



## Getting Around

Although many animal species engage in gliding or other aerial forms of locomotion, birds, bats and insects are the only living animals capable of powered flight. This is the most energetically demanding form of animal locomotion, and meeting these demands has shaped the evolution of many aspects of bird anatomy, physiology and behaviour.

Powered flight has several necessary components - wings, an engine, a flight stroke, control systems, small body size, lightweight design and an energy source (fuel) - but different species of birds meet these requirements in different ways using different flight styles. Birds do, however, share one common specialisation for powered flight: their forelimbs alone are used for flight, while their hindlimbs are used for walking, running and jumping forms of locomotion. These dual locomotory capacities contributed to the ability of birds to exploit a diverse range of environments and to inhabit every continent on Earth.

◀ White-vented plumeleteer (*Chalybura buffonii*).

# Aerodynamics

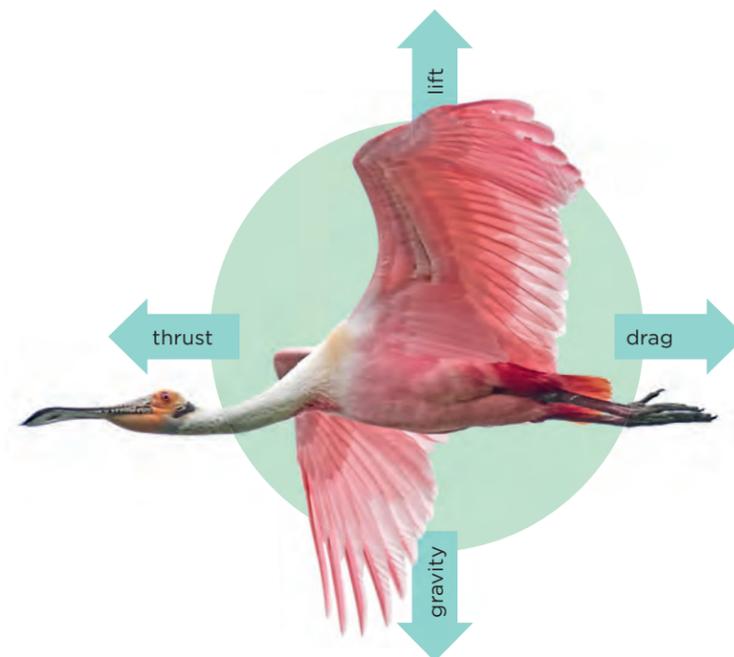
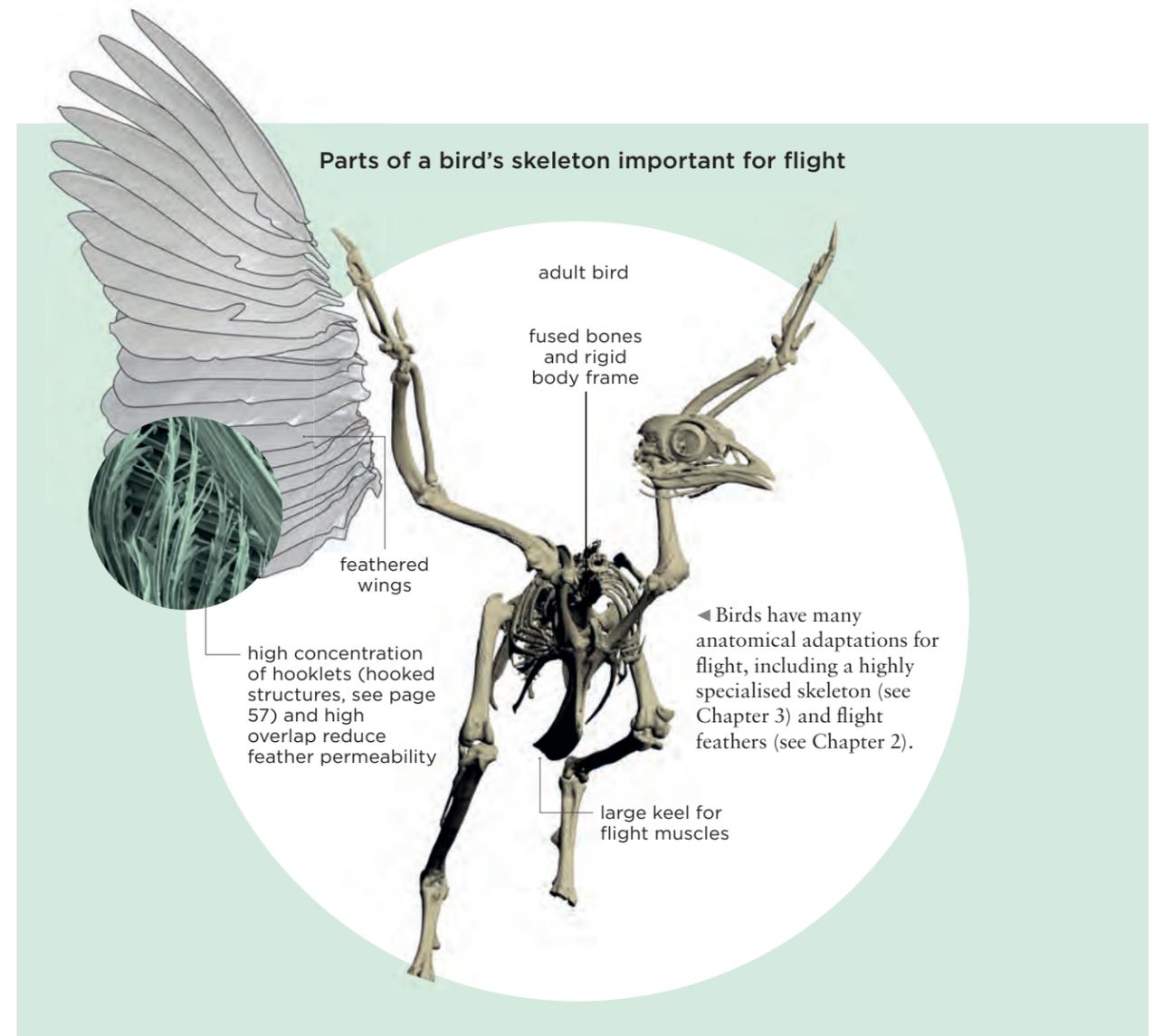
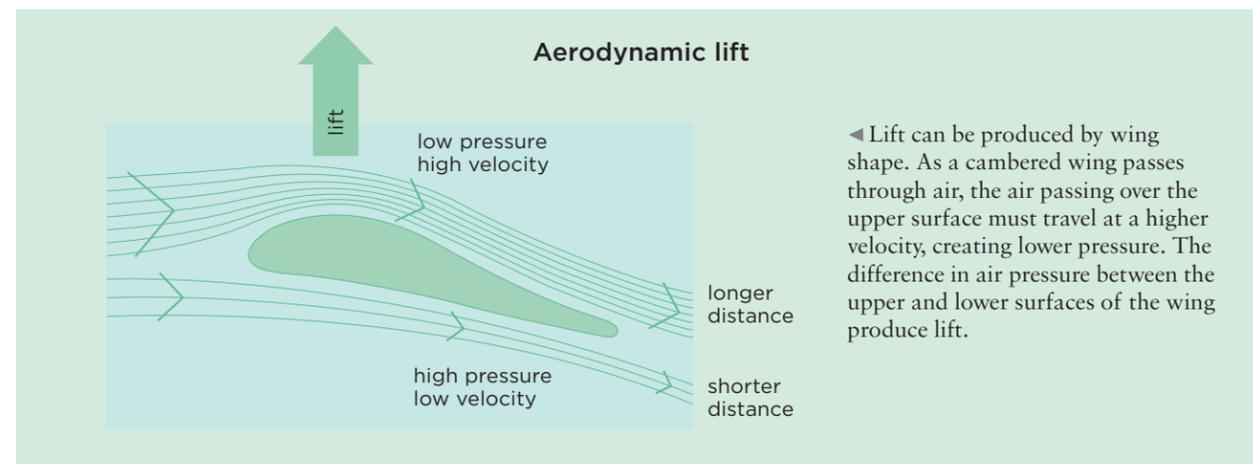
Powered flight requires the generation of forces to overcome gravity and drag. Overcoming the gravity is an acute problem for flying animals. Solid ground or the buoyancy of water counteract the force of gravity for walking and swimming animals, but the air provides little resistance to gravity for those that fly. Wings must provide enough lift to prevent a bird from falling to the ground, and they must also provide enough thrust to overcome drag forces in order to move the bird forward.

