CHAPTER 5  PRINCIPLES OF FLIGHT

5.1 Introduction

The study of flight in animals owes much to the work carried out on human- or machine-powered flight, but there has been relatively little information transfer in the other direction. Indeed, one of the surprising facts about the early pioneers of aviation is how little they drew on observations of flying animals, in pursuing their goal of human flight. One of the saddest clips of archive film of early aviators, shows a man at the top of the Eiffel Tower in Paris wearing a coat with extended arms that were intended to resemble the wings of birds. As he attempts to fly off the top of the tower, gravity takes over and he plummets to his death. The fact that the wings of birds are large relative to their body size should have challenged his confidence in his small wings. Did he really believe that he could flap his arms so powerfully with his muscles that he could maintain powered flight? As you read through this chapter and the next you will encounter the anatomical and physiological adaptations that enable birds and some other animals to fly and, in doing so, will appreciate why the early dream that humans could fly with wings strapped to their arms was always an impossible one.

There are significant parallels between the study of the mechanics of swimming in fish and the study of the aerodynamics of flight in birds, and there has been considerable cross-fertilization of ideas and techniques amongst researchers. However, although both swimming and flying involve moving through a three-dimensional medium, water and air respectively, water is much more viscous than air and is almost incompressible. In the earlier chapters of this book you have read about the mechanics of swimming in fish and the problems of maintaining position in the water against a gravitational force. In this chapter the principles of flight will be introduced, using birds as an example. Chapter 6 considers the application of these principles to a variety of other animal groups.

It is inevitable that much of the study of animal flight has been carried out using birds. Birds are numerically a most successful group of vertebrates, with about 25,000 species and sub-species recognized so far, compared with some 15,000 mammals and a similar number of fish species. Figures for the number of species can rarely be given precisely. Despite the general lack of study of birds by early flight enthusiasts, there was one particular feature of birds that influenced the most scientific of the early workers on flight and that was the shape of the wing. It is the relationship between shape and aerodynamic performance that is explored in the next section.

5.2 The aerofoil

Otto Lilienthal spent 20 years working on flight in the late nineteenth century and he studied bird flight with the intention of producing a workable glider. The wing design that he developed had a gently curved upper surface. This subtle parabola gave the wing lifting power, according to Lilienthal, and was the key feature of a bird’s wing that accounted for the lift (Chapter 2). The wingspan of his gliders was about 7 m, too small really from the aerodynamic point of view, but even so he made nearly 2,000 flights before crashing on 9th August 1896. He died one day later. His contribution to research on flight was the realization, from scientific observation, that a curved wing provided lift.
Prior to Lilienthal’s work, wings were generally constructed as flat sheets. The flat sheet does provide some lift and a simple experiment will demonstrate this. Hold a piece of paper (about A4 size) in front of your mouth (Figure 5.1a) and blow across the upper surface. If you blow gently, the paper will gradually rise (Figure 5.1b, c). This experiment demonstrates one of the properties of wings—that if air flows faster over an upper surface, an upward force is generated.

A structure that generates lift is called an aerofoil. In the experiment with the paper, the lift was generated in an upward direction, but you should be aware that the force that generates lift does not necessarily act vertically upwards (Section 2.3.3).

5.2.1 An introduction to flight dynamics

If you look at a bird wing in the flight position, or at an aircraft wing, you will see that it is curved in cross-section. A typical bird wing section is shown in Figure 5.2a. When positioned in an air flow, the air that passes over the top of the wing section moves faster than that travelling below, as a consequence of the curved shape of the wing. The difference in speed produces a difference in pressure between the upper and lower surfaces. Thus, there is a vertical pressure gradient across the wing, with the higher pressure below, providing lift (Figure 5.2a, b). The larger the surface area over which the air flows, the greater the lift. You have read about the generation of hydrodynamic lift as a fish fin moves through water, in Section 2.3.3. In the fish fin, lift was only generated if there was an angle of incidence and if this angle was small. Similarly, in an aerofoil, lift is only generated in the presence of a small angle of incidence (typically −5° to +15°). At large angles of incidence the lift disappears.

Why does the lift decrease at large angles of incidence?

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**Figure 5.1** Blowing on a sheet of paper to demonstrate lift.

**Figure 5.2** The air flow over an aerofoil.
(a) The curvature (camber) of the wing alters the velocity of the air above the wing, creating a pressure gradient.
(b) The forces generated on an aerofoil. The downward force due to gravity (the weight) is balanced by an upward force that is the resultant of lift and drag.
As you have read in Section 2.3.1, for the hydrofoil at small angles of incidence, the flow over an aerofoil is laminar (Figure 5.3a, b). As the angle of incidence increases (Figure 5.3b, c) the flow breaks up and spills off the upper surface of the aerofoil as turbulence. The velocity of the flow changes and the pressure gradient across the aerofoil is substantially reduced, leading to a loss of lift. At the point where the lift is so reduced that it does not counteract the gravitational force, the wing starts to fall and is said to have stalled. The optimum angle of incidence for an aerofoil is around 15°.

