially provided by a fast flapping rate which is higher than in normal forward flight. The amplitude of flapping is also greater. Similarly, during landing, the speed being low, the bird’s wings must generate the required lift to uphold the weight and also brake the forward motion. As a consequence, the wings are spread wide and the flapping motion adjusted. Figures 12 and 13 illustrate these two phases (also see figure 11c).

### 3.4 Propeller action

The details of the process of generation of forces required for sustained flight are discussed in the next section. Here we note that photographic observation of the



**Figure 12.** Slow flight of falcon (Ruppell 1977, pp. 82 & 83) (1 shows the downstroke with a sharp twist of wing tips; 2 shows the end of the stroke with alulae raised and wings pulled forward; 3 shows the upstroke with the inverted manus primaries splayed).



**Figure 13a.** Take-off and landing of large birds. (A) Stork take-off (1 – wing pulled forward on downstroke; 2 – end of upstroke). (B) Owl upstroke after take-off. (C) Take-off of large heron (1 – downstroke beginning, 2 – downstroke end with outer wing pulled forward and twisted). (D) Stork landing (1 – steep glide with alulae raised and wings extended; 3 – braking wing beats; 4 – landing on nest). (From Ruppell 1977, pp. 64, 65, 80 & 81.)

flight phases shows that, while a downward motion of the wings during flapping flight can be expected to generate lift, this, by itself, cannot propel the bird forward. As already pointed out, the "propeller" function is performed by the outer and faster moving part of the wing through a change in attitude i.e. twist, which moves the leading edge downwards as the wing moves forward. In this orientation the outer wings behave like the blades of a propeller. In fact, an observer viewing the bird from the front can easily imagine the flapping wings as equivalent parts of two contra-rotating propellers as shown in figure 16. This can also be seen in the case of the gull in fast flight (figure 11a – D) and the birds in figure 11b (crow etc.). The wing tips in their orientation and curvature clearly indicate the aerodynamic forces acting on them. It must, however, be noted that in each bird the precise orientation is not the same and, depending on the size and form, the functional kinematic aspects of wing flapping vary – only confirming the complexities of flight. Figure 12 shows the wing attitudes during the slow flight of a falcon. The earlier remarks relating to slow flight hold here also. The falcon's wings show significant upward curvature of the primary flight

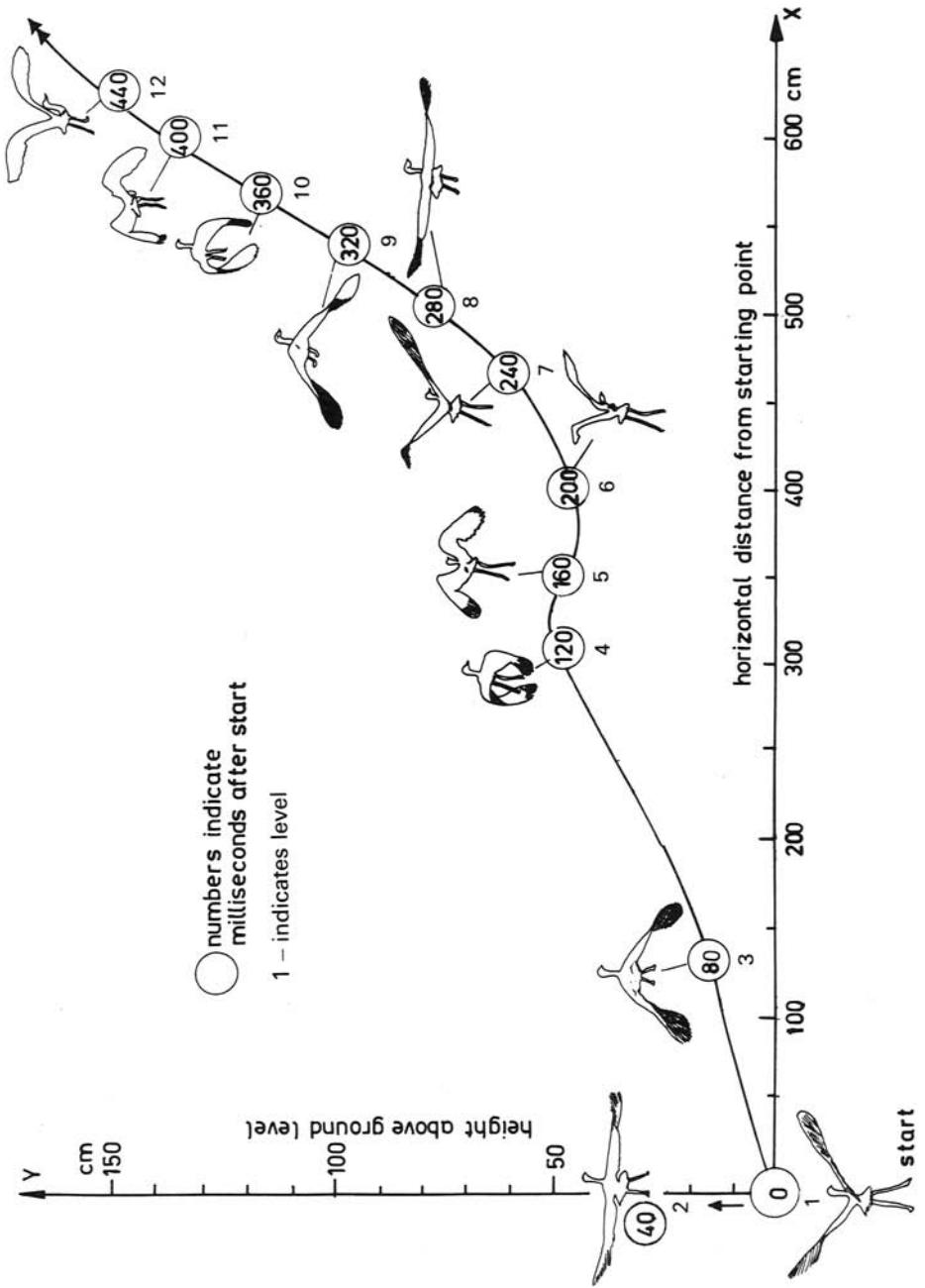


Figure 13b. A study of the egret take-off. The horizontal distance from the starting point (in cm) is plotted against the height above ground level. The number within the circle indicates milliseconds after start. The number below the circle indicates the level. Note that between levels 4 and 6 the bird drops about 10 cm as its flight has not fully stabilised. At level 12 the bird's speed is approximately 10 m/s and its climbing rate is about 0.33 m/s.

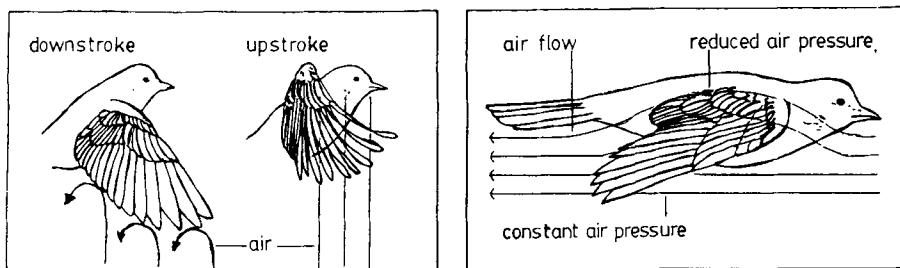


Figure 14. Wing attitudes in flight. (From *World Book Encyclopedia*, p. 287.)

feathers exhibiting the lifting function. The raised alulae and forward position at the end of the downstroke show the combined lift and propulsive forces. The inverted *manus* (hand) and splayed tip feathers, and the raised elbow moving the wings closer to the body, display the features of the upstroke which re-positions the wings for another power stroke.

### 3.5 Illustrations of flapping kinematics

Figure 13 shows some sketches of the wing flapping kinematics during landing and take off. The essential feature noted earlier can be observed in stork, heron and egret take offs. The landing stork uses its spread wings first, as a sort of parachute, for slowing down its flight and then large amplitude wing beats allow it to descend gradually before alighting on its nest. Figure 13b shows an egret (*Bubulcus ibis*) taking off.

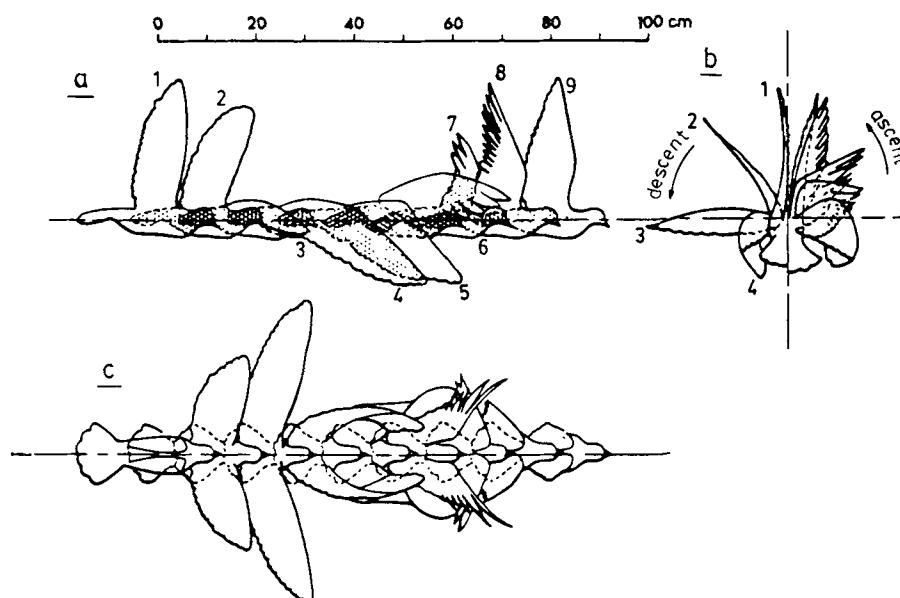


Figure 15. Wing motions of pigeon in normal flight (Guido 1939). (a) Side view, (b) view from rear, (c) top view.

## Bird flight

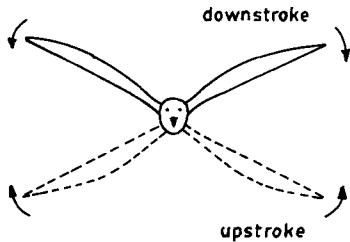


Figure 16. Flapping wings as propellers.

### 3.6 Hovering flight

The ultimate in low speed flight of course occurs when the forward speed diminishes to zero, or practically zero, and yet the bird has to be airborne. The classic example of this type of flight are the humming-birds of the American continents which hover stationary in front of flowers while sipping the nectar. Other birds such as sunbirds of the old world are also capable of hovering for short periods of time – this is because of the extraordinarily heavy demands of energy that hovering entails. Only the humming-birds are equipped with the musculature which allows them to continuously hover. The kinematics of hovering flight demand wing movements such that, apart from a vertical reaction, forces are also generated in the horizontal plane. Figure 17 shows how the humming-bird accomplishes this in still air with forward and backward strokes during which the wing reverses its inclination. The flapping frequency is high compared to other birds – being between 50–100 Hz – depending on the size and weight of the humming-bird (cf 2–10 Hz for other birds in normal flight). Figure 17 also shows a sequence of drawings of a kingfisher hovering just before diving into a pond to catch its prey. Such hovering usually occurs in a prevailing wind current so that, relative to the bird, there is wind velocity and some lift available, while, relative to the observer, the slow forward motion of the bird is neutralised by the wind and the bird appears stationary. The wing flapping motion of the kingfisher in figure 17 shows that it has both up-and-down as well as back-and-forth motions. Similar hovering patterns can be observed in other birds e.g., the kestrel, as also smaller birds alighting or manoeuvring to catch insects. The humming-bird also, in transitioning from hovering to forward flight, changes the flapping pattern of its wings so that an up-and-down motion appears in addition to the back-and-forth. This occurs along with a change in attitude of the body which was nearly vertical during hover and becomes horizontal during forward flight.

### 3.7 Gliding and soaring

Gliding flight occurs when the bird does not flap its wings but uses gravity to provide the means for flight. In still air the path of the bird with wings spread is inclined downwards and the combination of the aerodynamic forces generated by the motion through the air and the force of gravity create a balance of forces allowing steady gliding flight. Soaring takes place when a gliding bird is able to use air currents with vertical velocity components such as thermals, slope currents near mountains, cliffs etc. A particular form of soaring, known as dynamic soaring, can occur only when the wind has a velocity gradient with the speed increasing in the upwards direction (i.e. away from the ground). Figure 18 pictorially depicts some of the gliding and soaring situations. The most familiar gliding and soaring birds are the vultures and

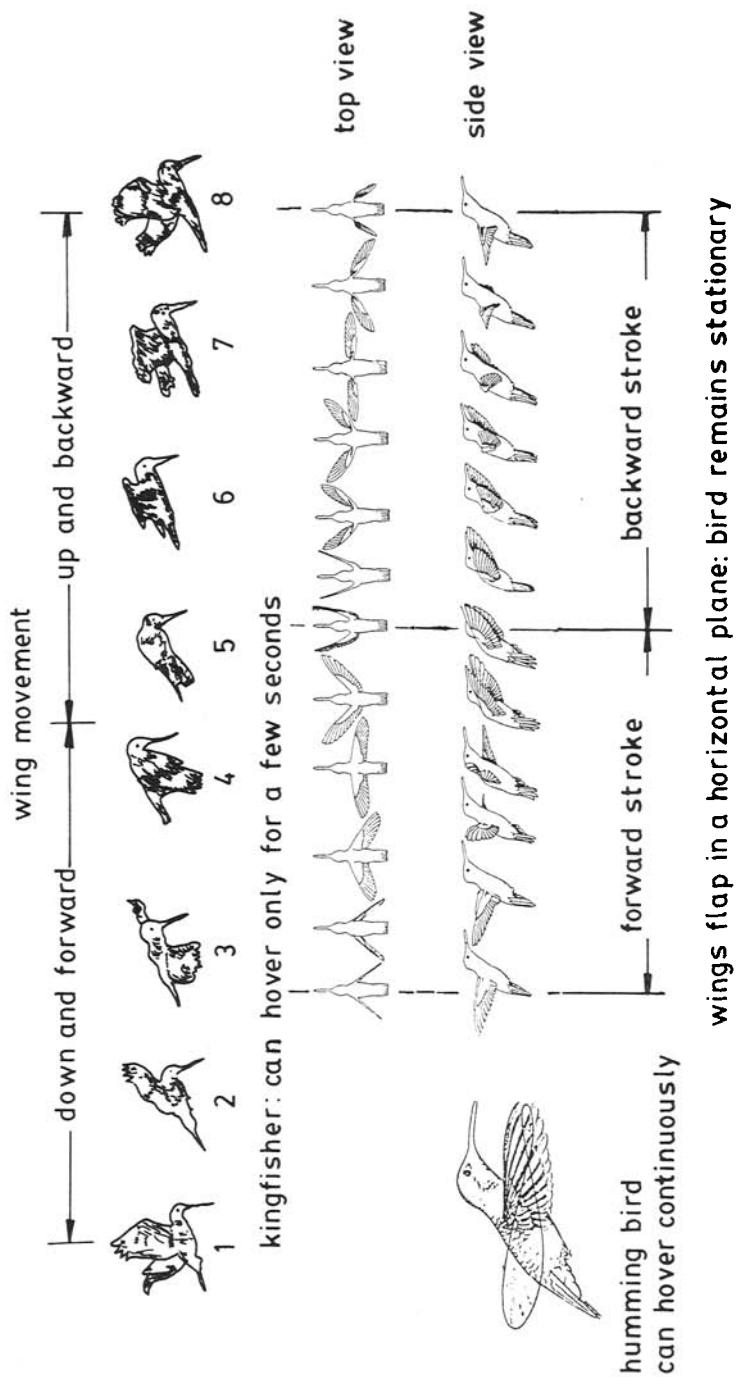
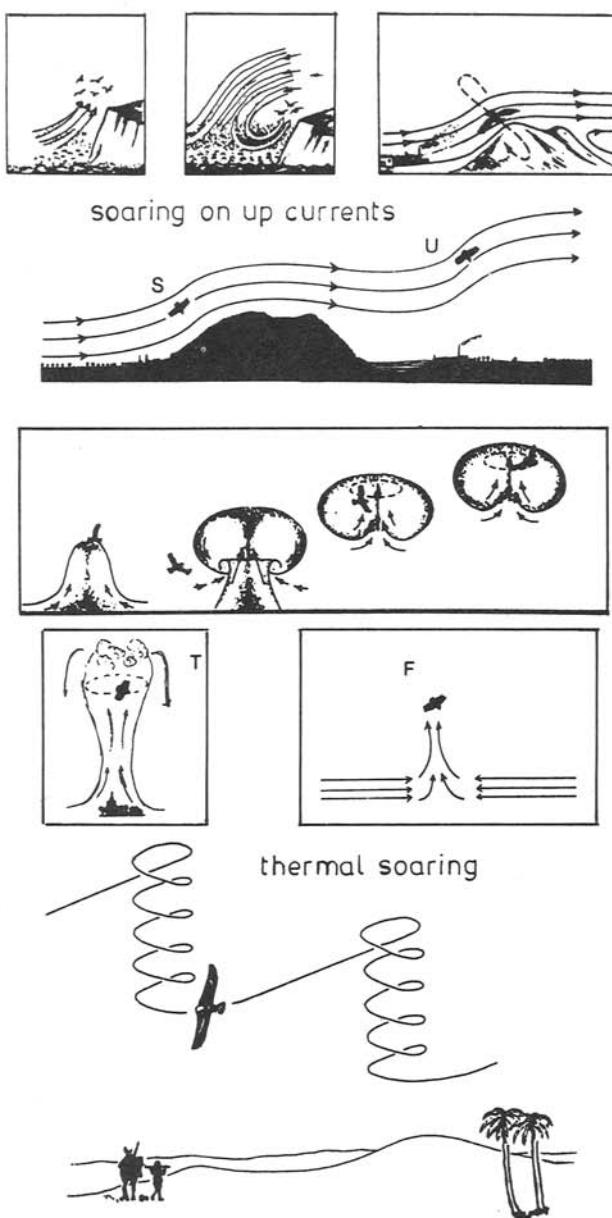


Figure 17. Hovering flight. (From Petersen 1968, pp. 44, 45.)

### Bird flight



**Figure 18.** Soaring flight (Ruppell 1977, p. 69).

kites. However most birds – except the smallest – have the capability to glide and often use it during landing. It is interesting to recall that very careful observations of gliding and soaring birds were made by Hankin in India in the early years of this century (Hankin 1913). Stationed in Agra, Hankin observed that birds of different weight and size followed soaring in succession after sunrise – the heavier ones coming later. He related this observation to the rising up-currents caused by differential heating of the atmosphere by the sun's rays. The attributes which make for efficient gliders and soarers will be discussed in § 5.7. Here we note that, during gliding, while the bird expends virtually no muscle power it does have to exercise some small

movement of the wings for flight control and maintenance of stable flight. There are numerous birds other than the raptors which resort to periods of gliding. Examples are sea birds like the gulls (Laridae), pelicans (Pelicanidae), crows (Corvidae) etc. As mentioned earlier, just before landing pigeons, pheasants, ducks, parrots and other smaller birds such as the common mynas (Sturinda) and pheasants (Phasianidae) may go through a gliding phase. Appendix C consists of high speed photographs of different birds in flight.

#### **4. Production of aerodynamic forces by the wings**

As indicated in § 3, in order to fly through the air a bird has to overcome gravity and generate a force which propels it forward. The science of aerodynamics and fluid mechanics seeks to understand and explain how forces arise on bodies moving immersed in a fluid (air, water). The foundations of the subject were laid in the last half of the 17th century when Newton enunciated the laws of motions of bodies. The development of aerodynamics has been a unique example of contributions by mathematicians on the one hand and creative engineers on the other. The names of Cayley (England), d'Alembert (France), Borda (France), Eiffel (France), Joukowski (Russia), Rankine and Reynolds (England), Prandtl (Germany), and Von Karman (Hungary) appear prominently among the scientists and engineers who developed the subject. Von Karman (1954) has given an excellent account of the historical development of the subject.

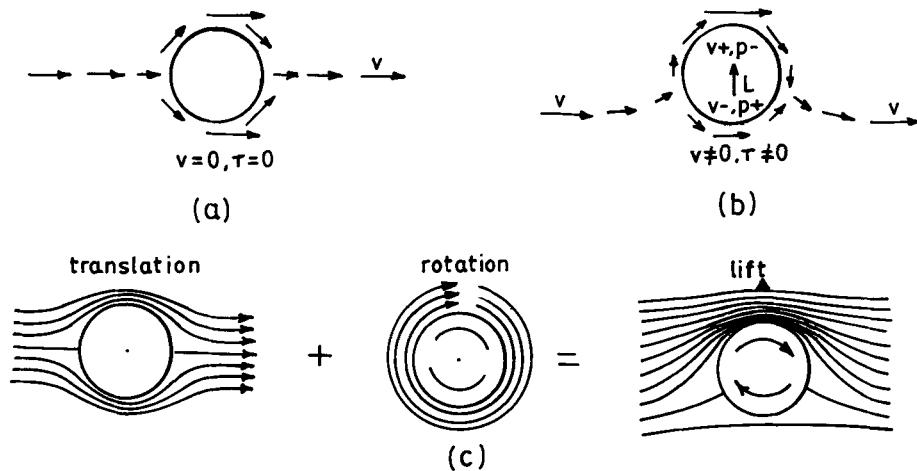
We rapidly recapitulate, in an elementary form, the manner in which lift and drag arise on a body moving through a fluid medium such as air.

##### *4.1 Flow patterns and forces on airfoils*

When a body – a bird or an aeroplane – moves through the atmosphere, the air is disturbed. These disturbances take the form of minute pressure and density changes in the vicinity of the body. Depending on the size of the body, and its speed, they propagate to distances away from the body up to a few body lengths. The scale of the atmosphere being large, compared to even the largest bird, the propagation distances are comparatively small. According to Bernoulli's principle, the total energy in a moving fluid is conserved. Thus in air flowing past a bird, the regions of higher velocity near the bird, caused by the disturbances created by the presence of the bird, would be regions of lower pressure and vice versa.

The simplest case to consider is a circular cylinder moving with uniform speed through air. This is equivalent, by the principle of relative motion, to considering the cylinder being stationary and exposed to parallel uniform flow. If there were no viscous friction, the theory shows that there would be no net force acting on the cylinder. The air stream would divide symmetrically, as shown in figure 19a, around the cylinder – there being higher velocities at the top and bottom, and low speeds adjacent to the front and back faces. The associated pressure changes would be symmetrical; so no net force would act on the cylinder. Now if a clockwise circulatory motion is imposed around the cylinder the velocity due to this motion will add (vectorially) to the earlier velocity field at each point. In particular, near the top of the cylinder, velocities would increase while, near the bottom, the velocities would diminish. The effect of these changes on the pressures would be to reduce the pressure

## Bird flight

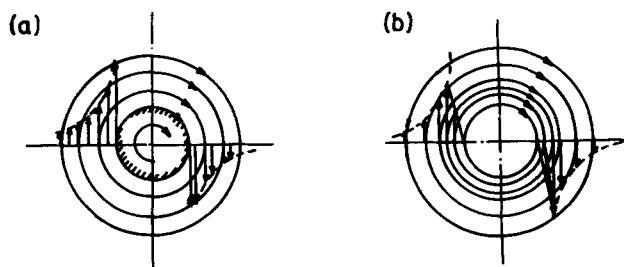


**Figure 19.** Flow past a circular cylinder. (a) Uniform flow – no lift force. (b) Flow with circulation – upward lift. (c) Flow patterns – superposition of uniform and circulatory flows.

on the upper surface and increase it on the lower one. Thus an upwards net force – the lift – would be created by the circulatory motion added to the streaming motion. It is clear that the greater the amount of circulatory motion, or ‘circulation’, greater would be the lift. When we deal with actual cases of wings and airfoils, whose shapes are not circular, the question arises: how much circulation would appear? Before we take up this issue we must recognise the role of viscous friction (and the fact that practical airfoils usually have sharp trailing edges). Recall that actual fluids, including air, would stick to the surface, gradually speed up in a thin layer, called the boundary layer, and reach the full velocity outside. A rotating circular cylinder in still air would then generate a velocity field such as shown in figure 20a. Due to viscosity the air next to the surface, would have the same velocity as the surface but rapidly fall off as we move away. If, on the other hand, we placed a solid circular cylinder in a rotating circulatory flow then the situation in figure 20b would develop. The velocity would rapidly increase from zero at the surface to a large value at the edge of the boundary layer and then diminish in proportion to the distance.