## Overcoming drag

Drag is the force that acts in opposition to the forward movement of an object through air or water (see diagram opposite). There are three main types of drag: pressure drag, friction drag and induced drag. Flying birds have adapted to overcome these drag forces in various ways. Pressure drag is generated by low pressure forming behind an object as it moves through air, and can be reduced by having a streamlined fusiform shape. Friction drag is created by shear forces between air molecules as they flow over a surface, and increases with velocity. Friction drag can be reduced by body and wing shape, and by having smooth feather surfaces. Induced drag is created during flapping flight. On the downstroke of a wing, air is pushed downward to create lift, but some of this lift is in a backwards direction, creating drag. Induced drag can be reduced by having long, narrow wings (typical of petrels and albatrosses), and having open slots between primary flight feathers (as in some eagles and vultures; see page 161).

## Producing lift

Gravity is the force pulling objects towards the centre of the Earth (see diagram opposite). Birds overcome both gravity and drag primarily through the use of their wings. During forward motion the body and tail can also provide lift, but most of the aerodynamic force to power flight is generated by the wings. Lift can be intuitively understood by thinking of the forces acting on your outstretched hand on a windy day, or if you carefully hold your arm out of the window of a moving vehicle. The wings of a gliding bird, or of a fixed-wing aircraft, generate lift – as does any solid object moving through a fluid medium. Lift is generated perpendicular to the wing due to lower air pressure forming above it, and wings are effective at generating this force thanks to their aerofoil shape. This causes differential airflow across the upper and lower surfaces of the wing, thereby increasing the pressure differential across the wing.



The amount of lift generated by a wing depends on several factors, including wing shape (aspect ratio), wing curvature (camber), feather structure, and orientation of the wing relative to the direction of motion (angle of attack). The wings of a flapping bird also generate lift, but the airflow due to forward motion of the body (as in gliding) and downstroke of the wing combine to create lift that acts both upward and forward, counteracting both gravity and drag. Lift and drag production vary across species depending on wing and feather shapes, and also from moment to moment within an individual bird as it flaps its wings. Birds rely on complex neuromuscular control to continuously change the shape of their wings during flapping in order to modify the size and direction of these forces, thereby staying aloft.

◀ The four forces experienced by any flying animal or aircraft.

# Wings and tails

Different birds have different flight speeds and styles depending on their habitat, lifestyle and behaviour. Some need high manoeuvrability to navigate their way through a cluttered environment, while others are adapted to soar over the open ocean. And while some must generate massive force for quick acceleration and take-off, others need to keep their energy expenditure during flight to a minimum. These and other factors have led to the evolution of diverse wing and tail shapes.

## Wing shape

The aerodynamic forces of lift and drag vary depending on wing size and shape. Aspect ratio is the measure of wing shape, and is calculated as the wing length (wingspan) divided by the wing width (wing chord). The long, pointed wings of swifts and albatrosses have high aspect ratios, providing greater efficiency (i.e. more lift relative to drag), and thus the

birds require less energy for flight. In contrast, the shorter, wider wings of sparrows and titmice have low aspect ratios, which facilitate rapid take-offs and manoeuvring through a cluttered environment (see also pages 32–3).

In some birds such as hawks and eagles, the outermost feathers (the primaries) on their wings have wide spaces or slots between them. These open



slots change wing shape to reduce the formation of vortexes at the wing tips and thus reduce the induced drag and increase lift.

The aspect ratio of the wing is usually considered in tandem with the wing loading, or the ratio of bird weight to wing area. This is because heavy birds with the same aspect ratio as lighter birds will have relatively reduced flight performance.

▲ Large raptors and other soaring birds can modify their wing shape by adjusting the gaps between the outermost primary flight feathers, as seen in this brahminy kite (*Haliastur indus*).

## Two extremes of wing aspect ratio



▲ The long, tapered wings of this northern royal albatross (*Diomedea sanfordi*), soaring near New Zealand, have a high aspect ratio, making them more efficient.



▲ Most sparrows, such as this Eurasian tree sparrow (*Passer montanus*), have relatively broad, short wings with a low aspect ratio, allowing manoeuvrability.

## Forked tails improve lift



▲ Forked tails, such as that of tree swallows (*Tachycineta bicolor*), can be used as visual displays, but they also provide more lift compared to a wedge-shaped tail of equivalent length.

## Tail shape

Besides the wings, the tail (and the body) can be important in generating more lift than drag – in fact, they provide up to 15 per cent of the lift required to overcome gravity. On first glance, bird tails would seem to provide drag and be costly to carry through the air. However, they actually provide substantial lift in many species. Aerodynamic modelling suggests that slightly forked tails that become triangular when fanned, as in American tree swallows (*Tachycineta bicolor*) and common terns (*Sterna hirundo*), provide high lift relative to their drag. In addition, tail feathers can effectively extend the length of the body during flight, contributing to a long fusiform shape that reduces pressure drag and the width of the wake behind a flying bird. Increasing the length of an object relative to its width creates a more aerodynamic shape by reducing pressure drag, and accounts for the shape not only of birds but of rowing shells, canoes and missiles.

# Wing strokes

Aeroplanes have fixed wings that provide lift, and engines or propellers that provide thrust. In contrast, birds must provide both lift and thrust with their wings, and do so by stroking the wing up and down, essentially rowing through the air. As birds flap their wings, they continuously control their shape, camber and attack angle to modify aerodynamic forces.

## Downstrokes and upstrokes

The power stroke is the downstroke of the wing that provides lift and propulsion, and is generated primarily by the large pectoralis flight muscles in the chest. During this stroke the wing can be swept down and forward, or down and backward, and is also rotated at the shoulder and other joints to adjust the angle of attack. These aspects of the downstroke vary

during take-off, forward motion and hovering. The downstroke is followed by an upstroke, which serves as a recovery phase. Upward motion of the wing is powered by contraction of the supracoracoideus flight muscle (see pages 94–5) and adjusted by using other muscles controlling the upper limb. Compared to the downstroke, the upstroke is more variable across species and during different types of flight.



◀ This multiple-exposure composite image reveals the undulating upstrokes and downstrokes of the wings of a Mediterranean Audouin's gull (*Ichthyaetus audouinii*), creating lift and propulsion.

▼ Birds can change the shape of their wings as they manoeuvre, as in this western barn owl (*Tyto alba*) preparing to land.



## Flight gaits

Variation in the upstroke creates different flight gaits, including vortex-ring gait and continuous-vortex gait. In the vortex-ring gait, lift is produced only during the downstroke of the wing, and drag is minimised during the upstroke by either rotating the wing tips backward or opening the primary flight feathers like a venetian blind. Continuous-vortex gait wing strokes create lift during both the downstroke and upstroke by keeping the wings partially or fully extended. Although lift is provided on both strokes, most is produced during the downstroke.

Some birds can use both types of gait, depending on their wing shape. At slower speeds all birds generally use vortex-ring gait during flight. At higher

▲ American kestrels (*Falco sparverius*) can use different wing gaits depending on their flight speed, from 60 km/h during rapid flight to almost stationary as they scan for prey.

speeds, birds whose wings have a low aspect ratio (e.g. sparrows or pigeons) continue using vortex-ring gait, but those whose wings have a high aspect ratio (e.g. falcons) switch to a continuous-vortex gait. For example, American kestrels (*Falco sparverius*) use continuous-vortex gait at high speeds, and vortex-ring gait at intermediate speeds (by opening the primary feathers) and slow speeds (via wing-tip rotation).

# Power for flight: physics meets biology

Newton's third law of motion states that for every action there is an equal and opposite reaction. For a flying bird, the downward force of gravity is counteracted by an opposing upward force of lift, and the forward force of thrust is counteracted by a backward force of drag. The good news for birds is the energy required to move a given distance during flight is quite low compared to swimming or running the same distance. The bad news, however, is that gravity causes them to use much more energy per unit of time.

## Generating power

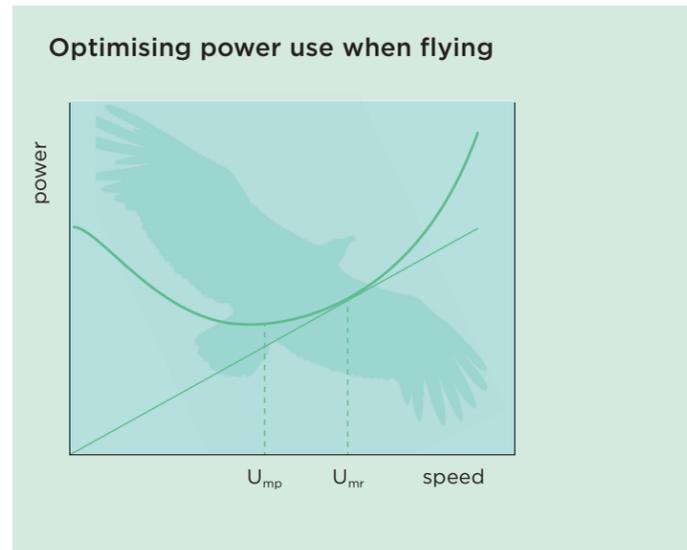
When hawks soar, they usually combine the lift generated by the aerodynamic shape of their wings with that from rising warm air currents. Flapping flight is more complicated than fixed-wing flight (e.g. soaring or gliding like an aeroplane), in that a bird's flexible wings essentially paddle through the wind to get aloft – a very energy-expensive manoeuvre. In this, lift generated by the aerodynamic shape of the wings is combined with the forward thrust and additional lift gained by flapping to sustain forward flight over longer distances.