![Diagram](image)

**Figure 5.3** (a)–(c) The development of turbulent air flow across an aerofoil as the angle of incidence increases. (d) As the angle of incidence of the aerofoil increases, lift (L) decreases and drag (D) increases. The length of the arrows for L and D indicate the magnitude of these forces.
You should now be able to list three key factors that affect lift. What are they?

Three key factors that affect lift are:

(a) wing area \((a)\);
(b) speed of air flow \((v)\);
(c) angle of incidence \((\alpha)\).

The lift \((L)\) that a wing can generate is derived from:

\[
L \propto av^2 \\
\text{or } L = kav^2
\]

where \(k\) is a constant incorporating measures of the shape of the wing.

The maximum lift is generated at the optimum angle of incidence for the wing.

The mass of the whole bird (or aircraft) divided by the total wing area gives the **wing loading** in N m\(^{-2}\). Obviously the lift has to be greater than the downward force due to wing loading or the bird would not fly. The area of the wings is related to the size of the bird. A plot of the logarithm of wing loading against the logarithm of body mass for a large number of bird species gives a strong positive correlation between the two parameters (Figure 5.4). So, although large birds have a greater wing area than small ones, their wing loading is greater. A consequence of this scale effect is that the minimum velocity of air over the wings necessary to provide sufficient lift for flight is higher in large birds than small ones. You can see this need for a higher air flow if you watch large birds take off from the ground. They have to run to build up speed before getting into the air, whereas small birds can just jump into the air and start flying. Of course a large bird may intentionally run into the wind, since it needs to maximize air flow across the wings, not its speed across the ground.

The shapes of bird wings vary substantially. In some species they are long and thin, like those of the albatross, while in others they are short and broad, like those of a pheasant. Two birds can have the same wing area, but very different wing shapes (Figure 5.5). Wing shape is defined by the **aspect ratio**, the ratio of the wing span to the chord (the mean distance between the leading and trailing edges of the wing). You should recall that an alternative method is used to calculate aspect ratio in the tail fin of a fish (Section 2.3.2):

\[
\text{aspect ratio} = \frac{\text{span}}{\text{surface area}}
\]

*Figure 5.4* A plot of wing loading against body mass for 70 species of birds. Note that both axes are logarithmic.
Figure 5.5 Two bird wings that have the same area but different aspect ratios. The two measurements that are made to calculate the aspect ratio are illustrated. Note that the span is a measurement made from wing-tip to body, not wing-tip to wing-tip. (a) A shearwater (Puffinus puffinus) wing; (b) a pheasant (Phasianus colchicus) wing.

There are some correlations between aspect ratio and the style of flight. In general, birds that glide or use high speed flight have wings with higher aspect ratios. Birds capable of a rapid take-off or of soaring on thermals generally have wings with low aspect ratios. Some reasons for these distinctions will become apparent when we consider soaring and gliding in Section 5.4.

Summary of Section 5.2
An aerofoil can generate lift and a bird’s wing acts like an aerofoil. Three key factors influence the generation of lift: the area of the wing, the speed of the air flowing over it and the angle of incidence of the wing to the direction of air flow. The area of the wing is related to the size of the bird and larger birds have larger wings. However, the wing loading (mass of the bird divided by the total area of the wings) is greater in larger birds. The shape of the wings of a bird reflects its lifestyle. Wings can be short or long, broad or narrow, but the shape can be described by calculating the aspect ratio (the ratio of the wing span to the chord).
5.3 The forces acting on a bird in flight

Up to this point we have discussed the bird wing as if it were a static aerofoil like the wing of an aeroplane. However, the bird wing is only analogous to an aircraft wing in a bird that is gliding. Since power in a bird comes from movement of the wings, the aerodynamics become more complicated. Figure 5.6 shows the fundamental difference between the forces acting on a bird and those acting on an aircraft. As a bird flies through the air, it experiences a frictional drag due to the airflow over the body and a downward force due to the weight of the bird. Similar forces act on an aircraft but, in an aircraft they are counteracted by two separate forces: the lift derived from the wings and the forward thrust derived from the engine(s). In the bird, there is only one force: that provided from the wings, so the wings must beat such that the force developed (wingbeat in Figure 5.6b) has both a vertical component—lift—and a horizontal component—thrust. The wingbeat must counteract the weight, as well as providing forward movement.

