All About Birds

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Bird

Birds Temporal range: Late Jurassic–Recent, 150–0 Ma

Australian Wood Duck, *Chenonetta jubata*

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
(unranked):	Reptiliomorpha
(unranked):	Amniota
(unranked):	Avialae
Class:	**Aves** Linnaeus, 1758
Subclasses & orders	
• About two dozen modern orders and several extinct orders and subclasses	

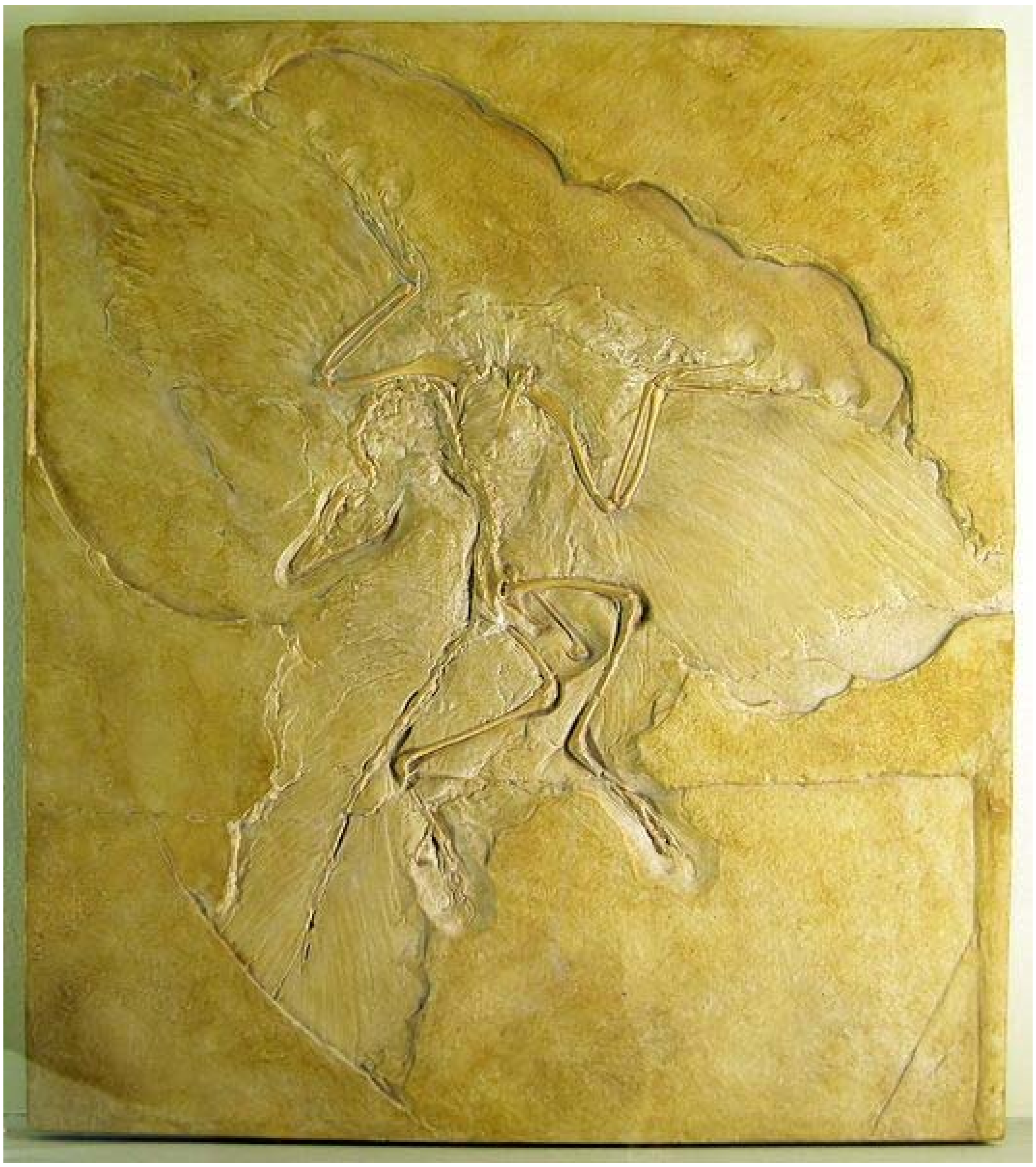
Birds (class **Aves**) are winged, bipedal, endothermic (warm-blooded), egg-laying, vertebrate animals. There are around 10,000 living species, making them the most varied of tetrapod vertebrates. They inhabit ecosystems across the globe, from the Arctic to the Antarctic. Extant birds range in size from the 5 cm (2 in) Bee Hummingbird to the 2.75 m (9 ft) Ostrich. The fossil record indicates that birds evolved within theropod dinosaurs during the Jurassic period, around 150–200 Ma (million years ago), and the earliest known bird is the Late Jurassic *Archaeopteryx*, *c* 150–145 Ma. Most paleontologists regard birds as the only clade of dinosaurs to have survived the Cretaceous–Tertiary extinction event approximately 65.5 Ma.

Modern birds are characterised by feathers, a beak with no teeth, the laying of hard-shelled eggs, a high metabolic rate, a four-chambered heart, and a lightweight but strong skeleton. All *living* species of birds have wings - the now extinct flightless Moa of New Zealand were the only exceptions. Wings are evolved forelimbs, and most bird species can fly, with some exceptions including ratites, penguins, and a number of diverse endemic island species. Birds also have unique digestive and respiratory systems that are highly adapted for flight. Some birds, especially corvids and parrots, are among the most intelligent animal species; a number of bird species have been observed manufacturing and using tools, and many social species exhibit cultural transmission of knowledge across generations.

Many species undertake long distance annual migrations, and many more perform shorter irregular movements. Birds are social; they communicate using visual signals and through calls and songs, and participate in social behaviours including cooperative breeding and hunting, flocking, and mobbing of predators. The vast majority of bird species are socially monogamous, usually for one breeding season at a time, sometimes for years, but rarely for life. Other species have breeding systems that are polygynous ("many females") or, rarely, polyandrous ("many males"). Eggs are usually laid in a nest and incubated by the parents. Most birds have an extended period of parental care after hatching.

Many species are of economic importance, mostly as sources of food acquired through hunting or farming. Some species, particularly songbirds and parrots, are popular as pets. Other uses include the harvesting of guano (droppings) for use as a fertiliser. Birds figure prominently in all aspects of human culture from religion to poetry to popular music. About 120–130 species have become extinct as a result of human activity since the 17th century, and hundreds more before then. Currently about 1,200 species of birds are threatened with extinction by human activities, though efforts are underway to protect them.

Evolution and taxonomy



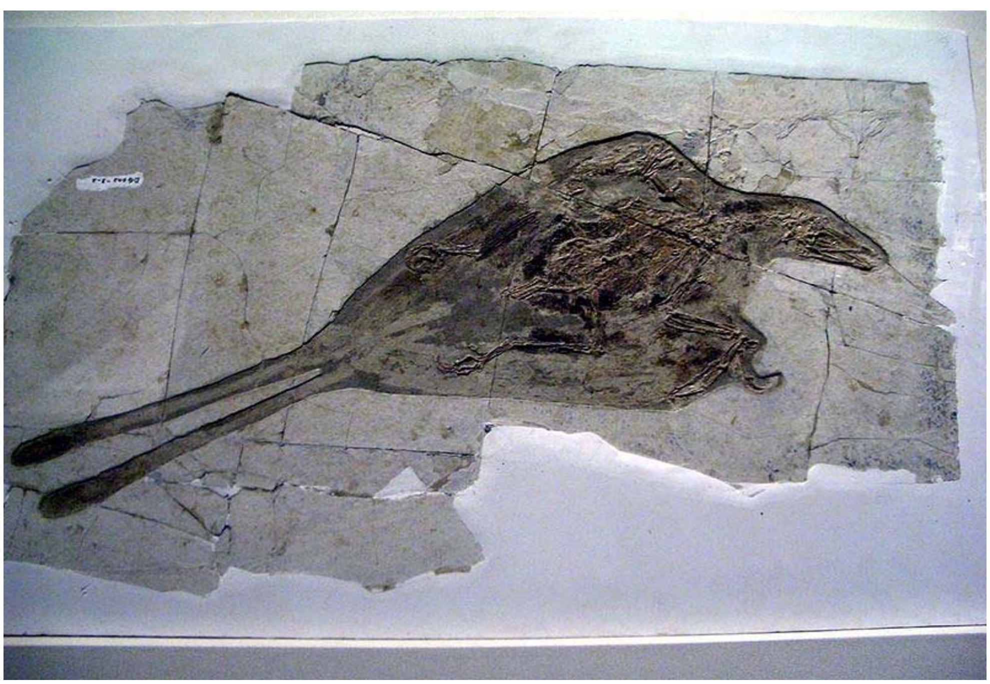
Archaeopteryx, the earliest known bird

The first classification of birds was developed by Francis Willughby and John Ray in their 1676 volume *Ornithologiae*. Carolus Linnaeus modified that work in 1758 to devise the taxonomic classification system currently in use. Birds are categorised as the biological class Aves in Linnaean taxonomy. Phylogenetic taxonomy places Aves in the dinosaur clade Theropoda. Aves and a sister group, the clade Crocodilia, contain the only living representatives of the reptile clade Archosauria. Phylogenetically, Aves is commonly defined as all descendants of the most recent common ancestor of modern birds and *Archaeopteryx lithographica*.

Archaeopteryx, from the Tithonian stage of the Late Jurassic (some 150–145 million years ago), is the earliest known bird under this definition. Others, including Jacques Gauthier and adherents of the Phylocode system, have defined Aves to include only the modern bird groups, the crown group. This has been done by excluding most groups known only from fossils, and assigning them, instead, to the Avialae in part to avoid the uncertainties about the placement of *Archaeopteryx* in relation to animals traditionally thought of as theropod dinosaurs.

All modern birds lie within the subclass Neornithes, which has two subdivisions: the Palaeognathae, containing birds that are flightless (like ostriches) or weak fliers, and the wildly diverse Neognathae, containing all other birds. These two subdivisions are often given the rank of superorder, although Livezey and Zusi assigned them "cohort" rank. Depending on the taxonomic viewpoint, the number of known living bird species varies anywhere from 9,800 to 10,050.

Dinosaurs and the origin of birds



Confuciusornis, a Cretaceous bird from China

Based on fossil and biological evidence, most scientists accept that birds are a specialized sub-group of theropod dinosaurs. More specifically, they are members of Maniraptora, a group of theropods which includes dromaeosaurs and oviraptorids, among others. As scientists discover more non-avian theropods that are closely related to birds, the previously clear distinction between non-birds and birds has become blurred. Recent discoveries in the Liaoning Province of northeast China, which demonstrate that many small theropod dinosaurs had feathers, contribute to this ambiguity.

The consensus view in contemporary paleontology is that the birds, Aves, are the closest relatives of the deinonychosaurs, which include dromaeosaurids and troodontids. Together, these three form a group called Paraves. The basal dromaeosaur *Microraptor* has features which may have enabled it to glide or fly. The most basal deinonychosaurs are very small. This evidence raises the possibility that the ancestor of all paravians may have been arboreal, may have been able to glide, or both.

The Late Jurassic *Archaeopteryx* is well-known as one of the first transitional fossils to be found and it provided support for the theory of evolution in the late 19th century. *Archaeopteryx* has clearly reptilian characteristics: teeth, clawed fingers, and a long, lizard-like tail, but it has finely preserved wings with flight feathers identical to those of modern birds. It is not considered a direct ancestor of modern birds, but is the oldest and most primitive known member of Aves or Avialae, and it is probably closely related to the real ancestor.

Alternative theories and controversies

There have been many controversies in the study of the origin of birds. Early disagreements included whether birds evolved from dinosaurs or more primitive archosaurs. Within the dinosaur camp there were disagreements as to whether ornithischian or theropod dinosaurs were the more likely ancestors. Although ornithischian (bird-hipped) dinosaurs share the hip structure of modern birds, birds are thought to have originated from the saurischian (lizard-hipped) dinosaurs, and therefore evolved their hip structure independently. In fact, a bird-like hip structure evolved a third time among a peculiar group of theropods known as the Therizinosauridae. A few scientists suggest that birds are not dinosaurs, but evolved from early archosaurs like *Longisquama*.

Early evolution of birds

Birds diversified into a wide variety of forms during the Cretaceous Period. Many groups retained primitive characteristics, such as clawed wings and teeth, though the latter were lost independently in a number of bird groups, including modern birds (Neornithes). While the earliest forms, such as *Archaeopteryx* and *Jeholornis*, retained the long bony tails of their ancestors, the tails of more advanced birds were shortened with the advent of the pygostyle bone in the clade Pygostylia.

The first large, diverse lineage of short-tailed birds to evolve were the Enantiornithes, or "opposite birds", so named because the construction of their shoulder bones was in reverse to that of modern birds. Enantiornithes occupied a wide array of ecological niches, from sand-probing shorebirds and fish-eaters to tree-dwelling forms and seed-eaters. More advanced lineages also specialised in eating fish, like the superficially gull-like subclass of Ichthyornithes ("fish birds").

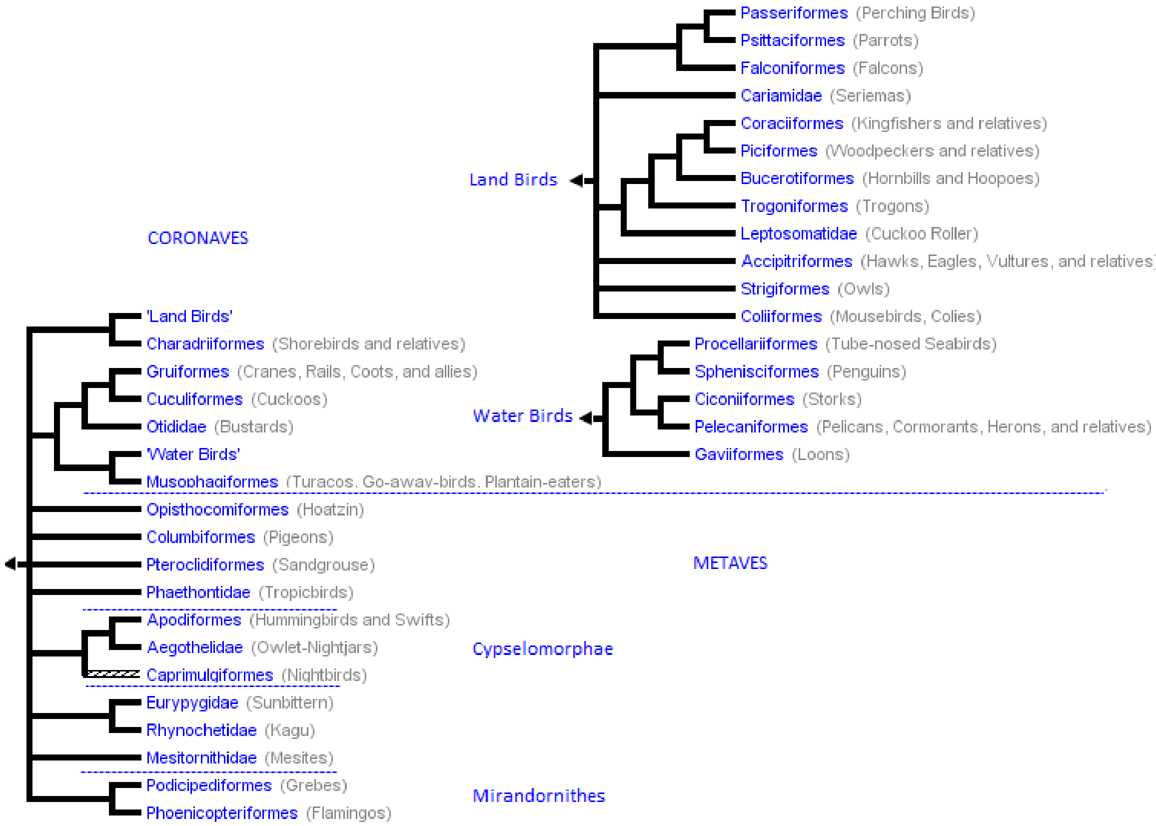
One order of Mesozoic seabirds, the Hesperornithiformes, became so well adapted to hunting fish in marine environments that they lost the ability to fly and became primarily aquatic. Despite their extreme specializations, the Hesperornithiformes represent some of the closest relatives of modern birds.

Diversification of modern birds

Containing all modern birds, the subclass Neornithes is, due to the discovery of *Vegavis*, now known to have evolved into some basic lineages by the end of the Cretaceous and is split into two superorders, the Palaeognathae and Neognathae. The paleognaths include the tinamous of Central and South America and the ratites. The basal divergence from the remaining Neognathes was that of the Galloanserae, the superorder containing the Anseriformes (ducks, geese, swans and screamers) and the Galliformes (the pheasants, grouse, and their allies, together with the mound builders and the guans and their allies). The dates for the splits are much debated by scientists. It is agreed that the Neornithes evolved in the Cretaceous, and that the split between the Galloanseri from other Neognathes occurred before the K–T extinction event, but there are different opinions about whether the radiation of the remaining Neognathes occurred before or after the extinction of the other dinosaurs. This disagreement is in part caused by a divergence in the evidence; molecular dating suggests a Cretaceous radiation, while fossil evidence supports a Tertiary radiation. Attempts to reconcile the molecular and fossil evidence have proved controversial.

The classification of birds is a contentious issue. Sibley and Ahlquist's *Phylogeny and Classification of Birds* (1990) is a landmark work on the classification of birds, although it is frequently debated and constantly revised. Most evidence seems to suggest that the assignment of orders is accurate, but scientists disagree about the relationships between the orders themselves; evidence from modern bird anatomy, fossils and DNA have all been brought to bear on the problem, but no strong consensus has emerged. More recently, new fossil and molecular evidence is providing an increasingly clear picture of the evolution of modern bird orders.

Modern bird orders: Classification



Cladogram showing the most recent classification of Neoaves, based on several phylogenetic studies.

This is a list of the taxonomic orders in the subclass Neornithes, or modern birds. This list uses the traditional classification (the so-called Clements order), revised by the Sibley-Monroe classification. The list of birds gives a more detailed summary of the orders, including families.

Subclass Neornithes
The subclass Neornithes has two superorders –

Superorder Palaeognathae:

The name of the superorder is derived from 'paleognath', the ancient Greek for "old jaws" in reference to the skeletal anatomy of the palate, which is described as more primitive and reptilian than that in other birds. The Palaeognathae consists of two orders which comprise 49 existing species.

- Struthioniformes—ostriches, emus, kiwis, and allies
- Tinamiformes—tinamous

Superorder Neognathae:

The superorder Neognathae comprises 27 orders which have a total of nearly ten thousand species. The Neognathae have undergone adaptive radiation to produce the staggering diversity of form (especially of the bill and feet), function, and behavior that are seen today.

The orders comprising the Neognathae are:

- Anseriformes—waterfowl
- Galliformes—fowl
- Charadriiformes—gulls, button-quails, plovers and allies
- Gaviiformes—loons
- Podicipediformes—grebes
- Procellariiformes—albatrosses, petrels, and allies
- Sphenisciformes—penguins
- Pelecaniformes—pelicans and allies
- Phaethontiformes—tropicbirds
- Ciconiiformes—storks and allies
- Cathartiformes—New World vultures
- Phoenicopteriformes—flamingos
- Falconiformes—falcons, eagles, hawks and allies
- Gruiformes—cranes and allies
- Pteroclidiformes—sandgrouse
- Columbiformes—doves and pigeons
- Psittaciformes—parrots and allies
- Cuculiformes—cuckoos and turacos
- Opisthocomiformes—hoatzin
- Strigiformes—owls
- Caprimulgiformes—nightjars and allies
- Apodiformes—swifts and hummingbirds
- Coraciiformes—kingfishers and allies
- Piciformes—woodpeckers and allies
- Trogoniformes—trogons
- Coliiformes—mousebirds
- Passeriformes—passerines

The radically different Sibley-Monroe classification (Sibley-Ahlquist taxonomy), based on molecular data, found widespread adoption in a few aspects, as recent molecular, fossil, and anatomical evidence supported the Galloanserae.