### 4.2 Circulation and lift

The applications of these ideas to the lift on airplanes and bird wings were pioneered by F W Lanchester (England), M V Kutta (Germany) and N E Joukowski (Russia).



**Figure 20.** Cylinder in a viscous fluid. (a) Rotating cylinder in viscous fluid, (b) fixed cylinder in rotating viscous flow.

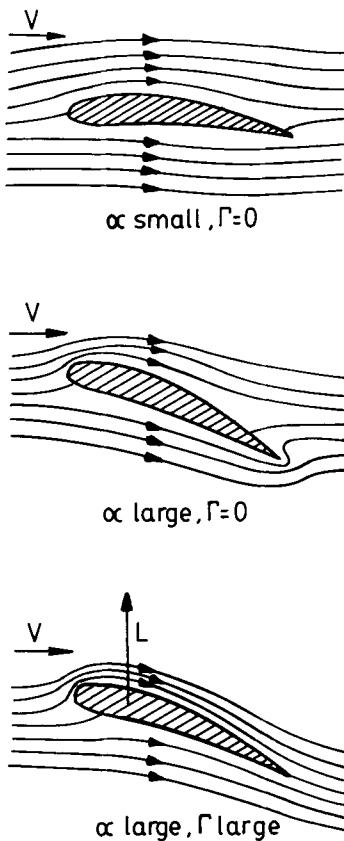


Figure 21. Flow past an airfoil.

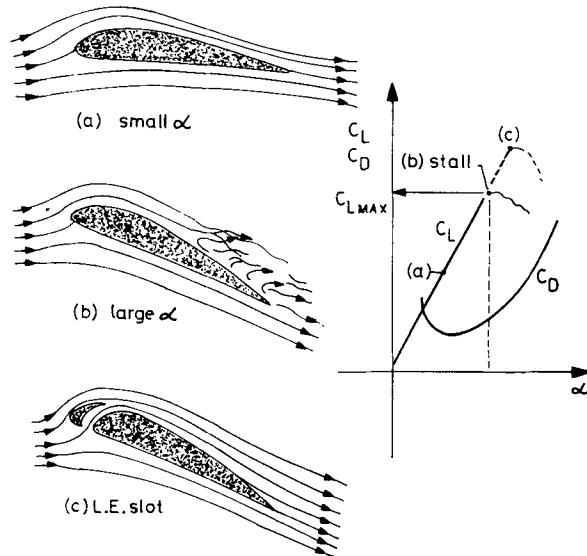


Figure 22. Lift on an airfoil.

They argued that on an airfoil placed in a moving stream of air, just enough circulation develops so that the rear stagnation point moves to the trailing edge, thereby avoiding the very high (infinite in theory) velocities the flow would have to encounter in going round the sharp trailing edge (see figure 21). In the process a trailing vortex is shed with strength equal and opposite to the 'bound' vortex around the profile – thus preserving the conservation laws. The lift force on the wing is generated by the difference in velocities on the two sides leading to difference in pressure analogous to the case of the circular cylinder with circulation. The magnitude of the lift is roughly proportional to the angle of incidence and increases linearly up to a certain maximum value after which it suddenly decreases. This phenomenon, known as stalling, is caused by the viscous boundary layer on the upper surface breaking away; thus causing a loss of the suction pressures. The flow can be reattached by re-energising the upper surface flow, for instance by a leading edge slot. The lift can then be increased to higher incidences. Figure 22 indicates the forces on the wing in the three instances. Incidentally, it is usual in aerodynamics to represent the forces on the wing by non-dimensional parameters or coefficients.

#### 4.3 The finite wing

The picture on a finite wing can be completed by noting that towards the tips the pressure differences between the upper surface (lower pressure) and lower surface

## Bird flight

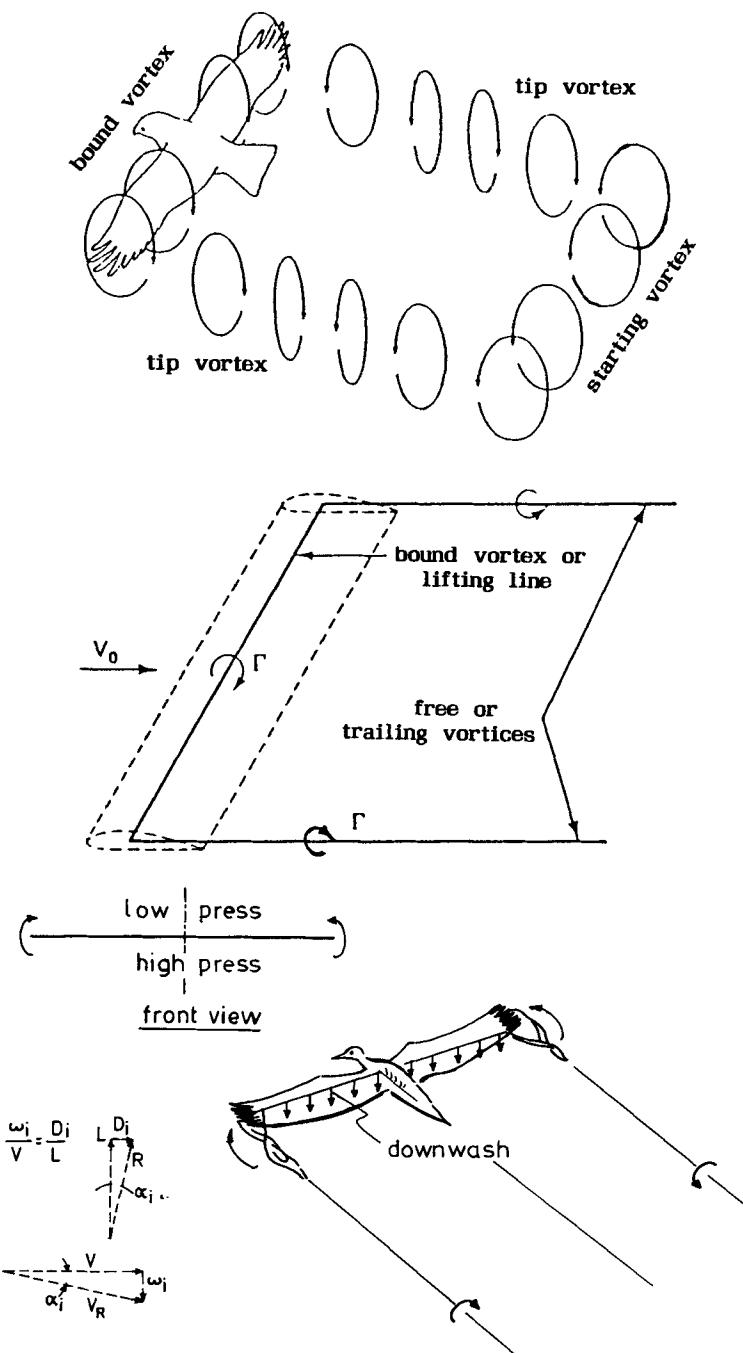


Figure 23. Prandtl's horseshoe vortex system.

(higher pressure) have to equalise giving rise to the tip vortices as shown. In theoretical treatments of lift the picture gets idealised (following Prandtl) into the horseshoe vortex system, with a bound vortex replacing the wing and trailing vortices which influence the flow on the wing and account for the drag due to lift. Figure 23 summarises the process.

#### 4.4 Downwash and induced drag

The above discussion can be summed up by noting that the flow pattern around a finite wing with an airfoil cross-section generates the velocity field shown in figure 23. The resulting forces are also shown. The trailing vortex system creates a ‘downwash’ at the wing which vectorially rotates the free stream velocity downwards. Thus the resultant lift force vector rotates backwards. This gives rise to a force in the direction of the flow – i.e. drag – in addition to lift, the upward force at right angles to the flow direction. Apart from this drag “induced” by production of lift we also have the drag caused by viscosity or friction.

#### 4.5 Linearised theory

So far we have discussed the forces generated by the uniform motion of aerodynamic elements i.e. airfoils and wings. In the case of birds, sustained flight requires the generation of both lift and thrust from the *same* aerodynamic surfaces, in contrast to flying machines in which the mechanisms of lift and thrust generation are separated. Lighthill (1974) has argued that the flapping wing motions that achieve the required forces can be approximately viewed as a linear combination of a simple up and down oscillation, with a twist of the wing surface at each extreme of the oscillation *and* a simple constant angle of attack for lift. Figure 24 (adapted from Lighthill 1975) shows the scheme. During the up and downstrokes the wing surface retains an approximately fixed inclination such that the movement always has a backward facing component which generates thrust. The wing remains approximately inclined at a small angle during the downstroke and then twists into a ‘nose-up’ position for the upstroke. The air forces producing thrust oppose the wing movements during both the down and the upstrokes. On the other hand, in lift production, they oppose the wing movement downward but assist it during the upstroke. As a consequence the wing is heavily loaded during the downstroke, and this explains the large size of the main pectoralis muscles responsible for the power stroke: and the much smaller supracoracoideus muscle which acts during the upstroke. Another important aspect relates to the essentially unsteady nature of flapping wing aerodynamics. The complexity of bird flight essentially arises from the nonlinear interactive relationships between the wing motions and the aerodynamic and elastic forces.

#### 4.6 Flapping amplitudes and frequency

In normal horizontal flight the flapping amplitudes are comparatively low – approximately  $60^\circ$  up and down from the horizontal. The frequency of flapping varies

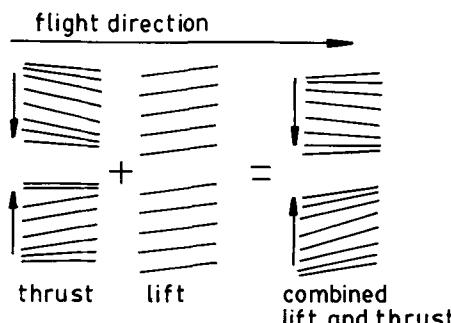


Figure 24. Lift and thrust generation in flapping flight (from Lighthill 1974).

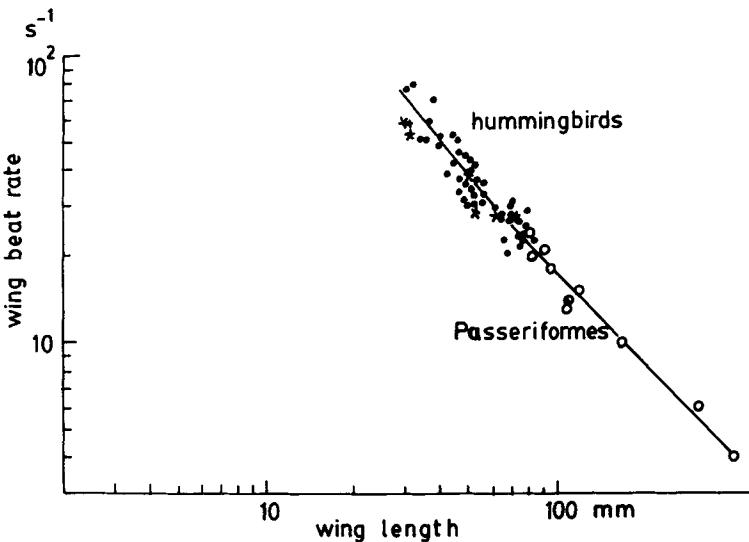


Figure 25. Flapping frequency (adapted from Greenewalt 1975).

with the size of the bird and has been found to vary inversely with size i.e.  $f \propto 1/l$ . Figure 25 shows data from Greenewalt (1975). The oscillating wing can be regarded as a forced mechanical oscillator with damping. It is known that such oscillating systems have, for small damping, resonant frequencies close to the natural frequency of the system. In such systems the amplitude of oscillation is controlled by the impedance which itself is a function of the phase difference between the forcing and the natural frequency of the system. Apparently, during normal flight, the bird maintains the flapping frequency close to the resonant value for minimum expenditure of energy and control is exercised by phase and amplitude changes. In such an approximate and very simplified theory the details of flapping can be ignored and the main features of the flight can be ascertained by considering the average values of the aerodynamic parameters.

#### 4.7 Summary of discussion

To recapitulate, we have noted that bird flight can be characterised by flapping and/or gliding. Birds' wings are essentially forms of airfoils which, when moving through the air, generate lift and thrust and are subject to drag or resistance. In order to understand the broad features of bird flight in terms of aerodynamic theory, we note that drastic simplifications of the complex wing motions are called for. In discussing how wings generate enough lift and thrust to move the birds' weight through the air, overcoming the resistance, we have to make simplifying assumptions which may not be accurate in detail but are physically plausible and lead to results which can be checked and compared with observation.

#### 4.8 Velocity and forces

Figure 26 shows velocity and force diagrams for flapping flight. The general shape of the wing – particularly the twist along the span can be clearly discerned from figures 11–13. During the downstroke, or a part of it, the outermost part of the wing is moving faster and at the same time it is twisted downwards producing thrust. On

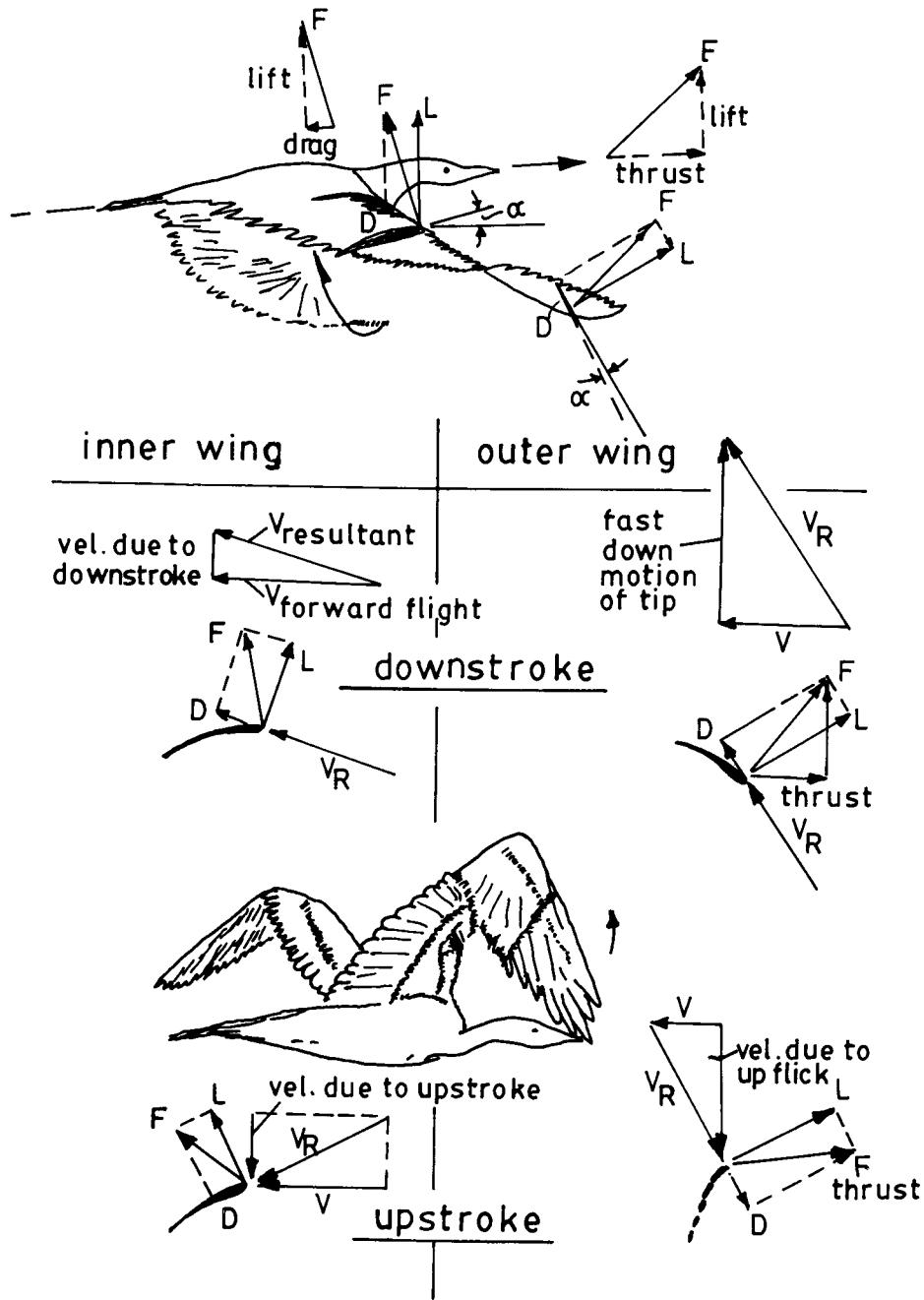


Figure 26. Velocity and force diagrams.

the upstroke the inner part of the wing has a reduced angle of attack but the orientation is generally similar to the downstroke configuration. As the wing is raised from the shoulder, the outer part drops and the leading edge gets twisted upwards. Just after the upstroke starts the twisted outer wing is flung rapidly up and back relative to the body. This results in a forward thrust as well as lift. These motions of the wing during the up- and downstrokes get modified during take off and landing as well as

during the transition from climbing to steady forward flight. The flapping rates and amplitudes also vary – being higher at lower speeds than during normal flight. As examples the hovering kingfisher in figure 17 flaps its wings at about 8 Hz while the pelican and stork in figure 11b have flapping rates of 2.5 and 3 Hz respectively.

## 5. Flight mechanics of the bird

The basic aerodynamic requirements for sustained flight are:

- enough lift to balance body weight, and
- enough forward thrust to balance backward body drag.

As the wings of birds have to generate both lift and thrust, their motions, and forces on them which arise due to interaction with the air, are much more complex to analyse and quantify than on aircraft. The main aim in applying mechanical principles to bird flight is to relate the forces acting during flight to parameters such as wing dimensions and total weight and arrive at estimates of the power required and speed attained. In this process many simplifications of, and approximations to, the observed flight phenomenon become necessary. The estimates and calculations provide information and, sometimes, explanations of wing shape, overall weight or musculature and their relation to the flight habit or habitat. A knowledge of the aerodynamic parameters often allows appreciation of the difference between types and species of birds.

The amount of lift ( $L$ ) and drag ( $D$ ) generated by the motion of a wing through the air depend upon five main factors:

- shape of the wing (cross-section as well as planform);
- angle between the surface of wing and direction of air stream ( $\alpha$ );
- area of the wing ( $S$ );
- density of the air ( $\rho$ ) and its kinematic viscosity ( $v$ );
- velocity of the air stream relative to the wing ( $V$ ).

The relationship between these factors can be expressed as:

$$L = \frac{1}{2} \rho V^2 S C_L, \quad D = \frac{1}{2} \rho V^2 S C_D, \quad (1)$$

where  $C_L$  and  $C_D$  are non-dimensional coefficients which depend upon the properties of the airfoil section and Reynolds number (representing the ratio of the dynamical to the viscous forces).

We note that the wing area  $S$  is the product of the wing span ( $b$ ) and the mean chord  $c$ .  $c$  is easily defined as the average chord and is  $S/b$  for a wing shape with curved leading and trailing edges. For a rectangular shape  $c$  would be just the width.

### 5.1 Estimates of lift

Referring to the discussion on airfoil characteristics we note that while, in general, the coefficients  $C_L$  and  $C_D$  are functions related to the shape and Reynolds number (viscous effects) of an airfoil, aerodynamic theory has established that, to a very good approximation,

$$C_L \approx a \cdot \alpha, \quad (2)$$

where  $\alpha$  is the angle of incidence below the stall and  $a$  is the slope of the lift curve  $\partial C_L / \partial \alpha$ . Theory indicates a value of  $2\pi$  for  $a$  for thin two-dimensional wings in frictionless flow. For finite wings of shape and form usually found in birds it is reasonable to take:

$$5 < a < 6, \quad (2a)$$

with  $\alpha$  being measured in radians. An approximate value for  $C_L$  below the stall can be obtained quickly from  $C_L \approx \alpha^\circ / 10$  where  $\alpha$  is now expressed in degrees.

## 5.2 Estimates of drag

Similarly we can arrive at approximate working formulas for  $C_D$ . In this case we have to recognise that the drag of the flying bird essentially consists of two parts: (a) frictional drag and (b) induced drag. The frictional component arises due to viscosity of the air and results in the formation of the viscous boundary layers on the wing and body surfaces in which dissipation of energy takes place. These boundary layers separate near the rear part of the surface and cause the pressure distributions on the wings and body to deviate from the ideal thus causing 'pressure' or 'form' drag. The drag associated with the friction layers is usually called profile drag. Aerodynamicists have evolved various schemes over the years to estimate these components of drag caused by viscosity. For our purposes we will use coefficient  $C_{D_0}$  at zero lift i.e. when the bird orientation at the flight velocity is such that no net lift is produced. The remaining component  $C_{D_i}$  is lift dependent and is a penalty paid for the generation of lift and we will estimate this separately. Estimates for  $C_{D_0}$  can be derived from boundary layer theory which treats the viscous boundary layers in the laminar (smooth) flow and turbulent states. It is usual to calculate from theory the friction losses on smooth flat plates and then make allowances for shape, roughness etc. In the case of the flapping wings of birds we would also need to make allowances for the increase in drag due to the unsteady nature of the flow over the wings. Boundary layer theory gives the form of skin friction dependence on Reynolds number  $Re$ , which is a parameter indicating the ratio of inertial and viscous forces in a flow and is defined as  $Re = Vl/v$ . For a bird flying in air, Reynolds number can be calculated from the equation  $Re = 6.8 Vc$ . Established theory gives  $C_F \propto (Re)^{-1/n}$ , where the friction coefficient  $C_F$  is equivalent to  $C_{D_0}$  when the proper surfaces etc. are taken and  $n$  is an index which has the value 2.0 in laminar flow and about 4.0 in turbulent flow. The constant of proportionality has to be determined from experiment. Using these relations and allowing for both wing surfaces, the body of the bird, surface roughness and the local velocity near the bird being greater than the flight velocity, we can approximate the behaviour of  $C_{D_0}$  by the relation

$$C_{D_0} = 0.77/Re^{0.3}. \quad (3)$$

This is plotted in figure 27 for the normal range of birds and the velocities (close to  $V_{MP}$ ) they fly at. The experimental data is from Withers (1981).

