Bird flight

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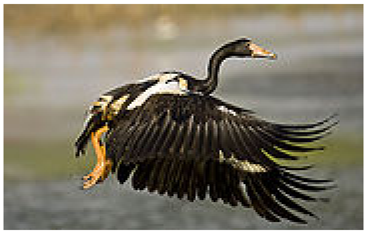


A magpie-goose taking off

Flight is the main mode of locomotion used by most of the world's bird species. Flight assists birds while feeding, breeding and avoiding predators.

This article discusses theories on the evolution of **bird flight**. The mechanics of bird flight is covered, with emphasis on the varied forms of bird's wings. The specifics of hovering, take-off and landing are also examined. Finally, additional adaptations of bird's bodies relating to their flying ability are covered.

Contents

Evolution of bird flight

Marine birds fly at Cape Hay in the High Arctic

Most paleontologists agree that birds evolved from small theropod dinosaurs, but the origin of bird flight is one of the oldest and most hotly contested debates in paleontology. The four main hypotheses are: "from the trees down", that birds' ancestors first glided down from trees and then acquired other modifications that enabled true powered flight; "from the ground up", that birds' ancestors were small, fast predatory dinosaurs in which feathers developed for other reasons and then evolved further to provide first lift and then true powered flight; and "wing-assisted incline running" (WAIR), a version of "from the ground up" in which birds' wings originated from forelimb modifications that provided *downforce*, enabling the proto-birds to run up extremely steep slopes such as the trunks of trees; and "Pouncing Proavis", which posits that flight evolved by modification from arboreal ambush tactics.

There has also been debate about whether the earliest known bird, *Archaeopteryx*, could fly. It appears that *Archaeopteryx* had the brain structures and inner-ear balance sensors that birds use to control their flight. *Archaeopteryx* also had a wing feather arrangement like that of modern birds and similarly asymmetrical flight feathers on its wings and tail. But *Archaeopteryx* lacked the shoulder mechanism by which modern birds' wings produce swift, powerful upstrokes; this may mean that it and other early birds were incapable of flapping flight and could only glide. The presence of most fossils in marine sediments in habitats devoid of vegetation has led to the hypothesis that they may have used their wings as aids to run across the water surface in the manner of the basilisk lizards.

From the trees down

This was the earliest hypothesis, encouraged by the examples of gliding vertebrates such as flying squirrels. It suggests that proto-birds like *Archaeopteryx* used their claws to clamber up trees and glided off from the tops.

Some recent research undermines the "trees down" hypothesis by suggesting that the earliest birds and their immediate ancestors did not climb trees. Modern birds that forage in trees have much more curved toe-claws than those which forage on the ground; the toe-claws of Mesozoic birds and of closely-related non-avian theropod dinosaurs are like those of modern ground-foraging birds.

From the ground up

Feathers are very common in coelurosaurid dinosaurs (including the early tyrannosauroid Dilong). Modern birds are classified as coelurosaurs by nearly all palaeontologists, though not by a few ornithologists. The original functions of feathers may have included thermal insulation and competitive displays. The most common version of the "from the ground up" hypothesis argues that bird's ancestors were small ground-running predators (rather like roadrunners) that used their forelimbs for balance while pursuing prey and that the forelimbs and feathers later evolved in ways that provided gliding and then powered flight. Another "ground upwards" theory argues the evolution of flight was initially driven by competitive displays and fighting: displays required longer feathers and longer, stronger forelimbs; many modern birds use their wings as weapons, and downward blows have a similar action to that of flapping flight. Many of the *Archaeopteryx* fossils come from marine sediments and it has been suggested that wings may have helped the birds run over water in the manner of the *Jesus Christ Lizard* (Common basilisk).