The power requirements for walking and running increase with speed, whereas those of birds in flight are more complicated owing to the additional difficulty of staying aloft. Specifically, at relatively

slow speeds birds must work harder to stay aloft than when flying at moderate speeds. The resulting graph that plots power requirements against flying speeds, which forms a shallow U-shaped curve (see below left), indicates that there is a flight speed at which birds can optimise their power requirements.

▼ Whooper swans (*Cygnus cygnus*) are among the heaviest living birds (15–23 kg) that can still fly. The extra power required for take-off for these very large, heavy birds must be augmented by running.

▼ Power required at take-off is high. As the bird picks up speed, the power required decreases to a minimum ( $U_{mp}$ ), then increases again. Best 'fuel economy' is achieved at  $U_{mr}$  (maximum range).



## Heavy birds

An interesting corollary of the laws of physics applied to bird flight is that, as the weight of a bird increases, there comes a point at which the downward force of gravity cannot be overcome and the bird cannot lift off the ground. Among the heaviest living birds that can fly under their own power for a sustained period are the New World trumpeter swan (*Cygnus buccinator*; 10–14 kg), and Old World mute swan (*C. olor*; 15–23 kg) and great bustard (*Otis tarda*; 15–20 kg). However, most similarly heavy birds, including the largest of the vultures (11–15 kg), fly mainly by gliding and soaring with the assistance of thermals, and use flapping flight only for initial take-off. The heaviest-known ancient bird that could fly was *Argentavis magnificens* (c. 70 kg), from the

▲ *Argentavis magnificens* is an extinct species from the Upper Miocene (c. 6 million years ago) that is believed to be the largest flying bird (with a wingspan of 7 m and weighing 70 kg) that ever lived. Given the laws of physics, it was likely a soarer incapable of powered, flapping flight.

Upper Miocene (around 6 million years ago) of Argentina, although it was probably too large to be capable of continuous flapping flight and instead presumably flew by gliding and soaring like modern-day vultures. The heaviest extant birds, including the ostriches (100–150 kg), are relegated to a running form of locomotion.

# Power for flight: the necessary metabolism

Given that flying is a relatively expensive form of locomotion, birds have evolved ways to lighten their load in order to reduce the effective force of gravity, and evolution has shaped their wings and feathers to maximise lift. In addition, they have specialised their fuel use, using fat as their primary source of energy for powering sustained flight.

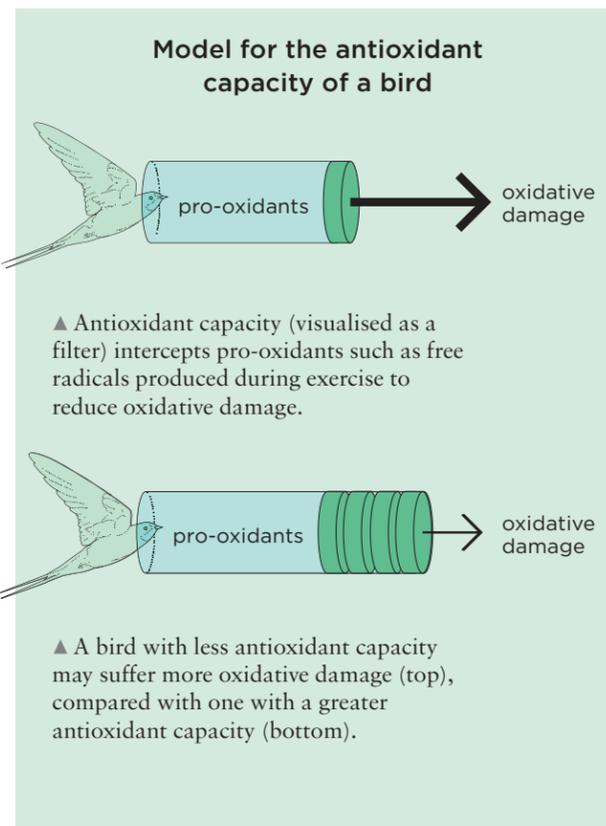
## Fuel for flight

Roughly 90 per cent of the energy birds use during long-distance flight comes from fat, with the remainder from protein and some carbohydrate stores. Some proteins and carbohydrates are also metabolised during such flights to provide necessary nutrients and water, rather than to meet the bird's primary energy needs directly. In contrast, a fast-running mammal (including a human) uses primarily carbohydrates (mostly glycogen stored within muscles) as fuel. Fat is the best fuel for weight-economising birds, however, because when stored it contains eight to ten times more energy per unit of wet mass (37 kJ/g) than alternative fuels such as proteins and carbohydrates (4–5 kJ/g).

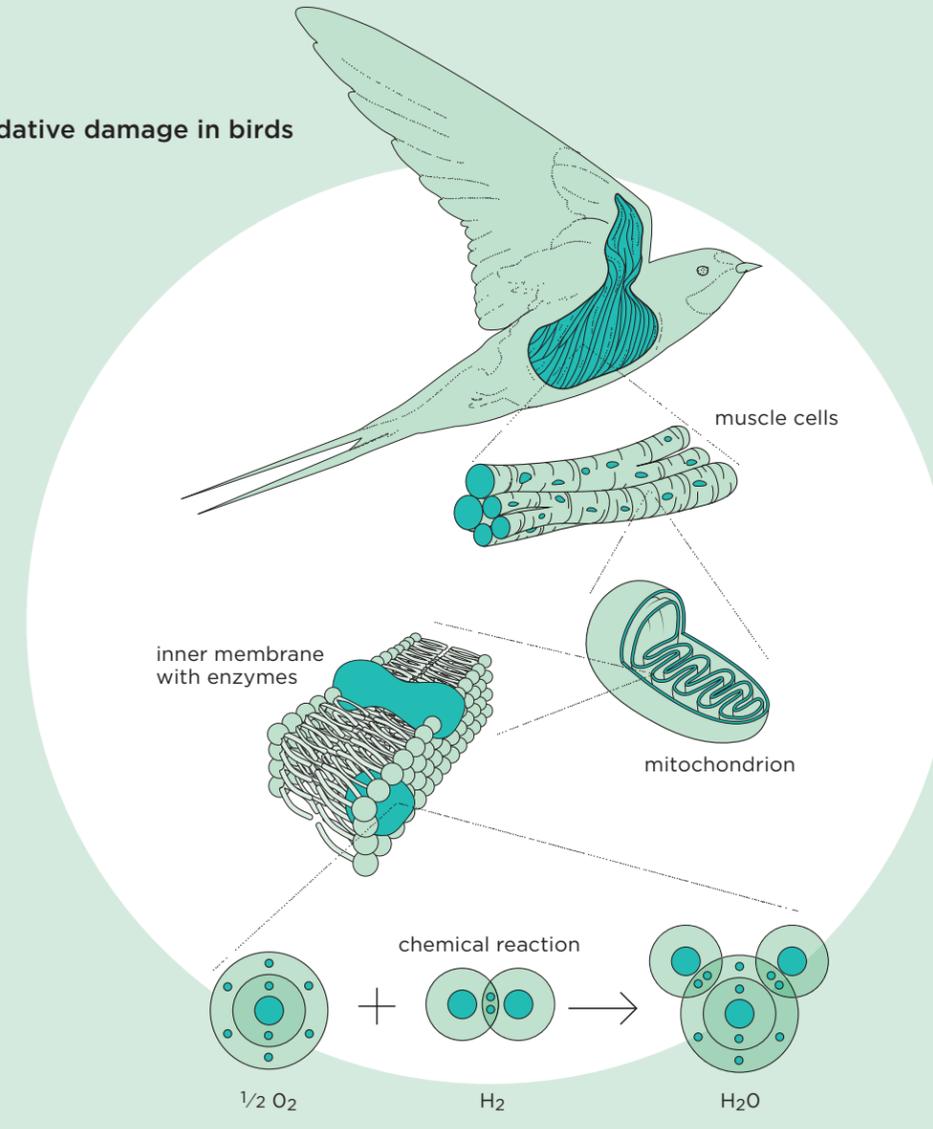
However, the use of fats as fuel during intense exercise such as flying is difficult because fat metabolism requires more oxygen, and fats must be chaperoned by fatty acid transporters from where they are stored in the body to the site of oxidation in the muscle cells. Birds increase the number of these fatty acid transporters (as well as oxidative enzymes) during migration, and it appears that this response is essential in enabling birds to rely on fats as their primary fuel while flying long distances. As noted in Chapter 4, the increased oxygen needed for fat metabolism is provided by a flow-through respiratory system that is well coordinated with the circulatory system.