In order to get an estimate of the induced drag  $C_{D_i}$  we need to consider the momentum imparted to the air by the birds' flapping wings. In view of the complex nonlinear interactions between the moving wing surfaces and the air, it is not possible so far to set out a detailed theory for the aerodynamic forces. We will use a very simple approach often used by aerodynamicists in such situations. In this approach

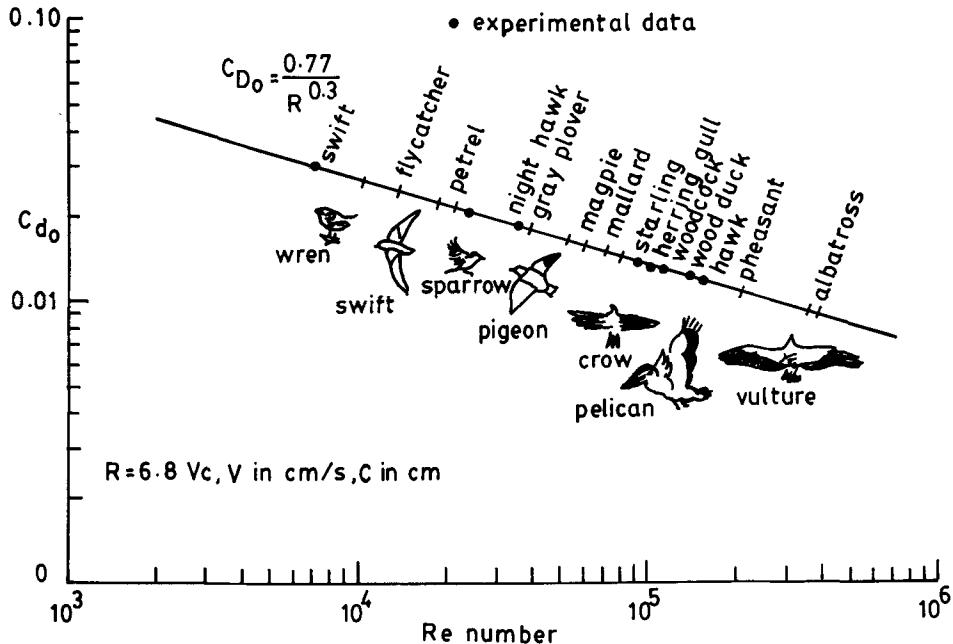


Figure 27. Zero-lift drag of birds (experimental data from Withers 1981).

we neglect all details of the flow near the bird and argue that eventually, as a result of the expenditure of energy by the bird, some air gets accelerated backwards and downwards. The aerodynamic force ( $L$ ) perpendicular to wing motion, is caused by the rate of transfer of momentum downwards in a region whose extent is approximately defined by the wing span  $b$ . Since the forces on the bird are a result of relative motion we consider, for convenience, the bird to be at rest and the air flowing past it at a velocity  $V$ . The situation is illustrated in figure 28. The bird can be considered idealised into a device which imparts momentum to the air and therefore experiences a force. In the application of this very simplified theory the following assumptions are implicit:

- no rotational velocities are imparted to the air;
- the pressure remains constant far ahead and far behind the bird;
- no losses, such as due to mixing, occur in the moving air.

If  $w_i$  is the downward velocity increment induced at the plane of the bird then a simple calculation using Bernoulli's equation to the flow ahead and after the wing shows that the increase in induced velocity far behind the wing reaches the value  $2w_i$ . It is to be noted that since energy is added at the wing, Bernoulli's equation is not applicable across the disc containing the wing. Prandtl's lifting line theory, which replaces the wing and its velocity field by a 'bound' and 'trailing' horseshoe vortex – the front bound with the wing with two counter-rotating trailing vortices (see figure 23) also predicts the same results. A consideration of the velocities and force diagrams shows that the ratio of the induced velocity  $w_i$  to the free stream velocity  $V$  is the same as the ratio of the drag  $D_i$  to the lift  $L$  – these ratios being equal to the tangent of the angle by which the free stream is deflected downward (see figure 19). Thus we have the equation

$$w_i/V = (D_i/L) = (C_{D0}/C_L). \quad (4)$$

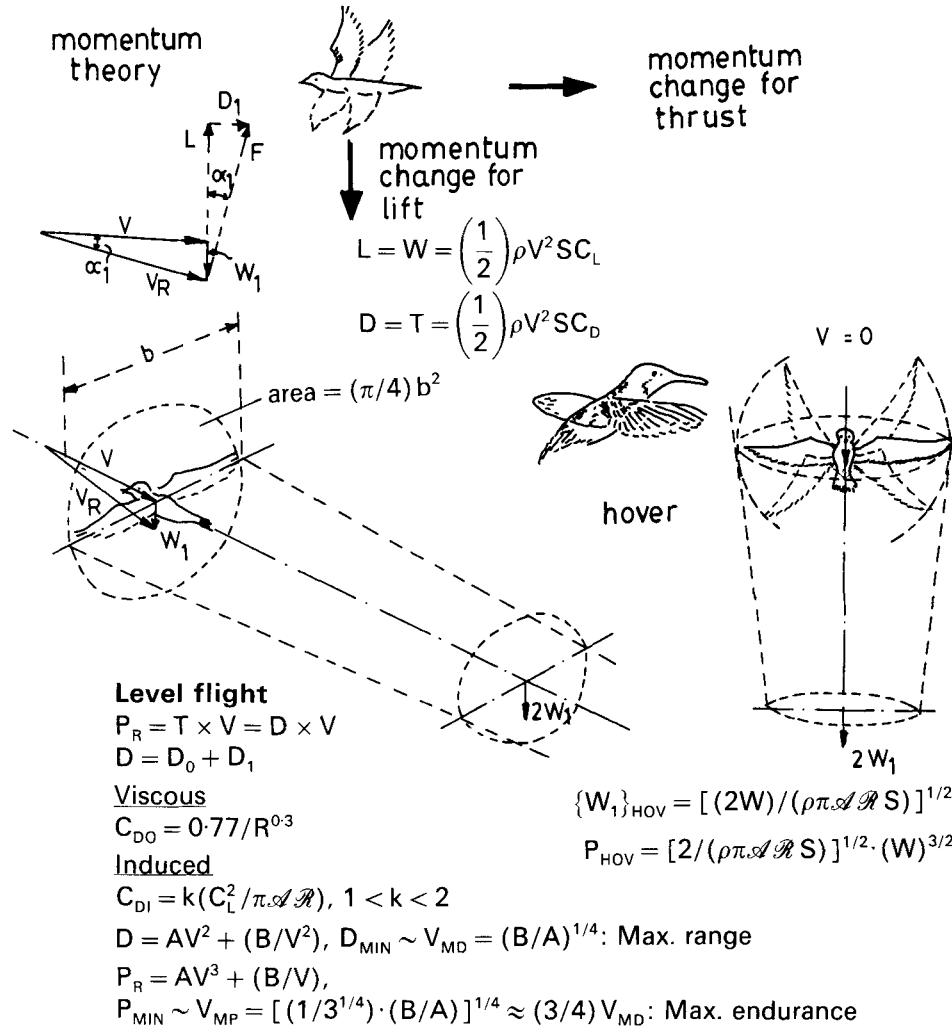


Figure 28. Power required for flight.

In general the induced velocity  $w_i$  is not constant across the wing span but depends on the wing geometry and the incidence of the various sections of the wing along the span. We will make the rather drastic assumption that  $w_i$  remains constant along the span. It turns out that aerodynamic theory predicts that this can occur only for elliptic wings with elliptic planforms. For non-elliptic wings a correction can be made.

We can now proceed to calculate the rate at which the vertical momentum is increased. For this we consider flow through the circular area swept by the wings i.e.  $\pi b^2/4$  and get the expression  $(\rho\pi b^2/4) \cdot (w_i)$  for the momentum change. The first bracket represents the rate of mass flow through the disc swept by the wings (this remains constant in the stream tube) and the second is the downward velocity far behind and represents the total downward velocity change. In this calculation the squares of the velocity increments have been neglected in comparison to the flight velocity. This rate of change of momentum supports the bird weight  $W$ . Using the expression for the induced velocity  $w_i$  and noting that the lift  $L$  is equal to  $W$ , we get for the induced drag coefficient,

$$C_{Di} = C_L^2 / \pi A R, \quad (5)$$

## Bird flight

where  $\mathcal{A}\mathcal{R} = b^2/S$ , the aspect ratio, represents an important dimensionless aerodynamic parameter.

As noted before, this expression is strictly valid for wings of elliptic planform which produce a constant downwash across the wing span. Making allowance for departures from constant downwash we write

$$C_{Di} = k C_L^2 / \pi \mathcal{A}\mathcal{R}, \quad (6)$$

where  $k$  is a parameter with values between 1 and 2 depending on the planform of the wing. In terms of standard aerodynamics terminology,  $k$  is the reciprocal of the “span efficiency factor” by which an equivalent elliptic wing with a modified aspect ratio of  $\mathcal{A}\mathcal{R}/k$  is used to replace the actual wing.

### 5.3 Power required for flight

Having estimated the components of drag we are now in a position to estimate the power required for steady horizontal flight. The rate of expenditure of energy represents the power  $P$  to keep the bird in flight. The energy must come from the bird's muscles which in turn derive it from the bio-chemical energy generated by the oxidation of fuel – which may be a carbohydrate or a fat. The mechanical power finally available for flying is only a fraction of the metabolic power since part of the energy is converted into heat and another fraction is used to maintain the basal metabolism for circulation of blood and oxygen in the bird's system. The overall efficiency of energy conversion has been estimated by physiologists to be between 20 and 25%. When flying horizontally the lift  $L$  must equal the weight  $W$  and the thrust  $T$  must balance the drag  $D$ . Since the power  $P$  is the rate of doing work we get the following:

$$\begin{aligned} L &= W, \\ D &= T, \\ P &= T \cdot V = D \cdot V, \end{aligned} \quad (7)$$

where  $V$  is the constant horizontal flight velocity. Using (1) with  $L$  being replaced by  $W$ , we immediately see that the flight velocity  $V$  can be expressed as a function of weight  $W$  and wing area,  $S$ . Thus:

$$V = [(2/\rho C_L) \cdot (W/S)]^{1/2}. \quad (8)$$

The flight velocity is thus proportional to the square root of the wing loading ( $W/S$ ) and, for a given wing loading, the speed is determined by the inverse square root of the lift coefficient and would be a minimum for  $C_L = (C_L)_{\max}$ . This property of the airfoil fixes the stalling speed  $V_{\min}$ , the minimum at which the bird can normally fly. Actually, as we will see later, birds can be seen to fly, especially during landing and take-off at forward speeds well below  $V_{\min}$ . During these conditions the kinematics of wing flapping i.e. the shape, rates and amplitudes of the wing change considerably and the simple theory outlined above does not provide the explanation. From (8) we also note that higher wing loading implies faster speeds. The effects of size etc., are discussed later in § 8.

Reverting to the estimation of power required for flight, we note that the total drag in flight consists of  $D_0$ , the drag at zero lift and  $D_i$ , the component induced by the production of lift which is equal to  $(1/2) \cdot \rho V^2 S \cdot k C_L^2 / (\pi \mathcal{A}\mathcal{R})$  by using the expression

$C_{D_i}$  from (5). Thus the total drag can be expressed as

$$D = D_o + D_i = A V^2 + (B/V^2), \quad (9)$$

where  $A = (\rho/2) \cdot S C_{D_o}$  and  $B = [(2/\rho) \cdot [k/(\pi \mathcal{A} R)] \cdot W^2]$  or, equivalently,  $[(2/\rho) \cdot (k/\pi) \cdot (W^2/b^2)]$  in terms of wing span.  $A$  &  $B$  are fixed for a given bird.

Thus the power required ( $D \cdot V$ ) is

$$P_R = A V^3 + (B/V). \quad (10)$$

#### 5.4 Discussion

In order to aid our understanding of the physical principles of flight it is useful to discuss briefly the drag and power equations (9) and (10). The first term in the drag equation represents the frictional resistance of the bird (wing and body combined) in its motion through the air. It represents the rate of transfer of momentum from the surface of the bird to the mass of air close to it, i.e. the boundary layers, which are dragged along due to the motion of the bird. The second term, i.e.  $B/V^2$ , is the induced drag and is due to a nonlinear interaction between weight support and the resistance to motion. Recall that the induced drag is proportional to  $L^2$  and involves a region whose diameter is approximately equal to the wing span  $b$ . The lift force involves motions (and momentum transfer) perpendicular to the bird's flight. These motions behind the bird take on the form of rolled up vortices forming a pair as seen in figure 23. So the induced drag can be looked upon as the extra force the wing has to exert to produce the kinetic energy of these motions. Note that the form of the drag equation shows the first term increasing and the second term decreasing with  $V^2$ . So we can conclude that when these two terms are equal the drag has a minimum value. The flight speed which corresponds to minimum drag ( $V_{MD}$ ) is given by:

$$V_{MD} = (B/A)^{1/4} = [(2W)/(\rho S)]^{1/2} \cdot [k/(\pi \mathcal{A} R C_{D_o})]^{1/4}. \quad (11)$$

At  $V_{MD}$ , friction and induced drags being equal, the total drag coefficient  $C_D$  is just  $2C_{D_o}$ . In aeronautical terminology this is the best cruising speed.

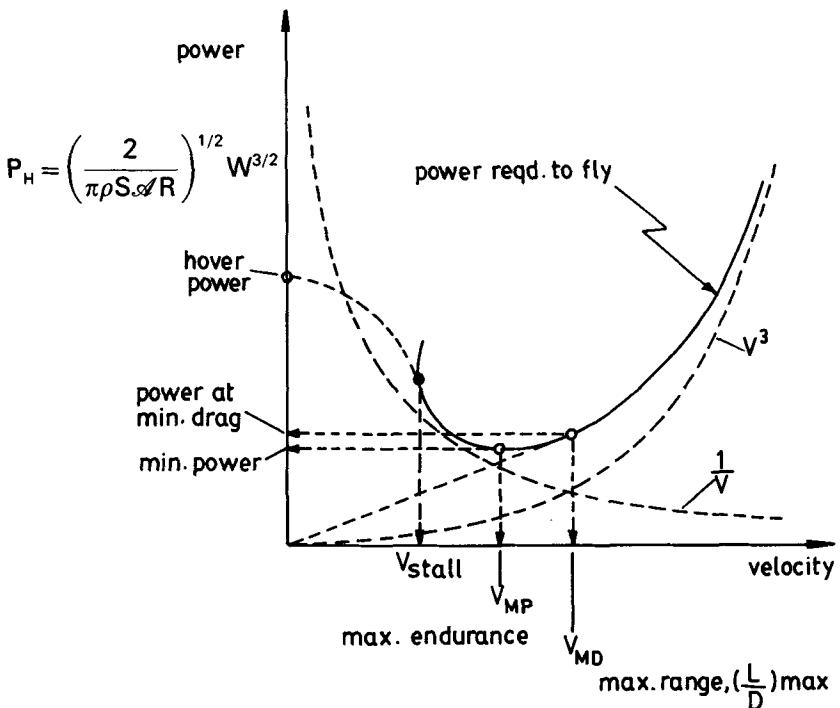
The power equation (10), consists of two terms, a cubic and a hyperbolic term. The cubic term represents the power required to overcome the air resistance and rapidly increases with the speed of flight. The hyperbolic term, representing the induced power, diminishes with increasing  $V$ . This is because the induced power depends on lift which in turn is proportional to  $V^2$ . So to lift a given weight an increase in velocity rapidly reduces the power expended. The velocity for which  $P_R$  is a minimum ( $V_{MP}$ ) can be obtained by differentiating (10) and this gives:

$$V_{MP} = [(1/3) \cdot (B/A)]^{1/4}, \quad (12)$$

which is  $(1/3)^{1/4} \approx 0.76$  times the minimum drag speed  $V_{MD}$ . Approximately we can write:

$$V_{MP} = (3/4) V_{MD}. \quad (13)$$

The drag and power relations are shown in figure 29 where the full expression for  $V_{min}$ ,  $V_{MD}$  and  $V_{MP}$  are also given. These characteristic speeds are:



$$D = AV^2 + (B/V^2) \quad A = (\rho/2) C_{D0} S$$

$$P_R = AV^3 + (B/V) \quad B = (2/\rho) (W^2/S) (k/\pi A R)$$

$$V = [(2/\rho) (W/S) (1/C_L)]^{1/2}$$

Min. drag: Max. range

$$\begin{aligned} V_{MD} &= 2^{1/2} [W/(\rho S)]^{1/2} [k/(\pi A R C_{D0})]^{1/4} \\ D_{min} &= 2W [ (kC_{D0})/(\pi A R) ]^{1/2} \\ P_{MD} &= [\{(2)^{3/2} (W)^{3/2}/(\rho S)^{1/2}\}] \\ &\times [k/(\pi A R)]^{3/4} (C_{D0})^{1/4} \end{aligned}$$

$$(C_L)_{MD} = [(\pi A R/k) C_{D0}]^{1/2}$$

$$(C_D)_{MD} = 2 C_{D0}$$

Min. power: Max. endurance

$$\begin{aligned} V_{MP} &= [1/(3^{1/4})] \cdot V_{MD} \approx (3/4) V_{MD} \\ D_{MD} &= [2/(3^{1/2})] D_{MD} \\ P_{min} &= [2/(3^{3/4})] \cdot P_{MD} \approx (7/8) P_{MD} \\ (C_L)_{MP} &= 3^{1/2} (C_L)_{MD} \\ (C_D)_{MP} &= 4 C_{D0} \end{aligned}$$

Figure 29. Drag and power relations.

- $V_{min} = V_{stall}$  – the speed below which the wings would stall and therefore cannot support the weight of the bird;
- $V_{MD}$  – the speed for minimum drag (at this speed  $C_{Di} = C_{D0}$ );
- $V_{MP}$  – the speed for minimum power (at this speed  $C_{Di} = 3C_{D0}$ ).

Flight at  $V_{MD}$ , when the drag is minimum, corresponds to  $(L/D)_{max}$  conditions since the lift remains equal to the weight. This is the condition of maximum aerodynamic efficiency and aerodynamicists would recognise it as the 'maximum range' condition. On the power vs. speed curve of figure 29 this condition is defined by drawing a

tangent to the curve from the origin. Note that the most economical flight speed  $V_{MP}$  (in terms of power and hence of fuel) lies to the left of this point. Thus  $V_{MP}$  corresponds to maximum duration of flight. In the performance aerodynamicist's language this is the maximum endurance speed. One can speculate that birds may choose to fly close to  $V_{MD}$  during migration or when they seek new habitats at large distances from their usual places in search of food. They can be expected to use  $V_{MP}$  when they circle or fly around locating food etc. close to their usual habitat and wish to remain aloft for long periods.

### 5.5 Power for hovering flight

The power equation, (10), clearly cannot hold for  $V = 0$ , which is the case for a hovering bird. To get an estimate of the power required for hovering we again use the simple momentum or 'actuator disc' theory (see figure 28).

For the hovering condition  $V$  is zero and  $C_{DO}$  would normally be negligible. We calculate the vertical momentum change supporting the weight  $W$  to be  $(2\rho w_i^2) \cdot (\pi b^2/4)$ . From this the induced velocity  $w_i$  (assumed constant across the span) is

$$w_i [(2/\pi\rho) \cdot (W/b^2)]^{1/2}, \quad (14)$$

and induced power for hovering ( $P_H$ ) is

$$\begin{aligned} P_H &= W \cdot w_i = [2/(\rho\pi)]^{1/2} \cdot (1/b^2) \cdot (W)^{3/2} \\ &= [2/(\rho\pi\mathcal{AR})]^{1/2} \cdot (W)^{3/2}, \end{aligned} \quad (15)$$

in terms of aspect ratio and wing area.

We note that this calculation of hovering power has again assumed uniform induced velocity and neglected the friction drag on the flapping wings as well as the body. Thus (14) can be expected to give values which are somewhat on the low side. Lighthill (1977) discusses the effect of non-uniform induced velocity and other factors and concludes that (15) gives reasonable estimates for the minimum hover power. In order to have an idea of magnitudes we can compare the minimum hovering power with the minimum power required for horizontal flight at  $V_{MP}$  given by (10) with the appropriate speed from (11) and (12) thus

$$P_H/P_{R\min} = ((3)^{3/4}/4) \cdot (\pi\mathcal{AR}/C_{DO})^{1/4} \cdot (1/k)^{3/4}. \quad (16)$$

Using numerical values of  $\mathcal{AR}$ ,  $C_{DO}$  and  $k$  for birds ranging in size and weight from small sparrows to larger birds such as pelicans, storks and vultures we can confirm that the ratio  $P_H/P_{R\min}$  is always greater than 1·0 and ranges from about 1·25 to 3.

### 5.6 Transition to and from hovering flight to forward flight

It must be noted that sustained hovering flight is uncommon in birds except in the humming-bird family. Most birds use the typical horizontal wing motions of hovering for brief periods in transition flight during take off and landing. The transition between hovering and fast forward flight is much more complex aerodynamically. We have noted that birds have to remain airborne during take-off and landing at speeds lower than the stalling speed. The analysis of this speed regime is much more complex and requires combined consideration of the thrust and lift generation modes. Quantitative estimates



require a consideration of the wing flapping cycle in greater detail with each wing section from shoulder to wing tip being given consideration. Lighthill (1975, 1977) has considered this approach with an averaging process over the flapping cycle. It is found that, due to flapping motions, there is an additional drag penalty to be paid in thrust generation. This implies using higher values of the parameter  $k$  in (6) than indicated by just planform considerations. Lighthill also finds that in conditions of slow forward flight, with large amplitude flapping, the local air speed over the wing sections is significantly enhanced during the downstroke and this results in an "effective" lift coefficient significantly larger than the normal forward flight  $C_{L\max}$ . The increase may be as large as 75%. It is also found that for slow forward flight with enhanced weight support (due to large flapping amplitudes) the power penalty is relatively modest, being of the order of a factor of 1.5 and therefore well within the musculature of most birds for short periods.

### 5.7 Gliding and soaring

Gliding in still air, in a 'slope current', or rising air can be analysed as a special case of horizontal powered flight with the power being supplied by gravity and the bird with outstretched wings moving in a straight line inclined downwards. In still air the plane of flight would be inclined downwards at an angle to the horizontal, the weight  $W$  acting vertically downwards. The weight  $W$  can be resolved into two components:  $W \sin \alpha$  along the flight path and  $W \cos \alpha$  normal to it as shown in figure 30. For a steady glide the total  $D$  must be equal to the driving weight component  $W \sin \alpha$  and the lift must balance  $W \cos \alpha$ , i.e.

$$\begin{aligned} D &= W \sin \alpha = (1/2) \rho V^2 C_D, \\ L &= W \cos \alpha = (1/2) \rho V^2 C_L, \end{aligned} \quad (17)$$

The speed  $V$  with which the bird glides is therefore  $[(2/\rho) \cdot (W \cos \alpha / C_L S)]^{1/2}$  analogous

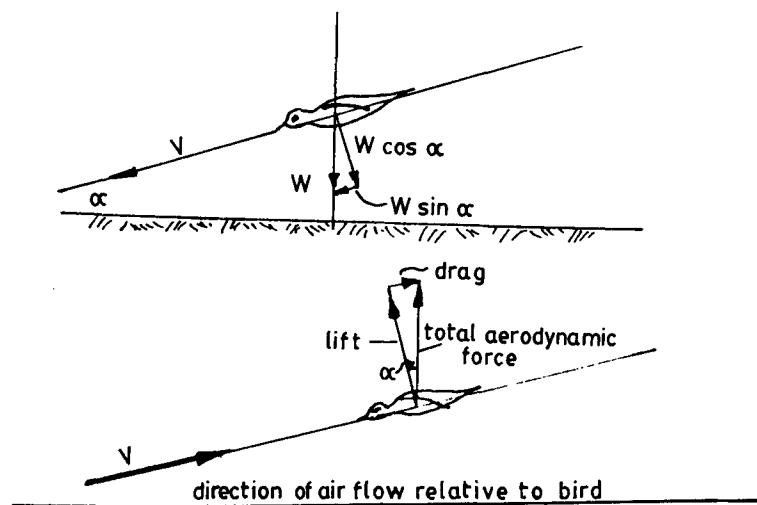


Figure 30. Forces on a gliding bird.

to (8) in the powered flapping case. Thus

$$V \propto \text{const} (W/S)^{\frac{1}{2}}, \quad (18)$$

indicating that birds with relatively heavier bodies and smaller wings glide faster than those with light bodies and large wings.

A bird gliding with speed  $V$  at an angle  $\alpha$  to the horizon will lose height  $t$  at a rate  $w_s = V \tan \alpha$ .  $w_s$  is the 'sinking speed' which aerodynamicists are familiar with in case of gliders and sailplanes. Two aspects of bird flight are of special interest:

- ability to glide long distances at high speed with minimum loss of height; and
- conditions under which the bird can sustain itself in the air for the longest possible time while losing a given height.