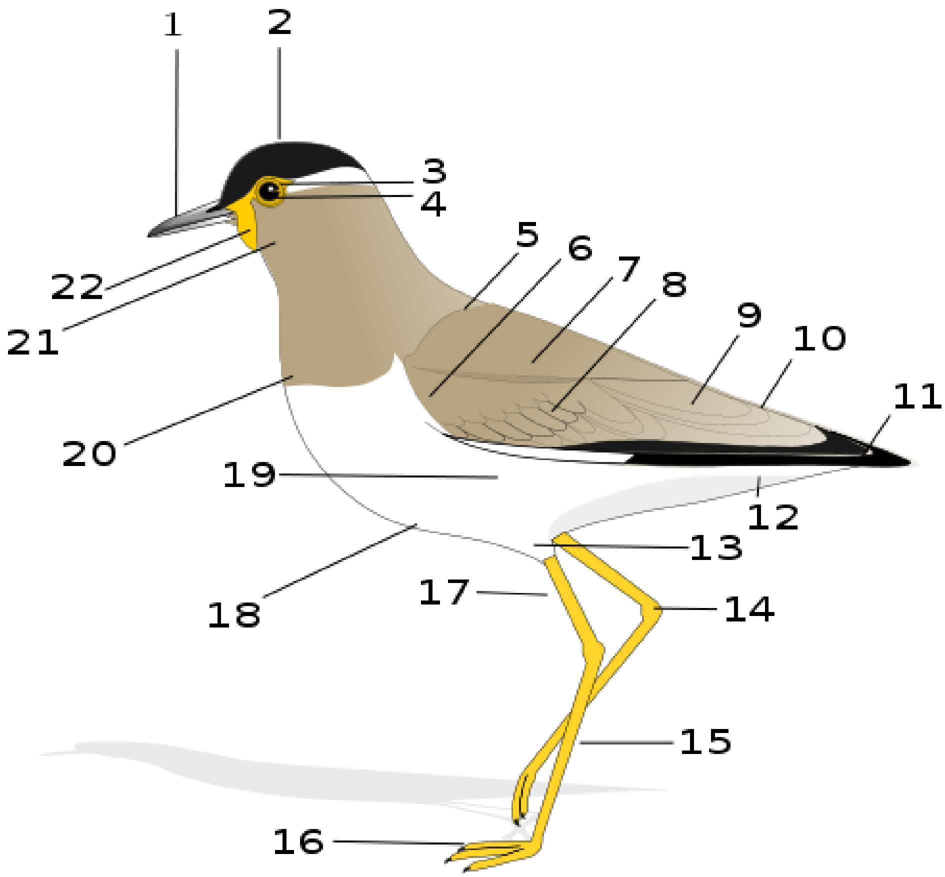
Distribution

The range of the House Sparrow has expanded dramatically due to human activities.

Birds live and breed in most terrestrial habitats and on all seven continents, reaching their southern extreme in the Snow Petrel's breeding colonies up to 440 kilometres (270 mi) inland in Antarctica. The highest bird diversity occurs in tropical regions. It was earlier thought that this high diversity was the result of higher speciation rates in the tropics, however recent studies found higher speciation rates in the high latitudes that were offset by greater extinction rates than in the tropics. Several families of birds have adapted to life both on the world's oceans and in them, with some seabird species coming ashore only to breed and some penguins have been recorded diving up to 300 metres (980 ft).

Many bird species have established breeding populations in areas to which they have been introduced by humans. Some of these introductions have been deliberate; the Ring-necked Pheasant, for example, has been introduced around the world as a game bird. Others have been accidental, such as the establishment of wild Monk Parakeets in several North American cities after their escape from captivity. Some species, including Cattle Egret, Yellow-headed Caracara and Galah, have spread naturally far beyond their original ranges as agricultural practices created suitable new habitat.

Anatomy and physiology



External anatomy of a bird: 1 Beak, 2 Head, 3 Iris, 4 Pupil, 5 Mantle, 6 Lesser coverts, 7 Scapulars, 8 Median coverts, 9 Tertials, 10 Rump, 11 Primaries, 12 Vent, 13 Thigh, 14 Tibio-tarsal articulation, 15 Tarsus, 16 Foot, 17 Tibia, 18 Belly, 19 Flanks, 20 Breast, 21 Throat, 22 Wattle

Compared with other vertebrates, birds have a body plan that shows many unusual adaptations, mostly to facilitate flight.

The skeleton consists of very lightweight bones. They have large air-filled cavities (called pneumatic cavities) which connect with the respiratory system. The skull bones in adults are fused and do not show cranial sutures. The orbits are large and separated by a bony septum. The spine has cervical, thoracic, lumbar and caudal regions with the number of cervical (neck) vertebrae highly variable and especially flexible, but movement is reduced in the anterior thoracic vertebrae and absent in the later vertebrae. The last few are fused with the pelvis to form the synsacrum. The ribs are flattened and the sternum is keeled for the attachment of flight muscles except in the flightless bird orders. The forelimbs are modified into wings.

Like the reptiles, birds are primarily uricotelic, that is, their kidneys extract nitrogenous wastes from their bloodstream and excrete it as uric acid instead of urea or ammonia via the ureters into the intestine. Birds do not have a urinary bladder or external urethral opening and (with exception of the Ostrich) uric acid is excreted along with feces as a semisolid waste. However, birds such as hummingbirds can be facultatively ammonotelic, excreting most of the nitrogenous wastes as ammonia. They also excrete creatine, rather than creatinine like mammals. This material, as well as the output of the intestines, emerges from the bird's cloaca. The cloaca is a multi-purpose opening: waste is expelled through it, birds mate by joining cloaca, and females lay eggs from it. In addition, many species of birds regurgitate pellets. The digestive system of birds is unique, with a crop for storage and a gizzard that contains swallowed stones for grinding food to compensate for the lack of teeth. Most birds are highly adapted for rapid digestion to aid with flight. Some migratory birds have adapted to use protein from many parts of their bodies, including protein from the intestines, as additional energy during migration.

Birds have one of the most complex respiratory systems of all animal groups. Upon inhalation, 75% of the fresh air bypasses the lungs and flows directly into a posterior air sac which extends from the lungs and connects with air spaces in the bones and fills them with air. The other 25% of the air goes directly into the lungs. When the bird exhales, the used air flows out of the lung and the stored fresh air from the posterior air sac is simultaneously forced into the lungs. Thus, a bird's lungs receive a constant supply of fresh air during both inhalation and exhalation. Sound production is achieved using the syrinx, a muscular chamber incorporating multiple tympanic membranes which diverges from the lower end of the trachea. The bird's heart has four chambers and the right aortic arch gives rise to systemic circulation (unlike in the mammals where the left arch is involved). The postcava receives blood from the limbs via the renal portal system. Unlike in mammals, the red blood cells in birds have a nucleus.

The nictitating membrane as it covers the eye of a Masked Lapwing

The nervous system is large relative to the bird's size. The most developed part of the brain is the one that controls the flight-related functions, while the cerebellum coordinates movement and the cerebrum controls behaviour patterns, navigation, mating and nest building. Most birds have a poor sense of smell with notable exceptions including kiwis, New World vultures and tubenoses. The avian visual system is usually highly developed. Water birds have special flexible lenses, allowing accommodation for vision in air and water. Some species also have dual fovea. Birds are tetrachromatic, possessing ultraviolet (UV) sensitive cone cells in the eye as well as green, red and blue ones. This allows them to perceive ultraviolet light, which is involved in courtship. Many birds show plumage patterns in ultraviolet that are invisible to the human eye; some birds whose sexes appear similar to the naked eye are distinguished by the presence of ultraviolet reflective patches on their feathers. Male Blue Tits have an ultraviolet reflective crown patch which is displayed in courtship by posturing and raising of their nape feathers. Ultraviolet light is also used in foraging—kestrels have been shown to search for prey by detecting the UV reflective urine trail marks left on the ground by rodents. The eyelids of a bird are not used in blinking. Instead the eye is lubricated by the nictitating membrane, a third eyelid that moves horizontally. The nictitating membrane also covers the eye and acts as a contact lens in many aquatic birds. The bird retina has a fan shaped blood supply system called the pecten. Most birds cannot move their eyes, although there are exceptions, such as the Great Cormorant. Birds with eyes on the sides of their heads have a wide visual field, while birds with eyes on the front of their heads, such as owls, have binocular vision and can estimate the depth of field. The avian ear lacks external pinnae but is covered by feathers, although in some birds, such as the *Asio*, *Bubo* and *Otus* owls, these feathers form tufts which resemble ears. The inner ear has a cochlea, but it is not spiral as in mammals.

A few species are able to use chemical defenses against predators; some Procellariiformes can eject an unpleasant oil against an aggressor, and some species of pitohuis from New Guinea have a powerful neurotoxin in their skin and feathers.

Chromosomes

Birds have two sexes: male and female. The sex of birds is determined by the Z and W sex chromosomes, rather than by the X and Y chromosomes present in mammals. Male birds have two Z chromosomes (ZZ), and female birds have a W chromosome and a Z chromosome (WZ).

In nearly all species of birds, an individual's sex is determined at fertilization. However, one recent study demonstrated temperature-dependent sex determination among Australian Brush-turkeys, for which higher temperatures during incubation resulted in a higher female-to-male sex ratio.

Feathers, plumage, and scales

The plumage of the African Scops Owl allows it to blend in with its surroundings.

Feathers are a feature characteristic of birds (though also present in some dinosaurs not currently considered to be true birds). They facilitate flight, provide insulation that aids in thermoregulation, and are used in display, camouflage, and signaling. There are several types of feathers, each serving its own set of purposes. Feathers are epidermal growths attached to the skin and arise only in specific tracts of skin called pterylae. The distribution pattern of these feather tracts (pterylosis) is used in taxonomy and systematics. The arrangement and appearance of feathers on the body, called plumage, may vary within species by age, social status, and sex.

Plumage is regularly moulted; the standard plumage of a bird that has moulted after breeding is known as the "non-breeding" plumage, or – in the Humphrey-Parkes terminology – "basic" plumage; breeding plumages or variations of the basic plumage are known under the Humphrey-Parkes system as "alternate" plumages. Moulting is annual in most species, although some may have two moults a year, and large birds of prey may moult only once every few years. Moulting patterns vary across species. In passerines, flight feathers are replaced one at a time with the innermost primary being the first. When the fifth of sixth primary is replaced, the outermost tertiaries begin to drop. After the innermost tertiaries are moulted, the secondaries starting from the innermost begin to drop and this proceeds to the outer feathers (centrifugal moult). The greater primary coverts are moulted in synchrony with the primary that they overlap. A small number of species, such as ducks and geese, lose all of their flight feathers at once, temporarily becoming flightless. As a general rule, the tail feathers are moulted and replaced starting with the innermost pair. Centripetal moults of tail feathers are however seen in the Phasianidae. The centrifugal moult is modified in the tail feathers of woodpeckers and treecreepers, in that it begins with the second innermost pair of feathers and finishes with the central pair of feathers so that the bird maintains a functional climbing tail. The general pattern seen in passerines is that the primaries are replaced outward, secondaries inward, and the tail from center outward. Before nesting, the females of most bird species gain a bare brood patch by losing feathers close to the belly. The skin there is well supplied with blood vessels and helps the bird in incubation.

Red Lory preening

Feathers require maintenance and birds preen or groom them daily, spending an average of around 9% of their daily time on this. The bill is used to brush away foreign particles and to apply waxy secretions from the uropygial gland; these secretions protect the feathers' flexibility and act as an antimicrobial agent, inhibiting the growth of feather-degrading bacteria. This may be supplemented with the secretions of formic acid from ants, which birds receive through a behaviour known as anting, to remove feather parasites.

The scales of birds are composed of the same keratin as beaks, claws, and spurs. They are found mainly on the toes and metatarsus, but may be found further up on the ankle in some birds. Most bird scales do not overlap significantly, except in the cases of kingfishers and woodpeckers. The scales of birds are thought to be homologous to those of reptiles and mammals.

Flight

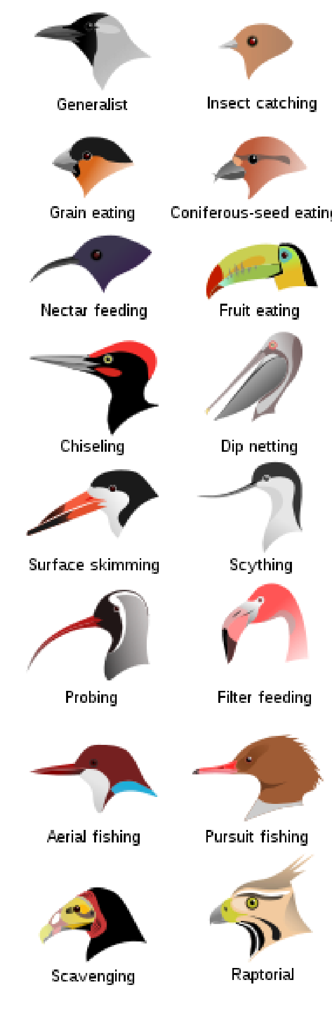
Restless Flycatcher in the downstroke of flapping flight

Most birds can fly, which distinguishes them from almost all other vertebrate classes. Flight is the primary means of locomotion for most bird species and is used for breeding, feeding, and predator avoidance and escape. Birds have various adaptations for flight, including a lightweight skeleton, two large flight muscles, the pectoralis (which accounts for 15% of the total mass of the bird) and the supracoracoideus, as well as a modified forelimb (wing) that serves as an aerofoil. Wing shape and size generally determine a bird species' type of flight; many birds combine powered, flapping flight with less energy-intensive soaring flight. About 60 extant bird species are flightless, as were many extinct birds. Flightlessness often arises in birds on isolated islands, probably due to limited resources and the absence of land predators. Though flightless, penguins use similar musculature and movements to "fly" through the water, as do auks, shearwaters and dippers.

Behaviour

Most birds are diurnal, but some birds, such as many species of owls and nightjars, are nocturnal or crepuscular (active during twilight hours), and many coastal waders feed when the tides are appropriate, by day or night.

Diet and feeding



Feeding adaptations in beaks

Birds' diets are varied and often include nectar, fruit, plants, seeds, carrion, and various small animals, including other birds. Because birds have no teeth, their digestive system is adapted to process unmasticated food items that are swallowed whole.

Birds that employ many strategies to obtain food or feed on a variety of food items are called generalists, while others that concentrate time and effort on specific food items or have a single strategy to obtain food are considered specialists. Birds' feeding strategies vary by species. Many birds glean for insects, invertebrates, fruit, or seeds. Some hunt insects by suddenly attacking from a branch. Those species that seek pest insects are considered beneficial 'biological control agents' and their presence encouraged in biological pest control programs. Nectar feeders such as hummingbirds, sunbirds, lories, and lorikeets amongst others have specially adapted brushy tongues and in many cases bills designed to fit co-adapted flowers. Kiwis and shorebirds with long bills probe for invertebrates; shorebirds' varied bill lengths and feeding methods result in the separation of ecological niches. Loons, diving ducks, penguins and auks pursue their prey underwater, using their wings or feet for propulsion, while aerial predators such as sulids, kingfishers and terns plunge dive after their prey. Flamingos, three species of prion, and some ducks are filter feeders. Geese and dabbling ducks are primarily grazers.

Some species, including frigatebirds, gulls, and skuas, engage in kleptoparasitism, stealing food items from other birds. Kleptoparasitism is thought to be a supplement to food obtained by hunting, rather than a significant part of any species' diet; a study of Great Frigatebirds stealing from Masked Boobies estimated that the frigatebirds stole at most 40% of their food and on average stole only 5%. Other birds are scavengers; some of these, like vultures, are specialised carrion eaters, while others, like gulls, corvids, or other birds of prey, are opportunists.

Water and drinking

Water is needed by many birds although their mode of excretion and lack of sweat glands reduces the physiological demands. Some desert birds can obtain their water needs entirely from moisture in their food. They may also have other adaptations such as allowing their body temperature to rise, saving on moisture loss from evaporative cooling or panting. Seabirds can drink seawater and have salt glands inside the head that eliminate excess salt out of the nostrils.

Most birds scoop water in their beaks and raise their head to let water run down the throat. Some species, especially of arid zones, belonging to the pigeon, finch, mousebird, button-quail and bustard families are capable of sucking up water without the need to tilt back their heads. Some desert birds depend on water sources and sandgrouse are particularly well-known for their daily congregations at waterholes. Nesting sandgrouse carry water to their young by wetting their belly feathers.

Migration

Many bird species migrate to take advantage of global differences of seasonal temperatures, therefore optimising availability of food sources and breeding habitat. These migrations vary among the different groups. Many landbirds, shorebirds, and waterbirds undertake annual long distance migrations, usually triggered by the length of daylight as well as weather conditions. These birds are characterised by a breeding season spent in the temperate or arctic/antarctic regions and a non-breeding season in the tropical regions or opposite hemisphere. Before migration, birds substantially increase body fats and reserves and reduce the size of some of their organs. Migration is highly demanding energetically, particularly as birds need to cross deserts and oceans without refuelling. Landbirds have a flight range of around 2,500 km (1,600 mi) and shorebirds can fly up to 4,000 km (2,500 mi), although the Bar-tailed Godwit is capable of non-stop flights of up to 10,200 km (6,300 mi). Seabirds also undertake long migrations, the longest annual migration being those of Sooty Shearwaters, which nest in New Zealand and Chile and spend the northern summer feeding in the North Pacific off Japan, Alaska and California, an annual round trip of 64,000 km (39,800 mi). Other seabirds disperse after breeding, travelling widely but having no set migration route. Albatrosses nesting in the Southern Ocean often undertake circumpolar trips between breeding seasons.

The routes of satellite-tagged Bar-tailed Godwits migrating north from New Zealand. This species has the longest known non-stop migration of any species, up to 10,200 km (6,300 mi).

Some bird species undertake shorter migrations, travelling only as far as is required to avoid bad weather or obtain food. Irruptive species such as the boreal finches are one such group and can commonly be found at a location in one year and absent the next. This type of migration is normally associated with food availability. Species may also travel shorter distances over part of their range, with individuals from higher latitudes travelling into the existing range of conspecifics; others undertake partial migrations, where only a fraction of the population, usually females and subdominant males, migrates. Partial migration can form a large percentage of the migration behaviour of birds in some regions; in Australia, surveys found that 44% of non-passerine birds and 32% of passerines were partially migratory. Altitudinal migration is a form of short distance migration in which birds spend the breeding season at higher altitudes elevations and move to lower ones during suboptimal conditions. It is most often triggered by temperature changes and usually occurs when the normal territories also become inhospitable due to lack of food. Some species may also be nomadic, holding no fixed territory and moving according to weather and food availability. Parrots as a family are overwhelmingly neither migratory nor sedentary but considered to either be dispersive, irruptive, nomadic or undertake small and irregular migrations.

The ability of birds to return to precise locations across vast distances has been known for some time; in an experiment conducted in the 1950s a Manx Shearwater released in Boston returned to its colony in Skomer, Wales, within 13 days, a distance of 5,150 km (3,200 mi). Birds navigate during migration using a variety of methods. For diurnal migrants, the sun is used to navigate by day, and a stellar compass is used at night. Birds that use the sun compensate for the changing position of the sun during the day by the use of an internal clock. Orientation with the stellar compass depends on the position of the constellations surrounding Polaris. These are backed up in some species by their ability to sense the Earth's geomagnetism through specialised photoreceptors.