## A robust antioxidant system

One of the other consequences of oxidising fats as fuel during flight is the greater potential for damage from the resulting reactive by-products. At the most basic chemical level, metabolising fats to produce energy involves the conversion of oxygen into water. During this process, some reactive intermediates (reactive oxygen species or free radicals) escape and can then react with, and damage, other useful

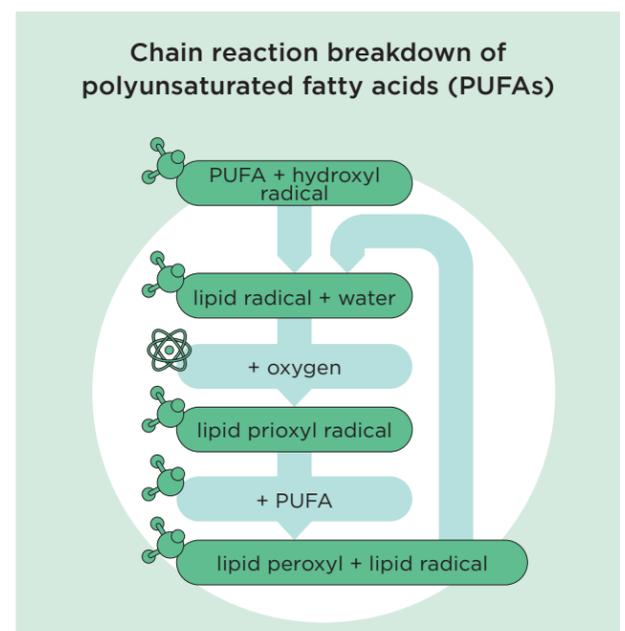


## Site of oxidative damage in birds



▲► Chemical reactions taking place in the mitochondria generate pro-oxidants such as lipid radicals during aerobic respiration, which can affect muscle metabolism and whole-animal flight performance.

molecules (e.g. proteins, lipids, DNA). However, the antioxidant system of birds can convert or quench these free radicals and thereby avoid oxidative damage to these useful molecules. Thus, flying birds must have a robust antioxidant system – including antioxidant enzymes such as superoxide dismutase, and metabolites such as uric acid – as well as eating dietary antioxidants (e.g. carotenoids).





## Flying at altitude

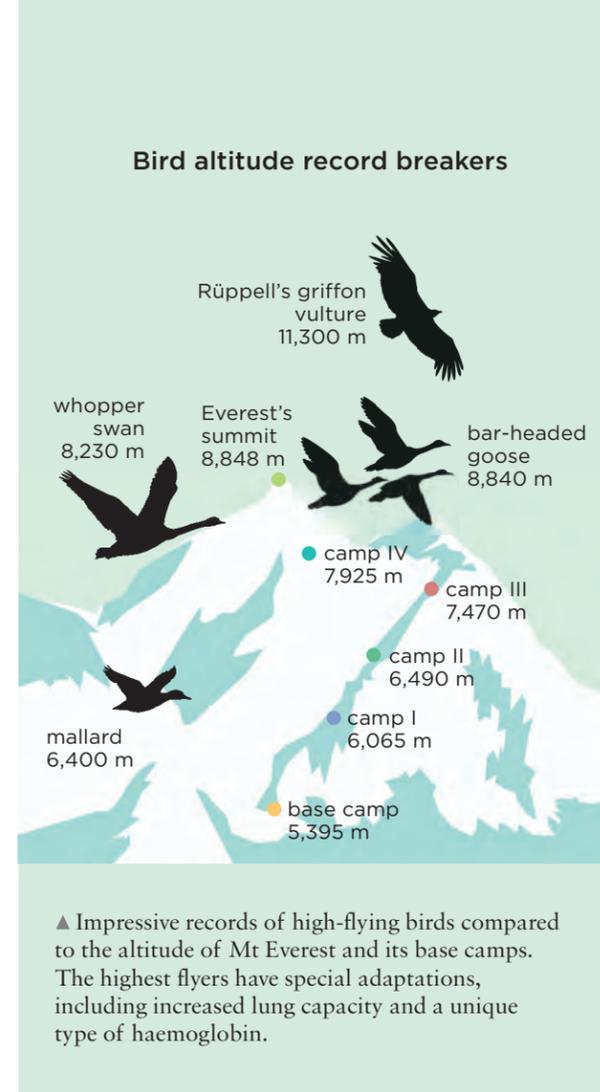
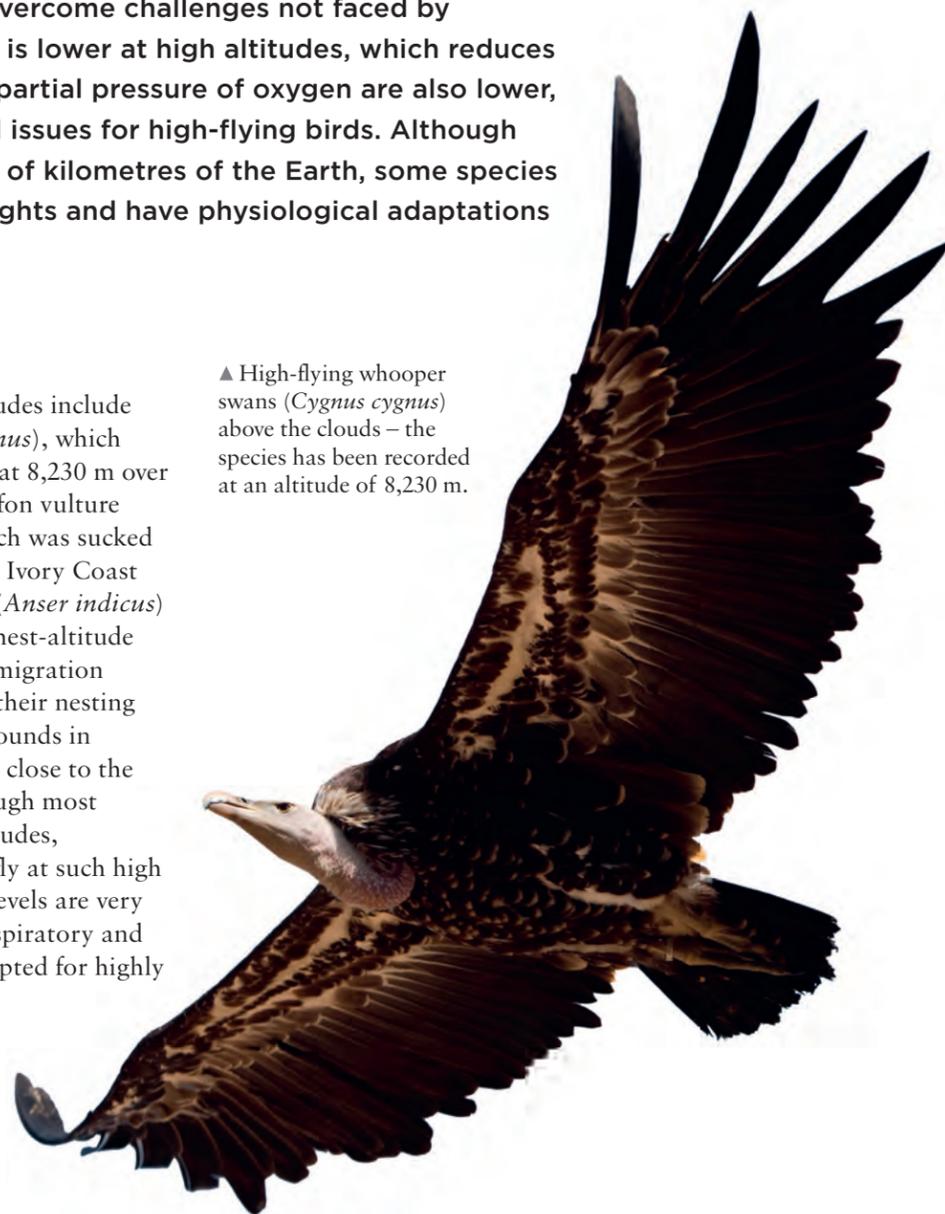
Birds that fly at altitude must overcome challenges not faced by terrestrial animals. Air pressure is lower at high altitudes, which reduces drag, but temperature and the partial pressure of oxygen are also lower, creating metabolic and thermal issues for high-flying birds. Although most birds stay within a couple of kilometres of the Earth, some species are known to fly at extreme heights and have physiological adaptations allowing them to do so.