These are the 'maximum range' and 'maximum endurance' conditions associated with the performance analysis of fixed wing aircraft. The first i.e. maximum range is associated with minimum  $\alpha$  or angle of glide, which implies  $w_s$  being a minimum and, from (17) can be seen to be equivalent to an  $(L/D)_{\max}$  condition. This in turn implies the minimum drag condition since the weight must be supported in any case by the lift  $L$ . For small angles of glide we can, to a good approximation, take  $\cos \alpha \approx 1.0$  so that the lift is equal to the weight. Then, from (11), we can estimate the velocity  $V_{MD}$  for maximum range. Analogous to the powered flight case the ratio of the sinking speed to the flight speed can be expressed for small angles of glide as:

$$(w_s/V) = D/L = C_D/C_L. \quad (19)$$

Using the expressions for  $C_D$  and  $C_L$ , (3) and (6), and noting that the lift is approximately equal to the weight, we get

$$w_s = A_1 V^3 + (B_1/V), \quad (20)$$

as the equation of the glide polar where

$$\begin{aligned} A_1 &= (\rho/2) \cdot (S/W) \cdot C_{D0}, \\ B_1 &= (2/\rho) \cdot (k/A) \cdot (W/S). \end{aligned} \quad (20a)$$

The glide polar is analogous to the power-required curve but by convention is plotted as shown in figure 31 with the sinking speed as the negative ordinate versus the gliding speed  $V$ . Again three characteristic speeds  $V_{stall}$ ,  $V_{\max \text{ range}}$  and  $V_{\max \text{ endurance}}$  can be calculated from the earlier expressions in (11), (12) and (13). Corresponding to these three speeds are the related sinking speeds  $[w_s]_{\min}$  for the 'best glide' and minimum angle of glide,  $[w_s]_{BG}$ , the lowest sinking speed the bird is capable of. The minimum sinking speed corresponding to  $V_{\max \text{ endurance}}$  can be determined from [20] by differentiation, the result is

$$[w_s]_{\min} = (2/3)^{3/4} \cdot [(2^{3/2} \cdot (C_{D0})^{1/4} \cdot (k/A)^{3/4} \cdot (W/S)^{1/2})]. \quad (21)$$

The expression in the square brackets on the right hand side is the sinking speed corresponding to the least glide angle i.e  $[w_s]_{BG}$ . Hence

$$[w_s]_{\min} = (2/3)^{3/4} [w_s]_{BG} \approx 0.88 [w_s]_{BG} \quad (22)$$

and is lower than the 'best glide' sinking speed.

### Bird flight

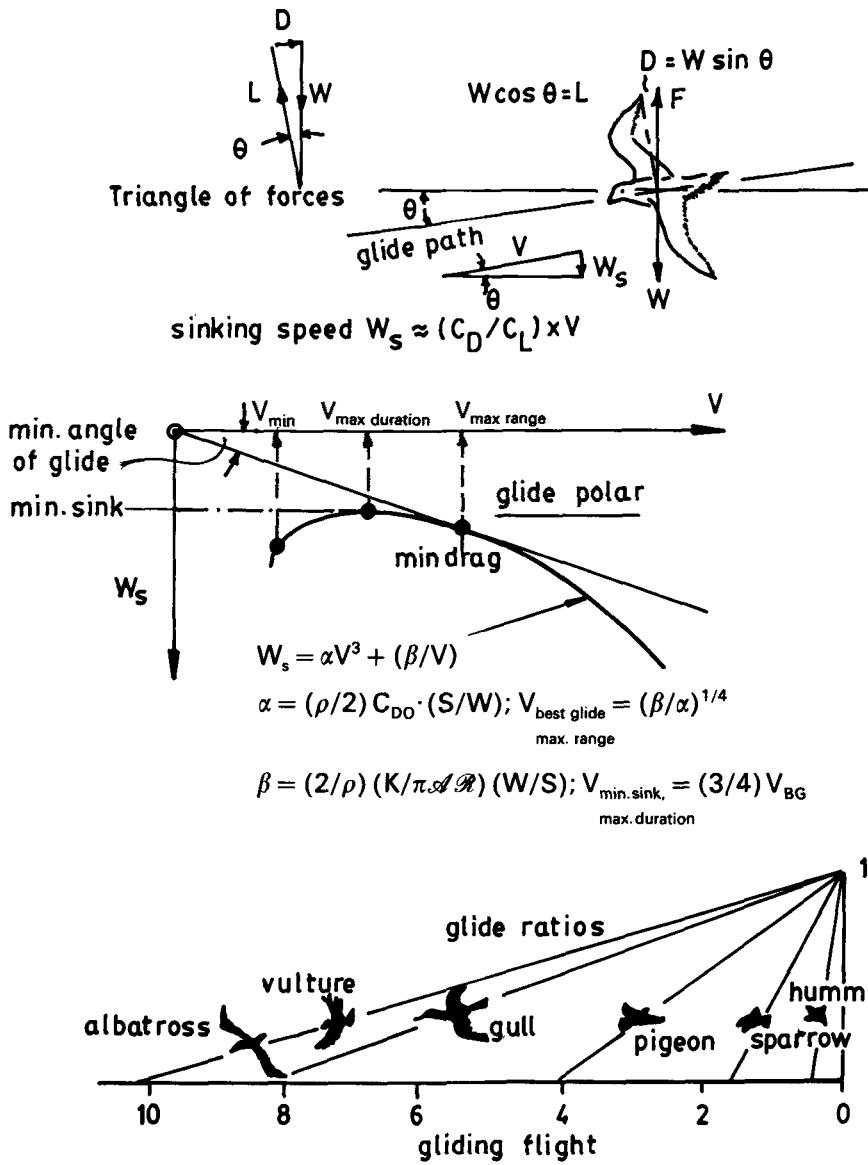


Figure 31. Gliding flight (adapted from Petersen 1968, p. 43).

### 5.8 Discussion

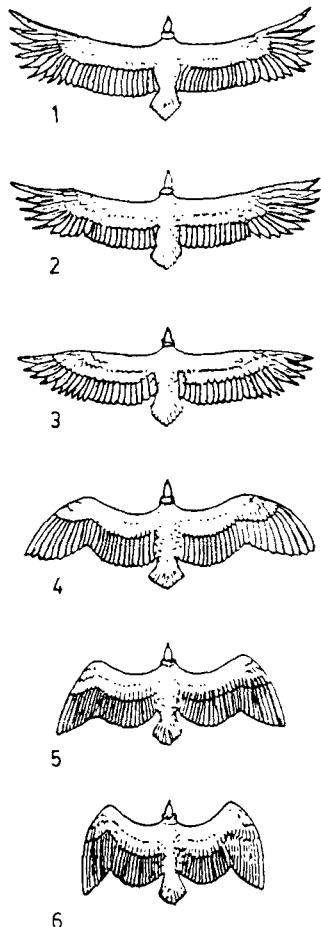
Several interesting observations can be made about the features of gliding birds from the above expressions. If the wings are held in a *fixed* configuration the glide can be stable only for speeds equal to or greater than  $V_{BG}$ . If a bird gliding at  $V_{BG}$  suffers a small disturbance which *reduces* the velocity the drag gets *increased* and the velocity would be further reduced until the process leads to the stall. Similarly a *positive* disturbance in flight velocity would reduce the drag and increase the glide speed and the rate of descent. The birds overcome this inherent stability problem by small changes in their wing geometry. The condition for stable gliding is that the induced

drag does not exceed the friction drag. The expressions for these two components of drag are

$$\text{frictional drag} = (1/2)\rho V^2 S C_{D0}, \quad (23)$$

$$\begin{aligned} \text{induced drag} &= [k/(\rho A\mathcal{R})] \cdot (W^2/S) \cdot [(2/(\rho V^2))] \\ &= k/[(1/2)\rho V^2 \pi b^2]. \end{aligned}$$

Neglecting small variations in  $C_{D0}$  and  $k$  we see that the stable glide condition depends upon the span  $b$ . Thus for slowing its glide a bird must *spread* its wings while for faster glide velocities it must pull them in. For attaining stable flight at any glide speed these span changes are small and the bird accomplishes them effortlessly. Significant changes in glide speed away from the  $V_{BG}$  and  $V_{\max \text{ range}}$  can of course be accomplished by flexing the wings and changing the wing loading  $W/S$  as well as the aspect ratio  $A\mathcal{R}$  i.e. essentially through wing planform modifications in flight. Of course such changes are accompanied by changes in sink rate etc. Figure 32 depicts a case for the vulture. The ultimate in steady gliding occurs when the bird increases its speed by drawing its wing very close together. From a shallow glide the bird then enters a dive – the speed, glide angle and sink all increase. This manoeuvre taken to an extreme can result in an almost vertical dive. In this configuration the resultant aerodynamic



**Figure 32.** Glide speed changes with wing planform. Wing configurations during gliding of vulture (*Gyps*). (1 – minimum sink, lowest speed; 2 – low speed glide; 3 – normal soaring,  $V_{\min \text{ sink}} < V < V_{\min \text{ drag}}$ ; 4 – increased speed; 5 – high speed glide; 6 – fast dive). Notice the reduction of span, wing area, and aspect ratio in stages 4,5,6. (From Ward-Smith 1984, p. 82)



drag at high speed dominates and is almost equal to the weight. The terminal velocity is then given by

$$V_{\max} = [2W/(\rho SC_{DO})]^{1/2}. \quad (24)$$

Here  $S$  and  $C_{DO}$  correspond to the bird's folded wings.

Raptors are typical examples of birds which adopt such aerial manoeuvres. The peregrine falcon kills its prey in the air by striking it from a steep high speed dive. Ward-Smith (1984) gives experimental data for a falcon with  $(SC_{DO}) = 3.1 \times 10^3 \text{ cm}^2$ . With  $W = 0.59 \text{ kg}$ , and  $\rho_{\text{air}} = 1.21 \text{ kg/m}^3$  we get the  $V_{\max}$  as  $55 \text{ m/s}$  or  $200 \text{ km/h}$ !

### 5.9 Effects of head and tail winds

While for aerodynamic performance the relative motion of a gliding bird is of importance, from a biological viewpoint the motion relative to the earth is of considerable significance. In still air the air speed and the ground speed are identical but when the air is in motion, as it often is in the atmosphere, the bird's ground speed is the vectorial sum of the flight speed and the speed of the air relative to the ground. The situations which obtain with a head or tail wind are shown in figure 33a.

### 5.10 Soaring flight

A gliding bird can, without much muscular effort, maintain its height or even increase it if it can derive energy from the air through which it is flying. Clearly a horizontal current of uniform speed cannot provide the necessary energy. However if the wind has an upward component, or an updraft, then depending on the magnitude of the upward component, the gliding bird may reduce its angle of glide. Figure 33b shows how a gliding bird may maintain its height or even increase it. The updraft velocities required are related to the sinking speed  $w_s$ . The minimum updraft required is equal to  $[w_s]_{\min}$ , (21). Air streams having upward components of velocity are often found to occur on the windward side of cliffs and mountains. Birds with low wing loading and/or high aspect ratio wings can, with relatively low minimum drag speeds, often exploit these wind conditions. This technique, known as 'slope-soaring', is often adopted by birds such as crows, ravens, gulls and various birds of prey. As a typical example, a vulture with an  $\mathcal{AR}$  of  $6.5$ ,  $k = 1.9$ , wing loading  $W/S$  of  $7.1 \text{ kg/m}^2$  and  $C_{DO} = 0.03$  would have a  $[w_s]_{\min} = 1.33 \text{ m/s}$  at sea level i.e. approximately  $5 \text{ km/h}$ , a wind speed which can often be found in nature.

The substantial vertical components of wind velocity in atmospheric thermals make them ideal for soaring. Thermals occur when disparate heating of the ground takes place. This may be due to vegetation bordering bare or sandy ground or water bodies or even differential cloud cover. Indian cities afford a familiar sight – especially in the mornings – of raptors such as buzzards, vultures, kites and eagles circling aloft for long periods of time.

### 5.11 Turning flight

The soaring flight of vultures and other birds usually consists of two phases: circling and gliding. In the circling phase, the bird's flight consists of a series of circles or loops with a continuous increase in height. In this phase the wings are fully extended

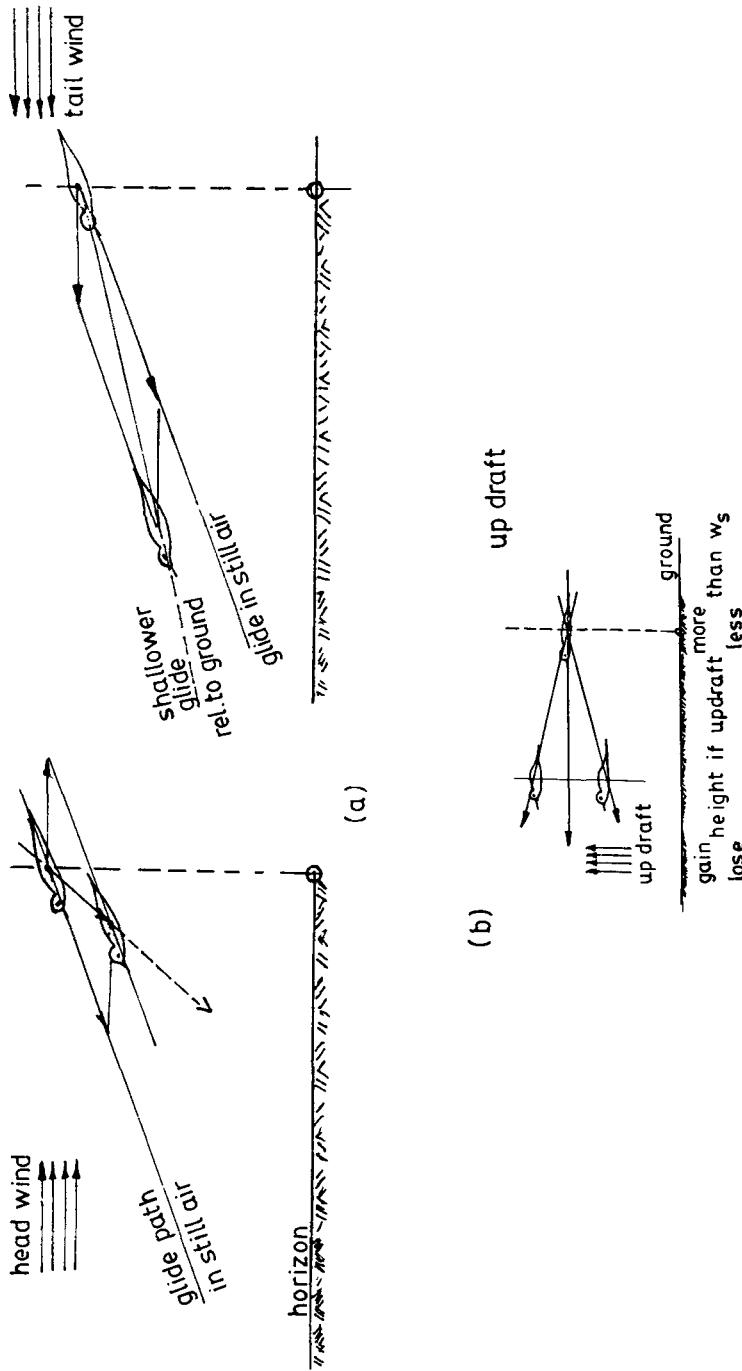


Figure 33. (a) Effect of wind on ground speed and glide path. (b) Shows how a gliding bird may maintain its height or change it.

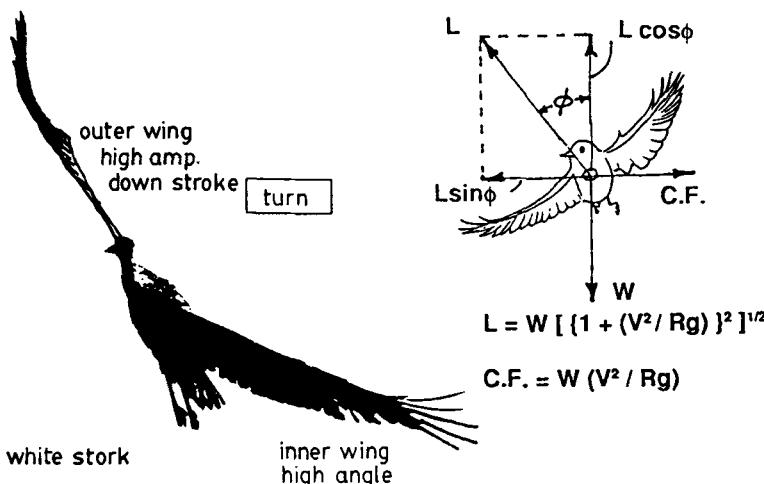


Figure 34. Forces in a turning flight. (From Ruppell 1977, pp. 92, 93)

and the tips of the primary feathers spread wide. As the bird moves in the circular path its wings are banked towards the centre of the circle and a centripetal force  $WV^2/R$ , where  $R$  is the radius of turn, comes into play so that the turn occurs without side slip. At constant height the lift  $L$  from the wings not only has to support the weight  $W$  but also supply the component  $WV^2/R$ . From figure 34 we have

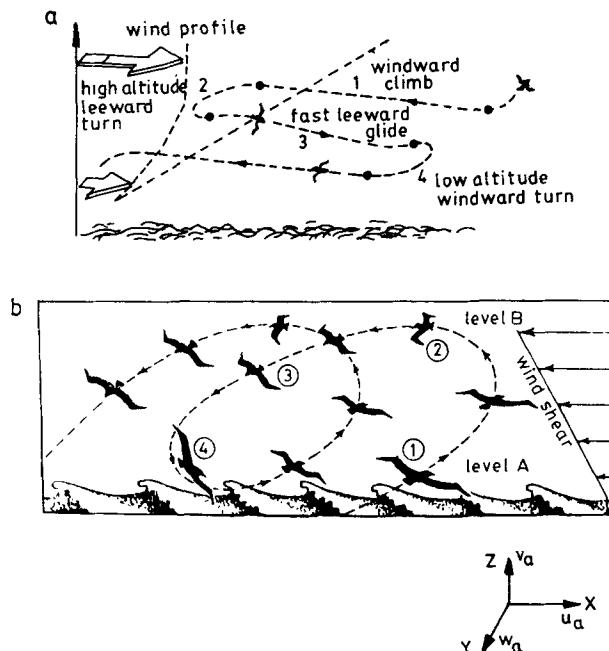
$$\tan \phi = [CF/W] = [W\{V^2/(Rg)\} \cdot (1/W)] = [V^2/(Rg)] \quad (25)$$

where  $CF$  is the centrifugal force.

The extra lift  $\Delta L$  necessary for a radius of turn  $R$  can be approximately expressed as  $[W/2] \cdot [(V^2/Rg)]^2$ . We note that  $\Delta L$  increases as  $V$  increases or  $R$  decreases. As the bird moves in the circular path, and if there is a horizontal component of the wind, it drifts downwind and gains height tracing out a characteristically looped trachoidal path (see Cone 1962). Gaining height, the bird partially flexes its wings; it may remain circling, but no longer gaining height. This configuration would be adopted in searching for food etc. On the other hand, after reaching a certain height, the bird may flex its wings into a fast glide configuration and glide along a straight path losing height as it glides. After some time, and at a variable height above the ground, the bird may again adopt the soaring configuration, fully extending its wing, and resume circling and gaining height. Hankin (1913) described in detail the soaring flight of Indian birds in Agra. He found that soaring began at a definite period of the day and was closely correlated to the intensity of sunshine. The time of soaring depends on the wing loading of the birds. The first to appear were the cheels or pariah kites (*Milvus m. govinda*) with a wing loading of approximately  $0.27 \text{ g/cm}^2$ . About half an hour later came the scavenger vultures (*Neophron p. ginginianus*) with  $W/S$  of  $0.42 \text{ g/cm}^2$ . Whitebacked vultures (*Gyps bengalensis*) with  $W/S$  of  $0.55 \text{ g/cm}^2$  followed another half an hour later. Then appeared the black or king vultures (*Sarcogyps calvus*) with  $W/S$  of  $0.6 \text{ g/cm}^2$  about an hour and a half after the cheels began. In general the circling diameters increase with the wing loading. Cheels circle in about 15 m diameter circles while the heavily laden vultures have circles of diameters of the order of 50 m.

### 5.12 Dynamic soaring

In contrast to land birds such as vultures, oceanic birds, notably petrels and albatrosses (Diamedeidae), usually restrict their gliding flight to relatively low altitudes. They have evolved a special soaring technique known as 'dynamic soaring' which involves flight within the shear layers of air just above the surface of the sea. Close to the sea surface the wind increases with height, rapidly reaching appreciable speeds. In fact the wind profile approximates a typical shear or boundary layer and the ability of the albatross to soar in this approximately 10 to 15 m layer of wind does not depend upon vertical air components but on an entirely different mechanism for extracting energy from the wind. It is interesting to note that the explanation of this mechanism of energy extraction from a shear layer was first given by Lord Rayleigh in 1883 (Rayleigh 1883). Figure 35a shows the flight path adopted by the albatross as it would appear to an observer at rest. Figure 35b shows the analysis in a frame of reference with the observer moving with the bird (after Lighthill 1975). During the first phase



Frame or ref. moving with bird velocity  $V_a$  ( $u_a, v_a, w_a$ )

Energy equation in moving frame of reference:

Total energy of bird = rate of working of inertia force  
– rate of loss by drag

$$(1/2)mV_a^2 + mgz = - [mv_a(dV/dZ)]u_a - DV_a$$

K.E.      P.E.      Inertia force      Loss due to drag  
Positive if  $(u_a v_a)$  is negative

**Figure 35.** Theory of dynamic soaring (Lighthill 1975). (a) Phases in the soaring flight of an albatross. (b) Dynamic soaring: (1) rise into wind, (2) turn at highest point, (3) glide down wind – build up of speed, (4) turn and repeat (1). (From Petersen 1968, p. 43, and Lighthill 1975.)



the bird glides directly into the wind gaining height but losing ground speed as a result of the combined effects of gravity and drag. Near the peak of its climb the bird executes a 180° turn and faces downwind to start the second phase of its flight. During this high speed glide the bird loses height and rapidly increases its ground speed thus increasing its kinetic energy at the expense of the potential energy (height loss). Approximately close to the sea surface the bird again executes a 180° turn and repeats the first phase. The reason that the albatross is able to repeat its flight pattern indefinitely is because during the long downwind glide it is able to extract sufficient energy from the wind to counteract the energy being dissipated in overcoming drag. The explanation lies in the extra inertial force term in the energy balance for the motion, given by minus mass times acceleration.

The rate of working of this inertial force, i.e. the energy can be expressed as:

$$(-mu_a v_a dV/dZ), \quad (26)$$

where  $dV/dZ$  is the wind velocity gradient.

At any instant of time, the energy equation expresses the fact that the rate of change of kinetic energy plus potential energy must equal the rate of working of the inertial force less the depletion due to drag. The quantities  $m$  and  $dV/dZ$  are always positive. During climb  $u_a$  is negative and  $v_a$  is positive, whereas during descent  $u_a$  is positive and  $v_a$  is negative. Thus throughout most of the flight pattern the product  $(u_a v_a)$  is negative and the rate of working of the inertia force is *positive* (due to the minus sign). Thus the albatross extracts energy from the wind profile. Of course during the 180° turns there is some energy depletion. However if we take a long term average of the motion the bird extracts enough energy from the wind to sustain its flight. The high aspect ratio wing is especially suited to minimize the energy loss due to drag. The criterion that the bird can extract enough energy turns out to be

$$dV/dZ > g/U. \quad (27)$$

Typically the albatross' air speed is about 30 m/s (100 km/h) and with  $g = 9.81 \text{ m/s}^2$ , the gradient of wind  $dV/dZ$  has to exceed  $1/3 \text{ m/s per meter}$ . This is usually available in the lowest 10 to 15 metres of the air above open sea. For higher gradients the bird's air speed can be less. It is interesting to note the analogy between the albatross' dynamic soaring and the energy balance governing turbulent shear flows in fluid mechanics. The condition for the large eddies extracting energy from the mean flow turns out to be similar to that for the bird, (27).

## 6. Power available

In §§ 5·3, 5·4 and 5·5 we have discussed, in an elementary manner, along with many simplifications and approximations, the flapping flight of birds. The power for flight is supplied by the muscles – primarily the pectoralis and supracoracoideus – for the down- and upstrokes respectively with other muscular ligaments acting to trim the shape and attitude of the wings. The muscular power for flight comes from the metabolic energy conversion in the bird's system. Although many studies have been conducted on the musculature, metabolic energy conversion processes etc., it is as yet not possible to directly calculate the flight power available for a given bird. We summarise the known information and provide some working estimates of the power available.