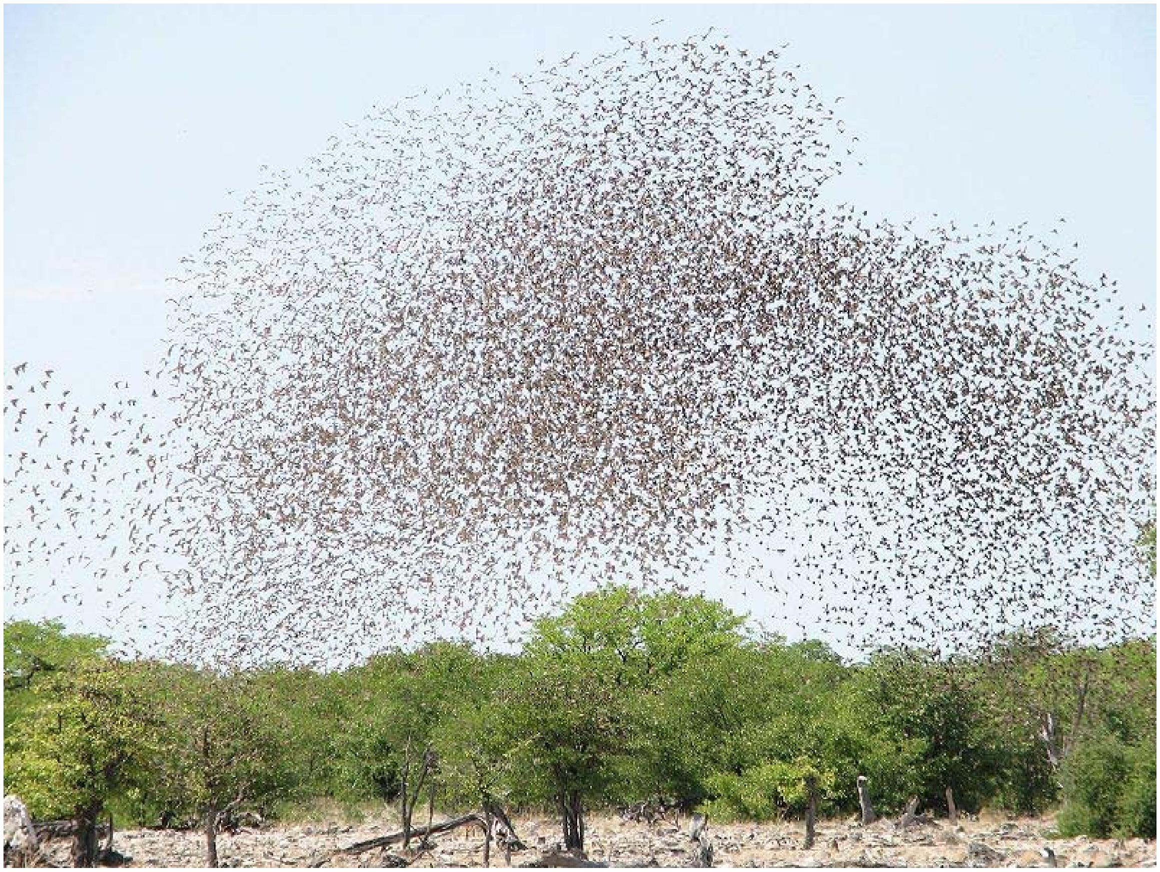
Communication

The startling display of the Sunbittern mimics a large predator.

Birds communicate using primarily visual and auditory signals. Signals can be interspecific (between species) and intraspecific (within species).

Birds sometimes use plumage to assess and assert social dominance, to display breeding condition in sexually selected species, or to make threatening displays, as in the Sunbittern's mimicry of a large predator to ward off hawks and protect young chicks. Variation in plumage also allows for the identification of birds, particularly between species. Visual communication among birds may also involve ritualised displays, which have developed from non-signalling actions such as preening, the adjustments of feather position, pecking, or other behaviour. These displays may signal aggression or submission or may contribute to the formation of pair-bonds. The most elaborate displays occur during courtship, where "dances" are often formed from complex combinations of many possible component movements; males' breeding success may depend on the quality of such displays.

Bird calls and songs, which are produced in the syrinx, are the major means by which birds communicate with sound. This communication can be very complex; some species can operate the two sides of the syrinx independently, allowing the simultaneous production of two different songs. Calls are used for a variety of purposes, including mate attraction, evaluation of potential mates, bond formation, the claiming and maintenance of territories, the identification of other individuals (such as when parents look for chicks in colonies or when mates reunite at the start of breeding season), and the warning of other birds of potential predators, sometimes with specific information about the nature of the threat. Some birds also use mechanical sounds for auditory communication. The *Coenocorypha* snipes of New Zealand drive air through their feathers, woodpeckers drum territorially, and Palm Cockatoos use tools to drum.



Red-billed Queleas, the most numerous species of bird, form enormous flocks—sometimes tens of thousands strong.

Flocking and other associations

While some birds are essentially territorial or live in small family groups, other birds may form large flocks. The principal benefits of flocking are safety in numbers and increased foraging efficiency. Defence against predators is particularly important in closed habitats like forests, where ambush predation is common and multiple eyes can provide a valuable early warning system. This has led to the development of many mixed-species feeding flocks, which are usually composed of small numbers of many species; these flocks provide safety in numbers but reduce potential competition for resources. Costs of flocking include bullying of socially subordinate birds by more dominant birds and the reduction of feeding efficiency in certain cases.

Birds sometimes also form associations with non-avian species. Plunge-diving seabirds associate with dolphins and tuna, which push shoaling fish towards the surface. Hornbills have a mutualistic relationship with Dwarf Mongooses, in which they forage together and warn each other of nearby birds of prey and other predators.

Resting and roosting

Many birds, like this American Flamingo, tuck their head into their back when sleeping

The high metabolic rates of birds during the active part of the day is supplemented by rest at other times. Sleeping birds often use a type of sleep known as vigilant sleep, where periods of rest are interspersed with quick eye-opening 'peeks', allowing them to be sensitive to disturbances and enable rapid escape from threats. Swifts are believed to be able to sleep in flight and radar observations suggest that they orient themselves to face the wind in their roosting flight. It has been suggested that there may be certain kinds of sleep which are possible even when in flight. Some birds have also demonstrated the capacity to fall into slow-wave sleep one hemisphere of the brain at a time. The birds tend to exercise this ability depending upon its position relative to the outside of the flock. This may allow the eye opposite the sleeping hemisphere to remain vigilant for predators by viewing the outer margins of the flock. This adaptation is also known from marine mammals. Communal roosting is common because it lowers the loss of body heat and decreases the risks associated with predators. Roosting sites are often chosen with regard to thermoregulation and safety.

Many sleeping birds bend their heads over their backs and tuck their bills in their back feathers, although others place their beaks among their breast feathers. Many birds rest on one leg, while some may pull up their legs into their feathers, especially in cold weather. Perching birds have a tendon locking mechanism that helps them hold on to the perch when they are asleep. Many ground birds, such as quails and pheasants, roost in trees. A few parrots of the genus *Loriculus* roost hanging upside down. Some hummingbirds go into a nightly state of torpor accompanied with a reduction of their metabolic rates. This physiological adaptation shows in nearly a hundred other species, including owlet-nightjars, nightjars, and woodswallows. One species, the Common Poorwill, even enters a state of hibernation. Birds do not have sweat glands, but they may cool themselves by moving to shade, standing in water, panting, increasing their surface area, fluttering their throat or by using special behaviours like urohidrosis to cool themselves.

Breeding

Social systems

Like others of its family the male Raggiana Bird of Paradise has elaborate breeding plumage used to impress females.

Ninety-five percent of bird species are socially monogamous. These species pair for at least the length of the breeding season or—in some cases—for several years or until the death of one mate. Monogamy allows for biparental care, which is especially important for species in which females require males' assistance for successful brood-rearing. Among many socially monogamous species, extra-pair copulation (infidelity) is common. Such behaviour typically occurs between dominant males and females paired with subordinate males, but may also be the result of forced copulation in ducks and other anatids. For females, possible benefits of extra-pair copulation include getting better genes for her offspring and insuring against the possibility of infertility in her mate. Males of species that engage in extra-pair copulations will closely guard their mates to ensure the parentage of the offspring that they raise.

Other mating systems, including polygyny, polyandry, polygamy, polygynandry, and promiscuity, also occur. Polygamous breeding systems arise when females are able to raise broods without the help of males. Some species may use more than one system depending on the circumstances.

Breeding usually involves some form of courtship display, typically performed by the male. Most displays are rather simple and involve some type of song. Some displays, however, are quite elaborate. Depending on the species, these may include wing or tail drumming, dancing, aerial flights, or communal lekking. Females are generally the ones that drive partner selection, although in the polyandrous phalaropes, this is reversed: plainer males choose brightly coloured females. Courtship feeding, billing and allopreening are commonly performed between partners, generally after the birds have paired and mated.

Territories, nesting and incubation

Many birds actively defend a territory from others of the same species during the breeding season; maintenance of territories protects the food source for their chicks. Species that are unable to defend feeding territories, such as seabirds and swifts, often breed in colonies instead; this is thought to offer protection from predators. Colonial breeders defend small nesting sites, and competition between and within species for nesting sites can be intense.

Male Common Blackbird (*Turdus merula*) feeding it's chicks

Male Golden-backed Weavers construct elaborate suspended nests out of grass.

All birds lay amniotic eggs with hard shells made mostly of calcium carbonate. Hole and burrow nesting species tend to lay white or pale eggs, while open nesters lay camouflaged eggs. There are many exceptions to this pattern, however; the ground-nesting nightjars have pale eggs, and camouflage is instead provided by their plumage. Species that are victims of brood parasites have varying egg colours to improve the chances of spotting a parasite's egg, which forces female parasites to match their eggs to those of their hosts.

Bird eggs are usually laid in a nest. Most species create somewhat elaborate nests, which can be cups, domes, plates, beds scrapes, mounds, or burrows. Some bird nests, however, are extremely primitive; albatross nests are no more than a scrape on the ground. Most birds build nests in sheltered, hidden areas to avoid predation, but large or colonial birds—which are more capable of defence—may build more open nests. During nest construction, some species seek out plant matter from plants with parasite-reducing toxins to improve chick survival, and feathers are often used for nest insulation. Some bird species have no nests; the cliff-nesting Common Guillemot lays its eggs on bare rock, and male Emperor Penguins keep eggs between their body and feet. The absence of nests is especially prevalent in ground-nesting species where the newly hatched young are precocial.

Nest of an Eastern Phoebe that has been parasitised by a Brown-headed Cowbird

Incubation, which optimises temperature for chick development, usually begins after the last egg has been laid. In monogamous species incubation duties are often shared, whereas in polygamous species one parent is wholly responsible for incubation. Warmth from parents passes to the eggs through brood patches, areas of bare skin on the abdomen or breast of the incubating birds. Incubation can be an energetically demanding process; adult albatrosses, for instance, lose as much as 83 grams (2.9 oz) of body weight per day of incubation. The warmth for the incubation of the eggs of megapodes comes from the sun, decaying vegetation or volcanic sources. Incubation periods range from 10 days (in woodpeckers, cuckoos and passerine birds) to over 80 days (in albatrosses and kiwis).

Parental care and fledging

At the time of their hatching, chicks range in development from helpless to independent, depending on their species. Helpless chicks are termed *altricial*, and tend to be born small, blind, immobile and naked; chicks that are mobile and feathered upon hatching are termed *precocial*. Altricial chicks need help thermoregulating and must be brooded for longer than precocial chicks. Chicks at neither of these extremes can be semi-precocial or semi-altricial.

A female Calliope Hummingbird feeding fully grown chicks

The length and nature of parental care varies widely amongst different orders and species. At one extreme, parental care in megapodes ends at hatching; the newly hatched chick digs itself out of the nest mound without parental assistance and can fend for itself immediately. At the other extreme, many seabirds have extended periods of parental care, the longest being that of the Great Frigatebird, whose chicks take up to six months to fledge and are fed by the parents for up to an additional 14 months.

In some species, both parents care for nestlings and fledglings; in others, such care is the responsibility of only one sex. In some species, other members of the same species—usually close relatives of the breeding pair, such as offspring from previous broods—will help with the raising of the young. Such alloparenting is particularly common among the Corvida, which includes such birds as the true crows, Australian Magpie and Fairy-wrens, but has been observed in species as different as the Rifleman and Red Kite.

Among most groups of animals, male parental care is rare. In birds, however, it is quite common—more so than in any other vertebrate class. Though territory and nest site defence, incubation, and chick feeding are often shared tasks, there is sometimes a division of labour in which one mate undertakes all or most of a particular duty.

The point at which chicks fledge varies dramatically. The chicks of the *Synthliboramphus* murrelets, like the Ancient Murrelet, leave the nest the night after they hatch, following their parents out to sea, where they are raised away from terrestrial predators. Some other species, such as ducks, move their chicks away from the nest at an early age. In most species, chicks leave the nest just before, or soon after, they are able to fly. The amount of parental care after fledging varies; albatross chicks leave the nest on their own and receive no further help, while other species continue some supplementary feeding after fledging. Chicks may also follow their parents during their first migration.

Brood parasites

Reed Warbler raising a Common Cuckoo, a brood parasite.

Brood parasitism, in which an egg-layer leaves her eggs with another individual's brood, is more common among birds than any other type of organism. After a parasitic bird lays her eggs in another bird's nest, they are often accepted and raised by the host at the expense of the host's own brood. Brood parasites may be either *obligate brood parasites*, which must lay their eggs in the nests of other species because they are incapable of raising their own young, or *non-obligate brood parasites*, which sometimes lay eggs in the nests of conspecifics to increase their reproductive output even though they could have raised their own young. One hundred bird species, including honeyguides, icterids, estrildid finches and ducks, are obligate parasites, though the most famous are the cuckoos. Some brood parasites are adapted to hatch before their host's young, which allows them to destroy the host's eggs by pushing them out of the nest or to kill the host's chicks; this ensures that all food brought to the nest will be fed to the parasitic chicks.

Ecology

The South Polar Skua (left) is a generalist predator, taking the eggs of other birds, fish, carrion and other animals. This skua is attempting to push an Adelie Penguin (right) off its nest

Birds occupy a wide range of ecological positions. While some birds are generalists, others are highly specialised in their habitat or food requirements. Even within a single habitat, such as a forest, the niches occupied by different species of birds vary, with some species feeding in the forest canopy, others beneath the canopy, and still others on the forest floor. Forest birds may be insectivores, frugivores, and nectarivores. Aquatic birds generally feed by fishing, plant eating, and piracy or kleptoparasitism. Birds of prey specialise in hunting mammals or other birds, while vultures are specialised scavengers. Avivores are animals that are specialized at predating birds.

Some nectar-feeding birds are important pollinators, and many frugivores play a key role in seed dispersal. Plants and pollinating birds often coevolve, and in some cases a flower's primary pollinator is the only species capable of reaching its nectar.

Birds are often important to island ecology. Birds have frequently reached islands that mammals have not; on those islands, birds may fulfill ecological roles typically played by larger animals. For example, in New Zealand the moas were important browsers, as are the Kereru and Kokako today. Today the plants of New Zealand retain the defensive adaptations evolved to protect them from the extinct moa. Nesting seabirds may also affect the ecology of islands and surrounding seas, principally through the concentration of large quantities of guano, which may enrich the local soil and the surrounding seas.

A wide variety of Avian ecology field methods, including counts, nest monitoring, and capturing and marking, are used for researching avian ecology.

Relationship with humans

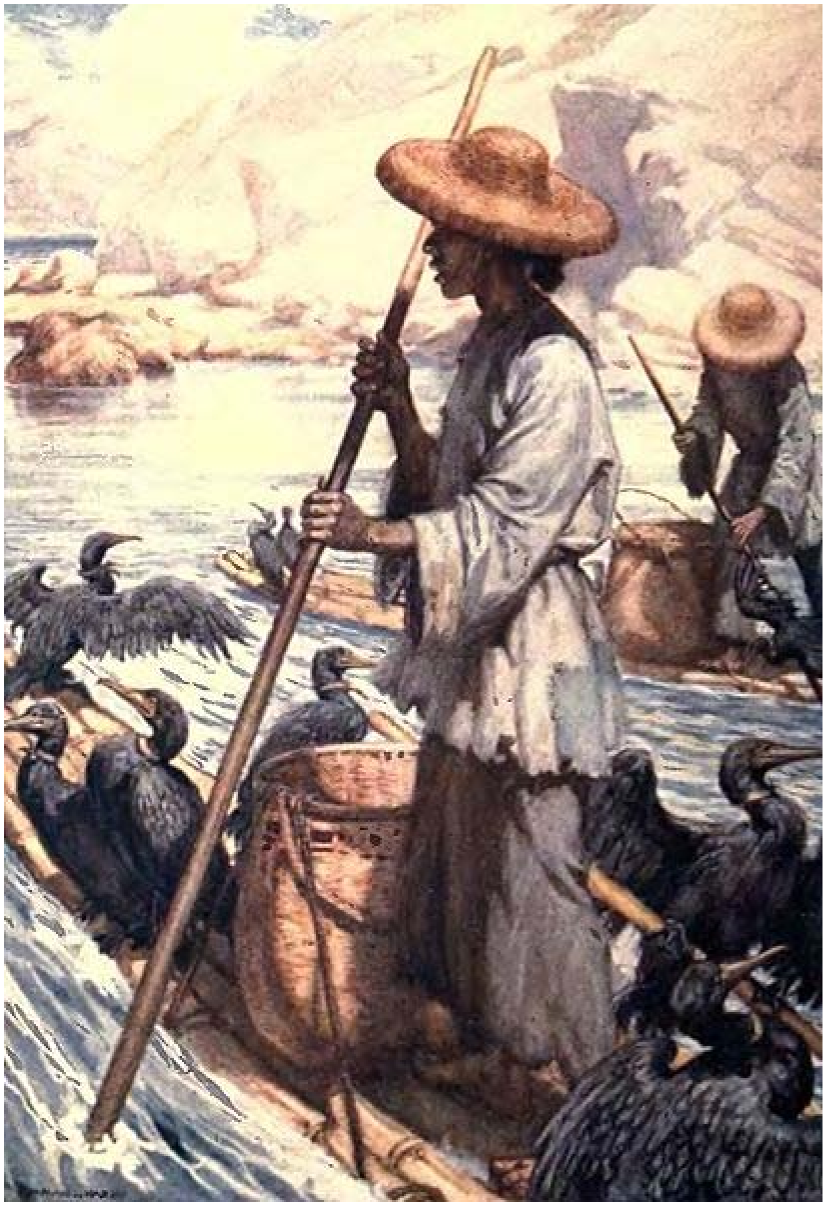
Industrial farming of chickens

Since birds are highly visible and common animals, humans have had a relationship with them since the dawn of man. Sometimes, these relationships are mutualistic, like the cooperative honey-gathering among honeyguides and African peoples such as the Borana. Other times, they may be commensal, as when species such as the House Sparrow have benefited from human activities. Several bird species have become commercially significant agricultural pests, and some pose an aviation hazard. Human activities can also be detrimental, and have threatened numerous bird species with extinction (hunting, avian lead poisoning, pesticides, roadkill, and predation by pet cats and dogs are common sources of death for birds).

Birds can act as vectors for spreading diseases such as psittacosis, salmonellosis, campylobacteriosis, mycobacteriosis (avian tuberculosis), avian influenza (bird flu), giardiasis, and cryptosporidiosis over long distances. Some of these are zoonotic diseases that can also be transmitted to humans.

Economic importance

Domesticated birds raised for meat and eggs, called poultry, are the largest source of animal protein eaten by humans; in 2003, 76 million tons of poultry and 61 million tons of eggs were produced worldwide. Chickens account for much of human poultry consumption, though turkeys, ducks, and geese are also relatively common. Many species of birds are also hunted for meat. Bird hunting is primarily a recreational activity except in extremely undeveloped areas. The most important birds hunted in North and South America are waterfowl; other widely hunted birds include pheasants, wild turkeys, quail, doves, partridge, grouse, snipe, and woodcock. Muttonbirding is also popular in Australia and New Zealand. Though some hunting, such as that of muttonbirds, may be sustainable, hunting has led to the extinction or endangerment of dozens of species.



The use of cormorants by Asian fishermen is in steep decline but survives in some areas as a tourist attraction.

Other commercially valuable products from birds include feathers (especially the down of geese and ducks), which are used as insulation in clothing and bedding, and seabird feces (guano), which is a valuable source of phosphorus and nitrogen. The War of the Pacific, sometimes called the Guano War, was fought in part over the control of guano deposits.