### High-flying migrants

Species that fly at extremely high altitudes include Eurasian whooper swans (*Cygnus cygnus*), which have been observed by an airline pilot at 8,230 m over the Atlantic Ocean, and Rüppell's griffon vulture (*Gyps rueppelli*), an individual of which was sucked into a jet engine at 11,552 m above the Ivory Coast in Africa. However, bar-headed geese (*Anser indicus*) can most regularly claim to be the highest-altitude migrants on the planet – during their migration through the Himalayas en route from their nesting grounds in Tibet to their wintering grounds in India, some individuals fly at altitudes close to the height of Mt Everest (8,848 m). Although most migratory birds fly at much lower altitudes, understanding how bar-headed geese fly at such high altitudes (where atmospheric oxygen levels are very low) provides insights into how the respiratory and circulatory systems of birds is pre-adapted for highly efficient oxygen uptake.

► Rüppell's griffon vulture (*Gyps rueppelli*) can soar at very high altitudes and is considered to be the highest-flying bird.

▲ High-flying whooper swans (*Cygnus cygnus*) above the clouds – the species has been recorded at an altitude of 8,230 m.



### Adaptations for high-altitude flying

Like other birds, bar-headed geese produce more haemoglobin, more red blood cells and more myoglobin (the haemoglobin equivalent in muscle cells) as they prepare for migration. These changes enhance their blood's capacity to bind and transport oxygen. However, the geese differ from other species in several exceptional ways that allow them to perform unusually well at high altitudes. For a start, they have relatively larger lungs and a special type of haemoglobin that allows them to extract more oxygen from each breath. This enables these geese to increase the oxygen-carrying capacity of their blood without unduly increasing its viscosity and potentially reducing circulatory efficiency. Bar-headed geese also have more blood capillaries in their heart and flight muscles than do other geese. In addition, the capillaries penetrate deep within the muscle, allowing them to deliver oxygen throughout key tissues under low-oxygen conditions. The birds also have a special form of the enzyme cyclooxygenase, which is involved in energy production within their muscle cells, increasing the efficiency of their oxygen use.

▼ Bar-headed geese (*Anser indicus*) must cross the Himalayas, the highest mountain range in the world, to reach their breeding grounds in Mongolia.



# Flight styles: flapping, gliding and soaring

Flapping of wings is usually necessary to generate enough lift for take-off, but once they are airborne birds vary in how much they flap and the nature of that flapping. Some birds soar for hours with virtually no wing flapping, while others flap continuously. And some birds have a bounding flight, while others flap and glide intermittently.

## Continuous flapping

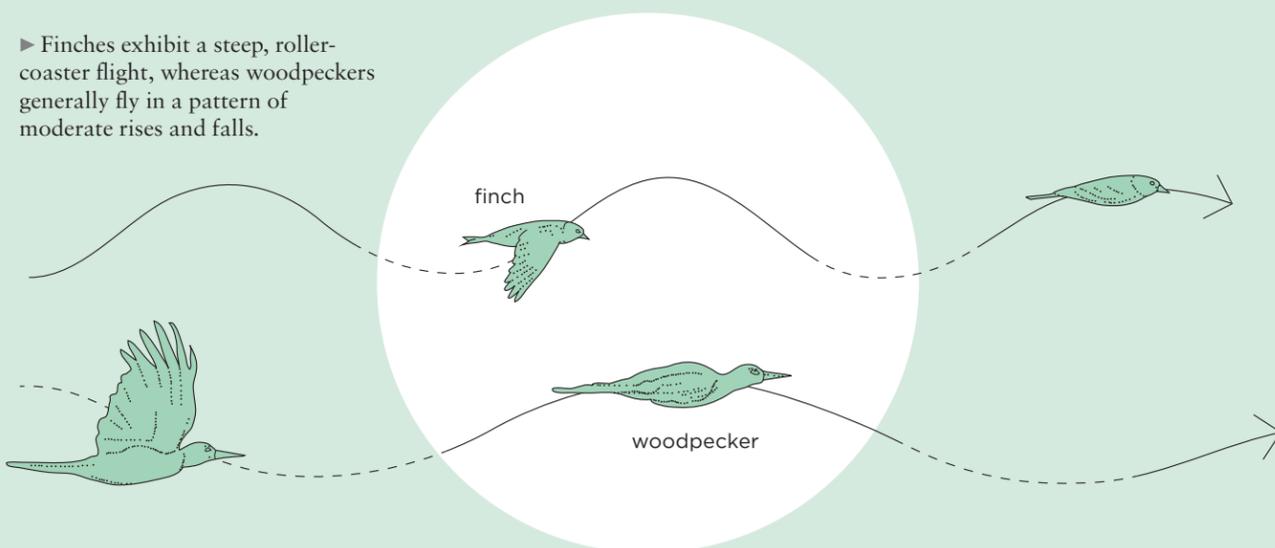
Continuous flapping flight is most common in species with a high wing loading (a high body mass relative to wing surface area), such as ducks and gamebirds. In some cases (ducks and divers) continuous flapping results in high-speed flight with low manoeuvrability, which requires long take-offs and landings. Some species can sustain continuous flapping for long periods. For example, the bar-tailed godwit (*Limosa lapponica*) can flap continuously for more than 11,000 km during its migration to and from Alaska and New Zealand. In other cases (pheasants, turkeys and tinamous) continuous flapping can be sustained for short bursts only and is mainly used to escape predators or move from the ground to a perch.

## Flapping and gliding

Many species do not flap continuously, but instead intersperse periods of flapping with periods of gliding on extended wings (called flap-gliding) or periods of bounding with wings closed (called flap-bounding). These non-flapping periods likely save the birds energy through brief rests and/or allow them to adjust their speed by briefly pausing their forward thrust. Flap-bounding is common among many passerines and woodpeckers, and likely saves energy when the birds are travelling near their maximum speed. Flap-gliding is common in small to medium-sized birds such as common swifts (*Apus apus*) and common starlings (*Sturnus vulgaris*), and likely also saves energy when the birds are travelling at slow or moderate speeds.

## Flap-bounding flight

► Finches exhibit a steep, roller-coaster flight, whereas woodpeckers generally fly in a pattern of moderate rises and falls.



▲ Great white pelicans (*Pelecanus onocrotalus*) are expert at ridge soaring along shorelines with minimal flapping using rising coastal air currents.

## Gliding

Gliding is non-flapping passive flight with wings outstretched. The wings and body provide aerodynamic lift, and the rate at which the bird sinks towards the ground depends on the lift-to-drag ratio. Expert gliders can produce very low glide angles and hence stay aloft for extended periods, whereas other species may glide only briefly during landing. Non-avian gliders such as flying squirrels, flying snakes, flying fish and flying frogs can glide moderate distances. However, some birds intersperse gliding with periods of flapping to regain altitude, allowing them to remain aloft almost indefinitely. For example, frigatebirds can remain on the wing for weeks, flapping to gain altitude when necessary and then gliding. If air conditions are favourable, they can glide for extended periods without flapping, a flight mode known as soaring.

## Soaring

Soaring is a form of gliding in which birds make use of rising air currents to counteract gravity and provide sufficient lift to stay aloft for long durations without flapping. There are three types of soaring: thermal soaring, ridge soaring and dynamic soaring. In thermal soaring, birds spiral upward within rising columns of warm air to gain altitude, then glide towards their goal. Hawks and vultures may glide from one rising thermal to another, spiralling upwards within each before gliding to the next. During migration, large numbers of birds may aggregate in warm air columns, forming so-called 'kettles' of spinning groups.

In ridge soaring, birds use rising air along ocean waves or ridges of land to stay aloft, such as when North American brown pelicans (*Pelecanus occidentalis*) soar along waves or coastlines. In dynamic soaring, birds alternately tack into prevailing winds to gain altitude and glide downwind to gain speed. Seabirds such as albatrosses and petrels use this form of soaring, taking advantage of the vertical gradient of wind speeds over the open ocean.

## HOVERING

Though hovering is most often associated with hummingbirds, many birds can hover, at least transiently. Hovering is a special form of flapping flight in which thrust is directed downward to keep a bird aloft without moving forward. Many birds hover briefly during landing, and kingfishers and ospreys may hover over water before diving to catch fish. Wind-hovering species such as Old World common kestrels (*Falco tinnunculus*) and American white-tailed kites (*Elanus leucurus*) hover while hunting by facing into the wind and flapping their wings, allowing them to survey the ground below for prey. However, hummingbirds are the most specialised hovering birds. They rely on a high attack angle and keep their wings extended during the upstroke, with the whole wing rotated in a similar way to the wing-tip rotation seen in other birds. As a result, the downstroke and upstroke combine with a figure-of-eight pattern made by the wings.

# Flight displays

In addition to being a form of locomotion, flight may be used in visual and acoustic communication. Many species of birds use flight as part of complex visual displays, combined with vocalisations or non-vocal sounds produced by feathers themselves. Flight may also be used to accentuate ornamental feathers, or to produce sounds that are carried great distances.