Figure 5.6 (a) The forces acting on an aeroplane in flight. (b) The forces acting on a bird in flight.
Describing lift as an upward force is not strictly accurate since it makes the assumption that the bird is flying parallel to the ground. It may well not be, so the more accurate definition of lift is: that part of the force acting on a wing which is perpendicular to the direction of the air flow. Drag acts in the same direction as the air flow (Figure 5.2b). Both lift and drag increase with the speed of air flow, roughly according to the square law—that is, lift and drag are proportional to the square of the speed of air flow which is comparable to the situation of a fish in water (Section 2.3.1). Both also depend upon the size of the bird and the density of the air.

The force shown as drag in Figure 5.6 has three components. The frictional force on the body produces parasite drag, $D_{par}$, which is dependent upon the shape and size of the body. The drag that results from the air flow over the wings is called profile drag, $D_{pro}$, and it is influenced by the structure of the wings. The third component is induced drag, $D_{i}$, which is associated with the beating of the wings to generate lift. $D_{i}$, unlike $D_{par}$ and $D_{pro}$, does not increase with the square of the speed, but is greatest at slow speeds close to stalling (Figure 5.7). We shall return to the phenomenon of induced drag in Section 5.7 in connection with wake analysis and vortex theory.

Most birds develop lift and thrust on the downstroke of the wing, flexing the wing on the upstroke to minimize $D_{pro}$. However, this is not the case for all birds. For example, the kestrel (*Falco tinnunculus*) generates lift on the upstroke also, which contributes to supporting its weight, but reduces the mean thrust. Analysis of the flight of birds in wind tunnels has shown that in small birds the upstroke—the ‘return’ stroke—generally has little or no aerodynamic effect. In the pigeon, for example, the wing tip is moved close to the body on the upstroke and only a small portion of each wing is in the air flow. This action reduces drag, but does not generate thrust or lift.

What is the consequence of this type of upstroke for the velocity of the bird?

If the upstroke does not generate lift or thrust, the bird decelerates during the upstroke. However, birds adapted for gliding may keep the wings extended during the upstroke in fast flight, generating lift. A bird that glides usually has thin wings with a high aspect ratio, factors that will give lower drag. For birds with a wing that produces high drag, generally the smaller birds and those with a low aspect ratio, the optimum strategy is to have a passive upstroke.

As you will read in Section 5.7, the differences between the wing movements of different species of bird have consequences for the air movements around these birds.
Summary of Section 5.3

The forces acting on a bird in flight are thrust, lift, drag and gravity. The wingbeat provides lift and also thrust for forward motion and the lift must counteract the force of gravity. Drag acts in the same direction as air flow and is divided into three components: parasite drag due to the shape and size of the body, profile drag due to the structure of the wings and induced drag due to the beating of the wings.

5.4 Soaring and gliding

Many large birds conserve energy by gliding, whenever wind conditions allow. In a glide, the bird holds its wings outstretched and descends relative to the direction of air flow. With a shallow angle of glide a bird can travel a considerable distance relative to the ground, particularly if it has started from a good height.

What other factors might affect gliding performance in a large bird?

Both wing loading and aspect ratio influence gliding performance. The speed of a glide depends on the wing loading, so generally a large bird travels faster than a small one and glides at a shallower angle. The angle is also dependent on the aspect ratio of the wing. A bird with a high-aspect-ratio wing, like the albatross (*Diomedea* sp.), can glide at a shallower angle than a vulture (e.g. *Gyps fulvus*), which has a lower aspect ratio.

The rate at which a bird descends is called the sinking speed. Measurements of sinking speed at different air speeds have shown that there are differences between species. The vulture has a minimum sinking speed of just under 2 m s\(^{-1}\) whereas for a pigeon the figure is 2.5 m s\(^{-1}\). By comparison, an aircraft built to glide can have a sinking speed of well under 1 m s\(^{-1}\).

Of the two birds mentioned above, the pigeon and the vulture, which would have the wings with the higher aspect ratio?

A high-aspect-ratio wing would be associated with good gliding ability and hence a slow sinking speed, so the vulture would have a higher aspect ratio wing than the pigeon.

5.4.1 Forces acting on a gliding bird

In Section 5.3 you considered the forces acting on a bird while it was flying. Obviously the forces acting on a gliding bird are similar, but the wing is held rigid. Figure 5.8 shows a gliding bird that is descending at an angle. The glide path is inclined to the horizontal so that the forward thrust is balanced by the drag. There is a vertical resultant force that counteracts the weight and the bird descends at a constant velocity and angle. If the glide path were rotated so that it was horizontal, then the lift would balance the weight and the bird would travel horizontally with a reducing velocity.