Birds have been domesticated by humans both as pets and for practical purposes. Colourful birds, such as parrots and mynas, are bred in captivity or kept as pets, a practice that has led to the illegal trafficking of some endangered species. Falcons and cormorants have long been used for hunting and fishing, respectively. Messenger pigeons, used since at least 1 AD, remained important as recently as World War II. Today, such activities are more common either as hobbies, for entertainment and tourism, or for sports such as pigeon racing.

Amateur bird enthusiasts (called birdwatchers, twitchers or, more commonly, birders) number in the millions. Many homeowners erect bird feeders near their homes to attract various species. Bird feeding has grown into a multimillion dollar industry; for example, an estimated 75% of households in Britain provide food for birds at some point during the winter.

Religion, folklore and culture

"The 3 of Birds" by the Master of the Playing Cards, 15th century Germany

Birds play prominent and diverse roles in folklore, religion, and popular culture. In religion, birds may serve as either messengers or priests and leaders for a deity, such as in the Cult of Makemake, in which the Tangata manu of Easter Island served as chiefs, or as attendants, as in the case of Hugin and Munin, two Common Ravens who whispered news into the ears of the Norse god Odin. Priests were involved in augury, or interpreting the words of birds while the "auspex" (from which the word "auspicious" is derived) watched their activities to foretell events. They may also serve as religious symbols, as when Jonah (Hebrew: יוֹנָה, dove) embodied the fright, passivity, mourning, and beauty traditionally associated with doves. Birds have themselves been deified, as in the case of the Common Peacock, which is perceived as Mother Earth by the Dravidians of India. Some birds have also been perceived as monsters, including the mythological Roc and the Māori's legendary *Pouākai*, a giant bird capable of snatching humans.

Birds have been featured in culture and art since prehistoric times, when they were represented in early cave paintings. Birds were later used in religious or symbolic art and design, such as the magnificent Peacock Throne of the Mughal and Persian emperors. With the advent of scientific interest in birds, many paintings of birds were commissioned for books. Among the most famous of these bird artists was John James Audubon, whose paintings of North American birds were a great commercial success in Europe and who later lent his name to the National Audubon Society. Birds are also important figures in poetry; for example, Homer incorporated Nightingales into his *Odyssey*, and Catullus used a sparrow as an erotic symbol in his Catullus 2. The relationship between an albatross and a sailor is the central theme of Samuel Taylor Coleridge's The Rime of the Ancient Mariner, which led to the use of the term as a metaphor for a 'burden'. Other English metaphors derive from birds; vulture funds and vulture investors, for instance, take their name from the scavenging vulture.

Perceptions of various bird species often vary across cultures. Owls are associated with bad luck, witchcraft, and death in parts of Africa, but are regarded as wise across much of Europe. Hoopoes were considered sacred in Ancient Egypt and symbols of virtue in Persia, but were thought of as thieves across much of Europe and harbingers of war in Scandinavia.

Conservation

The California Condor once numbered only 22 birds, but conservation measures have raised that to over 300 today.

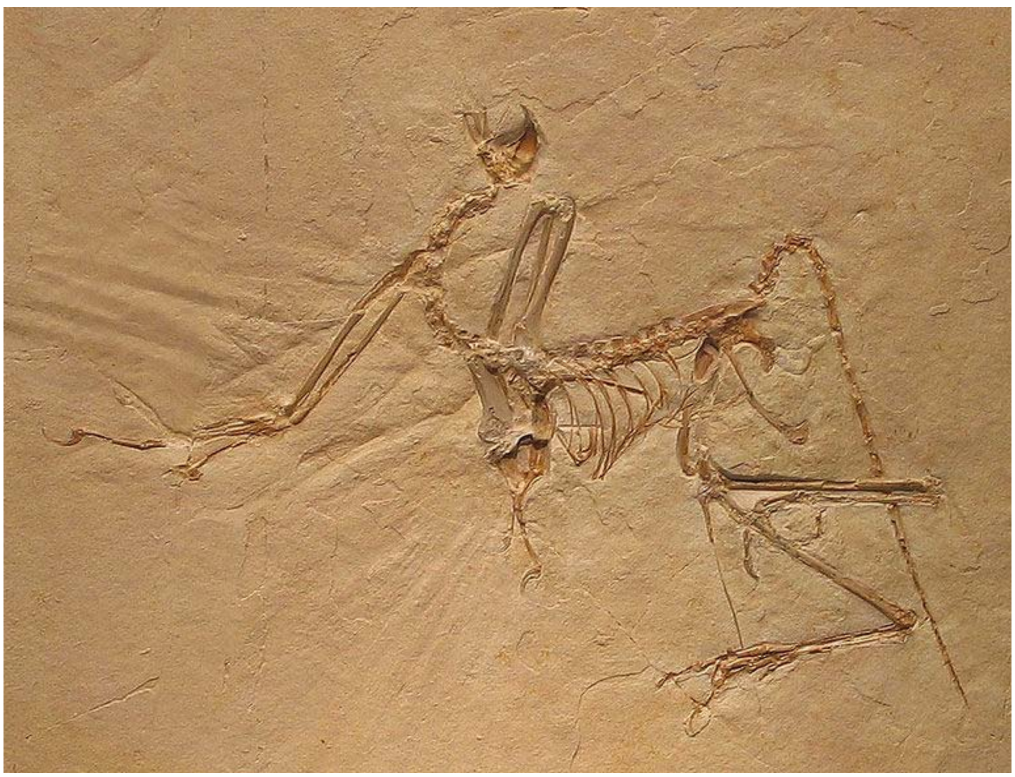
Though human activities have allowed the expansion of a few species, such as the Barn Swallow and European Starling, they have caused population decreases or extinction in many other species. Over a hundred bird species have gone extinct in historical times, although the most dramatic human-caused avian extinctions, eradicating an estimated 750–1800 species, occurred during the human colonisation of Melanesian, Polynesian, and Micronesian islands. Many bird populations are declining worldwide, with 1,227 species listed as threatened by Birdlife International and the IUCN in 2009.

The most commonly cited human threat to birds is habitat loss. Other threats include overhunting, accidental mortality due to structural collisions or long-line fishing bycatch, pollution (including oil spills and pesticide use), competition and predation from nonnative invasive species, and climate change.

Governments and conservation groups work to protect birds, either by passing laws that preserve and restore bird habitat or by establishing captive populations for reintroductions. Such projects have produced some successes; one study estimated that conservation efforts saved 16 species of bird that would otherwise have gone extinct between 1994 and 2004, including the California Condor and Norfolk Parakeet.

Chapter- 2

Evolution of Birds



Archaeopteryx at Paläontologisches Museum München

The **evolution of birds** is thought to have begun in the Jurassic Period, with the earliest birds derived from theropod dinosaurs. Birds are categorized as a biological class, **Aves**. The earliest known species of class Aves is *Archaeopteryx lithographica*, from the Late Jurassic period, though *Archaeopteryx* is not commonly considered to have been a true bird. Modern phylogenies place birds in the dinosaur clade Theropoda. According to the current consensus, Aves and a sister group, the order Crocodilia, together are the sole living members of an unranked "reptile" clade, the Archosauria.

Phylogenetically, Aves is usually defined as all descendants of the most recent common ancestor of a specific modern bird species (such as the House Sparrow, *Passer domesticus*), and either *Archaeopteryx*, or some prehistoric species closer to Neornithes (to avoid the problems caused by the unclear relationships of *Archaeopteryx* to other theropods). If the latter classification is used then the larger group is termed Avialae. Currently, the relationship between dinosaurs, Archaeopteryx, and modern birds is still under debate.

Origins

There is significant evidence that birds evolved within theropod dinosaurs, specifically, that birds are members of Maniraptora, a group of theropods which includes dromaeosaurs and oviraptorids, among others. As more non-avian theropods that are closely related to birds are discovered, the formerly clear distinction between non-birds and birds becomes less so. Recent discoveries in northeast China (Liaoning Province), demonstrating that many small theropod dinosaurs had feathers, contribute to this ambiguity.

The basal bird *Archaeopteryx*, from the Jurassic, is well-known as one of the first "missing links" to be found in support of evolution in the late 19th century, though it is not considered a direct ancestor of modern birds. *Confuciusornis* is another early bird; it lived in the Early Cretaceous. Both may be predated by *Protoavis texensis*, though the fragmentary nature of this fossil leaves it open to considerable doubt whether this was a bird ancestor. Other Mesozoic birds include the *Confuciusornis*, the Enantiornithes, *Yanornis*, *Ichthyornis*, *Gansus*, and the Hesperornithiformes - a group of flightless divers resembling grebes and loons. The recently (2002) discovered dromaeosaur *Cryptovolans* (which may be a *Microraptor*) was capable of powered flight, possessed a sternal keel and had ribs with uncinate processes. In fact, *Cryptovolans* makes a better "bird" than *Archaeopteryx* which lacks some of these modern bird features. Because of this, some paleontologists have suggested that dromaeosaurs are actually basal birds whose larger members are secondarily flightless, i.e. that dromaeosaurs evolved within birds and not the other way around. Evidence for this theory is currently inconclusive, but digs continue to unearth fossils (especially in China) of the strange feathered dromaeosaurs. At any rate, it is fairly certain that flight utilizing feathered wings existed in the mid-Jurassic theropods and was "tried out" in several lineages and variants by the mid-Cretaceous, such as in *Confuciusornis*. This latter species had some peculiar features. For example, its vestigial tail was unfit for steering, and its wing shape seems rather specialized although the arm skeleton was still quite "dinosaurian").

Although ornithischian (bird-hipped) dinosaurs share the same hip structure as birds, birds actually originated from the saurischian (lizard-hipped) dinosaurs if the dinosaurian origin theory is correct. They thus arrived at their hip structure condition independently. In fact, a bird-like hip structure also developed a third time among a peculiar group of theropods, the Therizinosauridae.

An alternate theory to the dinosaurian origin of birds, espoused by a few scientists, notably Larry Martin and Alan Feduccia, states that birds (including maniraptoran "dinosaurs") evolved from early archosaurs like *Longisquama*. This theory is contested by most other paleontologists and experts in feather development and evolution.

Adaptive radiation of birds

Modern birds are classified in Neornithes, which are now known to have evolved into some basic lineages by the end of the Cretaceous. The Neornithes are split into the paleognaths and neognaths.

Paleognathae
The paleognaths include the tinamous (found only in Central and South America) and the ratites which nowadays are found almost exclusively on the Southern Hemisphere. The ratites are large flightless birds, and include ostriches, rheas, cassowaries, kiwis and emus. A few scientists propose that the ratites represent an artificial grouping of birds which have independently lost the ability to fly in a number of unrelated lineages; in any case, the available data regarding their evolution is still very confusing.

Neognathae
The basal divergence from the remaining Neognathes was that of the Galloanserae, the superorder containing the Anseriformes (ducks, geese and swans), and the Galliformes (chickens, turkeys, pheasants, and their allies).

The dates for the splits are a matter of considerable debate amongst scientists. It is agreed that the Neornithes evolved in the Cretaceous and that the split between the Galloanserae and the other neognaths - the Neoaves - occurred before the K-T extinction event, but there are different opinions about whether the radiation of the remaining neognaths occurred before or after the extinction of the other dinosaurs. This disagreement is in part caused by a divergence in the evidence, with molecular dating suggesting a Cretaceous radiation, a small and equivocal neoavian fossil record from Cretaceous, and most living families turning up during the Paleogene. Attempts made to reconcile the molecular and fossil evidence have proved controversial.

On the other hand, two factors must be considered: First, molecular clocks cannot be considered reliable in the absence of robust fossil calibration, whereas the fossil record is naturally incomplete. Second, in reconstructed phylogenetic trees, the time and pattern of lineage separation corresponds to the evolution of the *characters* (such as DNA sequences, morphological traits etc.) studied, *not* to the actual evolutionary pattern of the lineages; these ideally should not differ by much, but may well do so in practice.

Considering this, it is easy to see that fossil data, compared to molecular data, tends to be more accurate in general, but also to underestimate divergence times: morphological traits, being the product of entire developmental genetics networks, usually only start to diverge some time *after* a lineage split would become apparent in DNA sequence comparison - especially if the sequences used contain many silent mutations.

Classification of modern species

The phylogenetic classification of birds is a contentious issue. Sibley & Ahlquist's *Phylogeny and Classification of Birds* (1990) is a landmark work on the classification of birds (although frequently debated and constantly revised). A preponderance of evidence suggests that most modern bird orders constitute good clades. However, scientists are not in agreement as to the precise relationships between the orders; evidence from modern bird anatomy, fossils and DNA have all been brought to bear on the problem but no strong consensus has emerged. As of the mid-2000s, new fossil and molecular data provide an increasingly clear picture of the evolution of modern bird orders, and their relationships. For example, the Charadriiformes seem to consititute an ancient and distinct lineage, while the Mirandornithes and Cypselomorphae are supported by a wealth of anatomical and molecular evidence. Our understanding of the interrelationships of lower level taxa also continues to increase, particularly in the massively diverse perching bird order Passeriformes.

On June 27, 2008, the largest study of bird genetics was published. It overturns several hypothesized relationships, and will likely necessitate a wholesale restructuring of the avian phylogenetic tree.

Current evolutionary trends in birds

Evolution generally occurs at a scale far too slow to be witnessed by humans. However, bird species are currently going extinct at a far greater rate than any possible speciation or other generation of new species. The disappearance of a population, subspecies, or species represents the permanent loss of a range of genes.

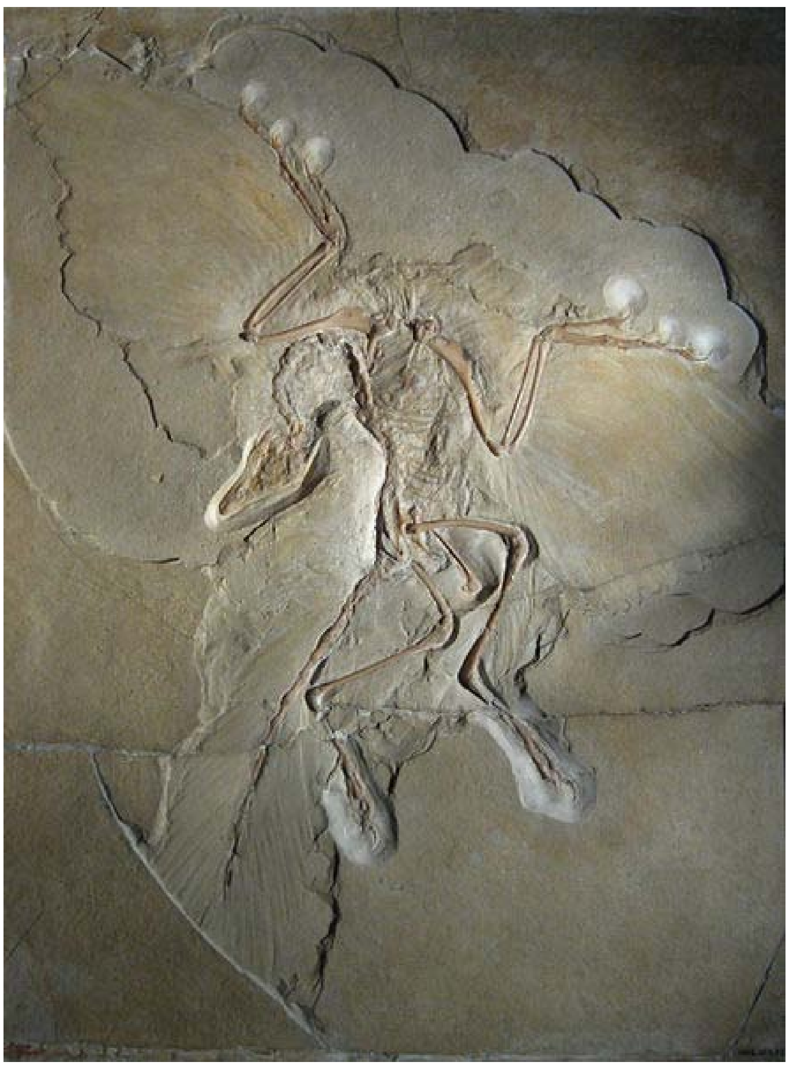
Another concern with evolutionary implications is a suspected increase in hybridization. This may arise from human alteration of habitats enabling related allopatric species to overlap. Forest fragmentation can create extensive open areas, connecting previously isolated patches of open habitat. Populations that were isolated for sufficient time to diverge significantly, but not sufficient to be incapable of producing fertile offspring may now be interbreeding so broadly that the integrity of the original species may be compromised. For example, the many hybrid hummingbirds found in northwest South America may represent a threat to the conservation of the distinct species involved.

Several species of birds have been bred in captivity to create variations on wild species. In some birds this is limited to color variations, while others are bred for larger egg or meat production, for flightlessness or other characteristics.

Some species, like the rock pigeon or several species of crows have been successful living in man made environments. Because these new habitats are different from their far less numerous "natural" habitats these species are to a certain extent evolutionary adapting to living close to man.

Chapter- 3

Origin of Birds



The famous Berlin specimen of *Archaeopteryx lithographica*

The **origin of birds** is a contentious and central topic within evolutionary biology. A close relationship between birds and dinosaurs was first proposed in the nineteenth century after the discovery of the primitive bird *Archaeopteryx* in Germany. To date, most researchers support the view that birds are a group of theropod dinosaurs that evolved during the Mesozoic Era.

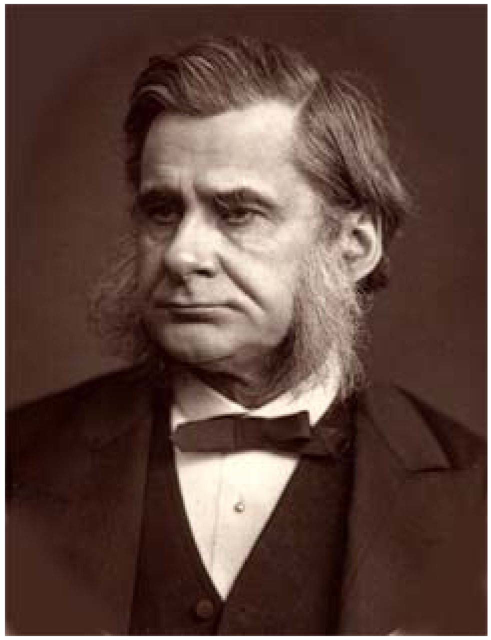
Birds share a myriad of unique skeletal features with dinosaurs. Moreover, fossils of more than twenty species of dinosaur have been collected which preserve feathers. There are even very small dinosaurs, such as *Microraptor* and *Anchiornis*, which have long, vaned, arm and leg feathers forming wings. The Jurassic basal avialan *Pedopenna* also shows these long foot feathers. Witmer (2009) has concluded that this evidence is sufficient to demonstrate that avian evolution went through a four-winged stage.

Fossil evidence also demonstrates that birds and dinosaurs shared features such as hollow, pneumatized bones, gastroliths in the digestive system, nest-building and brooding behaviors. The ground-breaking discovery of fossilized *Tyrannosaurus rex* soft tissue allowed a molecular comparison of cellular anatomy and protein sequencing of collagen tissue, both of which demonstrated that *T. rex* and birds are more closely related than either is to *Alligator*. A second molecular study robustly supported the relationship of birds to dinosaurs, though it did not place birds within Theropoda, as expected. This study utilized eight additional collagen sequences extracted from a femur of *Brachylophosaurus canadensis*, a hadrosaur.

Only a few scientists still debate the dinosaurian origin of birds, suggesting descent from other types of archosaurian reptiles. Among the consensus that supports dinosaurian ancestry, the exact sequence of evolutionary events that gave rise to the early birds within maniraptoran theropods is a hot topic. The origin of bird flight is a separate but related question for which there are also several proposed answers.