## Manakin dances

Flight is incorporated into the complex visual displays, or dances, of the Central and South American manakins, which hop, hover and fly during courtship. Manakin males court females at specific sites, and use a combination of complicated movements and sounds to attract them. These display flights may even be coordinated between multiple individuals, as seen in the dance of lance-tailed manakins (*Chiroxiphia lanceolata*), in which the males alternately hop and hover over one another. Golden-collared manakins (*Manacus vitellinus*) court females by leaping from stem to stem in an arena, and loudly snapping their wings together over their back while in mid-leap.

## Diving display flights

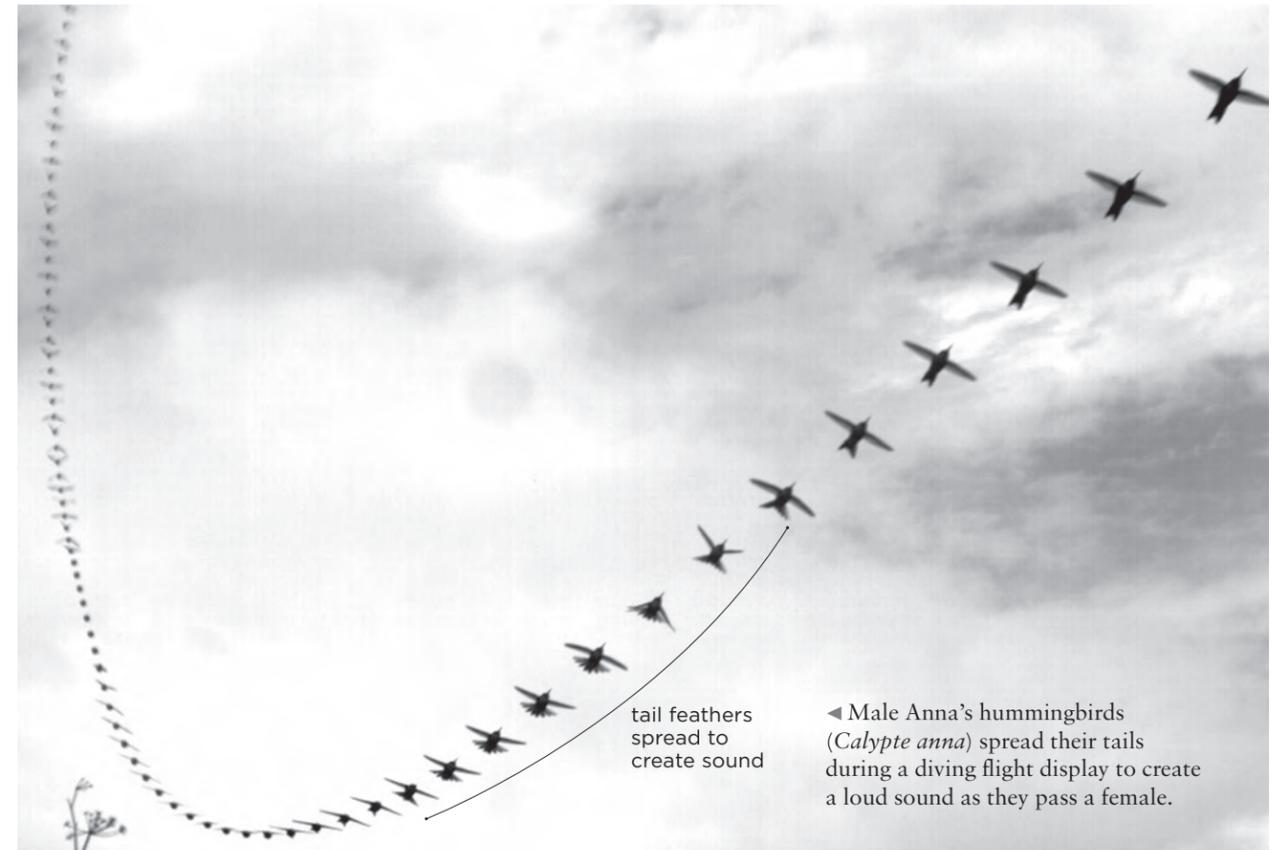
In other flight displays, birds may dive from high altitude and then sweep upward, showing off plumage features or making sounds as they do so. One magnificent example is the American Anna's hummingbird (*Calypte anna*), the males of which dive towards perched females. As they pass over the

female, they orient their iridescent throat feathers to create a flashing pattern, and then swoop upward while spreading their tail feathers, which vibrate to create a loud sound.

## Vocalising in flight

Some species sing or call during flight displays. The Old World rollers are so named for their rolling flight displays. For example, the African purple roller (*Coracias naevius*) rolls back and forth around its flight axis during long diving display flights that are combined with mating calls. Eurasian skylarks (*Alauda arvensis*) perform extended song flights, which may also last up to a half an hour. The males sing throughout the climb, level flight and descent of this display, and adjust their flight speed to maximise their endurance.

▼ These blue manakins (*Chiroxiphia caudata*) collaborate during their complex jump-hover flight displays, with an alpha male alternating with subordinates to perform in front of a female.



tail feathers spread to create sound  
◀ Male Anna's hummingbirds (*Calypte anna*) spread their tails during a diving flight display to create a loud sound as they pass a female.

## SOUNDING OFF

Like Anna's hummingbird (see main text), some birds make sounds in ways other than vocalisations during their flight displays. For example, Latham's snipe (*Gallinago hardwickii*) breeding in Japan have elaborate displays that incorporate sounds produced by their feathers. American common nighthawks

(*Chordeiles minor*) also perform a flight display that incorporates feather sounds. Around dusk, they fly to a height, then rapidly descend and swoop within a metre of the ground. At the bottom of this swoop they adjust their wings to produce a loud, low-pitched booming or whooshing sound.

► Male Latham's snipe (*Gallinago hardwickii*) perform elaborate flight displays to females. This sound spectrogram illustrates the short, loud calls (short vertical markings) and longer intermittent buzzes produced by their feathers.



# Sleeping on the wing

The majority of birds are diurnal, being active during the day and sleeping at night. However, when these birds migrate, they depart soon after sunset and often fly throughout the night. This switch to being nocturnally active is thought to have several potential benefits, including making it easier to avoid predators and providing more favourable flying conditions (the atmosphere is cooler and less stratified at night). However, flying throughout the night and then needing to feed and refuel during the day makes it very difficult to find time to sleep!

## Avian sleep versus mammalian sleep

Birds, like many other animals, sleep in the sense that their nervous system is relatively inactive, their muscles are relaxed, their eyes are usually closed and they themselves are largely unresponsive to the outside world. In both mammals and birds, sleep is categorised by certain patterns of brain activity: rapid eye movement (REM) sleep, with recognisable low-amplitude, fast-changing brainwaves; and non-REM sleep, with high-amplitude, slow-changing brainwaves. Active sleep periods are short in birds,

unlike in most mammals, and in some avian species sleep is interrupted frequently so that the birds can check for potential predators.

Birds can also sleep with only one-half of their brain at a time, a phenomenon known as unihemispheric sleep. The visual systems of birds are crossed in relation to the brain halves; that is, optic nerves from each eye go to the opposite sides of the brain. By alternating the sleeping half of the brain throughout the night, birds can watch out for predators with one eye open while resting the



## Effect of migration on behaviour of sleeping garden warblers

**Sleep position if condition is good**  
untucked;  
higher metabolic rate;  
higher heat dispersion;  
higher alertness

► Migratory warblers, including these garden warblers (*Sylvia borin*), adjust their sleeping behaviour (with the head tucked or untucked) depending on their condition and thereby trade off energy costs and predation risk.



**Sleep position if condition is poor**  
tucked;  
lower metabolic rate;  
lower heat dispersion;  
reduced alertness

other half of their brain. The advent of miniaturised wireless technology for recording the brain activity of flying birds has led to the remarkable discovery that birds such as the Old World alpine swifts (*Tachymarptis melba*) can fly for days at a time and sleep aloft using this unihemispheric sleep system. Great frigatebirds (*Fregata minor*) also use unihemispheric sleep in flight, but in addition they sometimes sleep with both brain hemispheres – so, it appears that the birds do not need to be awake to maintain the aerodynamic control of flight. That said, researchers have found that frigatebirds sleep for only 0.7 hours per day during flights that last up to ten days, whereas on land they sleep for 12.8 hours per day.

◀ Alpine swifts (*Tachymarptis melba*) can sleep while flying, resting one half of their brain while the other remains active.