Most recent attacks on the "from the ground up" hypothesis attempt to refute its assumption that birds are modified coelurosaurid dinosaurs. The strongest attacks are based on embryological analyses which conclude that birds' wings are formed from digits 2, 3 and 4 (corresponding to the index, middle and ring fingers in humans; the first of a bird's 3 digits forms the alula, which they use to avoid stalling on low-speed flight, for example when landing); but the hands of coelurosaurs are formed by digits 1, 2 and 3 (thumb and first 2 fingers in humans). However these embryological analyses were immediately challenged on the embryological grounds that the "hand" often develops differently in clades that have lost some digits in the course of their evolution, and therefore bird's hands do develop from digits 1, 2 and 3.

Wing-assisted incline running

The WAIR hypothesis was prompted by observation of young chukar chicks, and proposes that wings developed their aerodynamic functions as a result of the need to run quickly up very steep slopes such as tree trunks, for example to escape from predators. Note that in this scenario birds need *downforce* to give their feet increased grip. But early birds, including *Archaeopteryx*, lacked the shoulder mechanism by which modern birds' wings produce swift, powerful upstrokes; since the downforce on which WAIR depends is generated by upstrokes, it seems that early birds were incapable of WAIR.

Pouncing Proavis model

This theory was first proposed by Garner, Taylor, and Thomas in 1999:

> We propose that birds evolved from predators that specialized in ambush from elevated sites, using their raptorial hindlimbs in a leaping attack. Drag–based, and later lift-based, mechanisms evolved under selection for improved control of body position and locomotion during the aerial part of the attack.

Selection for enhanced lift-based control led to improved lift coefficients, incidentally turning a pounce into a swoop as lift production increased. Selection for greater swooping range would finally lead to the origin of true flight.

The authors believed that this theory had four main virtues:

- It predicts the observed sequence of character acquisition in avian evolution.
- It predicts an Archaeopteryx-like animal, with a skeleton more or less identical to terrestrial theropods, with few adaptations to flapping, but very advanced aerodynamic asymmetrical feathers.
- It explains that primitive pouncers (perhaps like Microraptor) could coexist with more advanced fliers (like Confuciusornis or Sapeornis) since they did not compete for flying niches.
- It explains that the evolution of elongated rachis-bearing feathers began with simple forms that produced a benefit by increasing drag. Later, more refined feather shapes could begin to also provide lift.

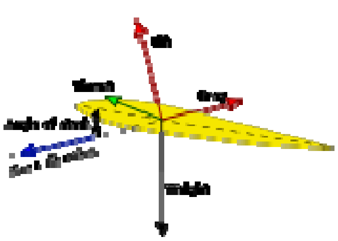
Uses and loss of flight in modern birds

Birds use flight to obtain prey on the wing, for foraging, to commute to feeding grounds, and to migrate between the seasons. It is also used by some species to display during the breeding season and to reach safe isolated places for nesting.

Flight is more energetically expensive in larger birds, and many of the largest species fly by soaring and gliding (without flapping their wings) most of the time. Many physiological adaptations have evolved that make flight more efficient.

Birds that settle on isolated oceanic islands that lack ground-based predators often lose the ability to fly. This illustrates both flight's importance in avoiding predators and its extreme demand for energy.

Basic mechanics of bird flight



Forces acting on a wing. The lift force has both a forward and a vertical component.

Lift

The fundamentals of bird flight are similar to those of aircraft. Lift force is produced by the action of air flow on the wing, which is an airfoil. The lift force occurs because the air has a lower pressure just above the wing and higher pressure below.

Gliding

When gliding, both birds and gliders obtain both a vertical and a forward force from their wings. This is possible because the lift force is generated at right angles to the air flow, which in gliding flight comes from slightly below the horizontal (because the bird is descending). The lift force therefore has a forward component which counteracts drag.

Flapping

When a bird flaps, as opposed to gliding, its wings continue to develop lift as before, but they also create an additional forward force, thrust, which counteracts drag and increases its speed, which has the effect of also increasing lift to counteract its weight, allowing it to maintain height or to climb. Flapping involves two stages: the down-stroke, which provides the majority of the thrust, and the up-stroke, which can also (depending on the bird's wings) provide some thrust. At each up-stroke the wing is slightly folded inwards to reduce upward resistance. Birds change the angle of attack between the up-stroke and the down-stroke of their wings. During the down-stroke the angle of attack is increased, and is decreased during the up-stroke.