### 6.1 Metabolic rate

The mechanical energy for flight (in general, animal locomotion) is derived from chemical energy which comes from the oxidation of suitable fuel (usually fat and carbohydrates). It is usual to measure the rate of metabolism as the rate of consumption of oxygen. One litre of  $O_2$  consumed corresponds to 20 kJ or 4.8 kcal. In the more usual units, one litre per hour  $O_2$  consumption represents 5.6 W of power output. In the absence of external activity the rate of metabolism can be called the 'resting', or 'maintenance' or 'basal' metabolic rate. In warm-blooded animals, mammals and birds, this basal metabolic rate is relatively well-defined and the body temperature of the animal remains relatively constant. That body temperature is a scale independent quantity is an empirical finding. The maintenance metabolic rate in watts and body mass (in kilograms) are correlated by the well-known "mouse to elephant" curve reproduced (figure 36) from Schmidt-Nielsen (1977). The slope of the regression line on the log-log plot is close to 0.75. Actually, for the birds, the following empirical formulas closely represent the data (see Tucker 1973): Basal metabolic rate in watts

$$\begin{aligned} &= 3.79 m_b^{0.723} \text{ for non-passenger birds} \\ &= 6.25 m_b^{0.724} \text{ for passengers,} \end{aligned} \quad (28)$$

where  $m_b$  is the mass in kilograms.

Although a wealth of information is available about the maintenance metabolic rates of animals and birds, our knowledge of maximum continuous performance or

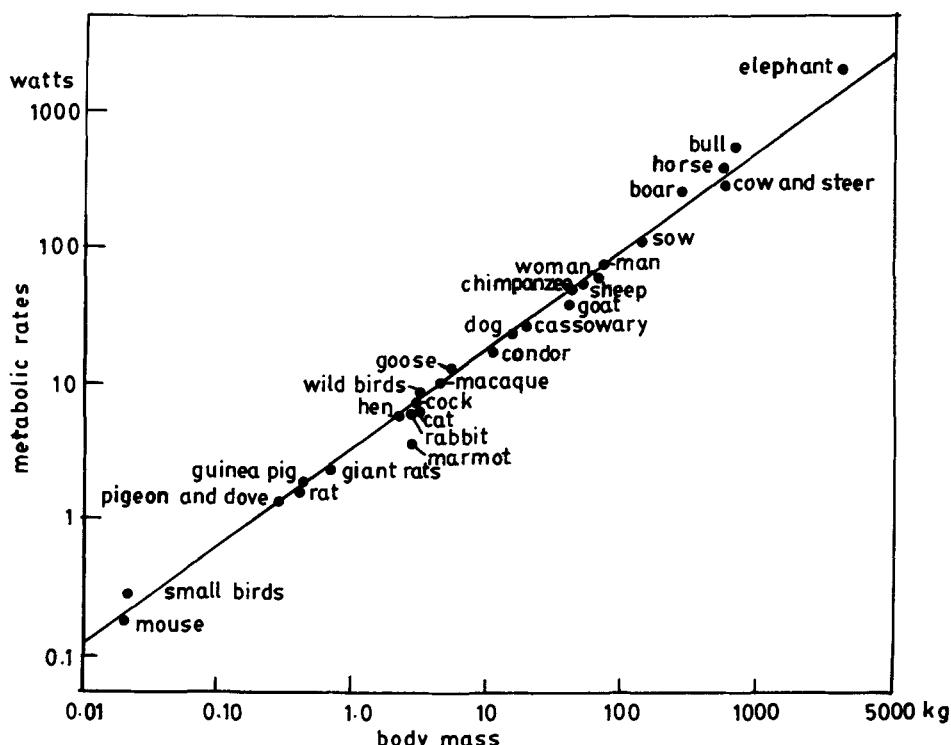


Figure 36. Metabolic rate and mass in animals (taken from Schmidt-Nielsen 1977, p. 11).



peak power output remains very meagre. It is known that in some animals the peak power output during maximum exertion may exceed the maintenance level by a factor of 10 or 15 or even 20. It has been suggested that power output of birds in flight exceeds their basal rate by a constant factor of about 10, independent of body size. However the available information is insufficient to conclude with any degree of certainty that this factor is really scale-independent. In fact it is known that peak power output in small birds (e.g. humming-birds) can be very high while in bigger birds like vultures it is not so large. In the absence of more comprehensive and precise data one can make the rough assumption that the ratio: peak power/maintenance power  $\approx$  10 to 15 for birds.

## 6.2 Muscle power

Extensive data for birds compiled by Greenewalt (1962) (see figure 8) indicates that the main flight muscle of birds, the pectoralis, makes up about 15% to 17% of the body mass. Obviously there are variations from this figure related to the flight muscles of individual species, but the percentage is a fairly constant fraction. The supracoracoideus (elevator) muscle weight is usually about 10% of the pectoralis. We have noted earlier the exceptional capabilities of humming-birds and it is therefore not surprising that their flight muscles make up a larger fraction of the body mass, some 25 to 30%. Also, in these birds, the secondary muscle responsible for the wing upstroke makes up about 30% of the total mass of the flight muscles compared to only about 10% in other birds. This suggests that lift is generated in both the strokes during hovering and, of course, is in agreement with the analysis of wing movements of hovering humming birds.

The maximum tension per unit area or stress that a muscle tissue can generate is roughly 300–400 kN/m<sup>2</sup> i.e., 3–4 kg/cm<sup>2</sup> (Schmidt-Nielsen 1977). This maximum stress is known to be independent of body size. Hill (1950) had arrived at the conclusion that the maximum work (force  $\times$  distance) performed in one contraction, when calculated per volume of muscle is invariant and is independent of size. This finding has been confirmed by later evidence. Thus if the work per contraction is constant, the power output during contraction will be a direct function of the speed of shortening, i.e. the strain rate. For repeated contractions, as in flight, the average power output of a muscle will be directly proportional to the frequency of contraction.

## 6.3 Fuel and oxygen

For steady state power output, the muscles must receive a continuous supply of fuel and oxygen at the appropriate rate. The bird's respiratory system is designed for high demands. The paired lungs are connected to five pairs of air sacs branching throughout the body – even to the bones. Bird lungs have two-way flow of oxygen. If the muscles get overworked it can lead to an oxygen crisis. To prevent such an emergency, birds, which must make a prolonged flight effort, have a built-in oxygen reserve. Two typical kinds of flight activity are: prolonged cruise – for example during migration, and sprint, where a sudden burst of power is required, for example when escaping from a predator. The muscular structure caters for such requirements through built-in oxygen reserves or by allowing anaerobic oxidation to take place

for short periods. The muscles used in locomotion are composed basically of filaments of two types –

- base protein myosin filaments which are thick,
- base protein actin filaments which are thin.

The supply of energy essentially is derived from oxidation of fuel which is in the form of fats and carbohydrates. The energy yield from oxidation of fat is nearly twice that from the same weight of carbohydrate. Also carbohydrates need to be stored in hydrated form. So, for a given amount of energy, the mass of fuel to be lifted is about eight times more for carbohydrate than for fat. For long flights maximum energy is required from the least weight of fuel. Thus fat is the most suitable form of fuel. However fat can be used only by aerobic oxidation in the muscle fibres themselves and cannot incur oxygen debt. Thus in prolonged flapping flight the muscles must operate under quasi-steady state conditions with the right amount of blood supply etc. It therefore turns out that such muscles for the 'long haul' are rich in mitochondria and also contain myoglobin. These components give to the muscle a red colour. Muscles used for sprints of short period generally contain glycogen which is oxidised anaerobically – at the expense of running up an oxygen debt. Such muscles are white in colour and generally larger in diameter than the red cruise muscles. Some birds (e.g., pigeons, terns, crows) have fibres of both types intermingled in the pectoralis muscles. The bird can then use the appropriate ones (red) for cruise and call forth the white ones for peak exertion during peak effort – e.g. at take-off or escape from attack by a predator. The game birds (Galliformes) are typical of birds which fly only briefly – they have preponderance of white fibres in their flight muscles. However in most birds which need to fly continuously for periods of time, red fibres predominate. To summarise, fat is the more efficient fuel for steady long period flight, while carbohydrate, which can be more quickly mobilised, is the fuel used for sprint or emergency power. In general, of the total metabolic energy produced, approximately 20–30% appears as mechanical work, the rest being dissipated as heat.

#### 6.4 Structure and action of muscles

Physiologists have established that broadly the structure and action of muscles in all vertebrates is more or less similar. Functionally most muscles require more or less regular cycles of contraction and relaxation. Figures 37 and 38 (adapted from Goldspink 1977 and Alexander 1989 respectively) schematically show the structure of muscles and the fibres they are composed of. Muscle fibres contain contractile material called 'myofibrils' approximately  $1\text{ }\mu\text{m}$  in diameter. As noted earlier, muscle contraction occurs due to interaction of two kinds of protein filaments:

- thick filaments composed mainly of *myosin*, and
- thin filaments containing *actin*.

The thick and thin filaments are arranged in a regular pattern which appears as bands when observed under the microscope. Each unit of the repeating pattern is called a 'sarcomere' which is the basic unit repeated along the length of the muscle. Each sacromere consists of one set of thick filaments and two sets of thin filaments which overlap with the thick ones. The thick filaments have protruding cross-bridges which, when activated, interact with the thin filaments and generate a force. The force per unit cross-sectional area that a muscle can generate depends upon the number

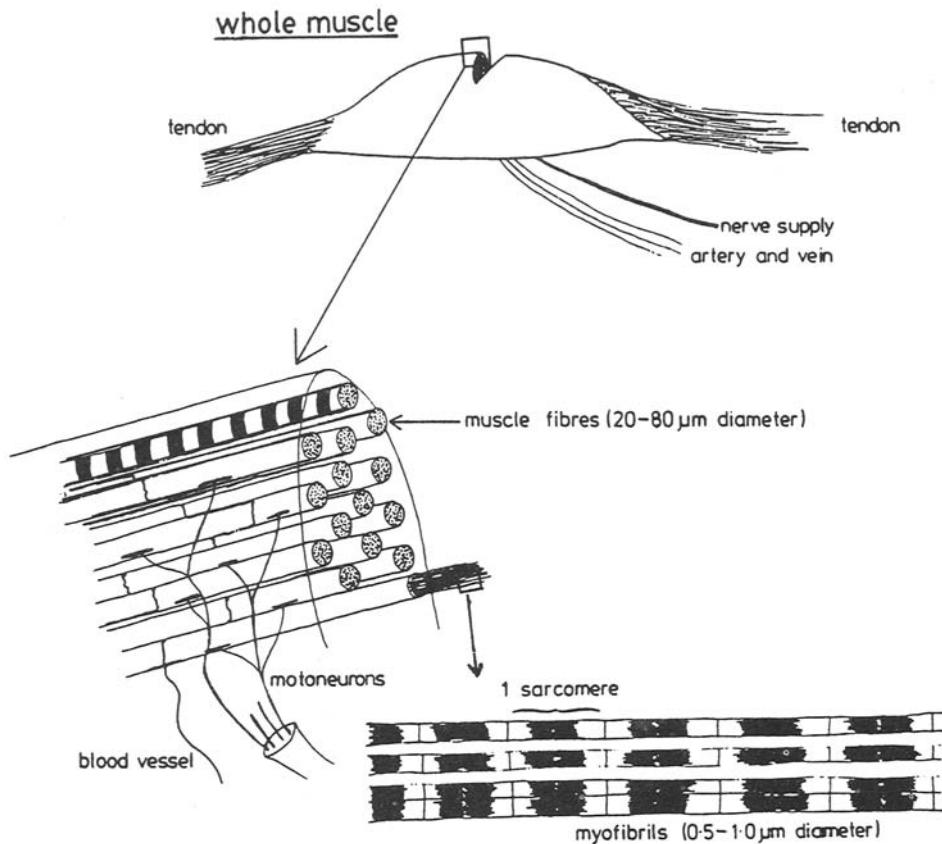


Figure 37. Structure of muscles. (Adapted from Goldspink 1977, p. 38.)

of filaments in parallel. It is found that the filaments and myofibril packing are about the same in most species. Therefore the force is scale independent. When muscles exert a constant force while shortening this is called *isotonic contraction*. When muscle fibres develop force (tension) without an appreciable change in their length this is referred to as *isometric contraction*. Figure 38 shows the force developed when muscles

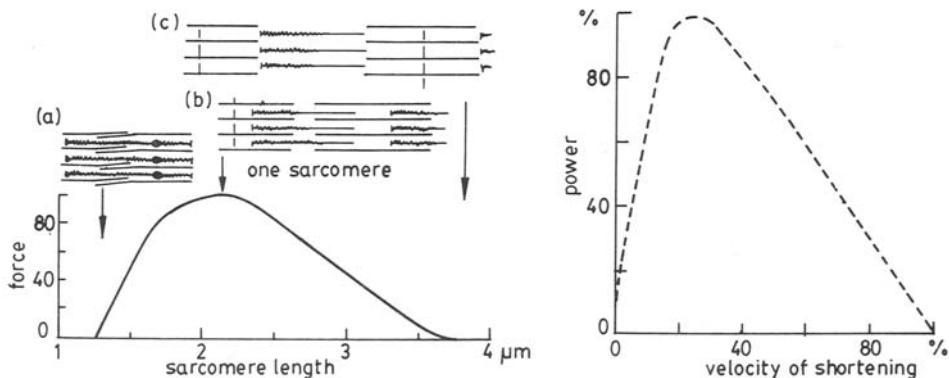


Figure 38. Output of muscles. The figure on the left shows that muscles can exert more forces at moderate lengths (b) than when contracted very short (a) or extended very long (c). (This first appeared in *New Scientist* magazine, London, the weekly review of science and technology, in an article by Alexander 1989; figure 1 on p. 50.)

are stretched and shows that muscles exert maximum force when all cross-bridges in the filaments can attach (which happens at moderate lengths). Figure 38 (adapted from Alexander 1989) also shows the power developed as a function of the velocity of shortening of muscle fibres and shows it to be maximum at medium low contraction rates.

*To summarise:* The power output of a muscle is limited by the rate at which its metabolic processes can produce ATP (adenosine triphosphate) and the rate at which its myofibrils can transduce the chemical energy into mechanical work. Metabolic and mechanical processes occur in separate fractions of the volume of the muscle: *Myofibrils* transduce chemical energy to mechanical work, *Mitochondria* are responsible for the production of ATP.

### 6.5 Muscle action during flight

*Flapping flight* involves *isotonic* contractions of roughly constant velocity and *gliding flight* involves mainly *isometric* contractions. Bird flight muscles are made up of fibres all of which have essentially the same rate of shortening. It would appear that the power requirements for flight are such that it would not be feasible to have more than one type of fibre as otherwise the pectoral muscles would become too bulky.

During flapping flight the bird can, in principle, alter its speed in several ways. However, it is found that in general it does not, to any appreciable extent, change the rate at which the pectoral muscle fibres contract, so the wing beat frequency remains roughly constant. Thus the bird changes the shape and force of the stroke (i.e. the number of muscle fibres recruited). It turns out that there is an optimum rate of shortening of the muscle fibres at which maximum power is produced. This implies that for each kind of bird there is a definite frequency of wing beat. We have seen this earlier also.

### 6.6 Wing frequency

Flapping frequency varies considerably between different species. Large birds like the stork or pelican flap at about 2 beats/second while for small birds, like a wren, the wing frequency is around 10 Hz. Other medium-size birds have flapping frequencies in between. Large birds do not need to flap their wings as fast as small birds in order to achieve the necessary power for flight. Power being force times displacement over time (velocity), the greater wing span of the larger birds means increased displacements. The time of displacement may also be increased. So they can have a longer beat cycle (lower frequency). It also turns out that there are limits to the wing beat frequency for large birds. The muscle fibres in large birds are long with a lot of sarcomeres and if they had the same intrinsic speed of shortening they would develop very high strain rates which the material, of which muscle fibre is made, cannot withstand.

### 6.7 Economy during gliding

The muscles involved in gliding are primarily those which hold the wings forward and outstretched, and the pectorals which maintain their horizontal position. The energy needed for gliding is known to be considerably less than that needed for flapping flight. Weis-Fogh (1977, pp. 405–420) shows that the metabolic rate during



gliding flight of herring gulls is only about twice the resting metabolic rate, while in flapping flight it may be about seven times. Roughly speaking these proportions seem to hold for most birds (the exceptions are the humming-birds which can continuously hover and can put out extraordinary amounts of power).

### 6.8 Power output from muscles

The total power that a bird can put out over and above the part required for maintaining the basal metabolism and circulation of blood and air can be called the 'power available'. Actually for flight the conversion efficiency to mechanical power (or energy rate) is only 20–25% of the chemical power produced. Compared to other animals, birds have a significantly higher metabolic rate and higher oxygen consumption. The heart beat rate of birds approximately follows the following relations:

Heart beat rate per minute

$$\begin{aligned} &= 24.1(W)^{-0.146} \text{ (flying),} \\ &= 12.4(W)^{-0.209} \text{ (resting).} \end{aligned} \quad (29)$$

While most mammals have hearts which are about 0.5% of their body weight, in birds it is about 1%. In this section we summarise the known information about the power the working muscles of birds can continuously deliver.

The maximum power output from a muscle occurs when the muscles are contracting at their optimum speed and developing the optimal stress. Weis-Fogh (1977, pp. 405–420) notes that contracting muscles can develop a maximum stress of 200 to 400 kN/m<sup>2</sup> but the maximum power occurs when they shorten against one-third of the maximum stress i.e. against 70 to 130 kN/m<sup>2</sup>. In this condition, the strain rate (shortening speed) is about 20% of the maximum value. It has been found empirically that the maximum work done per contraction, when calculated per unit volume, is invariable and independent of size. The power output is a direct function of the strain rate and, for repeated contractions, the average power output of a muscle is directly proportional to the frequency of contraction. The frequency varies with bird size. Typically large birds have low flapping rates around 2 Hz and small ones about 10 Hz. Weis-Fogh also finds that the average continuous power developed is about 70 to 260 W/kg of muscle (specific power) and that the specific power of birds is in the range 50–200 W/kg. Using typical values of stress exerted (about 90 kN/m<sup>2</sup>), strain rate (0.25) and the mass density of muscle (1060 kg/m<sup>3</sup>) it can be shown (Pennycuick 1975; Weis-Fogh 1977) that the maximum power available ( $P_A^*$ ) is given by the equation

$$P_A^* = 21f \text{ W/kg,} \quad (30)$$

here  $P_A^*$  = specific power =  $P_{A \text{ Max continuous}}/W_m$ ,  $f$  = frequency of flapping and  $W_m$  = weight of muscles in kilograms.

This can be checked against the few measurements that exist in the literature. Pennycuick (1975) finds that from observations on the pigeon and the Andean condor the sprint power ( $P_A^{**}$ ) is given by:

$$P_A^{** \text{ pigeon}} = 227 \text{ W at } 9.4 \text{ Hz, } W = 400 \text{ g}$$

$$P_A^{** \text{ condor}} = 54 \text{ W at } 2.5 \text{ Hz, } W = 800 \text{ g.}$$

Here  $P_A^{**}$  denotes the maximum specific power for a short period or 'sprint'. These

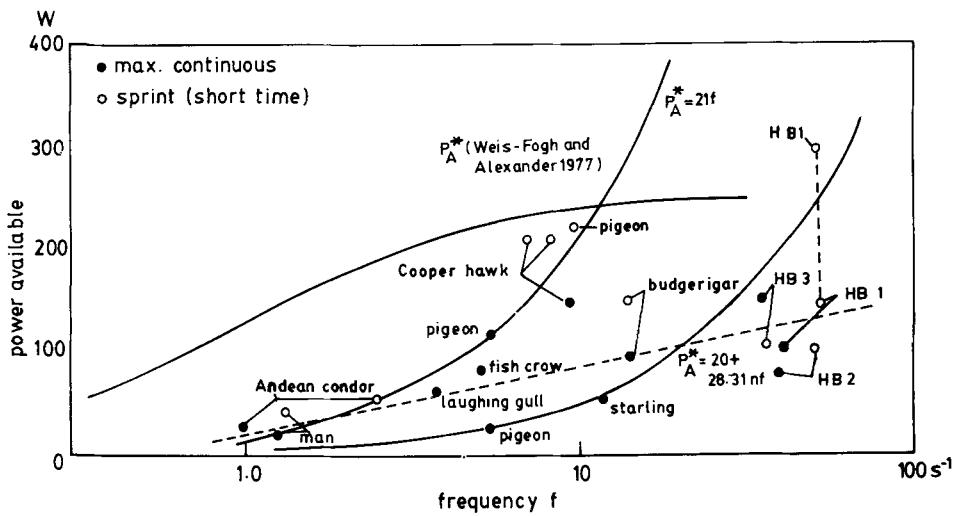


Figure 39. Maximum output of muscle. HB – humming-bird.

measurements indicate

$$P_A^* \text{ pigeon} = 24.1f : P_A^* \text{ condor} = 21.6f,$$

both of which are quite close to the empirical equation (30).

Figure 39 (adapted from Weis-Fogh & Alexander 1977, pp. 511–525) shows the results of more detailed calculations on the specific power output from muscles as a function of the frequency, along with some data from observations.

The specific power in watts per gram of mass of bird varies from 0.054 for the vulture to 0.235 for the humming-bird (see table 1). The vulture can sustain this power output only for short periods while the humming-bird can sustain the much higher output continuously for long periods. Perhaps the most detailed data available are for the pigeon (*Columba livia*) which has been studied in detail by Pennycuick (1968) and also by other scientists. The ratio: flight power/basic metabolic power varies from about 3.3 for *Regulus regulus* (3.8 gm mass) to nearly 20 for *Gyps fulvus* at 7300 gm.

Noting that the mass of the flight muscles bears a relationship with the bird's total weight and using the data from Greenewalt (1975) we can obtain simple working relations for estimation of the maximum sprint power available in the case of three main categories of birds discussed by Greenewalt.

- Passeriformes  $P_A^{**} = 3.6f$ ,
- Shorebirds  $P_A^{**} = 4.8f$ ,
- Ducks  $P_A^{**} = 6.54f$ , (30a)

where  $P_A^{**}$  is measured in watts,  $W$  in kilograms and  $f$  in hertz.

The maximum continuous power available ( $P_A^*$ ) would be less than is given by (30a) and the factor would vary for different bird species.

In the case of the pigeon (*Columba livia*), using Pennycuick's (1975) data we get

$$P_A^* = 1.93f. (30b)$$

Bird flight

Table 1. Observed data on power available for flight.