## The costs of sleeping safely

Garden warblers (*Sylvia borin*) migrate in spring from Africa to Europe, and they usually rest and refuel along the way. Researchers studied these long-distance migratory birds during a stopover on an island in the Mediterranean after they had been flying more than ten hours the previous night. Following the long nocturnal flight, the warblers must recover sleep and also refuel while avoiding being eaten themselves by predators. In a series of cleverly designed field experiments, the researchers discovered that the birds modify the depth of their sleep and resting posture so as to remain alert to predators, while at the same time conserving their energy. Specifically, leaner warblers sleep more deeply, saving more energy, but are more vulnerable to predators compared to fatter warblers, which sleep less deeply yet are better able to escape predators. In short, these migrating songbirds modify their sleep behaviour in such a way as to strategically trade off sleep-mediated energy conservation with antipredatory vigilance.

# Flock formations

Birds may fly individually, in large groups or in organised formations. Flocks of birds may consist of family groups, groups of unrelated birds of the same species or mixed-species flocks. Birds may fly together in a flock for self-defence, as many eyes have a greater chance of spotting predators, and to reduce the costs of flight.

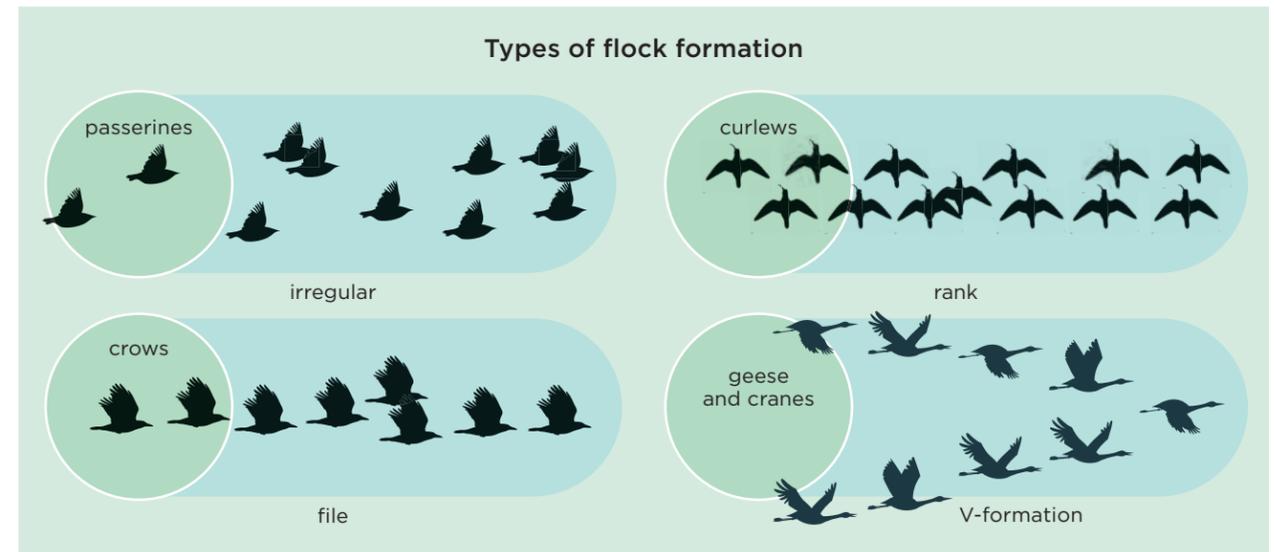
## Flocking

Most birds that migrate at night fly solo, even though hundreds of thousands of individuals may be aloft on any given night during a species' migration. Some birds, however, are more social and fly in groups. In the Americas, Harris's hawks (*Parabuteo unicinctus*) hunt in organised groups to capture prey, while other species fly in groups to avoid becoming prey. Mixed-species flocks of birds occur in a variety of ecosystems but are common in Neotropical forests. Individuals may benefit from being in a flock through increased foraging efficiency by increased detection of predators.



▼ Massive flocks of common starlings (*Sturnus vulgaris*) gather at dusk prior to roosting, forming visually stunning murmurations.

► Harris's hawks (*Parabuteo unicinctus*) of the Sonoran Desert are unusually social for a hawk species, hunting in coordinated groups.



▲ Species vary in whether their flocks are loosely organised or more coordinated. The V-formation provides aerodynamic benefits to birds within the flock.

Some birds flock seasonally, keeping to themselves in the breeding season but then joining groups in the non-breeding season. Flocking can also vary over a daily cycle, with massive gatherings of birds coming together at dusk, just before they descend to communal roosts. Such dusk flocking occurs in

red-ored Amazon parrots (*Amazona autumnalis*) in Panama and in many corvid species. However, it is perhaps most famous in common starlings, whose dusk flockings (called murmurations) can include thousands, or even hundreds of thousands, of individuals.

## Flying in formation

When birds fly together in a flock, they may be able to take advantage of the air movement created by those around them to gain some aerodynamic benefit. Consider the classic V-shaped groups of flying geese, pelicans and cormorants. In a study of endangered northern bald ibises (*Geronticus eremita*) raised at Salzburg Zoo in Austria, birds were fitted with transmitters that could record the precise movements of their wings while flying freely in V-formation behind an ultralight aircraft. This demonstrated that each bird positions itself with respect to adjacent individuals, and the birds time the flapping of their wings to maximise the capture of 'upwash' and minimise their exposure to 'downwash' (the helpful and unhelpful air from their neighbours, respectively). Much like the cyclists in a peloton slipstream behind one another, so birds in organised flock formations may reduce flight costs by flying close to one another.

▼▼ Australian budgerigars (*Melopsittacus undulatus*) can form massive flocks of tens of thousands of birds when in search of water.





# Getting around on land

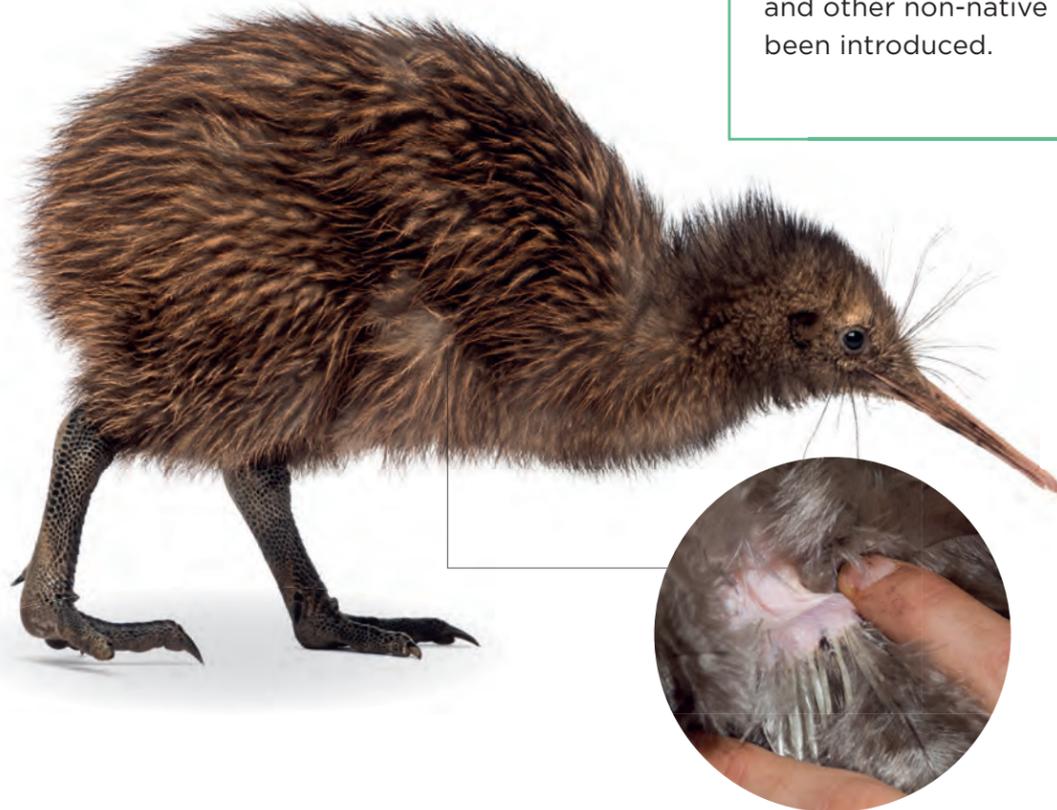
Present-day birds evolved from a walking (bipedal), featherless lizard-like animal(s) into an ancestral feathered, flying bird. While most contemporary birds fly, some have secondarily lost this ability, including the familiar ratites (ostriches, cassowaries, kiwi, rheas and emu, *Dromaius novaehollandiae*) and penguins, as well as more than 60 other species from a wide diversity of families. These birds rely on walking or running on land, and swimming at sea, to get around.