Drag

Apart from its weight, there are three major drag forces that impede a bird's aerial flight: frictional drag (caused by the friction of air and body surfaces), form drag (due to frontal area of the bird, also known as pressure drag), and lift-induced drag (caused by the wingtip vortices). These forces are reduced by streamlining the bird's body and wings.

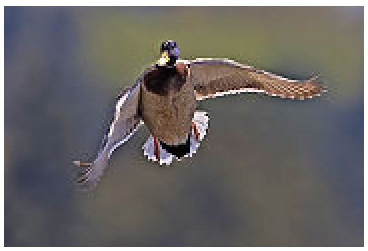
The wing

A kea in flight

The bird's forelimbs, the wings, are the key to bird flight. Each wing has a central vane to hit the wind, composed of three limb bones, the humerus, ulna and radius. The hand, or manus, which ancestrally was composed of five digits, is reduced to three digits (digit II, III and IV or I, II, III depending on the scheme followed), the purpose of which is to serve as an anchor for the primaries, one of two groups of flight feathers responsible for the wing's airfoil shape. The other set of flight feathers, which are behind the carpal joint on the ulna, are called the secondaries. The remaining feathers on the wing are known as coverts, of which there are three sets. The wing sometimes has vestigial claws. In most species these are lost by the time the bird is adult (such as the highly visible ones used for active climbing by Hoatzin chicks), but claws are retained into adulthood by the Secretary Bird, screamers, finfoots, ostriches, several swifts and numerous others, as a local trait, in a few specimens. The claws of the Jurassic theropod-like Archaeopteryx are quite similar to those of the Hoatzin nestlings.

Albatrosses have locking mechanism in the wing joints that reduce the strain on the muscles during soaring flight.

Wing shape and flight



A male Mallard in flight.

The shape of the wing is an important factor in determining the types of flight of which the bird is capable. Different shapes correspond to different trade-offs between beneficial characteristics, such as speed, low energy use, and maneuverability. The planform of the wing (the shape of the wing as seen from below) can be described in terms of two parameters, aspect ratio and wing loading. Aspect ratio is the ratio of wingspan to the mean of its chord (or the square of the wingspan divided by wing area). Wing loading is the ratio of weight to wing area.

Most kinds of bird wing can be grouped into four types, with some falling between two of these types. These types of wings are elliptical wings, high speed wings, high aspect ratio wings and soaring wings with slots.

Wing shapes

Elliptical wings

Elliptical wings are short and rounded, having a low aspect ratio, allowing for tight maneuvering in confined spaces such as might be found in dense vegetation. As such they are common in forest raptors (such as *Accipiter* hawks), and many passerines, particularly non-migratory ones (migratory species have longer wings). They are also common in species that use a rapid take off to evade predators, such as pheasants and partridges.

High speed wings

High speed wings are short, pointed wings that when combined with a heavy wing loading and rapid wingbeats provide an energetically expensive high speed. This type of flight is used by the bird with the fastest wing speed, the peregrine falcon, as well as by most of the ducks. The same wing shape is used by the auks for a different purpose; auks use their wings to "fly" underwater. The Peregrine Falcon has the highest recorded dive speed of 175 mph (282 km/h). The fastest straight, powered flight is the Spine-tailed Swift at 105 mph (170 km/h).

High aspect ratio wings

This Roseate Tern uses its low wing loading and high aspect ratio to achieve low speed flight, important for a species that plunge dives for fish

High aspect ratio wings, which usually have low wing loading and are far longer than they are wide, are used for slower flight, almost hovering (as used by kestrels, terns and nightjars) or alternatively by birds that specialize in soaring and gliding flight, particularly that used by seabirds, dynamic soaring, which use different wind speeds at different heights (wind shear) above the waves in the ocean to provide lift.