Bird	Body mass (kg)	Flight muscles (mass)	Flight conditions	Flight speed (m/s) ( $f(s^{-1})$ )	Flapping frequency	Power output (watts)	Specific power (watts/kg muscle)	References
Humming-bird (1) ( <i>Archilochus colubris</i> )	0.003	$8 \times 10^{-4}$	Hover Fast level Hover	0 13.5 0	52 40 38	0.112 0.085 0.24	140 105 300	Lasiewski (1963); Pennycuick (1968); Greenewalt (1975)
Humming-bird (2)	0.004	$12 \times 10^{-4}$	Hover Fast level	0 43.5	38 40	0.115 0.095	96 79	Greenewalt (1975)
Humming-bird (3) ( <i>Amazilia fimbriata</i> )	0.005	$15 \times 10^{-4}$	Hover	0	35	0.23	150	Weis-Fogh (1973); Weis-Fogh & Alexander (1977); Torre-Bieno & Larochele (1978)
Starling ( <i>Sturnus vulgaris</i> )	0.073	$1.24 \times 10^{-2}$	Level	18	12	9.4	55	Bernstein <i>et al</i> (1973)
Fish crow ( <i>Corvus ossifragus</i> )	0.275	$4.7 \times 10^{-2}$	Level	11	5.2	24.5	85	Bernstein <i>et al</i> (1973)
Laughing gull ( <i>Larus atricilla</i> )	0.277	$6.1 \times 10^{-2}$	Level	10-11.8	3.8	16.6	60	Bernstein <i>et al</i> (1973)
Budgerigar ( <i>Melopsittacus</i> )	0.035	$9 \times 10^{-3}$	Fast level	13	14	6	150	Tucker (1968); Weis-Fogh (1977, table-II)
Pigeon ( <i>Columba livia</i> )	0.400	$9 \times 10^{-3}$	Fast climb Level	16	5.5	20	220	Pennycuick (1968); Weis-Fogh & Alexander (1977)
Cooper's hawks ( <i>Accipiter cooperii</i> )	0.326	$6.3 \times 10^{-2}$	Level	18	4-8.5	10.5	120	March & Storer (1981)
Andean condor ( <i>Vultur gryphus</i> )	0.510	$9.3 \times 10^{-2}$	Take-off	18	7-8	9.5	150	McGahan (1973); Weis-Fogh & Alexander (1977)
Herring gull ( <i>Larus argentatus</i> )	8.00	$2.64 \times 10^{-2}$	Escape Fast level	11	2.5 1.0	14.2 61	210 54 23	Baudinette & Schmidt-Nielson (1974)
Man			Gliding Gliding Resting	0 0	12.5 15.4	gliding/rest ≈ 2.0 flapping/rest ≈ 7.0	6.6	Dickenson (1928); Parry (1948) Hendersen <i>et al</i> (1925); Parry (1948)

**Table 2.** Power available for flight.

● Flight power from: metabolic energy conversion through muscles	
● Birds have high heart beat rate	Galliformes • Turkey • Grouse ~ 100/min
	Apodiformes • Humming bird • Swift ~ 500/min
● Large hearts: 1% of body weight	
● Muscles	Large   – Pectorals – 15–20% of weight Small
● Energy source	Fuel + O <sub>2</sub>
↓	↓
Fat	Carbohydrates
• High cal. value/unit weight	• Stored in hydrated form – heavy
• Used through aerobic oxidation	• Water soluble and quick transport to site
• Rich in Mitochondria	• O <sub>2</sub> not essential – run on glycogen – oxidizes anaerobically – O <sub>2</sub> debt for short periods
• Myoglobin	
• Most suitable for cruise	
• Red	• White
<i>Examples</i>	
• Chicken	Red pigment in leg muscles
• Game birds	White in flight muscles for short flights
• Pigeons	Both red and white in muscles
• Crows	Red for long haul. White for quick take off and sprints
• Terns	
● Max. specific power available (W/kg muscle)	21f sprint (short period) 5f max. continuous

The margin between  $P_A^*$  (continuous) and  $P_A^{**}$  (sprint) would vary widely between birds. One can obtain an estimate of the  $P_A^*$  directly if the maximum speed of level flight is measured. It can be seen from the performance curves that  $P_A \max_{\text{cont}}$  equals power required ( $P_R$ ) at  $V_{\max}$ . Data on  $V_{\max}$  are very scarce but Greenewalt (1975, table 28, page 49) gives the results of estimates of  $V_{\max}$  for a range of birds. Equation (30) and other semi-empirical estimates for the specific power available are shown in figure 39. It would appear that while rough order of magnitude estimates can be made of the power available, in any specific case, actual observed or measured data would be necessary for reasonable accuracy.

Table 2 summarises information relating to the power available for flight.

## 7. Flight performance of birds

In earlier sections we have discussed the generation of aerodynamic forces by the wings and estimated the power required for flight. The relationships between flight speed  $V$ , wing loading  $W/S$  and the aspect ratio  $A/R$  are seen to relate the flight characteristics to the shape and size of the wings. The elementary treatment can be extended to cover hovering, gliding and soaring of birds. In order to estimate the 'range' and 'endurance', and other related aspects, we need to know the power available

from the metabolic energy conversion process. In § 6 we have discussed how the muscles produce power and the general relationship of flight muscle weight to the total weight of the bird – primarily from empirical data.

### 7.1 Flight characteristics

The availability of information on the power available and the power required for flight is usually presented in the form of power curves versus flight speed as shown in figure 40. We recall § 5·4 and figure 29 in the estimation of the characteristic speeds: the stalling speed, the speeds at which minimum power is required, and at which the bird can remain aloft for the longest time (max. endurance), and the speed at which maximum flight range can be attained. In figure 40 the power-available curve is superimposed as a horizontal line. As discussed in § 6, during normal flapping flight most birds have a characteristic frequency of flapping at which muscular power output can be sustained in horizontal flight for considerable periods of time. As figure 40 shows, the bird can choose a variety of speeds to suit the 'mission'.

From § 5·3 and equations (9) and (10) we note the dependence of the minimum power required for flight on the aerodynamic parameters of wing loading, aspect ratio, wing span and area, and wing section characteristics. Table 3 summarises the flight parameters for 36 birds, ranging in weight from the largest to the smallest. The flight characteristics are associated with wing shape and flight style which in turn are correlated to the habitat and evolutionary parameters. Through an extension of the analysis, the hovering, gliding and soaring of birds can also be understood reasonably well. However the landing and take off, and especially the manoeuvres that birds are capable of, are much more complex and it is not possible to calculate these in detail although many aspects can be understood qualitatively. During landing and take off we have noted that the explanation of forward climbing or descending flight at speeds lower than  $V_{\text{stall}}$  involves taking into account the essentially nonlinear and unsteady flow fields generated by the flapping wings, which, being elastic, take on shapes which

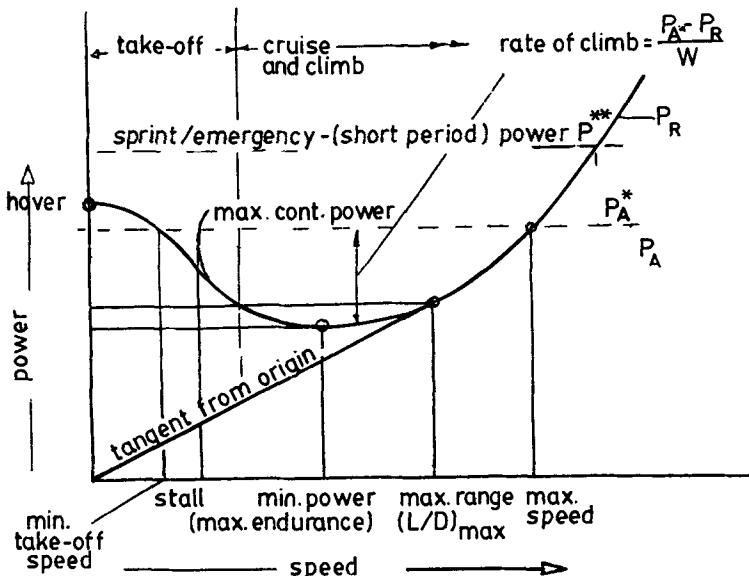


Figure 40. Performance curves.

**Table 3.** Flight parameters of birds.

Bird	<i>W</i> (g)	<i>b</i> (cm)	<i>S</i> (cm <sup>2</sup> )	$\mathcal{A}\mathcal{R}$	<i>W/S</i> (g/cm <sup>2</sup> )	<i>V<sub>s</sub></i> (m/s)	<i>V<sub>MP</sub></i> (m/s)	<i>P<sub>MF</sub>/W</i> × 10 <sup>2*</sup> (W/g)
Andean condor ( <i>Vultur gryphus</i> )	11700	300	11250	7.9	1.02	10.6	53.2	1.14
Great bustard ( <i>Otis tarda</i> )	8950	347	15897	7.6	0.56	7.9	66.1	1.49
Wandering albatross ( <i>Diomedea exulans</i> )	8500	341	6206	18.7	1.37	12.3	46.6	0.75
Griffon vulture ( <i>Gyps fulvus</i> )	7270	256	10540	6.2	0.69	8.8	46.5	1.16
Brown pelican ( <i>Pelecanus occidentalis</i> )	2650	210	4569	9.8	0.58	8.0	36.6	0.87
Sea gull ( <i>Larus marinus</i> )	1915	174	2736	11.0	0.70	8.8	38.4	0.91
Eagle owl ( <i>Bubo buho</i> )	1720	165	3739	7.3	0.46	7.1	35.5	0.99
White-fronted goose ( <i>Anser albifrons</i> )	1715	141	1833	10.8	0.93	10.2	44.5	1.07
American black vulture ( <i>Coragyps atratus</i> )	1702	141	3012	6.6	0.56	7.9	40.4	1.18
Pheasant ( <i>Phasianus colchicus</i> )	1660	85	1596	4.6	1.04	10.7	61.5	2.07
Serpent eagle ( <i>Spilornis cheela</i> )	1655	181	4138	8.0	0.40	7.4	32.1	0.87
Frigate bird ( <i>Fregata aquila</i> )	1620	202	3240	12.6	0.50	7.4	31.0	0.71
Velvet scoter ( <i>Melanitta fusca</i> )	1578	97	1010	9.3	1.56	13.1	60.3	1.52
Black throated loon ( <i>Gavia arctica</i> )	1495	120	1196	12.0	1.25	10.7	49.7	1.17
Herring gull ( <i>Larus argentatus</i> )	1189	146	2123	10.0	0.56	7.6	35.1	0.91
Mallard ( <i>Anas platyrhynchos</i> )	1100	117	928	8.6	1.20	11.5	45.2	1.02
Red kite ( <i>Milvus milvus</i> )	927	162	2897	9.0	0.32	5.9	27.3	0.76
Peregrine falcon ( <i>Falco peregrinus</i> )	712	101	1146	8.9	0.62	8.3	38.0	1.10
Carrion crow ( <i>Corvus corone</i> )	470	89	1058	7.7	0.44	7.0	33.6	1.09
Pigeon ( <i>Columba livia</i> )	330	63	635	6.3	0.52	7.6	38.3	1.39
Jackdaw ( <i>Corvus monedula</i> )	253	71	666	7.5	0.38	6.5	30.8	1.08
Long eared owl ( <i>Asio otus</i> )	247	94	1083	8.2	0.23	5.0	23.3	0.79
Kestrel ( <i>Falco tinnunculus</i> )	245	74	700	7.7	0.35	6.2	29.2	1.01
Montagu's harrier ( <i>Circus pygargus</i> )	237	11	1302	9.4	0.18	4.5	19.9	0.65
Gray plover ( <i>Pluvialis squatarola</i> )	216	66	413	10.4	0.52	7.6	32.6	1.03
Magpie ( <i>Pica pica</i> )	214	60	645	5.5	0.33	6.0	31.8	1.28
Little grebe ( <i>Tachybaptus ruficollis</i> )	180	44	236	8.2	0.76	9.1	42.2	1.49
Merlin falcon ( <i>Falco columbarius</i> )	173	61	410	9.0	0.42	6.8	30.3	1.03
House sparrow ( <i>Passer domesticus</i> )	30	25	101	6.0	0.23	5.0	27.8	1.35
Swift ( <i>Chaetura pelagica</i> )	17	42	104	17.0		13.7	15.2	0.54
House martin ( <i>Delichon urbica</i> )	14	29	93	9.3	0.16	4.1	17.1	0.81
Pied flycatcher ( <i>Ficedula hypoleuca</i> )	12	23	92	5.9	0.13	3.8	18.7	1.05
Citril finch ( <i>Serinus citrinella</i> )	12	25	74	8.1	0.16	4.2	18.7	0.92
Stone chat ( <i>Saxicola torquata</i> )	12	22	77	6.1	0.15	4.0	19.6	1.09
Wren ( <i>Troglodytes troglodytes</i> )	10	18	45	6.9	0.24	5.1	24.1	1.29
Gold crest ( <i>Regulus regulus</i> )	4	14	32	6.3	0.12	3.6	16.9	1.05

\*  $P_{MP}/W$  = Specific power

are influenced by the forces generated and in turn affect the forces and the flight behaviour. Some advance has been made (see Pennycuick 1975; Rayner 1979) in handling these situations but as yet we do not have a completely satisfactory theory for these situations.

## 7.2 Performance estimates

From figure 40 we see that, in the range of flight speeds possible, the bird may choose to adjust its power output to suit the performance it desires. We note that:

- the bird can have hover capability *only* if the  $P_A$  curve for  $V=0$  lies *above* the hover point  $P_H$ ;



- if  $P_A$  lies below the hover point the bird will have a minimum velocity for take off. It would need to achieve this either by running or by facing an oncoming wind or otherwise. The case of large gliding birds such as vultures is indicative of this situation;
- $(P_A - P_R)$  at a given velocity gives the differential power available for climbing. The steady rate of climb,  $RC$ , is given by

$$RC = (P_A - P_R)/W. \quad (31)$$

We note that, as the bird climbs, the drag would reduce due to the temperature effect on density and viscosity of air but the oxygen intake would also come down. In any case the power output cannot be sustained indefinitely and there is a ceiling height of roughly 3000 to 5000 metres for most birds. However, it is interesting to note that some birds can fly much higher. One of the geese species is known to regularly cross the Himalayas annually into its breeding grounds in Tibet at over 10,000 metres.

Another point of interest seen in figure 40 is the 'sprint power' curve. Most bird species can put out for a short time a burst of power. Situations such as escape from a predator or an emergency require this. Also, at landing and take off, conditions may arise when more than normal power output is called for. As noted before, such extraordinary muscular effort is often anaerobic and usually leads to an oxygen debt which must be replenished after a short interval of time. Partridges and pheasants are capable of very fast take offs but cannot sustain the high output of energy and therefore dive down into the bushes. Finally the condition  $P_A = P_R$  on the performance diagram determines the maximum horizontal speed of flight. Figure 41 (adapted from Pennycuick 1968) shows the performance curves for a pigeon (*Columba livia*) in detail and the conditions that obtain for a humming-bird, a vulture and a condor. Note that the larger birds have a minimum take off speed. The condor cannot take off with the maximum continuous power and needs to run and flap vigorously for a few seconds to attain the speed for take off. These limitations become even more restrictive when these birds have to carry food to their nests for feeding their young.

### 7.3 Endurance and range

The distance that a bird can fly or the time it can remain aloft are essentially controlled by the fuel (fat) consumption.

If  $E$  is the mechanical energy per unit mass of fat and  $\delta m$  = mass of fat used up in time  $\delta t$ , then  $\delta m = -(\delta W)/g$  where  $\delta W$  is the loss in weight. The energy required during an interval of time  $\delta t$  is  $P_R \delta t$ , where  $P_R$  is equal to  $D \cdot V$ . We have therefore

$$E \cdot \delta m = P_R \cdot \delta t,$$

or

$$\delta t = -(E/g) \cdot (L/D) \cdot (1/V) \cdot (\delta W/W). \quad (32)$$

Here we have recognised that the lift  $L = W$ , the weight, in horizontal steady flight. The endurance is then calculated as  $t = \int_i^f dt$ , where  $i$  and  $f$  refer to initial and final conditions. Substitution from (32) gives

$$T = -(E/g) \cdot (C_L^{3/2}/C_D) \cdot (\rho S/2) \cdot \int_i^f dW/W^{3/2}.$$

Here the velocity  $V$  has been substituted from

$$V = [(2/\rho) \cdot (W/C_L S)]^{1/2}.$$

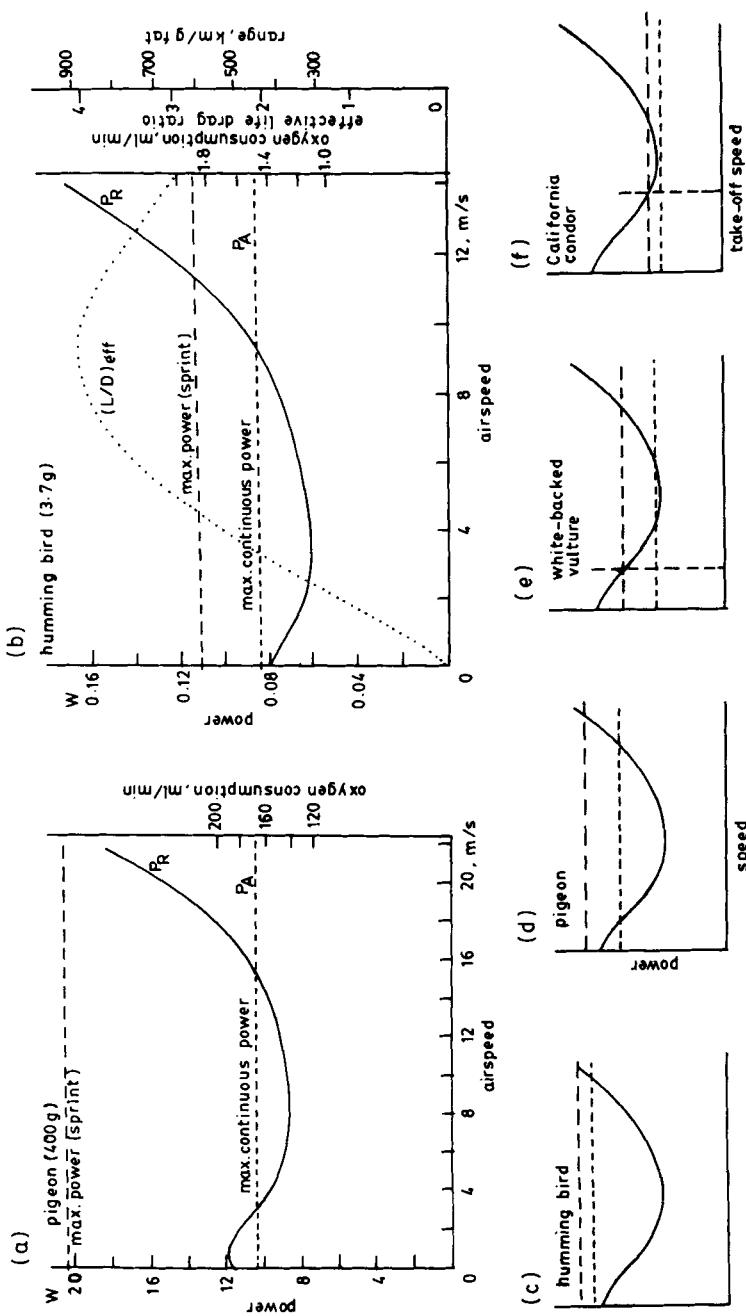


Figure 41. Performance curves of selected birds (adapted from Pennycuick 1968).



Integration gives

$$T = (E/g) \cdot (C_L^{3/2}/C_D) \cdot [(\rho S)/2]^{1/2} \cdot [(W_i/W_f)^{1/2} - 1] \cdot (2/W_i^{1/2}) \quad (33)$$

If  $\mathcal{F}$  is the fat fraction used up,  $\mathcal{F} = 1 - (W_f/W_i)$ , then the endurance is given by

$$T = (E/g) \cdot (C_L^{3/2}/C_D) \cdot [(2\rho S)/W_i]^{1/2} [\{1/(1 - \mathcal{F})\}^{1/2} - 1]. \quad (34)$$

Recalling that maximum endurance corresponds to minimum power required and that for this condition

$$(C_L)_{\min \text{ power}} = 3[(\pi \mathcal{A} \mathcal{R} C_{DO})/k]^{1/2}$$

and,

$$(C_D)_{\min \text{ power}} = 4 C_{DO},$$

we get for the maximum endurance

$$T_{\max} = (E/g) \cdot [(3\pi \mathcal{A} \mathcal{R} C_{DO})/k]^{3/4} \cdot [1/(4C_{DO})] \cdot [(2\rho S)/W_i]^{1/2} [\{1/(1 - \mathcal{F})\}^{1/2} - 1]. \quad (35)$$

For approximate calculations the endurance can be calculated from

$$T_{\text{in hours}} \approx 36(W_i)^{0.28}, \text{ with } W_i \text{ in grams.} \quad (35a)$$

Noting that the distance flown  $R$  in time  $t$  is given by  $V \cdot t$ , the range or distance flown can be calculated from (32) as

$$R = -(E/g) \cdot (L/D) \cdot \log[1/(1 - \mathcal{F})]. \quad (36)$$

We see that  $R$  does not depend on the weight but only on the fat fraction  $\mathcal{F}$ ,  $R_{\max}$  corresponds to  $(L/D)_{\max}$  which we have seen is equal to  $(1/2) \cdot [(\pi \mathcal{A} \mathcal{R})/(k C_{DO})]^{1/2}$ .

Also, an approximate value of  $E$ , the amount of work which can be obtained from a unit mass of fat, is

$$E = 8 \cdot 10^6 \text{ J/kg.}$$

With  $g = 9.81 \text{ m/s}^2$ , the range in kilometres can be written as

$$R = 800 \cdot (L/D) \cdot \log[1/(1 - \mathcal{F})], \quad (37)$$

or

$$R_{\max} \approx 400 \cdot [(\pi \mathcal{A} \mathcal{R})/(k C_{DO})]^{1/2} \cdot \log[1/(1 - \mathcal{F})]. \quad (38)$$

where we have taken the value of  $(L/D)_{\max}$  as given earlier. As a typical example, if  $(L/D)_{\max} \approx 6$ ,  $\mathcal{F} = 1/3$ ,  $[1 - (W_i/W_f)] = 1.5$ , the range would be 2000 km. Typically  $\mathcal{F}$  is approximately 30–40% in small birds and 25–30% in large ones.

If the bird flies (for max range) at constant altitude (constant density) then since  $V_{MP} = [K/(\pi \mathcal{A} \mathcal{R} C_{DO})]^{1/4} \cdot [2W/(\rho S)]^{1/2}$ , the birds' speed will diminish as  $W^{1/2}$ . Alternatively the bird may choose to fly at constant speed. In this case it would have to keep  $(W/\rho)$  constant and as  $W$  diminishes it would have to gain altitude. In either case the fuel consumption is the same. However, in the second case, the speed being higher the duration of flight would be less.

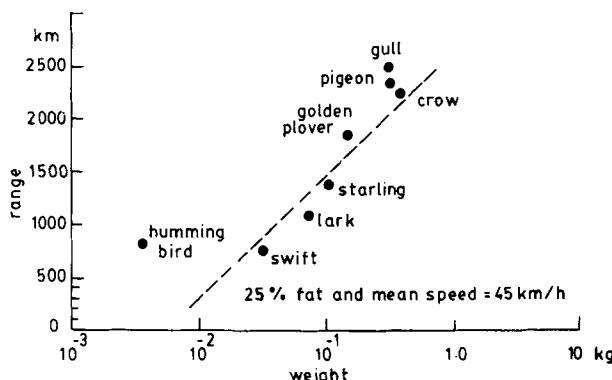


Figure 42. Range of migratory birds.

#### 7.4 Discussion

Calculations based on the above approximate theory show that a migratory bird with  $L/D = 6$  could have a range of 2000 km, using up one-third of its weight. Usually, during migration, birds often use 'staging' i.e. they stop for 're-fuelling' at intermediate points. Environmentalists often stress the protection of such areas. The destruction of re-fuelling areas – draining of marshes for example – can easily lead to the extinction of migratory species. Figure 42 gives the range of some birds and figure 43 the curves for estimating the range and endurance. Pennycuick (1975) has calculated the range of birds and gives charts for approximate calculations including the effects of winds.

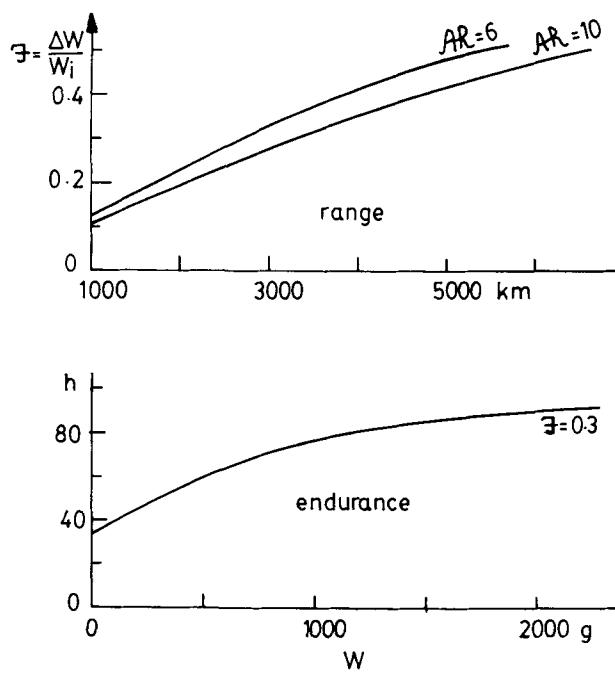


Figure 43. Range and endurance.