Research history

Huxley, *Archaeopteryx* and early research

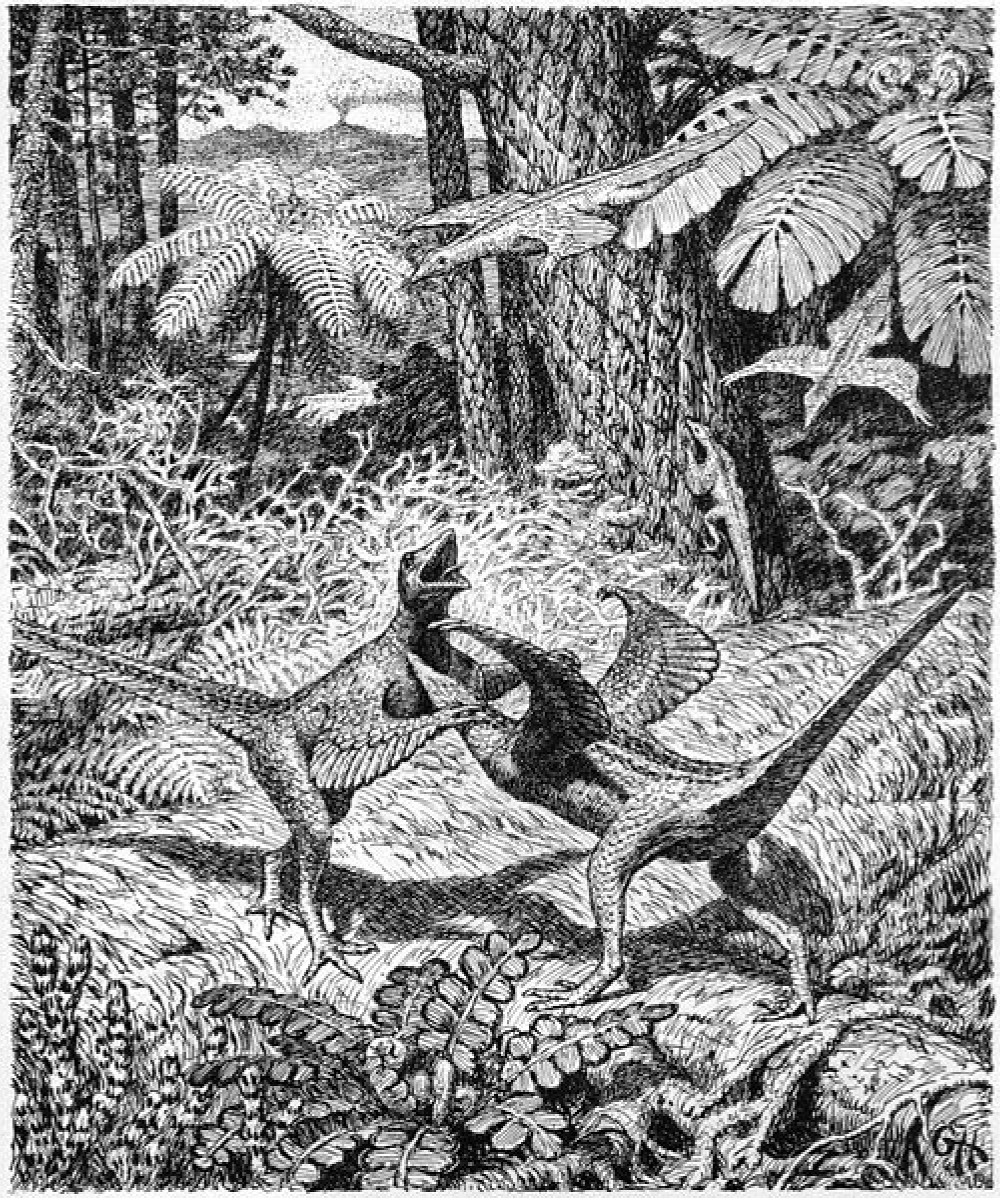


Thomas Henry Huxley (1825-1895)

Scientific investigation into the origin of birds began shortly after the 1859 publication of Charles Darwin's *On the Origin of Species*, the ground-breaking book which described his theory of evolution by natural selection. In 1860, a fossilized feather was discovered in Germany's Late Jurassic solnhofen limestone. Christian Erich Hermann von Meyer described this feather as *Archaeopteryx lithographica* the next year, and Richard Owen described a nearly complete skeleton in 1863, recognizing it as a bird despite many features reminiscent of reptiles, including clawed forelimbs and a long, bony tail.

Biologist Thomas Henry Huxley, known as "Darwin's Bulldog" for his ferocious support of the new theory of evolution, almost immediately seized upon *Archaeopteryx* as a transitional fossil between birds and reptiles. Starting in 1868, Huxley made detailed comparisons of *Archaeopteryx* with various prehistoric reptiles and found that it was most similar to dinosaurs like *Hypsilophodon* and *Compsognathus*. The discovery in the late 1870s of the iconic "Berlin specimen" of *Archaeopteryx*, complete with a set of reptilian teeth, provided further evidence. Huxley was the first to propose an evolutionary relationship between birds and dinosaurs, although he was opposed by the very influential Owen, who remained a staunch creationist. Huxley's conclusions were accepted by many biologists, including Baron Franz Nopcsa, while others, notably Harry Seeley, argued that the similarities were due to convergent evolution.

Heilmann and the thecodont hypothesis



Heilmann's hypothetical illustration of a pair of fighting 'Proaves' from 1916

A turning point came in the early twentieth century with the writings of Gerhard Heilmann of Denmark. An artist by trade, Heilmann had a scholarly interest in birds and from 1913 to 1916 published the results of his research in several parts, dealing with the anatomy, embryology, behavior, paleontology, and evolution of birds. His work, originally written in Danish as *Vor Nuvaerende Viden om Fuglenes Afstamning*, was compiled, translated into English, and published in 1926 as *The Origin of Birds*.

Like Huxley, Heilmann compared *Archaeopteryx* and other birds to an exhaustive list of prehistoric reptiles, and also came to the conclusion that theropod dinosaurs like

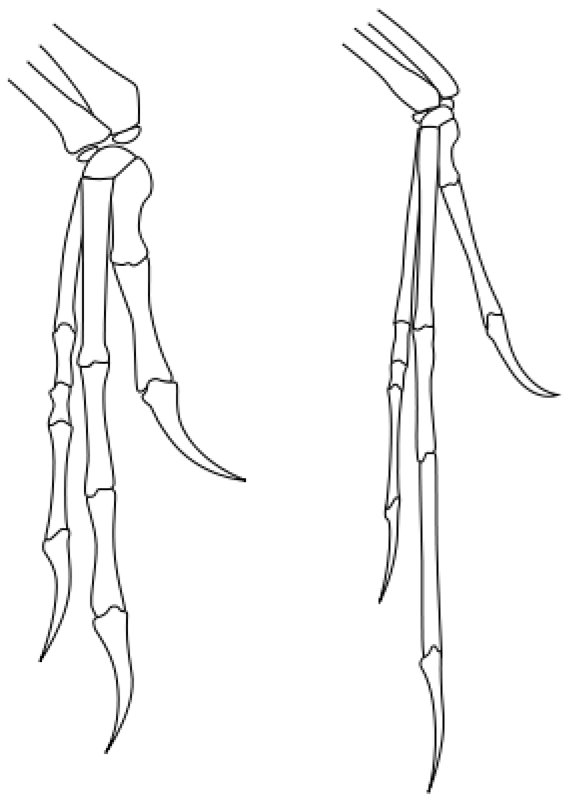
Compsognathus were the most similar. However, Heilmann noted that birds possessed clavicles (collar bones) fused to form a bone called the furcula ("wishbone"), and while clavicles were known in more primitive reptiles, they had not yet been recognized in dinosaurs. Since he was a firm believer in Dollo's law, which states that evolution is not reversible, Heilmann could not accept that clavicles were lost in dinosaurs and re-evolved in birds. He was therefore forced to rule out dinosaurs as bird ancestors and ascribe all of their similarities to convergent evolution. Heilmann stated that bird ancestors would instead be found among the more primitive "thecodont" grade of reptiles. Heilmann's extremely thorough approach ensured that his book became a classic in the field, and its conclusions on bird origins, as with most other topics, were accepted by nearly all evolutionary biologists for the next four decades.

Bronze cast of the furcula of "Sue" the *Tyrannosaurus*, Field Museum

Clavicles are relatively delicate bones and therefore in danger of being destroyed or at least damaged beyond recognition. Nevertheless clavicles had been found in theropod dinosaurs before Heilman wrote his book, but had gone unrecognized. The absence of clavicles in dinosaurs became the orthodox view despite the discovery of clavicles in the primitive theropod *Segisaurus* in 1936. The next report of clavicles in a dinosaur was in 1983, and that was in a Russian article published before the end of the Cold War.

Contrary to what Heilman believed, paleontologists now accept that clavicles and in most cases furculae are a standard feature not just of theropods but of saurischian dinosaurs. Up to late 2007 ossified furculae (i.e. made of bone rather than cartilage) have been found in nearly all types of theropods except the most basal ones, *Eoraptor* and *Herrerasaurus*. The original report of a furcula in the primitive theropod *Segisaurus* (1936) has been confirmed by a re-examination in 2005. Joined, furcula-like clavicles have also been found in *Massospondylus*, an Early Jurassic sauropodomorph.

Ostrom, *Deinonychus* and the Dinosaur Renaissance



The similarity of the forelimbs of *Deinonychus* (left) and *Archaeopteryx* (right) led John Ostrom to revive the link between dinosaurs and birds.

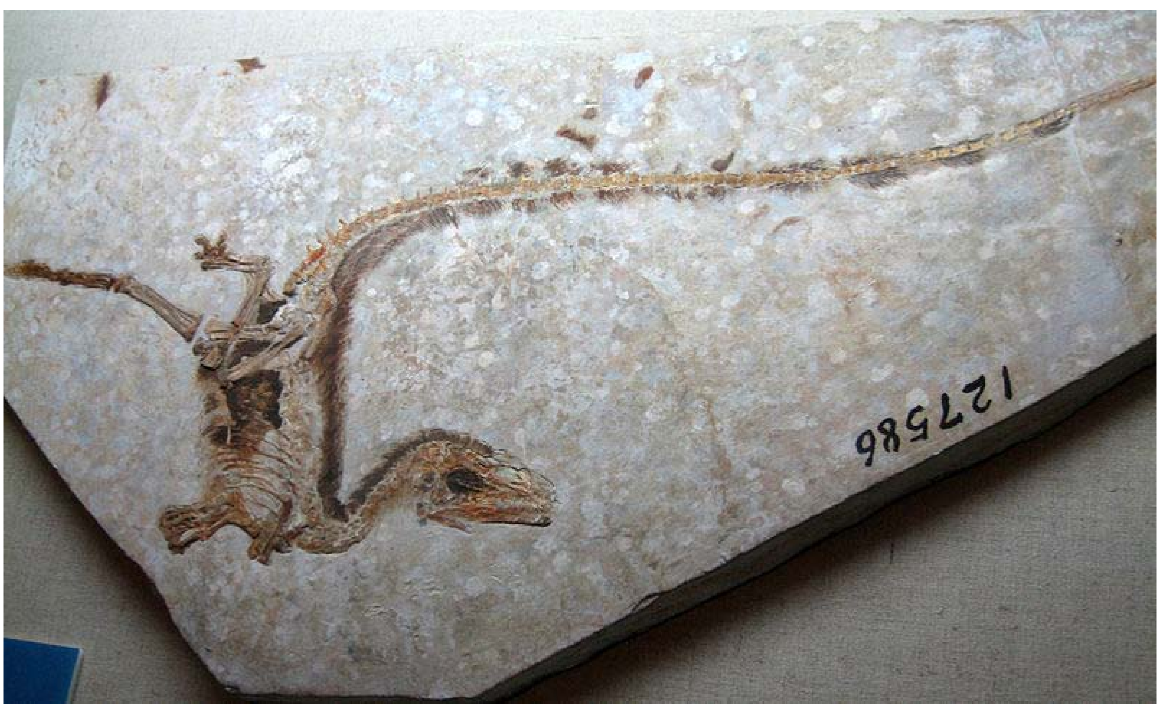
The tide began to turn against the 'thecodont' hypothesis after the 1964 discovery of a new theropod dinosaur in Montana. In 1969, this dinosaur was described and named *Deinonychus* by John Ostrom of Yale University. The next year, Ostrom redescribed a specimen of *Pterodactylus* in the Dutch Teyler Museum as another skeleton of

Archaeopteryx. The specimen consisted mainly of a single wing and its description made Ostrom aware of the similarities between the wrists of *Archaeopteryx* and *Deinonychus*.

In 1972, British paleontologist Alick Walker hypothesized that birds arose not from 'thecodonts' but from crocodile ancestors like *Sphenosuchus*. Ostrom's work with both theropods and early birds led him to respond with a series of publications in the mid-1970s in which he laid out the many similarities between birds and theropod dinosaurs, resurrecting the ideas first put forth by Huxley over a century before. Ostrom's recognition of the dinosaurian ancestry of birds, along with other new ideas about dinosaur metabolism, activity levels, and parental care, began what is known as the Dinosaur renaissance, which began in the 1970s and continues to this day.

Ostrom's revelations also coincided with the increasing adoption of phylogenetic systematics (cladistics), which began in the 1960s with the work of Willi Hennig. Cladistics is a method of arranging species based strictly on their evolutionary relationships, using a statistical analysis of their anatomical characteristics. In the 1980s, cladistic methodology was applied to dinosaur phylogeny for the first time by Jacques Gauthier and others, showing unequivocally that birds were a derived group of theropod dinosaurs. Early analyses suggested that dromaeosaurid theropods like *Deinonychus* were particularly closely related to birds, a result which has been corroborated many times since.

Modern research and feathered dinosaurs in China



Fossil of *Sinosauropteryx prima*.

The early 1990s saw the discovery of spectacularly preserved bird fossils in several Early Cretaceous geological formations in the northeastern Chinese province of Liaoning. In 1996, Chinese paleontologists described *Sinosauropteryx* as a new genus of bird from the Yixian Formation, but this animal was quickly recognized as a theropod dinosaur closely related to *Compsognathus*. Surprisingly, its body was covered by long filamentous structures. These were dubbed 'protofeathers' and considered to be homologous with the more advanced feathers of birds, although some scientists disagree with this assessment. Chinese and North American scientists described *Caudipteryx* and *Protarchaeopteryx* soon after. Based on skeletal features, these animals were non-avian dinosaurs, but their remains bore fully-formed feathers closely resembling those of birds. "Archaeoraptor," described without peer review in a 1999 issue of *National Geographic*, turned out to be a smuggled forgery, but legitimate remains continue to pour out of the Yixian, both legally and illegally. Feathers or "protofeathers" have been found on a wide variety of theropods in the Yixian, and the discoveries of extremely bird-like dinosaurs, as well as dinosaur-like primitive birds, have almost entirely closed the morphological gap between theropods and birds.

A small minority, including ornithologists Alan Feduccia and Larry Martin, continues to assert that birds are instead the descendants of earlier archosaurs, such as *Longisquama* or *Euparkeria*. Embryological studies of bird developmental biology have raised questions about digit homology in bird and dinosaur forelimbs. However, due to the cogent evidence provided by comparative anatomy and phylogenetics, as well as the dramatic feathered dinosaur fossils from China, the idea that birds are derived dinosaurs, first championed by Huxley and later by Nopcsa and Ostrom, enjoys near-unanimous support among today's paleontologists.

Phylogeny

Archaeopteryx has historically been considered the first bird, or *Urvogel*. Although newer fossil discoveries eliminated the gap between theropods and *Archaeopteryx*, as well as the gap between *Archaeopteryx* and modern birds, phylogenetic taxonomists, in keeping with tradition, almost always use *Archaeopteryx* as a specifier to help define Aves. Aves has more rarely been defined as a crown group consisting only of modern birds. Nearly all palaeontologists regard birds as coelurosaurian theropod dinosaurs. Within Coelurosauria, multiple cladistic analyses have found support for a clade named Maniraptora, consisting of therizinosauroids, oviraptorosaurs, troodontids, dromaeosaurids, and birds. Of these, dromaeosaurids and troodontids are usually united in the clade Deinonychosauria, which is a sister group to birds (together forming the node-clade Eumaniraptora) within the stem-clade Paraves.

Other studies have proposed alternative phylogenies in which certain groups of dinosaurs that are usually considered non-avian are suggested to have evolved from avian ancestors. For example, a 2002 analysis found oviraptorosaurs to be basal avians. Alvarezsaurids, known from Asia and the Americas, have been variously classified as basal maniraptorans, paravians, the sister taxon of ornithomimosaurs, as well as specialized early birds. The genus *Rahonavis*, originally described as an early bird, has been identified as a non-avian dromaeosaurid in several studies. Dromaeosaurids and troodontids themselves have also been suggested to lie within Aves rather than just outside it.

Features linking birds and dinosaurs

Many distinct anatomical features are shared by birds and theropod dinosaurs. Some of the more interesting similarities are discussed here:

Feathers

Parts of a feather

Archaeopteryx, the first good example of a "feathered dinosaur", was discovered in 1861. The initial specimen was found in the solnhofen limestone in southern Germany, which is a *lagerstätte*, a rare and remarkable geological formation known for its superbly detailed fossils. *Archaeopteryx* is a transitional fossil, with features clearly intermediate between those of modern reptiles and birds. Discovered just two years after Darwin's seminal *Origin of Species*, its discovery spurred the nascent debate between proponents of evolutionary biology and creationism. This early bird is so dinosaur-like that, without a clear impression of feathers in the surrounding rock, at least one specimen was mistaken for *Compsognathus*.

Since the 1990s, a number of additional feathered dinosaurs have been found, providing even stronger evidence of the close relationship between dinosaurs and modern birds. Most of these specimens were unearthed in Liaoning province, northeastern China, which was part of an island continent during the Cretaceous period. Though feathers have been found only in the lagerstätte of the Yixian Formation and a few other places, it is possible that non-avian dinosaurs elsewhere in the world were also feathered. The lack of widespread fossil evidence for feathered non-avian dinosaurs may be because delicate features like skin and feathers are not often preserved by fossilization and thus are absent from the fossil record.

A recent development in the debate centers around the discovery of impressions of "protofeathers" surrounding many dinosaur fossils. These protofeathers suggest that the tyrannosauroids may have been feathered. However, others claim that these protofeathers are simply the result of the decomposition of collagenous fiber that underlaid the dinosaurs' integument.

Fossil cast of NGMC 91, a probable specimen of *Sinornithosaurus*.

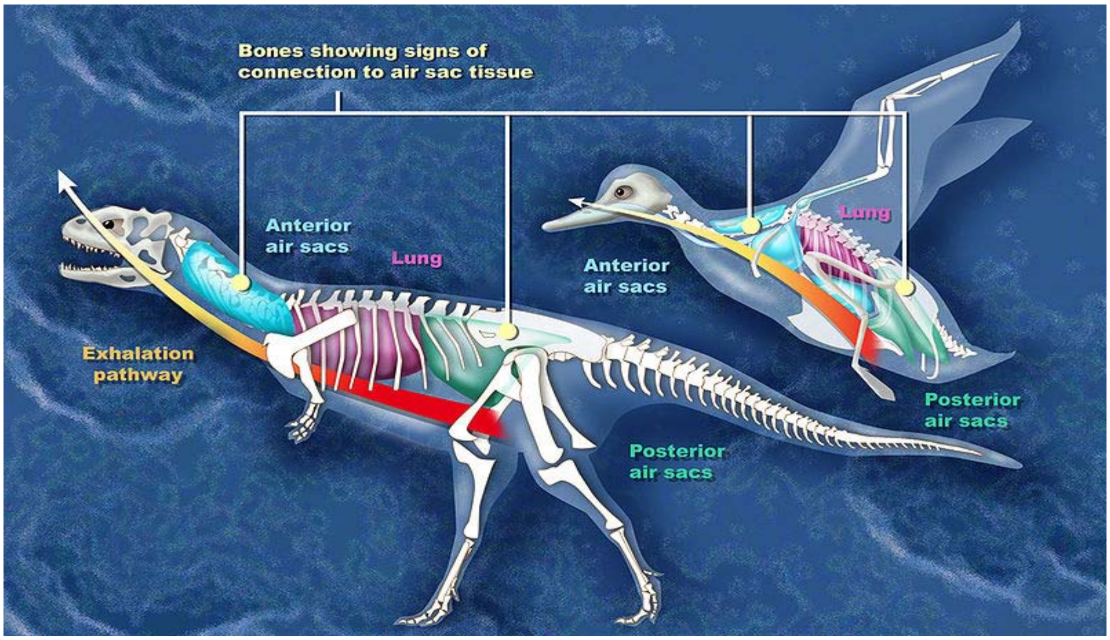
The feathered dinosaurs discovered so far include *Beipiaosaurus*, *Caudipteryx*, *Dilong*, *Microraptor*, *Protarchaeopteryx*, *Shuvuuia*, *Sinornithosaurus*, *Sinosauropteryx*, and *Jinfengopteryx*, along with dinosaur-like birds, such as *Confuciusornis*, which are anatomically closer to modern avians. All of them have been found in the same area and formation, in northern China. The Dromaeosauridae family, in particular, seems to have been heavily feathered and at least one dromaeosaurid, *Cryptovolans*, may have been capable of flight.