Why would the forward velocity decrease?

The drag would not be completely balanced by thrust, so velocity would decrease and, of course, the bird would be in a highly unstable state.
Figure 5.8 The forces acting on a gliding bird. Sinking speed = vertical distance moved/time taken (i.e. $d_v/t$).

Birds are able to change the characteristics of a glide. For example, at low speeds, the tail feathers are spread to increase lift. The vulture adjusts the angle of its body in the air, so changing the angle of descent. Then, as it approaches the ground, it extends its legs which act as brakes, steepening the angle of descent (Figure 5.9), and eventually lands on the ground. The mechanisms for altering the glide angle alter the glide distance. How then can some gliding birds apparently move horizontally or even rise?

5.4.2 Soaring on thermals

Hot air rises. Where there is uneven heating of air by the sun, for example on hillsides facing the sun, which are hotter than the surrounding land in shadow, warmer air rises, either as a column or a series of vortex rings. Such upward movements are called thermals. Gliding birds, by circling within the rising air use the lift that the air movement produces and glide upwards, or soar. Thermals over the plains of East Africa can rise as fast as 4 m s$^{-1}$.

What is the implication of the presence of thermals for a vulture gliding over the plains of East Africa?

Figure 5.9 The vulture in gliding flight. (a) and (b) Tilting the body produces different gliding angles. (c) At any speed, the vulture can glide more steeply if the legs are lowered, acting as air brakes. The length of the lift and drag arrows indicates the magnitude of the force.
The vulture has a sinking speed of approximately 2 m s\(^{-1}\) (Section 5.4), so a thermal would provide a net gain in lift. Observations made on Ruppell’s griffon vultures (Gyps rueppellii) over the Serengeti plains have shown that large distances can be travelled rapidly by soaring on a thermal and then gliding to the next. The vultures nest on cliffs at the edge of the plain and then travel to their feeding areas around the herds of mammals that inhabit the Serengeti. Colin Pennycuick of Bristol University followed the vultures in a motorized glider and discovered that one individual travelled 75 km in only 96 minutes entirely by using the thermals. The vultures can travel to great height on thermals, thus rising above the level of their cliff nest before returning from feeding.

Can you think of any limitations to soaring that would affect the vultures?

On cloudy days, and first thing in the morning, the vultures cannot go and feed because the temperatures are not high and hence not uneven enough to generate the thermals that they need.

### 5.4.3 Slope soaring

Rising air is also found over ridges—both ridges on land and waves on the sea. Sloping contours force wind upwards towards the ridge, it flows over the ridge and then rebounds. Over the long ocean stretches, the large waves can provide a whole series of rising and rebounding air currents that birds can utilize for soaring. The air currents do not give great vertical movement, unlike thermals, but they do still enable long distance travel because of their regular pattern (Figure 5.10).

Cliffs and sea margins also provide upward movement of air. Warm air flowing off the land rises over the cold air above the sea. Wind from the sea hitting the edge of a cliff is deflected upwards producing a localized, near vertical, air current—the obstruction current (Figure 5.11). The gannet (Sula bassana) shown in Plate 5.1 is gliding in the wind that blows almost continually around the Bass Rock in the Firth of Forth. The updraft is supporting the bird which, although moving relative to the air flow, appears almost stationary to an observer on the rock. Most birds that soar have prominent, separated feathers at the tips of their wings. These feathers spread out in both the vertical and horizontal plane. Their role appears to be to reduce drag.

Figure 5.10  Slope soaring over a wave.

Figure 5.11  Obstruction currents at the edges of cliffs allow birds to gain height.
Summary of Section 5.4

Large birds can conserve energy by gliding, holding the wings outstretched. With the wings in this position, a bird will descend, its speed of descent being influenced by the wing loading and the aspect ratio of the wing. In regions where there are columns or patches of hot air rising, birds can glide upwards—soar—by circling within the rising air. The bird will rise providing that the air is rising faster than the bird’s sinking speed in still air. Sloping ground or large ocean waves will deflect air upwards and birds can use this to rise, a strategy called slope soaring.

5.5 Structure of the bird wing

Birds first appeared in the fossil record during the Jurassic period 146–208 million years ago, evolving from the archosaurs, an ancient group of reptiles. The bird wing evolved from the front limb and so has similarities with the front limb of tetrapods such as reptiles and mammals. These similarities are apparent when a wing is compared with a human arm (Figure 5.12). Some of the bones are directly comparable, but from the wrist to the tip of the limb there is no immediate similarity. The birds evolved from reptiles which had a pentadactyl
limb with five digits, so substantial fusion and loss of bones has occurred as evolution has progressed. In birds, there are two ‘wrist’ bones, a carpal at the end of the radius (the radiale) and one at the end of the ulna (the ulnare). The ‘hand’ has what appears to be a single bone made up from two that are fused at each end, the carpometacarpus. In fact, some interesting developmental studies have shown that this bone is formed from fusion of the carpals and metacarpals of three digits, equivalent to the first, second and third digit of the pentadactyl limb of the reptiles. The second digit is long and robust and carries feathers.