Soaring wings with deep slots

These are the wings favored by the larger species of inland birds, such as eagles, vultures, pelicans, and storks. The slots at the end of the wings, between the primaries, reduce the induced drag at the tips, whilst the shorter size of the wings aids in takeoff (high aspect ratio wings require a long taxi in order to get airborne).

Hovering

Hovering is used by several species of birds (and specialized in by one family). True hovering, which is generating lift through flapping alone rather than as a product of the bird's passage through the air, demands a lot of energy. This means that it is confined to smaller birds; the largest bird able to truly hover is the pied kingfisher, although larger birds can hover for short periods of time. Larger birds that hover for prolonged periods do so by flying into a headwind, allowing them to remain stationary relative to the ground (or water). Kestrels, terns and even hawks use this windhovering.

The ruby-throated Hummingbird can beat its wings 52 times a second

Most birds that hover have high aspect ratio wings that are suited to low speed flying. One major exception to this are the hummingbirds, which are the most accomplished hoverers of all the birds. Hummingbird flight is different from other bird flight in that the wing is extended throughout the whole stroke, the stroke being a symmetrical figure of eight, with the wing producing lift on both the up- and down-stroke. Some hummingbirds can beat their wings 52 times a second, though others do so less frequently.

Take-off and landing

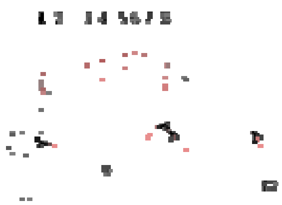
A male bufflehead runs atop the water while taking off

Take-off is one of the most energetically demanding aspects of flight, as the bird needs to generate enough airflow across the wing to create lift. With small birds a jump up will suffice, while for larger birds this is not possible. In this situation, birds need to take a run up in order to generate the airflow to take off. Large birds take off by facing into the wind, or, if they can, by perching on a branch or cliff so that all they need to do is drop off into the air.

Landing is also a problem for large birds with high wing loadings. This problem is dealt with in some species by aiming for a point below the intended landing area (such as a nest on a cliff) then pulling up beforehand. If timed correctly, the airspeed once the target is reached is virtually nil. Landing on water is simpler, and the larger waterfowl species prefer to do so whenever possible, landing into wind and using their feet as skids. In order to lose height rapidly prior to landing, some large birds such as geese indulge in a rapid alternating series of sideslips in a maneuver termed as *whiffling*.

Mute Swan *Cygnus olor*

Adaptations for flight



1 Axillaries; 2 Margin (Marginal underwing coverts); 3 Lesser underwing coverts; 4 Median underwing coverts (Secondary coverts); 5 Greater underwing coverts (Secondary coverts); 6 Carpal joint; 7 Lesser underwing primary coverts; 8 Greater undering primary coverts; 9 Secondaries; 10 Primaries

The most obvious adaptation to flight is the wing, but because flight is so energetically demanding birds have evolved several other adaptations to improve efficiency when flying. Birds' bodies are streamlined to help overcome air-resistance. Also, the bird skeleton is hollow to reduce weight, and many unnecessary bones have been lost (such as the bony tail of the early bird *Archaeopteryx*), along with the toothed jaw of early birds, which has been replaced with a lightweight beak. The skeleton's breastbone has also adapted into a large keel, suitable for the attachment of large, powerful flight muscles. The vanes of the feathers have hooklets called barbules that zip them together, giving the feathers the strength needed to hold the airfoil (these are often lost in flightless birds).

The large amounts of energy required for flight have led to the evolution of a unidirectional pulmonary system to provide the large quantities of oxygen required for their high respiratory rates. This high metabolic rate produces large quantities of radicals in the cells that can damage DNA and lead to tumours. Birds, however, do not suffer from an otherwise expected shortened lifespan as their cells have evolved a more efficient antioxidant system than those found in other animals.