Skeleton

Because feathers are often associated with birds, feathered dinosaurs are often touted as the missing link between birds and dinosaurs. However, the multiple skeletal features also shared by the two groups represent the more important link for paleontologists. Furthermore, it is increasingly clear that the relationship between birds and dinosaurs, and the evolution of flight, are more complex topics than previously realized. For example, while it was once believed that birds evolved within dinosaurs in one linear progression, some scientists, most notably Gregory S. Paul, conclude that dinosaurs such as the dromaeosaurs may have evolved within birds, losing the power of flight while keeping their feathers in a manner similar to the modern ostrich and other ratites.

Comparisons of bird and dinosaur skeletons, as well as cladistic analysis, strengthens the case for the link, particularly for a branch of theropods called maniraptors. Skeletal similarities include the neck, pubis, wrist (semi-lunate carpal), arm and pectoral girdle, shoulder blade, clavicle, and breast bone.

Lungs



Comparison between the air sacs of *Majungasaurus* and a bird

Large meat-eating dinosaurs had a complex system of air sacs similar to those found in modern birds, according to an investigation which was led by Patrick M. O'Connor of Ohio University. The lungs of theropod dinosaurs (carnivores that walked on two legs and had birdlike feet) likely pumped air into hollow sacs in their skeletons, as is the case in birds. "What was once formally considered unique to birds was present in some form in the ancestors of birds", O'Connor said. The study was funded in part by the National Science Foundation.

Heart and sleeping posture

Modern computed tomography (CT) scans of a dinosaur chest cavity (conducted in 2000) found the apparent remnants of complex four-chambered hearts, much like those found in today's mammals and birds. The idea is controversial within the scientific community, coming under fire for bad anatomical science or simply wishful thinking. A recently discovered troodont fossil demonstrates that the dinosaurs slept like certain modern birds, with their heads tucked under their arms. This behavior, which may have helped to keep the head warm, is also characteristic of modern birds.

Reproductive biology

When laying eggs, female birds grow a special type of bone in their limbs. This medullary bone, which is rich in calcium, forms a layer inside the hard outer bone that is used to make eggshells. The presence of endosteally-derived bone tissues lining the interior marrow cavities of portions of a *Tyrannosaurus rex* specimen's hind limb suggested that *T. rex* used similar reproductive strategies, and revealed the specimen to be female. Further research has found medullary bone in the theropod *Allosaurus* and ornithopod *Tenontosaurus*. Because the line of dinosaurs that includes *Allosaurus* and *Tyrannosaurus* diverged from the line that led to *Tenontosaurus* very early in the evolution of dinosaurs, this suggests that dinosaurs in general produced medullary tissue.

Brooding and care of young

A nesting *Citipati osmolskae* specimen, at the American Museum of Natural History in New York.

Several *Citipati* specimens have been found resting over the eggs in its nest in a position most reminiscent of brooding.

Numerous dinosaur species, for example *Maiasaura*, have been found in herds mixing both very young and adult individuals, suggesting rich interactions between them.

A dinosaur embryo was found without teeth, which suggests some parental care was required to feed the young dinosaur, possibly the adult dinosaur regurgitated food into the young dinosaur's mouth. This behaviour is seen in numerous bird species; parent birds regurgitate food into the hatchling's mouth.

Gizzard stones

Both birds and dinosaurs use gizzard stones. These stones are swallowed by animals to aid digestion and break down food and hard fibres once they enter the stomach. When found in association with fossils, gizzard stones are called gastroliths. Gizzard stones are also found in some fish (mullets, mud shad, and the gilaroo, a type of trout) and in crocodiles.

Molecular evidence and soft tissue

Fossil of a juvenile individual of Scipionyx samniticus. The fossil preserves clear traces of soft tissues.

One of the best examples of soft tissue impressions in a fossil dinosaur was discovered in Petraroia, Italy. The discovery was reported in 1998, and described the specimen of a small, very young coelurosaur, *Scipionyx samniticus*. The fossil includes portions of the intestines, colon, liver, muscles, and windpipe of this immature dinosaur.

In the March 2005 issue of *Science*, Dr. Mary Higby Schweitzer and her team announced the discovery of flexible material resembling actual soft tissue inside a 68-million-year-old *Tyrannosaurus rex* leg bone from the Hell Creek Formation in Montana. After recovery, the tissue was rehydrated by the science team. The seven collagen types obtained from the bone fragments, compared to collagen data from living birds (specifically, a chicken), suggest that older theropods and birds are closely related.

When the fossilized bone was treated over several weeks to remove mineral content from the fossilized bone marrow cavity (a process called demineralization), Schweitzer found evidence of intact structures such as blood vessels, bone matrix, and connective tissue (bone fibers). Scrutiny under the microscope further revealed that the putative dinosaur soft tissue had retained fine structures (microstructures) even at the cellular level. The exact nature and composition of this material, and the implications of Dr. Schweitzer's discovery, are not yet clear; study and interpretation of the specimens is ongoing.

The successful extraction of ancient DNA from dinosaur fossils has been reported on two separate occasions, but upon further inspection and peer review, neither of these reports could be confirmed. However, a functional visual peptide of a theoretical dinosaur has been inferred using analytical phylogenetic reconstruction methods on gene sequences of related modern species such as reptiles and birds. In addition, several proteins have putatively been detected in dinosaur fossils, including hemoglobin.

Debates

Origin of bird flight

Debates about the origin of bird flight are almost as old as the idea that birds evolved within dinosaurs, which arose soon after the discovery of *Archaeopteryx* in 1862. Two theories have dominated most of the discussion since then: the cursorial ("from the ground up") theory proposes that birds evolved from small, fast predators that ran on the ground; the arboreal ("from the trees down") theory proposes that powered flight evolved from unpowered gliding by arboreal (tree-climbing) animals. A more recent theory, "wing-assisted incline running" (WAIR), is a variant of the cursorial theory and proposes that wings developed their aerodynamic functions as a result of the need to run quickly up very steep slopes, for example to escape from predators.

Cursorial ("from the ground up") theory

Reconstruction of *Rahonavis*, a ground-dwelling feathered dinosaur that some researchers think was well-equipped for flight.

The cursorial theory of the origin of flight was first proposed by Samuel Wendell Williston, and elaborated upon by Baron Nopcsa. This hypothesis proposes that some fast-running animals with long tails used their arms to keep their balance while running. Modern versions of this theory differ in many details from the Williston-Nopcsa version, mainly as a result of discoveries since Nopcsa's time.

Nopcsa theorized that increasing the surface area of the outstretched arms could have helped small cursorial predators to keep their balance, and that the scales of the forearms became elongated, evolving into feathers. The feathers could also have been used as a trap to catch insects or other prey. Progressively, the animals would have leapt for longer distances, helped by their evolving wings. Nopcsa also proposed that there were three main stages in the evolution of flight. First, passive flight was realized, in which the developed wing structures served as a sort of parachute. Second, active flight was possible, in which the animal achieved flight by flapping its wings. He used *Archaeopteryx* as an example of this second stage. Finally, birds gained the ability to soar.

It is now thought that feathers did not evolve from scales, as feathers are made of different proteins. More seriously, Nopcsa's theory assumes that feathers evolved as part of the evolution of flight, and recent discoveries prove that assumption is false.

Feathers are very common in coelurosaurian dinosaurs (including the early tyrannosauroid *Dilong*). Modern birds are classified as coelurosaurs by nearly all palaeontologists, though not by a few ornithologists. The modern version of the "from the ground up" hypothesis argues that birds' ancestors were small, *feathered*, ground-running predatory dinosaurs (rather like roadrunners in their hunting style) 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. The most widely-suggested original functions of feathers include thermal insulation and competitive displays, as in modern birds.

All 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 refutations of the "from the ground up" hypothesis attempt to refute the modern version's assumption that birds are modified coelurosaurian 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 three digits forms the alula, which they use to avoid stalling in low-speed flight, for example when landing); but the hands of coelurosaurs are formed by digits 1, 2, and 3 (thumb and first two 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 that birds' "hands" do develop from digits 1, 2, and 3. This debate is complex and not yet resolved.

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. This makes it a specialized type of cursorial ("from the ground up") theory. 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.

Arboreal ("from the trees down") theory

The remarkable four-winged *Microraptor*, a "cousin" of the birds.

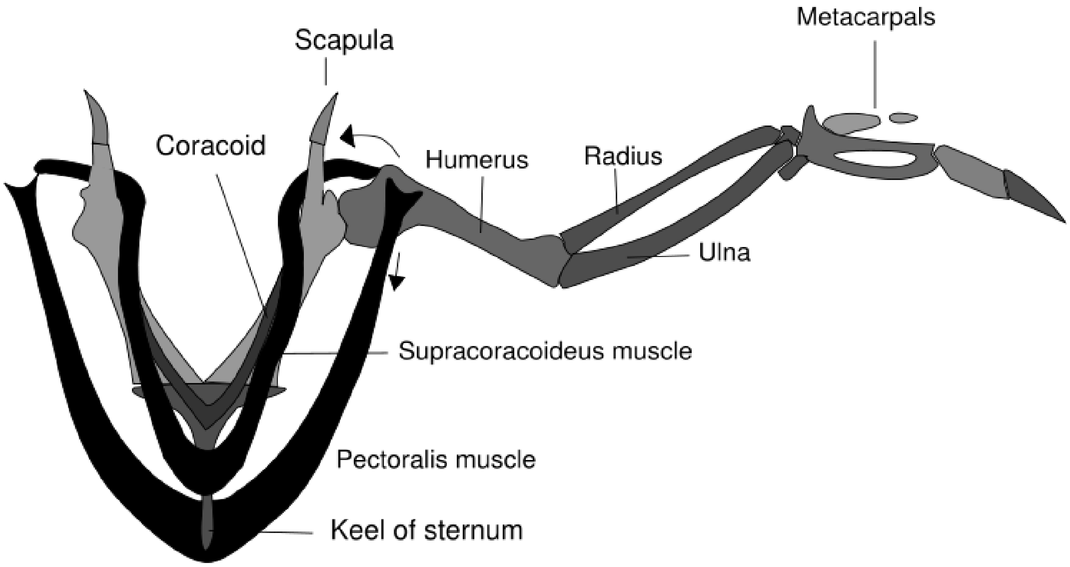
Most versions of the arboreal hypothesis state that the ancestors of birds were very small dinosaurs that lived in trees, springing from branch to branch. This small dinosaur already had feathers, which were co-opted by evolution to produce longer, stiffer forms that were useful in aerodynamics, eventually producing wings. Wings would have then evolved and become increasingly refined as devices to give the leaper more control, to parachute, to glide, and to fly in stepwise fashion. The arboreal hypothesis also notes that, for arboreal animals, aerodynamics are far more energy efficient, since such animals simply fall in order to achieve minimum gliding speeds.

Several small dinosaurs from the Jurassic or Early Cretaceous, all with feathers, have been interpreted as possibly having arboreal and/or aerodynamic adaptations. These include *Epidendrosaurus*, *Epidexipteryx*, *Microraptor*, *Pedopenna*, and *Anchiornis*. *Anchiornis* is particularly important to this subject, as it is the smallest known non - avian dinosaur, and it lived at the beginning of the Late Jurassic, long before *Archaeopteryx*.

Analysis of the proportions of the toe bones of the most primitive birds *Archaeopteryx* and *Confuciusornis*, compared to those of living species, suggest that the early species may have lived both on the ground and in trees.

One study suggested that the earliest birds and their immediate ancestors did not climb trees. This study determined that the amount of toe claw curvature of early birds was more like that seen in modern ground-foraging birds than in perching birds.

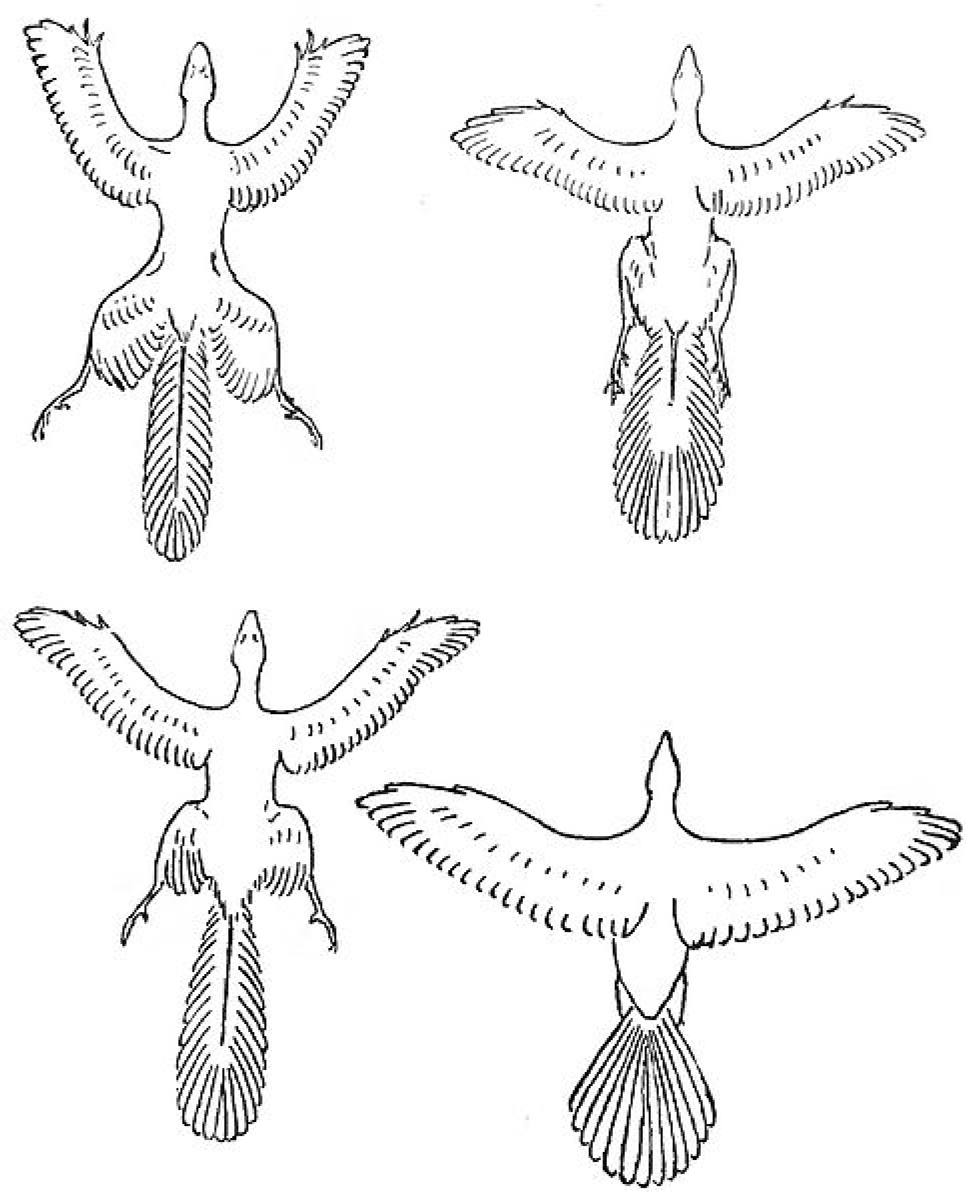
Diminished significance of *Archaeopteryx*



The supracoracoideus works using a pulley-like system to lift the wing while the pectorals provide the powerful downstroke

Archaeopteryx was the first and for a long time the only known feathered Mesozoic animal (or dinosaur, if one accepts the majority view that birds are modified dinosaurs). As a result, discussion of the evolution of birds and of bird flight centered on *Archaeopteryx* at least until the mid-1990s.

There has been debate about whether *Archaeopteryx* could really 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.



Proposed development of flight in a book from 1922: Tetrapteryx, *Archaeopteryx*, Hypothetical Stage, Modern Bird

But the discovery since the early 1990s of many feathered dinosaurs means that *Archaeopteryx* is no longer the key figure in the evolution of bird flight. Other small, feathered coelurosaurs from the Cretaceous and Late Jurassic show features that may be precursors of avian flight, for example: *Rahonavis*, a ground-runner which had a *Velociraptor*-like raised sickle claw on the second toe and which some paleontologists think was better adapted for flight than *Archaeopteryx*; *Epidendrosaurus*, an arboreal dinosaur that may provide some support for the "from the trees down" theory; *Microraptor*, an arboreal dinosaur that may have been capable of powered flight but, if so, more like a biplane, as it had well-developed feathers on its legs. As early as 1915, some scientists had argued that the evolution of bird flight may have gone through a four-winged (or *tetrapteryx*) stage.

Digit homology

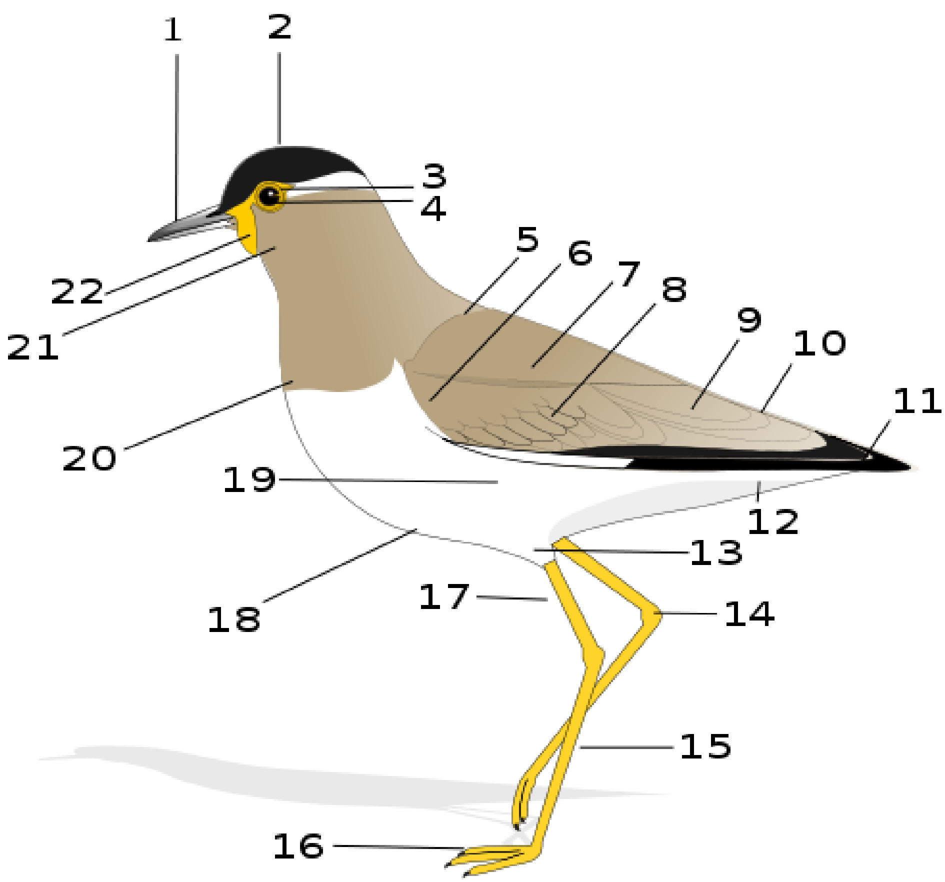
There is a debate between embryologists and paleontologists whether the hands of theropod dinosaurs and birds are essentially different, based on phalangeal counts, a count of the number of phalanges (fingers) in the hand. This is an important and fiercely debated area of research because its results may challenge the consensus that birds are descendants of dinosaurs.