The numbering of the digits of the bird is a controversial area of research. It is possible that the bones of the digits found in birds are derived from the second, third and fourth digits of the pentadactyl limb, rather than the first, second and third. This debate is an important one for evolutionary biology, but of no direct aerodynamic significance.

The feathers on the bird wing probably evolved from the scales of reptiles, but the stages of evolution are not known. Wing feathers can be divided broadly into two types—flight and contour—based on their means of attachment to the wing.

Look at the wing in Figure 5.12. The flight feathers are inserted onto the ulna, the carpometacarpus and the second digit of the wing. Those on the ulna are the secondary flight feathers, and those on the carpometacarpus and second digit, the primaries. The ulna is thicker than the radius, to allow for the insertion of the tips of the flight feathers—a strong attachment is needed to withstand the forces acting on them during flight.

Over both surfaces of the wing are spread the contour feathers which give the wing its curved shape. The contour feathers have been removed from the wing illustrated in Figure 5.12. They are inserted onto the skin membrane that covers the wings, so contour feathers, unlike the flight feathers, do not have a firm base.

The first digit carries a small group of feathers which together form the alula or bastard wing (visible on the gannet in Plate 5.1). The alula has a limited amount of movement. It can be raised into the air flow over the wing to enhance lift as the wing approaches a stall. The laminar flow of the layers of air over the wing begins to break up as air speed drops or the angle of incidence increases; air flow becomes turbulent, lift declines and the wing can stall. When a bird raises the alula into the airstream, there is an increase in the velocity of the air travelling through the small gap between the alula and the main wing. This increase generates extra lift and the presence of the alula helps maintain laminar flow, so greater angles of incidence can be reached before stalling and greater lift is produced.

When might you see a bird with the alula raised into the airflow over its wing?

The alula is often used as birds land. At this stage in flight the bird is decelerating and there is a risk of stalling.

The structure of flight and contour feathers is compared in Figure 5.13. The interlocking barbs and barbules of the flight feathers produce a structure that is almost airtight, yet is light enough to remain firm while only attached to the wing at one end.
Figure 5.13 (a) A primary flight feather with an enlargement which shows the barbs. (b) and (c) Magnified portions of the flight feather viewed from above (b) and below (c). (d) A contour feather.

The flight feather (Figure 5.13a) is asymmetrical, with the rachis offset from the centre (Figure 5.13a). This affects the behaviour of the feather during the wingbeat cycle because the centre of pressure of the air is not along the line of the stiffest part of the feather, the rachis. On the downstroke, the pressure acting on the vane of the feather rotates it slightly about the point of insertion, forcing the feathers on the wing together into a broad surface pushing against the air. On the upstroke, the pressure acts on the feather in the opposite way, from the upper surface, producing a twist in the other direction. The rotation opens gaps between the feathers which reduces the resistance to air flow as the wing readies itself for the next downward power stroke (Figure 5.14).

The bones of birds are much lighter than those of terrestrial vertebrates. The lightening results from thinner walls and the lack of blood-forming or fatty tissue filling the interior. To retain strength, the interior is stiffened with light struts of bone (Figure 5.15).
Figure 5.14 A cross-section through the feathers to show rotation during the wingbeat cycle. The arrows represent air movement.

Figure 5.15 A longitudinal section through the humerus of a bird showing how the thin wall is strengthened by struts of bone. The cavities between the bone struts are filled with air.

Summary of Section 5.5

The structure of the bird wing is homologous with the structure of the typical tetrapod forelimb from which it evolved. The feathers on the wing are probably derived from the scales of reptiles, the group from which the birds diverged in the Jurassic period. The bones of birds are much lighter than those of terrestrial vertebrates. There are air-filled cavities within the bones and the walls of the bones are much thinner.
5.6 Flapping flight

In the introduction to this chapter you read about an early attempt by a man to fly from the Eiffel Tower using wings attached to his arms. The anatomical arrangement of muscles in the human does not allow the arms to generate sufficient power for flight. In birds, the anatomy of the pectoral girdle is highly modified and the muscles that move the wings are massive. Figure 5.16a shows the skeleton of a bird and Figure 5.16b the position of the flight muscles.