## 8. Effects of size and shape

During the evolutionary processes three main kinds of morphological changes have taken place.

- The wings of birds have lengthened. The area swept during flapping has increased thus lowering the induced power to manageable levels at low speeds.
- The muscular system has become modified in such a way as to transmit large amounts of power to the wings.
- The body has become streamlined for drag reduction.

The above general observations need to be modified and supplemented when considering a particular species or order of bird. Here the evolutionary processes are intermingled with the environmental and ecological factors.

Bird flight has two major areas of complexity. The first derives from the fact that flight provides the bird an extended range of means for its life and development. Some of these are escape from predators and other dangers; seeking, finding and taking food; migration; and for reproductive purposes. Many different modes of flight are used. These include straight and level flight, climbing, diving, bounding, soaring, take off and landing, hovering and manoeuvres such as zig-zagging etc. The other area of complexity arises from the highly nonlinear interaction between a bird's flight activities which generate lift for weight support and propulsion for overcoming drag. The problem of scaling and explaining the effects of departures from geometrical similarity is indeed a very difficult and complex task. There are complex connections between the scaling of biological form and function and various aspects of geometrical, mechanical, physiological similitude. In particular, the unique bird organ represented by the wing shows variations in shape, form, size and weight which are difficult to correlate in detail with physiological and biological parameters dictated by the life style of bird species. Greenewalt (1962, 1975) has discussed the data available on birds as also the departures from similarity. The scale effects in aerial locomotion are also surveyed and analysed by Lighthill (1974, 1975, 1977). We will briefly discuss, using dimensional analysis in a very elementary way, the scaling laws and the relationships which can be expected on the basis of geometrical similarity. This provides a very broad (although no doubt a rough) picture of the effects of size and shape which can be seen to be on the whole confirmed by the available data.

### 8.1 Scaling laws

By considering the changes in size while generally maintaining the shape one can discuss changes in flight behaviour and characteristics of bird flight in a rational manner. Of course dimensional analysis is strictly applicable only for cases of geometrical similarity. However even when this does not hold precisely one can derive useful information.

We begin by noting that bird size may be expressed in terms of wing span, body weight, wing area etc. The main parameters which enter into discussion of bird flight are broadly the flight speeds and the power required and that available for a particular regime of flight. We note that the 'size' of a bird generally implies the weight as well as the dimensions of wings and body etc. A bird's weight is proportional to volume, which has the dimensions of  $l^3$  where  $l$  is a characteristic length or dimension. The wing area is proportional to  $l^2$ . Thus we note that the wing loading  $W/S$ , which

controls the flight speed, is proportional to  $l$ . We may therefore write

$$W/S \propto l \propto W^{1/3}. \quad (39)$$

Since velocity is proportional to  $(W/S)^{1/2}$ , (8), we note that flight speed  $V$  would vary as  $l^{1/2}$  or  $W^{1/6}$ . The minimum power required for sustained flight is given by the product of the drag and velocity and evaluated at the minimum power speed. In this condition the lift dependent drag  $C_{Dl}$  is three times  $C_{D0}$  (see table 2) and the minimum power required can be expressed as

$$(P_R)_{\min} \propto W^{7/6}. \quad (40)$$

For an estimate of the power available ( $P_A$ ) we note that there is an upper limit to the sustained rate of working of the muscles.

If

$m$  = mass of flight muscle

$P_A^*$  = power available per unit mass of muscle

$Q$  = work done in one contraction by unit mass of muscle

$f$  = flapping frequency, i.e. the number of contractions/s

then

$$P_A = m \cdot P_A^* = m \cdot Q \cdot f. \quad (41)$$

The mass of muscle is proportional to the weight of the bird (see figure 8). Therefore

$$m \propto l^3. \quad (42)$$

$Q$  can be expected to be the same for any muscle able to exert a given force by contraction through a given fraction of its length and therefore can be regarded as independent of  $l$ . For aerodynamic and mechanical reasons the frequency of flapping  $f$  is proportional to  $1/l$ . So we get

$$P_A \propto l^2 \propto W^{2/3}. \quad (43)$$

To summarise we have the following proportionalities or scaling laws:

- wing loading  $W/S \propto W^{1/3} (\propto l)$
- flight speed  $V \propto W^{1/6} (\propto l^{1/2})$
- power (available)  $P_A \propto W^{2/3} (\propto l^2)$
- power (required)  $P_R \propto W^{7/6} (\propto l^{7/2})$

## 8.2 Discussion

We can now assess and compare the flight behaviour and requirements of birds of different sizes. A bird A with twice the wing span of a bird B would fly  $\sqrt{2} = 1.4$  times as fast. In terms of weight, since  $l \propto W^{1/3}$ , the heavier bird would require  $(2)^{7/6} = 2.25$  times the power to fly at the same ( $L/D$ ). On the other hand the heavier bird will have only  $(2)^{2/3} = 1.59$  the power available. Thus, in relative terms, the power available and power required curves of figure 40 would come closer and the larger and heavier birds can be expected to have reduced capabilities of climbing flight by flapping – a point we have noticed already. This proportionate decrease in power margin with increase in size, suggests a limit to the size of birds that can fly (Pennycuick 1975).



On a plot of  $\log P_A$  and  $\log P_R$  against  $\log W$  (see figure 44), i.e. the proportionalities

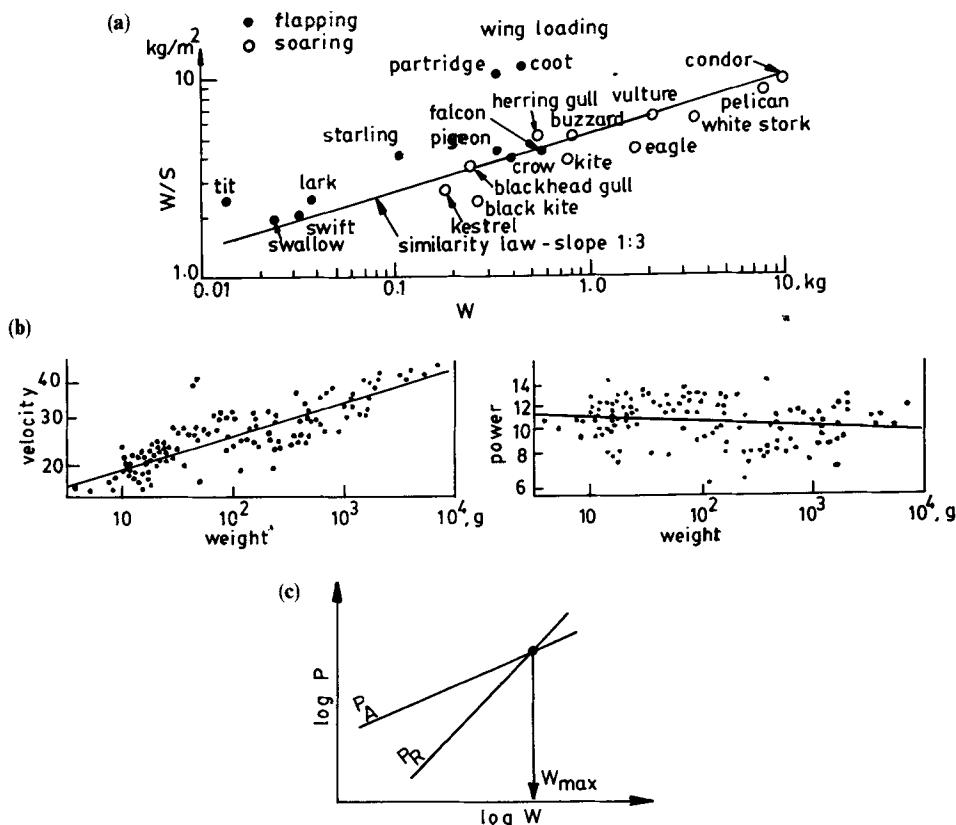
$$\begin{aligned}\log P_R &\propto 7/6 \log W, \\ \log P_A &\propto 2/3 \log W,\end{aligned}\quad (44)$$

we would get straight lines with slopes of  $7/6$  &  $2/3$ , and the intersection would indicate the limiting weight (size) of birds that can fly.

Such scaling arguments cannot, of course, provide the actual numerical estimate for the maximum practical limit for flying birds but they do indicate the existence of an upper limit which has to be determined from observation. From observational data it would appear that the four orders of birds given below generally conform to the scaling laws for a limiting weight for flying. This turns out to be about 12 kg (Pennycuick 1972, 1975):

- Kori bustard (Gruiformes),
- White pelican (Pelecaniformes),
- Mute swan (Anseriformes),
- California condor (Falconiformes).

The first proportionality, relating the wing loading and weight, is a well-known relationship which was already known to Helmholtz and given by Von Karman in 1954. Figures 44 and 45 show a confirmation of this law for a variety of birds.



**Figure 44.** Scaling laws and limits on size. (a) Wing loading. (b) Velocity + power (adapted from Greenewalt 1975). (c) Power required + power available.

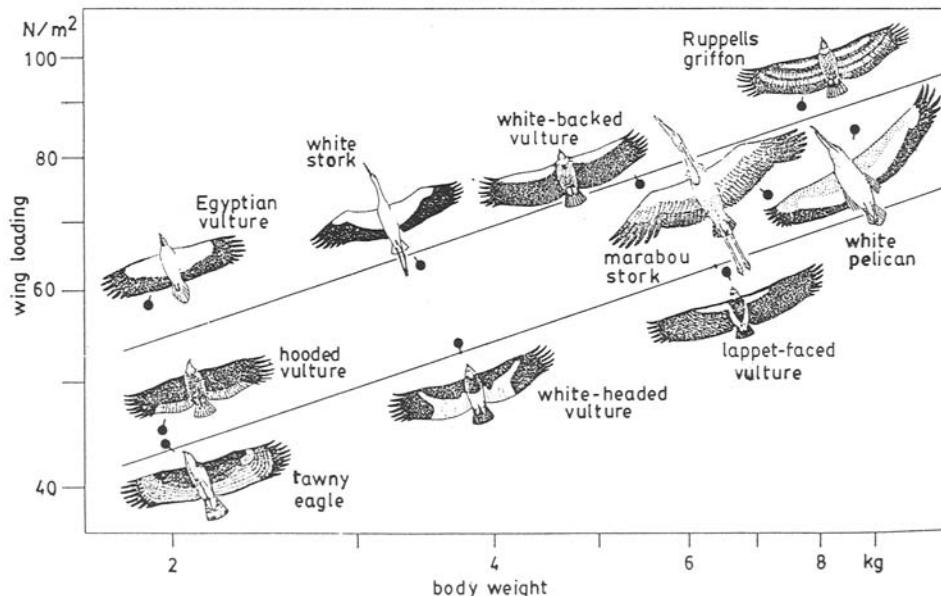


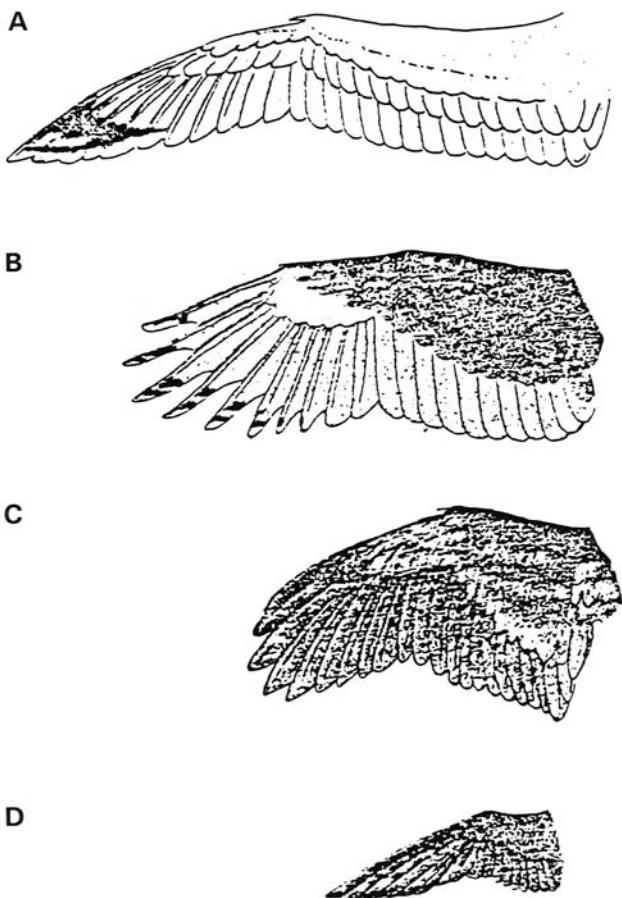
Figure 45. Wing loading and size of soaring birds. (Taken from Pennycuick 1973.)

Greenewalt (1962, 1975) has collected extensive data on birds showing dimensional relationships and confirming the scaling laws discussed above. One can of course expect departures from the one-third power law as well as those governing the characteristic velocities and power relations. It is not surprising that small birds like the partridge or the humming-bird significantly depart from the mean behaviour indicated by the scaling laws.

Greenewalt's extensive studies show that a large number of groups of birds very roughly conform to the scaling laws. These include: falcons, ducks, coots, divers, herons, woodpeckers, wrens, grebes, pigeons, swans, owls etc. Figure 44 shows this to be broadly true for other parameters e.g.  $V_{MP}$  and  $P_R$ . It should be noted that these arguments hold only broadly. Actually much further research is necessary to explain the departures in each case. Greenewalt discusses some of the departures in Passeriformes, shore birds and ducks by fitting regression curves to actual data and gives approximate expressions for calculating the performance. Figure 45 (from Pennycuick 1973) shows a plot of wing loading versus weight for ten soaring birds. Five of these, with relatively high wing loading, fall on one line while those with low wing loading fall on a lower line. The lightly loaded birds are able to soar in relatively weak thermals and so are able to hunt for food over relatively small territories. The heavily loaded birds often fly cross-country for food.

### 8.3 Wing shape

The wing is the bird's unique possession and is totally committed to flight. Adaptation of the wing to the bird's requirement for food and preservation in different habitats and to its mode of life, has produced a very large variety of wing shapes and forms. However avian morphologists distinguish four basic wing types with many intermediate forms (King & King 1979) (see figure 46).



**Figure 46.** The four basic wing shapes. (A) Long distance high speed gliders: albatrosses, gulls, shearwaters and other sea birds; (B) Endurance land soarsers: eagles, vultures, storks, etc.; (C) Fast flapping rapid take off game birds and woodpeckers, jays etc.; (D) High speed fliers: swifts, falcons, waders, etc. (From Petersen 1968, p. 42.)

- *The elliptical wing:* The shape is relatively short and broad with a low aspect ratio between 3 and 6. Wing loading is moderate or low. The wing beat is fairly fast and the amplitude moderately large. This shape typifies many game birds, woodpeckers, cuckoos, jays etc. (many Passeriformes and some Galliformes and Columbiformes) i.e. birds which have to manoeuvre through restricted openings in vegetation. The alula is relatively large and the primary feathers may separate to form additional wing slots to prevent stalling at low speeds.
- *The broad soaring wing:* This occurs in vultures, eagles, pelicans etc. The shape is moderately long and broad with aspect ratios between 5 and 7 and only moderate wing loading. The beat frequency is low. The alula and wing slots are prominent. This type of wing is particularly suited for low speed soaring.
- *The high speed wing:* This characterises swifts (Apodidae) falcons (Falconidae), humming-birds (Trochilidae) and, to a lesser extent, ducks (*Anas*) and terns (*Sterna*). The wing is relatively small with a moderately high aspect ratio of between 5 and 9. Drag is low and the wing loading high. The wing beat is rapid and the amplitude relatively small. The wing is tapered and the outer part may be swept back. There are no tip slots except in falcons who close them during fast flight.
- *The long soaring wing:* This is confined to oceanic soaring birds such as gulls (*Larus*), gannets (*Morus*) and albatrosses (Diomedeidae). Long, slender and pointed,

this type of wing has a high aspect ratio of between 8 and 18 and high wing loading. With high  $L/D$  these birds soar at high speed. There are no tip slots but the alula can be fairly large. Such wings have high aerodynamic efficiency and satisfactorily meet the contradictory requirements of gliding and flapping flight. However they are relatively fragile and demand a habitat free from obstacles.

These basic wing shapes are illustrated in figure 46. The detailed mechanics of the wing vary with different types of flight as discussed before. In fast level flight the propulsion comes almost solely from the downstroke, being provided by the outer half of the wing. During the upstroke the wing is lifted by air pressure and is more or less passive. Considerable lift is generated by the inner part of the wing on both up- and downstrokes. The slow flight of small woodland birds while ascending or descending is not very complicated. The main lift and propulsion come from the downstroke. The steep ascending and descending flight of strong fliers of medium size such as pigeons, ducks, hawks and pheasants is much more complex. The downstroke provides much lift but little propulsion. The upstroke is distinguished by a very rapid rotation at the shoulder and extension of the arm producing a backward flick of the primaries which results in strong propulsive forces. In hovering flight, as in the flight of humming-birds, much lift is obtained during the forward as well as backstroke. Each species has some peculiarities in its flight, and in the flight apparatus and the mode of using it, but the basic features are roughly similar.

## **9. Conclusion**

Flight in the atmosphere imposes limitations and restrictions on the shape, size and structure of flying animals as well as flying machines. If an animal like a bird has to fly, aerodynamic efficiency and power have to be combined with structural strength and muscular energy, and the weight must be kept at a minimum. Such requirements have imposed a certain degree of uniformity of basic structure in all birds. Every part of the bird's anatomy is attuned for its life in the air. A compact streamlined body combines strength with lightness and a versatile musculature controlling the unique feather-covered wings provides the bird with an unequalled system for flight.

Over the 150 million years of evolution the anatomy and physiology of birds have changed not only to combine strength and lightness but also to enhance efficiency of body functions such as breathing and blood circulation. The senses have been very finely tuned to the flight environment. Like all vertebrates, birds sense their attitude changes by means of the semi-circular canal of the inner ear and their marvellous flight control systems depend on this information. Their eyesight provides them with the maximum possible amount of information at the fastest speed reaching a perfection not found in any other animal.

Second only to insects, birds are the most biologically successful group of animals that have existed. This success, in which the ability to fly has played a vital part, has led to an extraordinary diversification into nearly 9000 species compared to about 4000 species of mammals. Birds cover virtually all regions of the earth, from the poles to the equator. In their quest for food and survival each species has evolved characteristic forms of flight which, while conforming generally to broadly similar features, have specific attributes peculiar to it. Smaller birds have adapted their flying to escape threat. Apart from being highly manoeuvrable, some of them adopt assembly and flight in flocks; e.g. starlings. Another technique is the capability for very high

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speed spurts for a short time in order to escape. Pheasants and partridges have an almost rocket-propelled take off and fast curving flight for short distances before finding a shrub shelter. Often the special modifications of flight which adapt a bird species to one habitat prevent their switching to another. However, some birds are equally adept in several bio-habitats. Gulls fly over stormy seas as well as the reed masses of inland lakes. Pigeons and crows seem to survive in forests as well as in the concrete jungle of urban surroundings.

The song birds are particularly successful survivors because of their great manoeuvrability in flight. Natural forests, bushes and shrub-covered plains provide ample food supply but are full of obstructions which small birds can easily navigate through – and also find nesting and hiding places in! Despite their lack of endurance some small birds have to migrate before winter and frost. Arctic terns, golden plovers, snipe, geese and many shore birds migrate over long distances in quest for food. Each species has interesting and intriguing features of flight.

Much empirical data is needed to relate the flight characteristics of a particular bird species to its habitat and environment and habits. There is great scope for naturalists and scientists to pursue these studies in India.

I am grateful to many colleagues in the Indian Space Research Organisation and the National Aeronautical Laboratory for help and support. Mr K R Seetharam was responsible for the high speed photographs of birds at SHAR and the Nelapettu Sanctuary. I thank Dr Ranjit Daniels of the Indian Institute of Science for his help with the names of birds and their classification. The editorial staff of the Indian Academy of Sciences have been most helpful and I thank them.

### List of symbols

$A, B$	constants in power equation;
$A_1, B_1$	constants in glide polar;
$a$	slope of the lift curve;
$\mathcal{A}\mathcal{R}$	aspect ratio;
$b$	wing span;
$C_D, C_L$	coefficients of drag and lift, respectively;
$C_{D0}, C_{Di}$	zero lift drag coefficient and induced drag coefficient, respectively;
$C_F$	friction coefficient;
$D$	drag;
$E, e$	energy content of fat per unit mass;
$F$	force;
$\mathcal{F}$	fat fraction;
$f$	frequency;
$\dot{g}$	acceleration due to gravity;
$k$	constant in induced drag expression to account for non-elliptic lift distribution;
$L$	lift;
$l$	length scale;
$M, m$	mass of bird;

$P$	power;
$P_A, P_A^*, P_A^{**}$	power available, specific power (max. continuous) and specific power (sprint), respectively;
$P_R$	power required;
$p$	power available for unit mass of muscle;
$Q, q$	work done in one contraction by unit mass of muscle;
$R$	radius of turn;
$Re$	Reynolds number;
$S$	wing area;
$T, t$	thrust or time of flight (endurance);
$U$	bird speed in moving coordinate system;
$u$	local horizontal velocity component;
$V, v$	velocity of the air stream relative to the wing/speed of flight;
$V_{BG}, V_{MD}, V_{MP}$	velocity for best glide angle, minimum drag and minimum power, respectively;
$V_s$	stalling speed i.e. minimum speed for flight;
$V_R$	resultant velocity;
$v$	local vertical velocity component;
$W, W_i, W_t$	weight, initial weight, final weight, respectively;
$W_m$	weight of muscles;
$W_{SM}$	minimum sinking speed in gliding flight;
$W_{SBG}$	sinking speed at best glide angle;
$w_i$	downwash velocity;
$Z$	coordinate in vertical direction;
$\alpha$	angle of attack;
$\alpha_i$	induced angle of attack;
$\eta$	efficiency of energy conversion;
$\nu$	kinematic viscosity;
$\rho$	density of air.



**Appendix A.** Hindi names of some common Indian birds mentioned in the article. A bar over a letter denotes a long syllable; a dot under the letter denotes a hard (retroflex) sound.

English	Hindi	English	Hindi
Blackbird	Kastūri	Osprey	Machchariyā,
Bluejay	Neelkant	Owl	Macchlimār
Bulbul	Bulbul	Oystercatcher	Ullu, Ghūghū
Bustard	Hūkna, Tūqdār	Parrot	Daryā gajpaon
Buzzard	Chūhāmār	Partridge	Totā
Coot	Aari, Thekāri	Peacock	Chukor, Teetar
Coppersmith	Tamerā, Chotābasant, Katphōrā	Pelican	Mōr, Mayūrā
Cormorant	Jal kowwā	Pheasant	Hawāsil
Crane	Sāras	Pigeon	Chir, Kaleej
Crow	Kowwā	Pipit	Kabūtar
Cuckoo	Papiyā	Plover	Chillu, Rūgēl, Charchari
Dove	Kabūtar, Fākhtā	Quail	Batān, Karvānaka
Drongo	Bujangā, Kālkalachi	Redstart	Batēr
Duck	Batak, Chakwa	Robin	Thirthirā
Eagle	Okāb, Sāmpmār	Rook	Kālchūri, Daiyār
Egret	Baglā	Shrike	Kowwā
Falcon	Shāheen, Kohi	Snipe	Latorā
Finch	Munia	Sparrow	Chahā, Ohādi
Flamingo	Bog hans, Rāj hans	Spoonbill	Gauriyā, Chiria
Flycatcher	Chakdil, Zakki, Turrā	Starling	Chamachbāzā
Goose	Hans, Rāj hans	Stork	Tilyār
Grebe	Dūbdūbi, Pāndūbi	Sunbird	Ghūngil, Laglag,
Grey tit	Rāmgangrā		Janghil
Gull	Dhomra		Shakar korā,
Hawk	Shikra		Phūl Soongi
Heron	Nāri, Sain, Baglā	Swallow	Abābeel
Hoopoe	Hūdhūd	Swan	Rāj hans
Ibis	Bāzā, Mūndā	Swift	Abābeel, Bābeela
Kestrel	Koruttia	Tern	Tehāri, Gangācheel
Kingfisher	Kilkilā, Kourillā	Thrush	Kastūrā
Kite	Cheel, Kapāsi	Tit	Rāmgangrā
Koel	Koel	Vulture	Gidh
Lark	Bharat, Chandūl	Wagtail	Pillakh, Pilkyā
Magpie	Duzd*, Khāshimbrah*	Warbler	Phūtki, Tikitiki
Mallard	Batak, Neelsir, Neerrūgi	Weaver bird	Bāyā
Myna	Mynā	Wood cock	Simteetar, Tuteetar
Nighthawk, nightjar	Chapkā, Dābchuri	Woodpecker	Katphora

References: Hindi names from Ali (1979) and Ali & Ripley (1987);

\* Kashmiri names

Please note that names listed in Hindi are, as far as possible, those of the most commonly occurring Indian species, and that regional variations may be quite common.