Embryologists and some paleontologists who oppose the bird-dinosaur link, have long numbered the digits of birds II-III-IV on the basis of multiple studies of the development in the egg. This is based on the fact that in most amniotes, the first digit to form in a 5-fingered hand is digit IV, which develops a primary axis. Therefore, embryologists have identified the primary axis in birds as digit IV, and the surviving digits as II-III-IV. The fossils of advanced theropod (Tetanurae) hands appear to have the digits I-II-III (some genera within Avetheropoda also have a reduced digit IV). If this is true, then the II-III-IV development of digits in birds is an indication against theropod (dinosaur) ancestry. However, with no ontogenical (developmental) basis to definitively state which digits are which on a theropod hand (because no non-avian theropods can be observed growing and developing today), the labelling of the theropod hand is not absolutely conclusive.

Paleontologists have traditionally identified avian digits as I-II-III. They argue that the digits of birds number I-II-III, just as those of theropod dinosaurs do, by the conserved phalangeal formula. The phalangeal count for archosaurs is 2-3-4-5-3; many archosaur lineages have a reduced number of digits, but have the same phalangeal formula in the digits that remain. In other words, paleontologists assert that archosaurs of different lineages tend to lose the same digits when digit loss occurs, from the outside to the inside. The three digits of dromaeosaurs, and *Archaeopteryx* have the same phalangeal formula of I-II-III as digits I-II-III of basal archosaurs. Therefore, the lost digits would be V and IV. If this is true, then modern birds would also possess digits I-II-III. Also, one research team has proposed a frame-shift in the digits of the theropod line leading to birds (thus making digit I into digit II, II to III, and so forth). However, such frame shifts are rare in amniotes and would have had to occur solely in the forelimbs and not the hindlimbs (a condition presently unknown in any animal) in the bird-theropod lineage in order to be consistent with the theropod origin of birds. This is called *Lateral Digit Reduction* (LDR) versus *Bilateral Digit Reduction* (BDR)

Chapter- 4

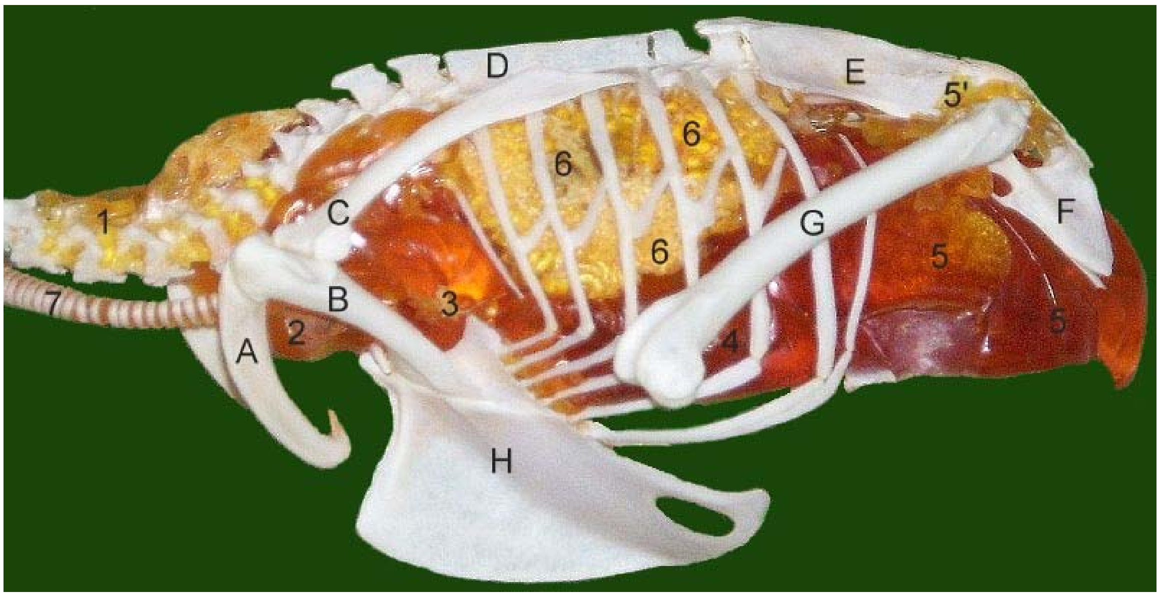
Bird Anatomy



External anatomy (topography) of a typical bird: 1 Beak, 2 Head, 3 Iris, 4 Pupil, 5 Mantle, 6 Lesser coverts, 7 Scapulars, 8 Coverts, 9 Tertials, 10 Rump, 11 Primaries, 12 Vent, 13 Thigh, 14 Tibio-tarsal articulation, 15 Tarsus, 16 Feet, 17 Tibia, 18 Belly, 19 Flanks, 20 Breast, 21 Throat, 22 Wattle

Bird anatomy, or the physiological structure of birds' bodies, shows many unique adaptations, mostly aiding flight. Birds have a light skeletal system and light but powerful musculature which, along with circulatory and respiratory systems capable of very high metabolic rates and oxygen supply, permit the bird to fly. The development of a beak has led to evolution of a specially adapted digestive system. These anatomical specializations have earned birds their own class in the vertebrate phylum.

Respiratory system

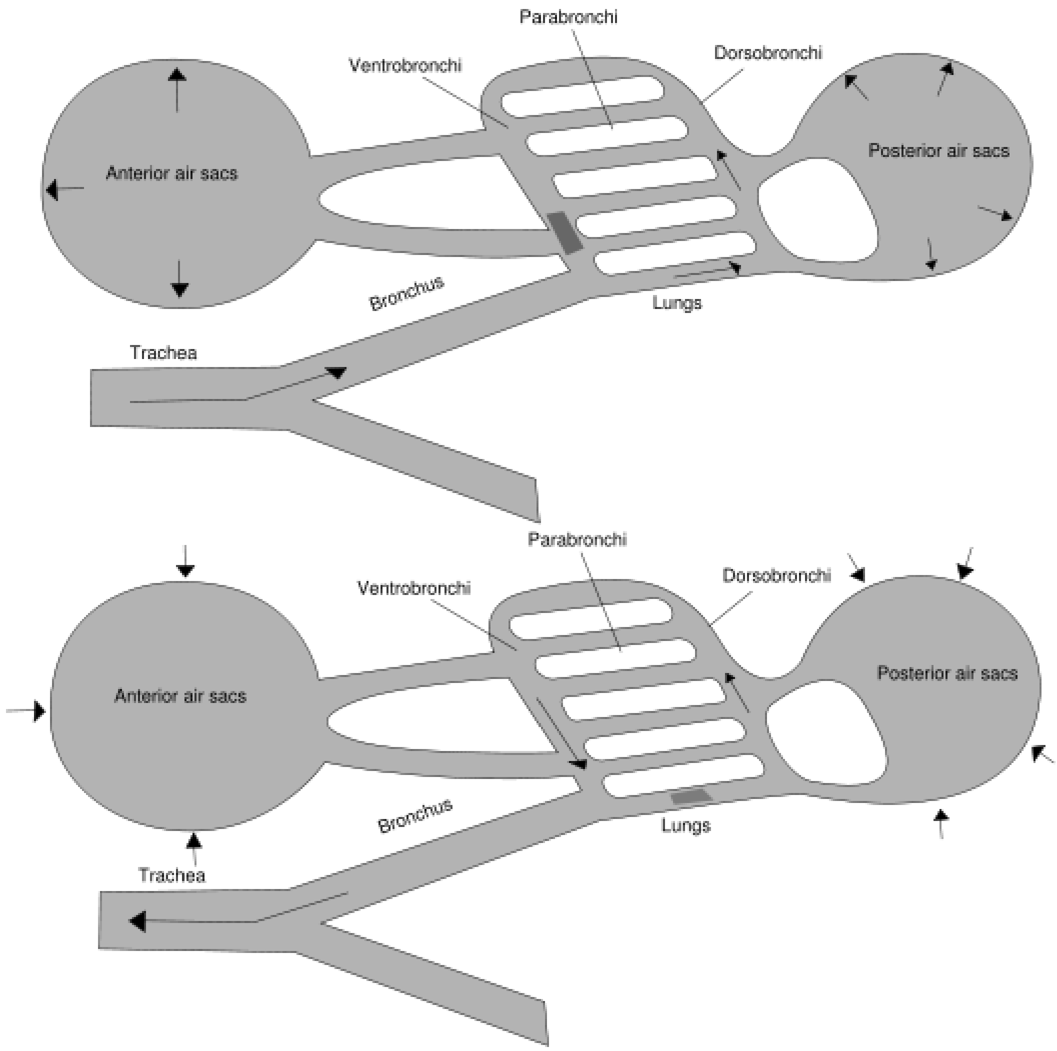


Air always flows from right (posterior) to left (anterior) through a bird's lungs during both inhalation and exhalation. Key to a Common Kestrel's circulatory lung system: 1 cervical air sac, 2 clavicular air sac, 3 cranial thoracic air sac, 4 caudal thoracic air sac, 5 abdominal air sac (5' diverticulus into pelvic girdle), 6 lung, 7 trachea

Due to their high metabolic rate required for flight, birds have a high oxygen demand. Development of an efficient respiratory system enabled the evolution of flight in birds. Birds ventilate their lungs by means of air sacs.

These sacs do not play a direct role in gas exchange, but to store air and act like bellows, allowing the lungs to maintain a fixed volume with fresh air constantly flowing through them.

Three distinct sets of organs perform respiration—the anterior air sacs (interclavicular, cervicals, and anterior thoracics), the lungs, and the posterior air sacs (posterior thoracics and abdominals). The posterior and anterior air sacs, typically nine, expand during inhalation. Air enters the bird via the trachea. Half of the inhaled air enters the posterior air sacs, the other half passes through the lungs and into the anterior air sacs. Air from the anterior air sacs empties directly into the trachea and out the bird's mouth or nares. The posterior air sacs empty their air into the lungs. Air passing through the lungs as the bird exhales is expelled via the trachea. Some taxonomic groups (Passeriformes) possess 7 air sacs, as the clavicular air sacs may interconnect or be fused with the cranial thoracic air sacs.



Birds lungs obtain fresh air during both exhalation and inhalation

As air flows through the air sac system and lungs, there is no mixing of oxygen-rich air and oxygen-poor, carbon dioxide-rich, air as in mammalian lungs. Thus, the partial pressure of oxygen in a bird's lungs is the same as the environment, and so birds have more efficient gas-exchange of both oxygen and carbon dioxide than do mammals. In addition, air passes through the lungs in both exhalation and inspiration, with the air sacs functioning as a reservoir for the next breath of air.

Avian lungs do not have alveoli, as mammalian lungs do, but instead contain millions of tiny passages known as parabronchi, connected at either ends by the dorsobronchi and ventrobronchi. Air flows through the honeycombed walls of the parabronchi into air vesicles, called atria, which project radially from the parabronchi. These atria give rise to air capillaries, where oxygen and carbon dioxide are traded with cross-flowing blood capillaries by diffusion.

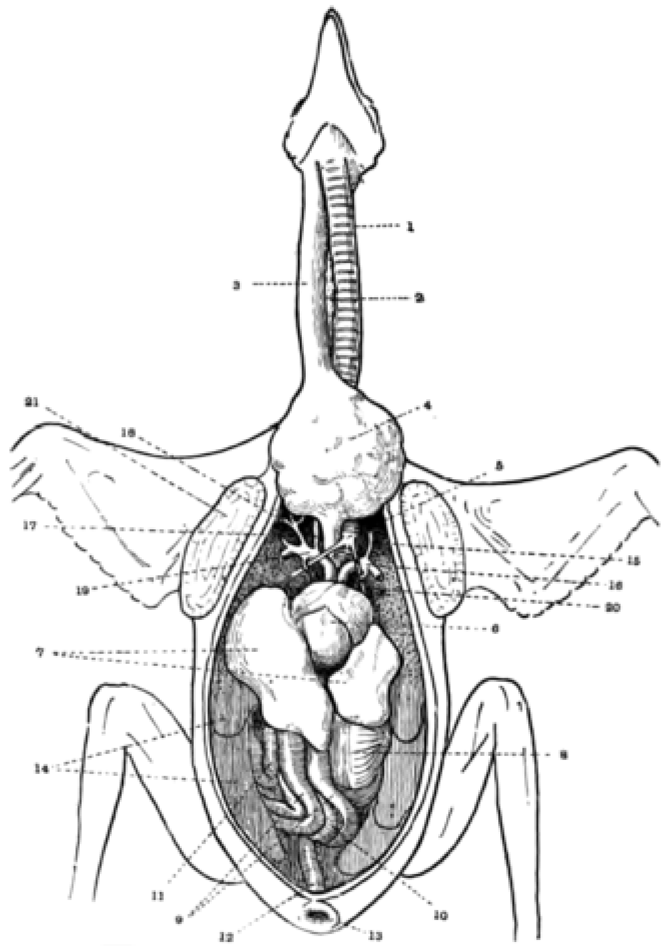
Birds also lack a [Thoracic diaphragm|diaphragm]. The entire body cavity acts as a bellows to move air through the lungs. The active phase of respiration in birds is exhalation, requiring muscular contraction.

The syrinx is the sound-producing vocal organ of birds, located at the base of a bird's trachea. As with the mammalian [larynx], sound is produced by the vibration of air flowing through the organ. The syrinx enables some species of birds to produce extremely complex vocalizations, even mimicking human speech. In some songbirds, the syrinx can produce more than one sound at a time.

Circulatory system

Birds have a four-chambered heart, in common with humans, most mammals, and some reptiles (namely the crocodilia). This adaptation allows for an efficient nutrient and oxygen transport throughout the body, providing birds with energy to fly and maintain high levels of activity. A Ruby-throated Hummingbird's heart beats up to 1200 times per minute (about 20 beats per second).

Digestive system



The chief Viscera of the Pigeon, *Columba livia*

1. Trachea. 2. Thymus gland. 3. Oesophagus. 4. Crop. 5. Syrinx. 6. Heart. 7. Liver. 8. Gizzard. 9. Duodenum. 10. Pancreas. 11. Small intestine. 12. Rectum. 13. Cloaca. 14. Air-sacs. 15. Left carotid. 16. Left subclavian. 17. Right carotid. 18. Brachial artery. 19. Right subclavian. 20. Muscles of syrinx. 21. Pectoralis major muscle cut across.

Alimentary canal of the bird exposed.

Sharp teeth like structures in this rooster's mouth called papillae help birds hold and move food around

Many birds possess a muscular pouch along the esophagus called a crop. The crop functions to both soften food and regulate its flow through the system by storing it temporarily. The size and shape of the crop is quite variable among the birds. Members of the order Columbiformes, such as pigeons, produce a nutritious crop milk which is fed to their young by regurgitation. Birds possess a *ventriculus*, or gizzard, composed of four muscular bands that rotate and crush food by shifting the food from one area to the next within the gizzard. The gizzard of some species contains small pieces of grit or stone swallowed by the bird to aid in the grinding process of digestion, serving the function of mammalian or reptilian teeth. The use of gizzard stones is a similarity between birds and dinosaurs, which left gizzard stones called gastroliths as trace fossils.

Drinking behavior

There are four general ways in which birds drink.

Most birds are unable to swallow by the "sucking" or "pumping" action of peristalsis in their esophagus (as humans do), and drink by repeatedly raising their heads after filling their mouths to allow the liquid to flow by gravity, a method usually described as "sipping" or "tipping up". The notable exception is the Columbiformes; in fact, according to Konrad Lorenz in 1939,

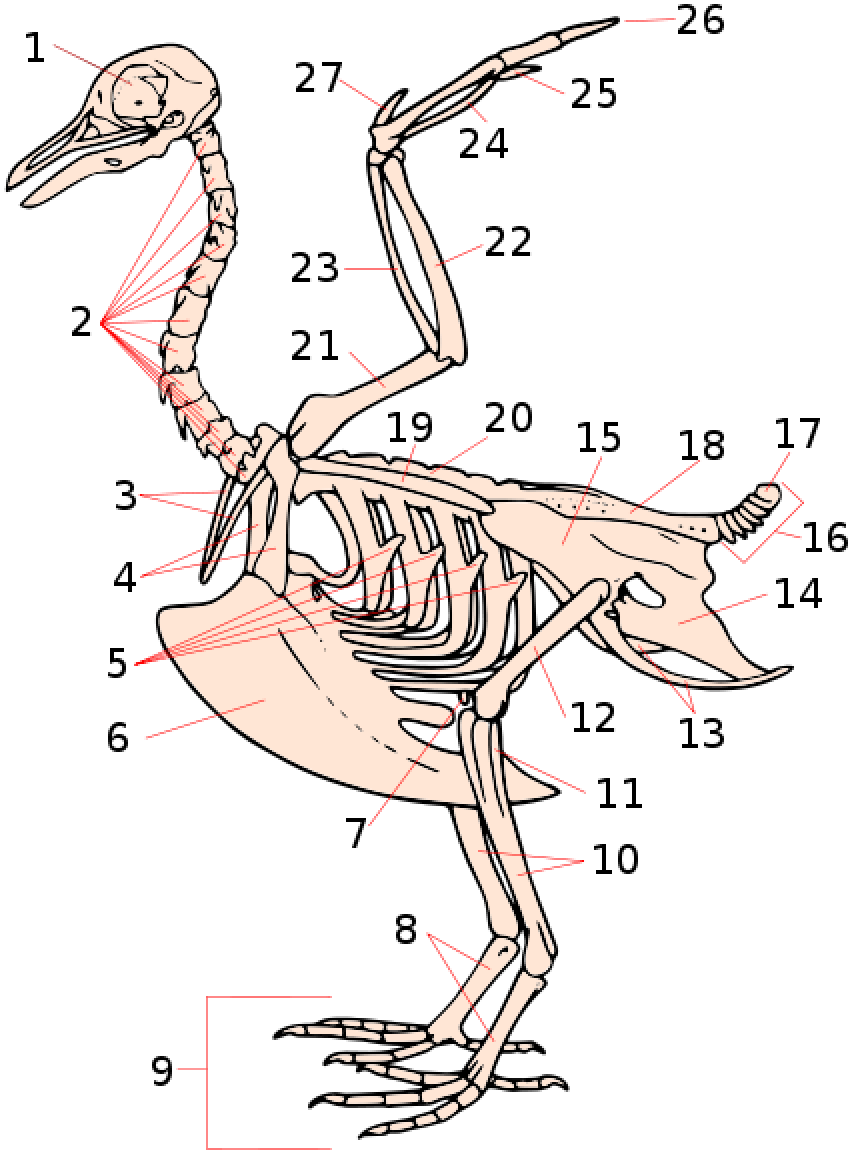
"one recognizes the order by the single behavioral characteristic, namely that in drinking the water is pumped up by peristalsis of the esophagus which occurs without exception within the order. The only other group, however, which shows the same behavior, the Pteroclidae, is placed near the doves just by this doubtlessly very old characteristic."

Although this general rule still stands, since that time, observations have been made of a few exceptions in both directions.,

In addition, specialized nectar feeders like sunbirds (Nectariniidae) and hummingbirds (Trochilidae) drink by using protrusible grooved or trough-like tongues, and parrots (Psittacidae) lap up water.

Many seabirds have glands near the eyes that allow them to drink seawater. Excess salt is eliminated from the nostrils. Many desert birds get the water that they need entirely from their food. The elimination of nitrogenous wastes as uric acid reduces the physiological demand for water.