**Figure 5.16** (a) Photograph of the skeleton of a common tern (*Sterno hirundo*) with the wings outstretched as in flight. (b) The attachments of the two major flight muscles to the skeleton (shown for one of the wings).
What is striking about the position of the muscles relative to the point of articulation of the wing?

Although the muscles raise and lower the wing, they lie below the point of articulation.

What is counter-intuitive about the muscle mass that raises the wing being below the point of articulation?

For a muscle to raise the wing it needs to pull the wing up and so needs to be above the wing or, to be more accurate, needs to exert a force on the upper surface of the wing. The muscle that raises the wing, the supracoracoideus (Figure 5.16b), has a long tendon that passes through a gap between the head of the humerus, the scapula and the coracoid bone. This gap is called the foramen triosseum. The tendon is attached to the deltoide ridge that runs along the dorsal surface of the humerus. Thus when the supracoracoideus contracts, the force is transmitted through the tendon and converted to an upward force on the humerus, so raising the wing. The system is just like a rope (the tendon) passing over a pulley (the foramen triosseum). The pectoralis muscle is responsible for the downstroke.

From what you know about the power stroke in flapping flight, which muscle is likely to be the larger, the supracoracoideus or the pectoralis?

In most birds the downstroke of the wing is the power stroke (Section 5.3) so you would expect the pectoralis muscle to be larger and indeed this is generally the case. For example, in the herring gull (Larus argentatus) the supracoracoideus muscle is very much smaller than the pectoralis, and if you get the opportunity to look at a domestic chicken you will find similarly that the pectoralis muscle is larger.

The contraction of both of the supracoracoideus muscles to produce an upstroke generates a force on the joint between the humerus and coracoid bones. If you look at Figure 5.16 and imagine the muscles contracting you can see that they will tend to pull the joint in towards the mid-line. Between the two joints is a U-shaped bone, the furcula, which is probably more familiar to you as the wishbone. It appears that this bone and its joint can store energy, like a spring, and perhaps act to provide an opposing force to the inward force generated when the supracoracoideus muscles contract. Information about the role of the furcula comes from cineradiographic analysis of starlings in flight. Traces from the film made in this study are shown in Figure 5.17. During the downstroke the furcula (Figure 5.18) bends laterally, springing back during the upstroke.

During the wingbeat cycle, the sternum also moves as the muscles attached to it contract. On the downstroke, the sternum moves upwards and backwards, dropping again and moving forward during the upstroke. A consequence of these bone movements is that the rib cage changes shape, altering the size of the thoracic cavity. So, there is a link between the wingbeat cycle and the respiratory cycle, though the scale of the contribution made by the flight muscle contractions to respiration is not yet known.
Figure 5.17  Analysis of the wingbeat cycle of a European starling (*Sturnus vulgaris*). (a) Dorsal and (b) lateral views of the bird in flight.

Figure 5.18  The furcula and the coracoids of the starling. These bones bend laterally during flight.

Summary of Section 5.6

The downstroke of the wing is the power stroke in most species of bird and in these species the pectoralis muscle, which produces the downstroke, is substantially larger than the supracoracoideus, which produces the upstroke. Both muscles lie below the point of articulation of the wing. The supracoracoideus has a long tendon which is attached to the dorsal surface of the humerus so that although the muscle lies below the point of articulation, the force it develops is transmitted via the tendon to the upper surface of the humerus, so raising the wing.
5.7 The wake

In Section 2.3.2 you read about the studies of locomotion in fluids that have concentrated on the wake left by fish moving through the water. There have also been a number of studies of the wake of birds, though as the wake is such a short-lived phenomenon, and normally invisible, such studies have not been easy. Nikolai Kokshaysky worked on this problem at the Severtsov Institute in Moscow in the late 1970s using chaffinches that he had trained to fly between two perches positioned a few metres apart. As a bird flew between the perches, he blew wood dust into the air. The dust took up the shape of the bird’s wake. To photograph the wake, he carried out the experiments in darkness and used an infrared beam to detect the flight of the bird and trigger a series of flash guns. Two cameras at right angles to each other recorded the wake pattern. Some of Kokshaysky’s photographs are shown in Figure 5.19.

Figure 5.19d shows a vortex ring formed behind the bird. This was not the first time that such vortices had been observed, but these are the first photographs to show vortex formation in birds.
The air movements that produce such effects were observed a long time ago in aircraft, but the significance was not immediately apparent. Here is an account of such observations, written many years after the event.

The author has vivid memories of an incident when, on a festive occasion, long streamers were attached to the wing-tips of his flying boat. When taxying on the water, these streamers rotated violently and they continued to do so in the air until, after a few minutes, they were nothing but shreds. The author and his colleagues dismissed the whole affair with such silly remarks as “That was funny, wasn’t it?” Had they been a little more intelligent they would have realized that a phenomenon of this kind does not occur without good reason and they would have followed it up by further experiment – and maybe it would have slowly dawned on them that this was one of the most significant facts of aviation and one that was to influence the whole trend of aeroplane design. But that discovery was left to others and, even then, it took a long time.