## Wings of flightless birds

All flightless birds except one group (the very large, herbivorous New Zealand moas, which were hunted to extinction around 600–700 years ago) retain the forelimb wing structure of their flying ancestors, albeit in a reduced form. These birds use their wings for non-flying purposes, including while running (e.g. ostriches) or for swimming (e.g. penguins), or quite extensively for courtship and displays. In the extreme, wings may be reduced to an almost vestigial state, as in the kiwi.

## NO ESCAPE

Kiwi, South Island takahē (*Porphyrio hochstetteri*) and kākāpō (*Strigops habroptila*) are New Zealand birds that evolved flightlessness in the absence of predators. Unfortunately, however, their populations are now very low owing to predation by rats, weasels and other non-native species that have been introduced.



vestigial wing position

◀ The North Island brown kiwi (*Apteryx mantelli*) of New Zealand, like all kiwi, has highly reduced wings (inset) and is a walker, not a flyer. This flightlessness evolved in the absence of predators.



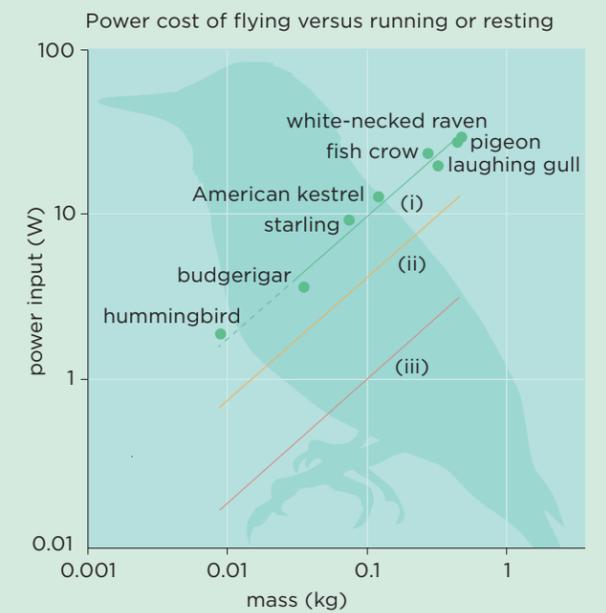
▲ The emu (*Dromaius novaehollandiae*) is the second-largest living bird (35–40 kg) and is flightless. Its relatively small wings are used for balance during running and for displays.

## Too large to fly

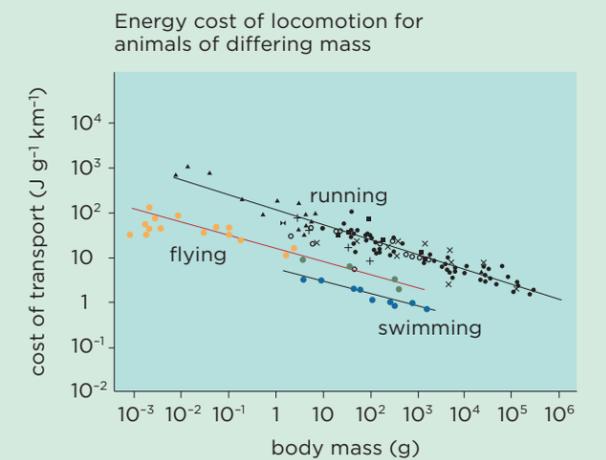
The energy expenditure (kilojoules per gram of body mass) required for flight is very high compared to that for running, and these energy costs increase with body weight – this means that at some point birds are too heavy to fly. Accordingly, the heaviest flying birds today are relatively light compared to flightless running birds. In general, the evolution of flightlessness in birds is associated with larger body size, as well as island environments with few or no predators and reduced competition (see box).

Ostriches are the largest living birds and among the fastest bird runners. Interestingly, if one considers the energy required for flying versus running per unit distance travelled – essentially like considering petrol mileage in vehicles – then running is more expensive than flying. That is, a running bird will expend more energy than a similar-sized flying bird to move a given distance. This advantage in fuel mileage for flying birds enables their long-distance migrations, but flight still requires many physiological and anatomical adaptations, as has been discussed earlier in the chapter.

## Power and energy requirements of locomotion of different groups and species



▲ For a given body mass, birds in flight (i) require more power (energy per unit time) than a running mammal (ii) and much less when simply at rest (iii).



● insects  
○ birds  
● mammals  
× birds  
■ reptiles  
◇ amphibians  
+ crustaceans  
▲ insects  
✱ myriapods

▲ Running animals have a much higher cost of transport (energy per gram body mass for a given distance) for a given body mass than flying or swimming animals.

# Swimming and diving

In addition to flying, running and perching, many birds use their wings and legs for aquatic locomotion. Swimming is an important or primary form of locomotion for many birds such as waterfowl, loons (divers), cormorants, pelicans and penguins. Convergent evolution has resulted in several common features among such birds, including webbed feet with narrow foot bones, posteriorly oriented hips and legs, smaller and sturdier wings (for species that flap underwater), wide bodies to increase flotation, and oily feathers.

## Swimming

Some species are so specialised for swimming and diving that they are very awkward on land (e.g. loons or divers) or have lost the ability to fly (e.g. penguins). Other species, including Atlantic puffins (*Fratercula arctica*), are adept at both swimming and flying.

Swimming on the water's surface involves overcoming drag, and although swimming speeds are slower than typical flying speeds, water is more viscous than air. Swimming at the surface creates a wave in front of the animal, limiting the speed at which it can travel. At slow speeds birds engage in paddling, such that propulsion is provided by pushing their webbed feet through the water. To achieve higher speeds, birds hydroplane to reduce the drag induced by water. Smaller (lighter) birds generate enough forward propulsion by paddling to hydroplane and lift their bodies above the surface of the water. Larger birds such as South American steamer ducks cannot generate sufficient speed to hydroplane by paddling alone, and instead use their wings as oars to steam over the water.

At higher speeds, birds can flap their wings with enough power to lift their body out of the water while they run across its surface, a behaviour known as taxiing, skittering or paddle-assisted flying. Taxiing differs from steaming in that the wings do not enter the water, and the recovery stroke of the feet is above the water. A few landbirds, including North American bald eagles (*Haliaeetus leucocephalus*) and western ospreys (*Pandion haliaetus*), occasionally swim slowly using their wings as oars, such as when they catch a fish with their talons that is too large to lift out of the water by flight.

◀ Atlantic puffins (*Fratercula arctica*) are adept at flying, swimming on the surface of the ocean and extended diving.

▼ Flightless Fuegian steamer ducks (*Tachyeres pteneres*) 'steam' over the water, using their wings as oars.

▶ Atlantic puffin (*Fratercula arctica*) diving.





▲ American dippers (*Cinclus mexicanus*) are an aquatic songbird, catching their food on the bottom of fast flowing streams by diving or running along it.

### Diving

Birds sometimes dive below the surface of the water to avoid predators or to forage, a behaviour that has been a way of life for some species since the Cretaceous period. Fossils of Hesperornithes, a group of theropod dinosaurs that colonised the oceans in the Mesozoic era (66–22 million years ago), indicate that they were likely poor at flying, if they flew at all, but they appear to have been adapted to foot-propelled swimming and diving. Diving is present in many different taxa of modern birds. Dippers are passerines that can run along the bottom of streams or rivers and occasionally also swim underwater using their wings. They forage like this even in turbulent streams during winter, gathering invertebrate prey from the streambed. Some species (e.g. kingfishers and terns) dive into the water from a height to capture fish and return to the surface quickly. These birds may hover over the water until they spot prey, and then plunge-dive from a great height. Other species (e.g. loons or divers, and penguins) may dive from the surface and then spend longer periods of time underwater on foraging trips.

### Underwater propulsion

Swimming underwater has an advantage over flying in that birds have natural buoyancy and so do not need to generate lift. However, water is many times more viscous than air, so much greater hydrodynamic force is required for propulsion, or thrust. Propulsion for diving is generated by either the wings, in which

the birds essentially fly underwater (e.g. penguins), or the feet (e.g. grebes, loons or divers, and cormorants). Foot propulsion can involve oscillating the feet horizontally or vertically, depending on the species. Ducks and cormorants kick their feet up and down like a paddle wheel, but loons (divers) and grebes kick their feet from side to side like a kayak paddle.

Puffins and penguins flap their wings underwater for propulsion. While they are underwater they need to generate downward force with their wings to prevent themselves from floating upward, as well as propulsion to move forward. Flying birds that use wing propulsion underwater commonly keep their wings partly folded while diving, as much less wing

area is required to produce the same force in water than in air. In a few cases, such as the scoters, both the wings and the feet are used for propulsion while the bird swims underwater.

▼ Propulsion while swimming underwater can be provided by the wings or feet. African penguins (*Spheniscus demersus*, main image) and other penguin species ‘fly’ through the water by flapping their wings. In contrast, common loons or great northern divers (*Gavia immer*, inset) propel themselves by kicking their feet from side to side.