## Appendix B

**Table B1.** Field-estimates of the rate of weight-loss in migrating birds.

Species	Weight-loss (% body mass h <sup>-1</sup> )	Basis of field estimate
Blackpoll warbler ( <i>Dendroica striata</i> )	0·6	Estimated arrival and departure weight for non-stop flight: from New England to Bermuda
European robin ( <i>Erithacus rubecula</i> )	0·9	from Norway to Scotland
Goldcrest ( <i>Regulus regulus</i> )	0·7	from Norway to Scotland
Wheatear ( <i>Oenanthe oenanthe</i> )	0·8, 1·3	from Greenland to Scotland
Knot ( <i>Calidris canutus</i> )	1·0	from England to Iceland and from Iceland to Ellesmere Island
Manx shearwater ( <i>Puffinus puffinus</i> )	0·3	from Wales to Brazil
Song sparrow ( <i>Melospiza melodia</i> )	0·7	Weight before and after a night of migration. Massachusetts
Thrush ( <i>Hylocichla mustelina</i> )	1·8	Weight at different times in the night 1 Migrants killed at TV-tower, Illinois
Tennessee warbler ( <i>Vermivora peregrina</i> )	1·8	Migrants killed at TV-tower, Wisconsin
Veery ( <i>Catharus fuscescens</i> )	1·3	Migrants killed/trapped at lighthouse, Ontario
Ovenbird ( <i>Seiurus aurocapillus</i> )	1·0	
Chaffinch ( <i>Fringilla coelebs</i> )	2·9, 2·0	Weights at trapping sites 50 km apart along the migratory pathway, East Baltic

Reference: Alerstam (1981).

**Table B2.** Morphometric parameters for bird wings and vulture primary feather, and morphometrics of wing cross-section at approximately mid-span.

(Thickness ratio = maximum thickness/chord; camber ratio = maximum deviation of centre of wing from line connecting leading and trailing edges; nose radius ratio = approximate radius of wing at leading edge/chord; 'twist' is base to tip twist angle).

Bird	Length (m)	Projected area (m <sup>2</sup> )	Wetted area (m <sup>2</sup> )	$\mathcal{A}\mathcal{R}$	Thickness ratio	Camber ratio	Nose radius ratio	Twist (degrees)
Swift	0·141	0·005	0·0104	3·9	0·054	0·054	0·012	5
Petrel	0·212	0·0116	0·024	4·1	0·048	0·065	0·011	9
Woodcock	0·171	0·0137	0·029	1·9	0·053	0·081	0·019	7
Wood duck	0·257	0·0211	0·044	3·1	0·100	0·069	0·020	11
Quail	0·145	0·0109	0·023	1·8	0·036	0·101	0·019	5
Starling	0·164	0·0088	0·035	3·0	0·036	0·112	0·032	13
Nighthawk	0·260	0·0165	0·035	4·1	0·062	0·069	0·036	5
Hawk	0·394	0·0522	0·122	3·0	0·068	0·099	0·032	10
Vulture primary	0·180	0·00410	0·0086	7·9	0·063	0·039	0	15

Reference: Withers (1981).

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**Table B3.** Observed air speeds in migrating birds, studies by radar, in comparison to speeds for minimum power ( $V_{MP}$ ) and maximum range ( $V_{MR}$ ) as predicted theoretically from the power equation.

Bird	Mass (kg)	Wing span (m)	$V_{MP}$ (ms <sup>-1</sup> )	$V_{MR}$ (ms <sup>-1</sup> )	Observed mean air speed (ms <sup>-1</sup> )
Chaffinch ( <i>Fringilla coelebs</i> )	0.020	0.30	5.1	9.5	11
Swift ( <i>Apus opus</i> )	0.043	0.45	5.4	9.4	11
Redwing thrush ( <i>Turdus iliacus</i> )	0.065	0.40	6.6	11.5	13
Wood pigeon ( <i>Columba palumbus</i> )	0.50	0.75	9.5	15.7	17
Oystercatcher ( <i>Haematopus ostralegus</i> )	0.55	0.80	9.5	15.7	14
Eider duck ( <i>Somateria mollissima</i> )	2.0	1.1	12.5	20.4	21
Bean goose ( <i>Anser fabalis</i> )	3.5	1.6	12.5	20.3	20
Crane ( <i>Grus grus</i> )	5.5	2.4	11.8	19.4	19
Whooper swan ( <i>Cygnus cygnus</i> )	10	2.4	14.4	23.5	17

Reference: Alerstam (1981, p. 12).

**Table B4.** Approximate value of the stalling speed at flight speeds: above this value the bird can maintain itself in the air without flapping the wings; below it, flapping is required. Calculations assume  $C_{1 \text{ max}} = 1.5$ .

Bird	Stalling speed (ms <sup>-1</sup> )
Wren	5.1
Pied flycatcher	3.8
Kestrel	6.2
Pigeon	7.6
Mallard	11.5
Frigate bird	7.4
Pheasant	10.7
Griffon vulture	8.8
Wandering albatross	12.3
Mute swan	14.8

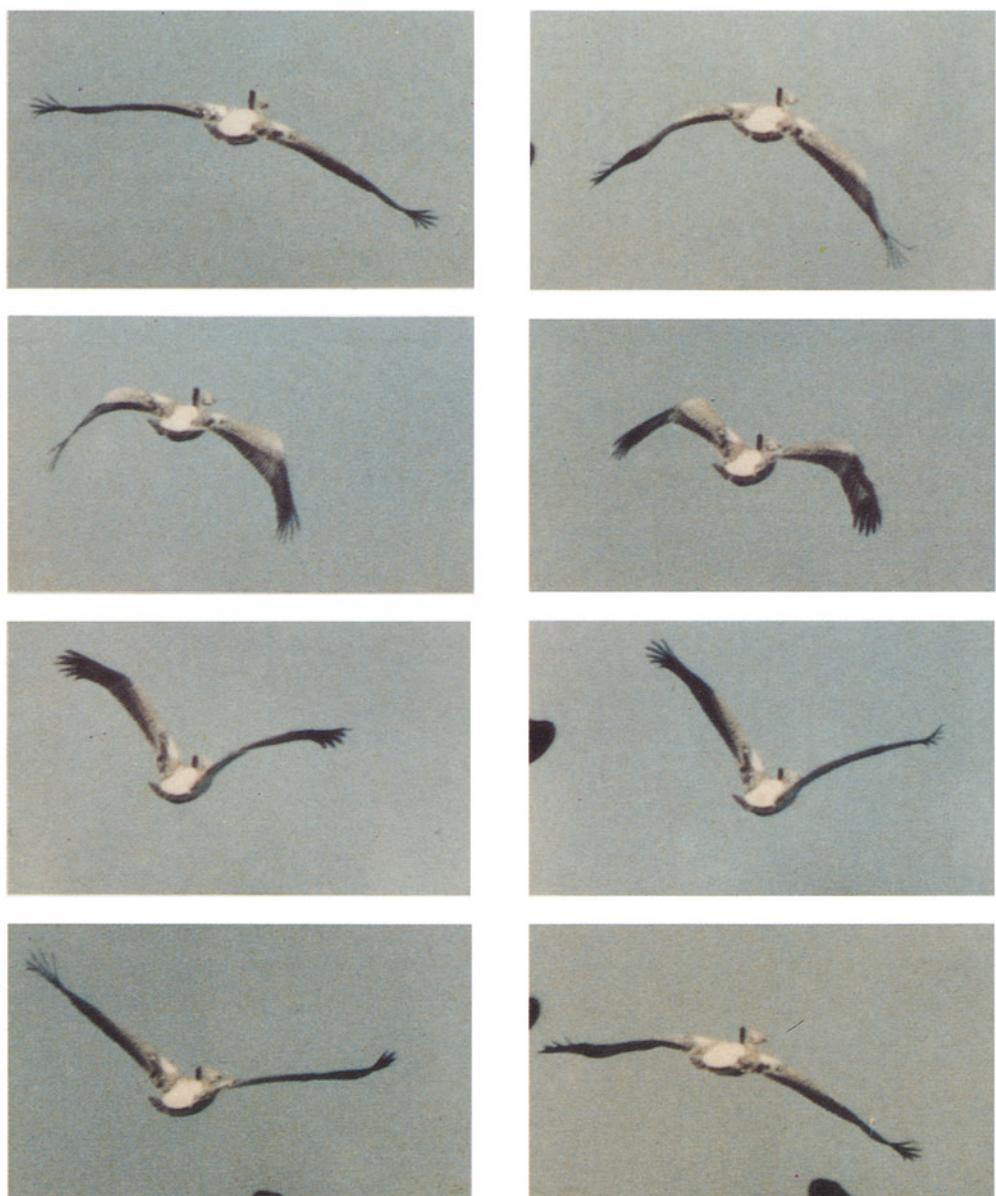
Reference: Ward-Smith (1984, p. 78).

## References

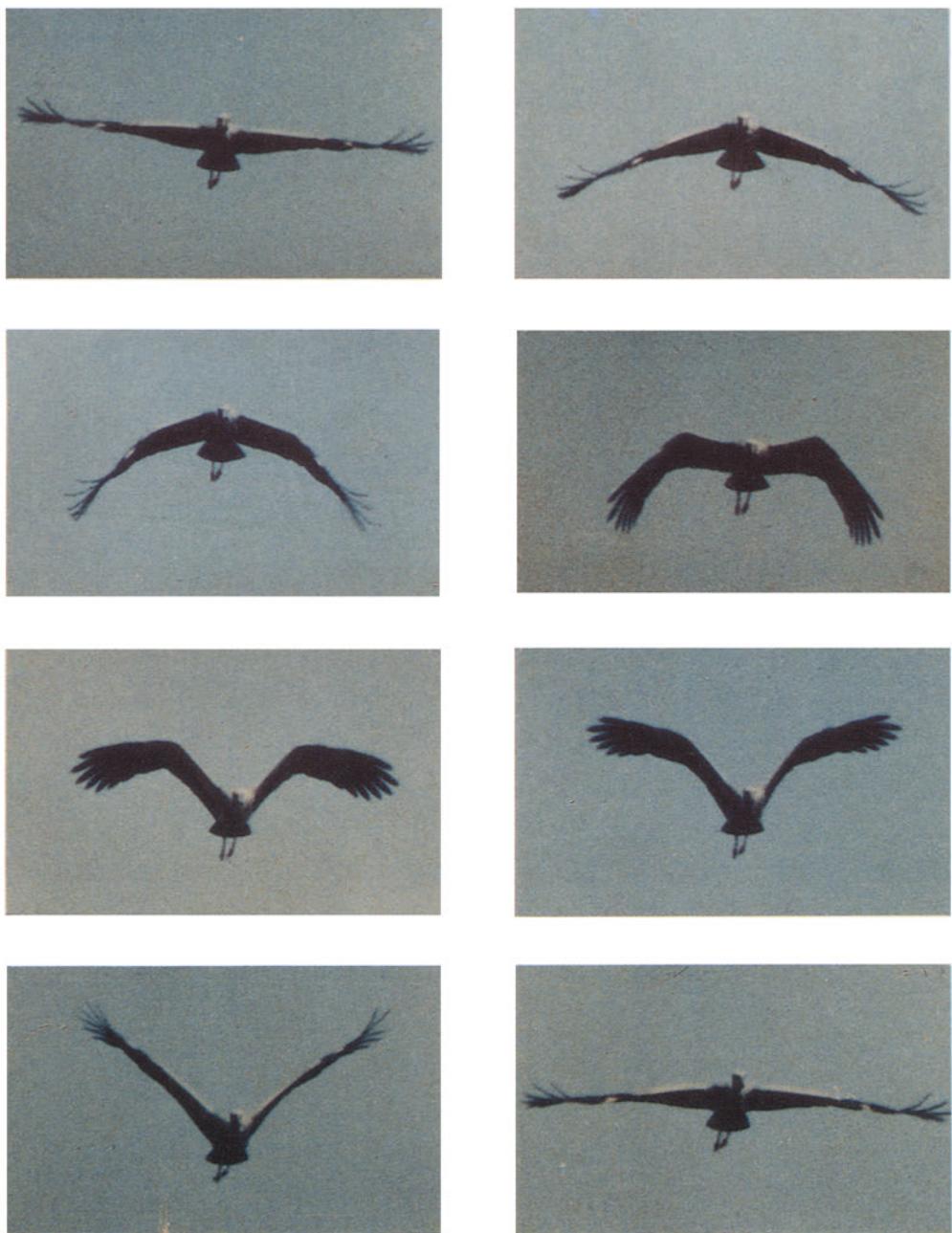
- Alerstam T 1981 *Animal migration* (ed.) D J Aidley (London: Cambridge University Press)
- Alexander R M 1989 Muscles for the job. *New Sci.* 122 (1960): 50–53
- Ali S 1979 *The book of Indian birds* 11th edn (Bombay: Bombay Natural History Society)
- Ali S, Ripley D 1983 *A pictorial guide to the birds of the Indian subcontinent* (Bombay: Bombay Natural History Society/Oxford Press)
- Ali S, Ripley S D 1987 *Compact handbook of the birds of India and Pakistan* 2nd edn (Delhi: Bombay Natural History Society/Oxford Press)
- Ardley N 1984 *Birds* (Leicester: Modern Knowledge Library/Galley Press)
- Baudinette R V, Schmidt-Nielson K 1974 Energy cost of gliding flight in herring gulls. *Nature (London)* 248: 83–84
- Bernstein M H, Thomas S P, Schmidt-Neilson K 1973 Power input during flight of the fish crow, *Corvus ossifragus*. *J. Exp. Biol.* 58: 401–410
- Brown R H J 1948 The flight of birds. The flapping flight of the pigeon. *J. Exp. Biol.* 25: 322–333
- Brown R H J 1953 The flight of birds. II. Wing function in relation to flight speed. *J. Exp. Biol.* 30: 90–103
- Brown R H J 1963 The flight of birds. *J. Biol. Rev.* 38: 460–489
- Cone C D 1962 Thermal soaring of birds. *Am. Sci.* 50: 180–209
- Dalton S 1977 *The miracle of flight* (Maidenhead, Berkshire: Sampson Low)
- Dickenson S 1928 The dynamics of bicycle pedalling. *Proc. R. Soc. London* B103: 225–233
- Freethy R 1982 *How birds work* (Poole, Dorset: Blanford Press)
- Goldspink G 1977 *Scale effects in animal locomotion* (ed.) T J Pedley (New York: Academic Press)
- Greenewalt C H 1962 Dimensional relationships for flying animals. *Smithsonian Misc. Coll.* 144(2): 1–46
- Greenewalt C H 1975 The flight of birds. *Trans. Am. Philos. Soc. (N.S.)* 65 (4): 1–67
- Guido L 1939 *Aeronautics* 18: 8–9
- Hankin E H 1913 *Animal flight: A record of observation* (London: Iliffe & Sons)
- Henderson, Haggard, Parry D A 1925 *Am. J. Physiol.* 72: 264–282
- Hill A V 1950 Dimensions of animals and their muscular dynamics. *Science* 38(150)
- King A S, King B Z 1979 *Form and function in birds* (eds) King, Melelland (New York: Academic Press) vol. 1 & 2
- Lasiewski R C 1963 Oxygen consumption of torpid, resting, active and flying hummingbirds. *Physiol. Zool.* 36: 122–140, quoted by Bernstein M H, Thomas S P, Schmidt-Neilson K 1973 *J. Exp. Biol.* 58: 407
- Lighthill M J 1974 Aerodynamic aspects of animal flight. *Bull. Inst. Maths. Appl.* 10: 369–393
- Lighthill M J 1975 Aerodynamic aspects of animal flight. In *Swimming and flying in nature* (eds) T Y T Wu, C J Brokaw, C Brennen (New York: Plenum) vol. 12
- Lighthill M J 1977 Introduction to the scaling of aerial locomotion. In *Scale effects in animal locomotion* (ed) T J Pedley (New York: Academic Press)
- March R L, Storer R W 1981 Correlation of flight-muscle size and body mass in Cooper's hawks: A natural analogue of power training. *J. Exp. Biol.* 91: 363–368
- McGahan J 1973 Flapping flight of the Andean condor in nature. *J. Exp. Biol.* 58: 239–253
- Parry D A 1948 The swimming of whales and a discussion of Gray's paradox. *J. Exp. Biol.* 26: 24–34
- Pennycuick C J 1968 A wind tunnel study of gliding flight in the pigeon, *Columba livia*. *J. Exp. Biol.* 49: 509–516
- Pennycuick C J 1972 *Animal flight: Studies in biology*, No. 33 (London: Edwin Arnold)
- Pennycuick C J 1973 The soaring flight of vultures. *Sci. Am.* 229 (6): 102–109
- Pennycuick C J 1975 The mechanics of flight. *Avian biology* (eds) D S Farner, J R King, K C Parkes (New York: Academic Press) vol. 4 & 14
- Peterson R T 1968 *The birds* (Time Inc.)
- Rayleigh Lord 1883 The soaring of birds. *Nature (London)* 27: 534–535
- Rayner J M V 1979a A vortex theory of avian flight. Part 1. The vortex wake of hovering animals. *J. Fluid. Mech.* 91: 697–730
- Rayner J M V 1979b A vortex theory of animal flight. Part 2. The forward flight of birds. *J. Fluid. Mech.* 91: 731–763
- Ruppell G 1977 *Bird flight* (New York: Van Nostrand Reinhold)
- Schmidt-Neilson K 1977 *Scale effects in animal locomotion* (ed.) T J Pedley (New York: Academic Press)
- Torre-Bueno J R, Larochelle J 1978 The metabolic cost of flight in unrestrained birds. *J. Exp. Biol.* 75: 223–229

*Bird flight*

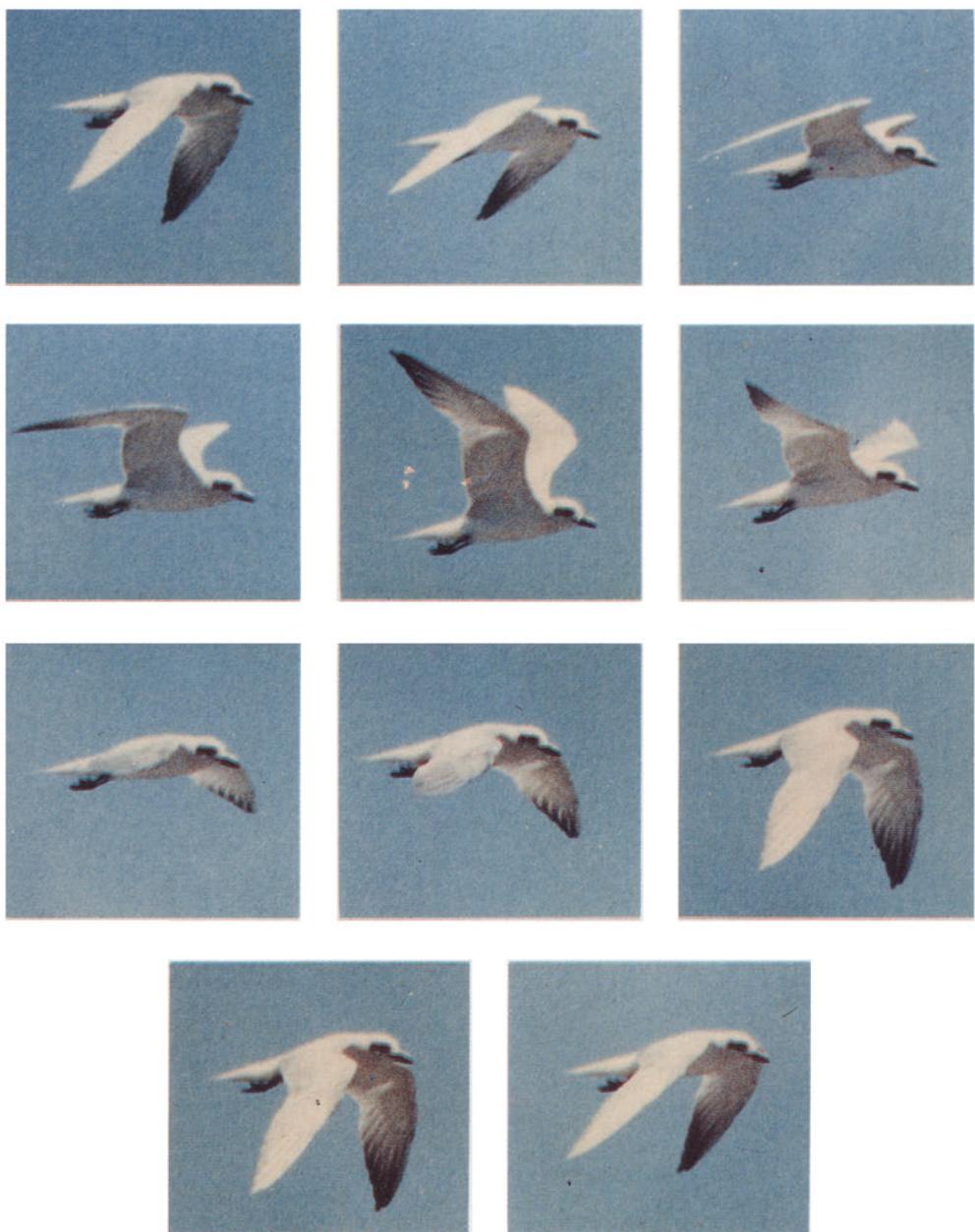
- Tucker V A 1968 Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* 48: 67-87
- Tucker V A 1973 Bird metabolism during flight: Evaluation of a theory. *J. Exp. Biol.* 50: 689-709
- Von Karman T 1954 *Aerodynamics* (Cornell: University Press)
- Ward-Smith A J 1984 *Biophysical aerodynamics and the natural environment* (New York: Wiley)
- Weis-Fogh T 1973 Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J. Exp. Biol.* 59: 169-230
- Weis-Fogh T 1977 *Scale effects in animal locomotion* (ed.) T J Pedley (New York: Academic Press)
- Weis-Fogh T, Alexander R M 1977 *Scale effects in animal locomotion* (ed.) T J Pedley (New York: Academic Press)
- Withers P C 1981 An aerodynamic analysis of bird wings as fixed aerofoils. *J. Exp. Biol.* 90: 143-162
- World Book Encyclopedia* (illustrations by Jean Helmer) (Chicago, London, Paris: World Book-Childcraft Int. Inc.) vol. 2

**Plate 1**

**Figure C1.** Pelican in flight. Average flapping frequency: 2·5 s. Framing rate: 100/s. Exposure: 500  $\mu$ s. Lens: 300 mm *f*/4·5. The number on each photograph indicates the time in milliseconds.

**Plate 2**

**Figure C2.** Painted stork in flight. Average flapping frequency: 3/s. Framing rate: 100/s. Exposure: 500  $\mu$ s. Lens: 300 mm f/4.5. The number on each photograph indicates the time in milliseconds.

**Plate 3**

**Figure C3.** Tern in flight. Average flapping frequency: 3.5/s. Framing rate: 100/s. Exposure: 500  $\mu$ s. Lens: 300 mm f/4.5. The number on the photograph indicates the time in milliseconds.