A. C. Kermode (1930)

What Kermode had observed was the consequence of the air flow being in a spiral form as it left the trailing edge of the wing of his aircraft. You can reproduce the observation by attaching thin, lightweight streamers to the tips of the wings of a balsa-wood glider and launching it into the air. The streamers should take up a spiral form, rotating clockwise on one side and anti-clockwise on the other. It may not be easy to see this! Alternatively, hold the glider in the air stream from a hairdryer and you should see the streamers spiral backwards from the wing.

Figure 5.20 shows the airflow over a fixed wing. As the air flows off the trailing edge of the wing it is deflected downwards and inwards, imparting a clockwise rotation to the airflow from the right-hand wing and an anti-clockwise one from the left-hand one. The wake that is formed is a continuous pair of spirals. How, then, is a vortex formed in birds?

![Diagram of airflow and vortex](image)

**Figure 5.20** The wake created by a fixed aerofoil as it moves through the air. Note that the direction of the spiral is inwards on each side, imparting a clockwise rotation (seen from the front) on the right of the aerofoil and an anti-clockwise one on the left.
In flapping flight, as Figure 5.19 shows, a vortex is formed on the downstroke of the wing. Figure 5.21a shows how, as the wings move down, two vortex sheets form, one from each wing. The sheets roll up to form a half-ring (Figure 5.21b) and then, as the downstroke is completed, the vortex is shed as a complete ring (Figure 5.21c). The wings are flexed during the upstroke, have little interaction with the air and produce little vorticity: recall that it is the downstroke that normally generates the power (Section 5.3).

The significance of the vortex for the physiologist is that because it represents the reaction of the air to the bird moving through it, observations and measurements of the vortices produced by birds can yield valuable information about aerodynamic forces, mechanical energetics, wing design and other features of flight. For example, Figure 5.22 shows that each vortex ring is tilted from the horizontal. The angle of tilt is related to the thrust-to-weight ratio of the bird. Jeremy Rayner, at Bristol University, has been in the forefront of this work. Indeed, he published a theoretical model of vortex formation in the same year that Nikolai Kokshaysky published his photographs of the chaffinch. Subsequently, Jeremy Rayner worked with bubbles to photograph the wake left by a number of species of birds and, with Gareth Jones at Bristol, the wake left by bats. He filled soap bubbles with a mixture of helium and air, such that they were neutrally buoyant. As the animal flew through the cloud of bubbles, a linear series of flashguns was triggered in sequence. A pair of cameras took stereo images which showed the moving bubbles as a series of dots, the distance between each position of a bubble on the film representing the time between two flashes and the distance that the bubble had travelled in that time.

A flying bird must expend energy to generate the vortices, and this is equivalent to the energy necessary to overcome induced drag. So, one might imagine that there would be an advantage in not producing vortices since a component of drag would be absent. However, this is not the case. The only way in which
Forward movement can be imparted to the bird by flapping flight is if there is a transport of momentum to the air. The direction and speed of movement of the vortex ring backwards is indicative of the magnitude and direction of the force that created it. So, for optimum flight conditions, the wake generated should provide the maximum momentum transport for the minimum energy input. Experiments and theory both suggest that there are only a few types of wake that are associated with efficient flight. The optimum structures are rings, loops or spirals. Figure 5.23 shows the wake produced by a falcon (Falco sp.) in cruising flight, where the wing produces some lift on the upstroke. The wake is very like that produced by an aircraft and, when the bird is gliding, the wake is a pair of linear vortices, the continuous vortex wake, as you would have seen in the balsa wood glider experiment mentioned earlier.

Figure 5.22 The chain of vortex rings that forms in the wake of a bird in forward flight.

Figure 5.23 The continuous vortex wake of a falcon.
The type of wake can be related to the lifestyle of the animal. In all species so far studied, a vortex ring wake is produced during slow flight and, where the wings are broader and more rounded, in fast and cruising flight. Animals with longer, thinner wings, such as falcons, kestrels, swallows, swifts and pipistrelle bats, change to a continuous vortex as speed increases. They may maintain this type of wake when subsequently decelerating. The types of wake are analogous with the gaits that are described for terrestrial animals. Only the two types of gait described above have been observed so far and it is unlikely that any more exist, apart perhaps from some very specialized cases.

5.8 Conclusion

Aerodynamic theory derived from the development of aviation has provided a theoretical framework for the study of flight in birds. The primary difference between an aircraft and a bird, in terms of the aerodynamic forces acting on them, is that the wings of an aircraft provide lift and it derives its thrust from an engine, whereas in a bird the wings provide both lift and forward movement. Birds evolved from reptiles, but as the ability to fly evolved the skeleton became lighter, the forelimbs became substantially modified, the scales were replaced by feathers and the muscles involved in forelimb movement changed substantially. The shape of the wings in a particular species is an adaptation to a particular mode of life such as soaring, gliding or fast flapping flight. A measure of the shape of a wing is the aspect ratio, the ratio of the wing span to the mean chord.

Birds in flight are subject to a drag force that has a number of components. One of these, induced drag, is a consequence of the formation of a wake. The wakes of birds flying under laboratory conditions have been visualized using wood particles or bubbles containing helium. The wake has revealed the formation of vortices in either rings or linear spirals. These two types of wake are called gaits, in a similar way to the locomotory patterns of terrestrial animals. The study of gaits has provided information about the aerodynamics of flight.

Studying the dynamics of bird flight throws up important energetic considerations—how do you estimate the costs of flight or, more importantly, measure them under realistic conditions? Wake visualization, together with vortex theory, has provided a means of estimating mechanical energy consumption in flight, but it is the coupling of aerodynamic theory and observation with the measurement of physiological parameters, such as heart rate in free-flying birds, that has provided the real advance in our understanding of the energetics of flight. It is the energetic cost of flying and the occurrence of flying in other groups of animals that we consider in the next chapter.
Objectives for Chapter 5

After completing Chapter 5 you should be able to:

5.1 Define and use, or recognize definitions and applications of, each of the **bold** terms.

5.2 Explain how an aerofoil moving through air generates lift.

5.3 Draw a diagram illustrating the forces acting on a bird in flight and describe the forces in non-mathematical terms.

5.4 Draw outline diagrams of, or label diagrams of, the shape of typical, identified, birds and explain how they are adapted to their particular flight strategy.

5.5 Use diagrams to explain how the musculature of a bird produces the flapping flight movements of the wing and how the wing generates both lift and thrust.

5.6 Describe techniques used for visualizing air flow in experiments with flying birds and explain the physiological significance of the results from such experiments.

5.7 Describe the two typical gaits observed in flying animals and relate them to particular types of flight.

Questions for Chapter 5

*Answers to questions are at the end of the book.*

**Question 5.1 (Objectives 5.1, 5.2 and 5.3)**

For each of the following statements about flight, decide whether the statement is true or false and explain why.

(a) Aspect ratio describes the cross-sectional area of a wing.

(b) A bird flying slowly would reduce the angle of incidence of its wings to increase lift.

(c) Induced drag and profile drag arise from the active flapping of the wings in birds.

**Question 5.2 (Objective 5.4)**

Look at the drawings of the two bird wings, in Figure 5.24a and b. For each describe the aspect ratio of the wing and the probable style of flight of the owner.

![Figure 5.24  Wing shapes of two birds (not drawn to scale). For use with Question 5.2.](image-url)
Question 5.3 (Objective 5.5)
In a few brief statements, describe the muscular events that occur, in sequence, from the bottom of one downstroke of a bird’s wing until the bottom of the next. Indicate the direction of the forces involved and the bones that the muscles act upon.

Question 5.4 (Objective 5.6)
Outline one technique that has been used to visualize the wake of a flying bird. What is the value, to physiologists, of the pictures of the wake that can be obtained.

Question 5.5 (Objective 5.7)
What are the two gaits observed in birds? Under what conditions can a bird change from one gait to another?
Plate 5.1 The gannet (*Sula bassana*) gliding near the Bass Rock.

Plate 6.1 Gliding vertebrates: (a) the Javan flying frog (*Rhacophorus reinwardti*, length 8 cm); (b) the flying fish *Exocoetus volitans*, length 20 cm); (c) the flying lizard or dragon *Draco volans*, length 20 cm); (d) Kuhl's gecko (*Ptychozoon kuhlii*, length 15 cm); (e) the paradise tree snake *Chrysopelia* sp., length 1.5 m); (f) the Southern flying squirrel *Glaucomys volans*, length 25 cm).
Plate 6.2 The largest of the extinct pterosaurs, *Quetzalcoatlus northropi*, wingspan 12 m; it survived to the end of the Cretaceous period.

Plate 6.3 The Costa Rican gliding frog (*Agalychnis spurrelli*, length 8 cm) showing the well-developed webs between the digits.

Plate 6.4 The flying gurnard (*Dactylopterus volitans*, length 50 cm).

Plate 6.5 The gecko (* Ptychozoon sp.*, length 15 cm).