Skeletal system

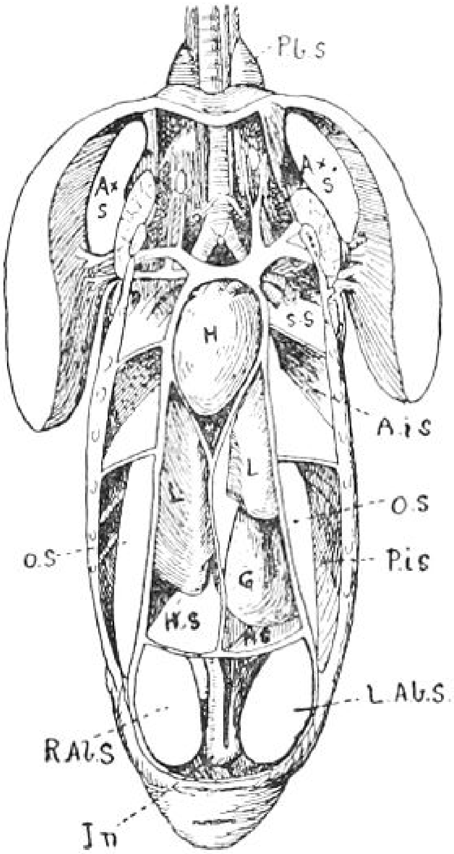


A stylised dove skeleton. Key:
1. skull
2. cervical vertebrae
3. furcula
4. coracoid
5. uncinate processes of ribs
6. keel
7. patella
8. tarsometatarsus
9. digits
10. tibia (tibiotarsus)
11. fibia (tibiotarsus)

12. femur
13. ischium (innominate)
14. pubis (innominate)
15. illium (innominate)
16. caudal vertebrae
17. pygostyle
18. synsacrum
19. scapula
20. lumbar vertebrae
21. humerus
22. ulna
23. radius
24. carpus
25. metacarpus
26. digits
27. alula

The bird skeleton is highly adapted for flight. It is extremely lightweight but strong enough to withstand the stresses of taking off, flying, and landing. One key adaptation is the fusing of bones into single ossifications, such as the pygostyle. Because of this, birds usually have a smaller number of bones than other terrestrial vertebrates. Birds also lack teeth or even a true jaw, instead having evolved a beak, which is far more lightweight. The beaks of many baby birds have a projection called an egg tooth, which facilitates their exit from the amniotic egg.

Birds have many bones that are hollow (pneumatized) with criss-crossing struts or trusses for structural strength. The number of hollow bones varies among species, though large gliding and soaring birds tend to have the most. Respiratory air sacs often form air pockets within the semi-hollow bones of the bird's skeleton. Some flightless birds like penguins and ostriches have only solid bones, further evidencing the link between flight and the adaptation of hollow bones.



DISSECTION SHOWING THE LUNGS AND AIR-SACS OF A BIRD

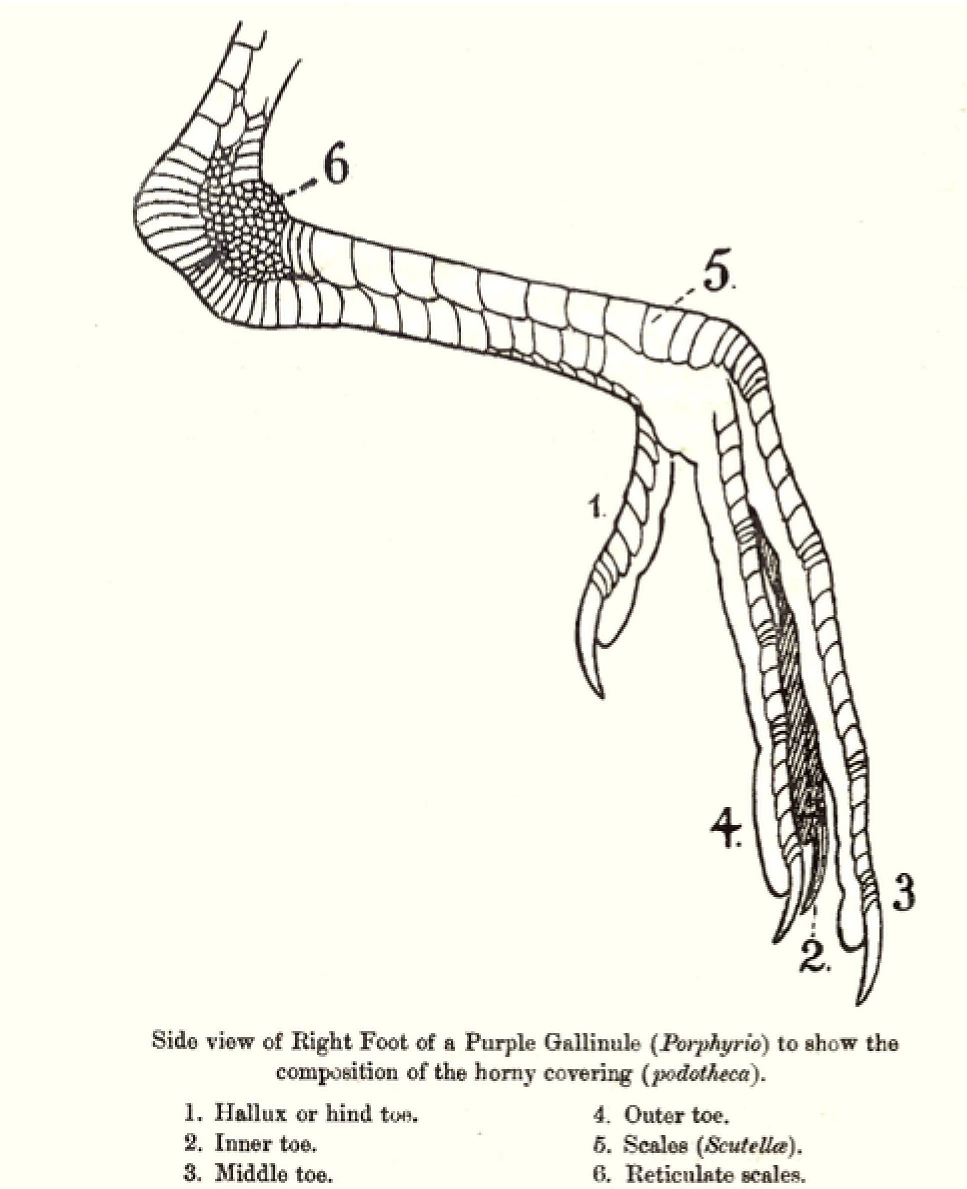
Pb. s. = Pre-bronchial sac. Ax. = Axillary sac bounded externally by the breast-muscles, seen here in section. S. s. = Partition dividing anterior intermediate sac (A.i.s.) from the sub-bronchial sac. P.i.s. = Posterior intermediate sac. O.s. = Oblique septum. H.s. = Horizontal septum. L. Ab. s. = Left abdominal sac. H. = Heart. G. = Gizzard. L. = Liver. In. = Intestine. (After Strasser.)

Air-sacs and their distribution

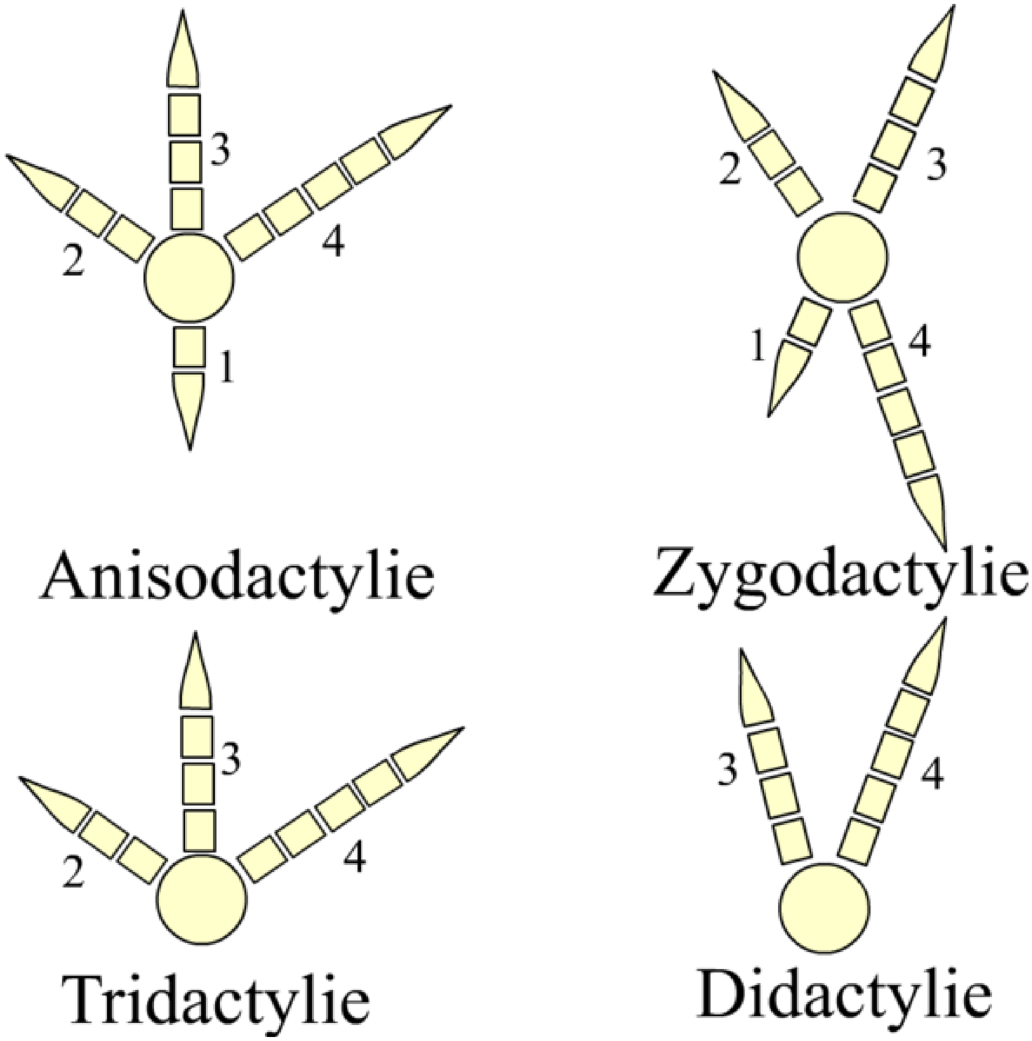
Birds also have more cervical (neck) vertebrae than many other animals; most have a highly flexible neck consisting of 13-25 vertebrae. Birds are the only vertebrate animals to have a fused collarbone (the furcula or wishbone) or a keeled sternum or breastbone. The keel of the sternum serves as an attachment site for the muscles used for flight, or similarly for swimming in penguins. Again, flightless birds, such as ostriches, which do not have highly developed pectoral muscles, lack a pronounced keel on the sternum. It is noted that swimming birds have a wide sternum, while walking birds had a long or high sternum while flying birds have the width and height nearly equal.

Birds have uncinate processes on the ribs. These are hooked extensions of bone which help to strengthen the rib cage by overlapping with the rib behind them. This feature is also found in the tuatara *Sphenodon*. They also have a greatly elongate tetradiate pelvis as in some reptiles. The hindlimb has an intra-tarsal joint found also in some reptiles. There is extensive fusion of the trunk vertebrae as well as fusion with the pectoral girdle. They have a diapsid skull as in reptiles with a pre-lachrymal fossa (present in some reptiles). The skull has a single occipital condyle.

Skeleton



Scalation and structure of the leg



Types of bird feet

The skull consists of five major bones: the frontal (top of head), parietal (back of head), premaxillary and nasal (top beak), and the mandible (bottom beak). The skull of a normal bird usually weighs about 1% of the birds total bodyweight.

The vertebral column consists of vertebrae, and is divided into three sections: cervical (13-16) (neck), Synsacrum (fused vertebrae of the back, also fused to the hips (pelvis)), and pygostyle (tail).

The chest consists of the furcula (wishbone) and coracoid (collar bone), which two bones, together with the scapula, form the pectoral girdle. The side of the chest is formed by the ribs, which meet at the sternum (mid-line of the chest).

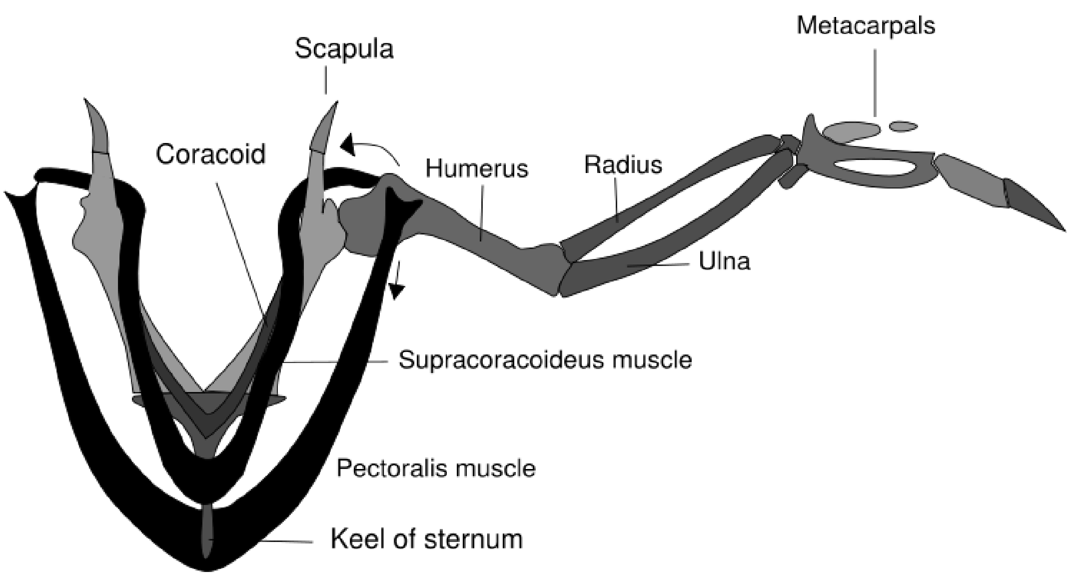
The shoulder consists of the scapula (shoulder blade), coracoid, and humerus (upper arm). The humerus joins the radius and ulna (forearm) to form the elbow. The carpus and metacarpus form the "wrist" and "hand" of the bird, and the digits (fingers) are fused together. The bones in the wing are extremely light so that the bird can fly more easily.

The hips consist of the pelvis which includes three major bones: Illium (top of the hip), Ischium (sides of hip), and Pubis (front of the hip). These are fused into one (the innominate bone). Innominate bones are evolutionary significant in that they allow birds to lay eggs. They meet at the acetabulum (the hip socket) and articulate with the femur, which is the first bone of the hind limb.

The upper leg consists of the femur. At the knee joint, the femur connects to the tibiotarsus (shin) and fibula (side of lower leg). The tarsometatarsus forms the upper part of the foot, digits make up the toes. The leg bones of birds are the heaviest, contributing to a low center of gravity. This aids in flight. A bird's skeleton comprises only about 5% of its total body weight

Birds feet are classificated as anisodactyl, zygodactyl, heterodactyl, syndactyl or pamprodactyl.

Muscular system



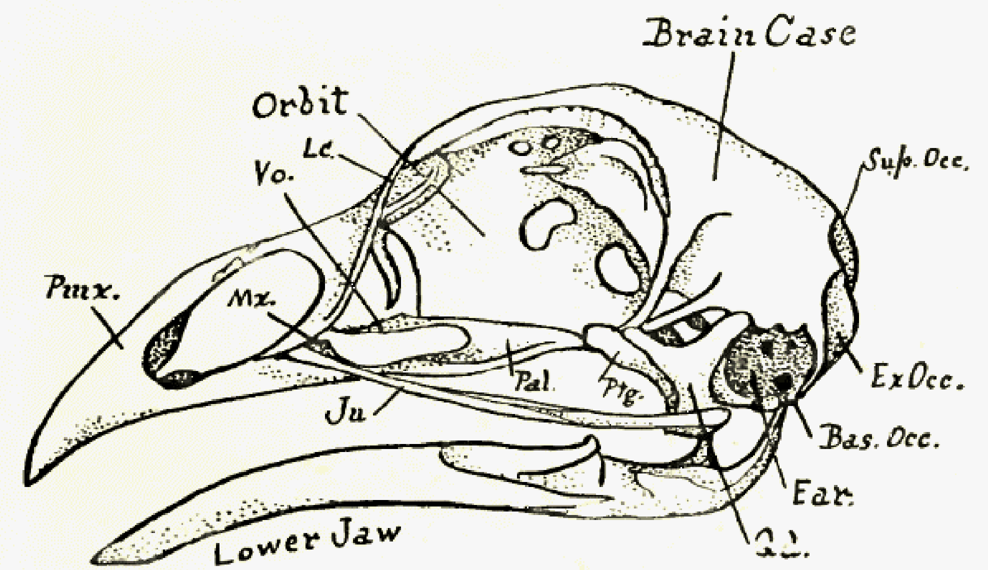
The supracoracoideus works using a pulley like system to lift the wing while the pectorals provide the powerful downstroke

Most birds have approximately 175 different muscles, mainly controlling the wings, skin, and legs. The largest muscles in the bird are the pectorals, or the breast muscles, which control the wings and make up about 15 - 25% of a flighted bird's body weight. They provide the powerful wing stroke essential for flight. The muscle ventral (underneath) to the pectorals is the supracoracoideus. It raises the wing between wingbeats. The supracoracoideus and the pectorals together make up about 25 – 35% of the bird's full body weight.

The skin muscles help a bird in its flight by adjusting the feathers, which are attached to the skin muscle and help the bird in its flight maneuvers.

There are only a few muscles in the trunk and the tail, but they are very strong and are essential for the bird. The pygostyle controls all the movement in the tail and controls the feathers in the tail. This gives the tail a larger surface area which helps keep the bird in the air.

Head



Skull of Fowl, showing orbit, brain-case, ear, lower jaw, premaxillary (*Pmx.*), maxillary (*Mx.*), vomer (*Vo.*), lacrymal (*Lc.*), jugal (*Ju.*), palatine (*Pal.*), pterygoid (*.Ptg*), quadrate (*Qd.*), and supra (*Sup. occ.*), ex (*Ex. occ.*), and basioccipital bones. (After Parker.)

Skull of a bird

Birds have acute eyesight - raptors have vision eight times sharper than humans - thanks to higher densities of photoreceptors in the retina (up to 1,000,000 per square mm in *Buteos*, compared to 200,000 for humans), a high number of optic nerves, a second set of eye muscles not found in other animals, and, in some cases, an indented fovea which magnifies the central part of the visual field. Many species, including hummingbirds and albatrosses, have two foveas in each eye. Many birds can detect polarised light. The eye occupies a considerable part of the skull and is surrounded by a sclerotic eye-ring, a ring of tiny bones that surround the eye. This character is also seen in the reptiles.

The bills of many waders have Herbst corpuscles which help them detect prey hidden under wet sand using minute pressure differences in the water. All extant birds can move the parts of the upper jaw relative to the brain case. However this is more prominent in some birds and can be readily detected in parrots.

Birds have a large brain to body mass ratio. This is reflected in the advanced and complex bird intelligence.

The region between the eye and bill on the side of a bird's head is called the lore. This region is sometimes featherless, and the skin may be tinted, as in many species of the cormorant family.

Reproduction

Fledgling

Although most male birds have no external sex organs, the male does have two testes which become hundreds of times larger during the breeding season to produce sperm. The testes in male birds are generally asymmetric with most birds having a larger left testis. The female's ovaries also become larger, although only the left ovary usually functions. However, if the left ovary is damaged by infection or other problems, the right ovary will try to function.

In the males of species without a phallus, sperm is stored in the semenal glomera within the cloacal protuberance prior to copulation. During copulation, the female moves her tail to the side and the male either mounts the female from behind or in front (in the stitchbird), or moves very close to her. The cloacae then touch, so that the sperm can enter the female's reproductive tract. This can happen very fast, sometimes in less than half a second.

The sperm is stored in the female's sperm storage tubules for a week to a year, depending on the species. Then, eggs will be fertilized individually as they leave the ovaries, before being laid by the female. The eggs continue their development outside the female body.

A juvenile Laughing Gull

Many waterfowl and some other birds, such as the ostrich and turkey, possess a phallus. When not copulating, it is hidden within the proctodeum compartment within the cloaca, just inside the vent.

After the eggs hatch, parents provide varying degrees of care in terms of food and protection. Precocial birds can care for themselves independently within minutes of hatching; altricial hatchlings are helpless, blind, and naked, and require extended parental care. The chicks of many ground-nesting birds such as partridges and waders are often able to run virtually immediately after hatching; such birds are referred to as nidifugous. The young of hole-nesters, on the other hand, are often totally incapable of unassisted survival. The process whereby a chick acquires feathers until it can fly is called "fledging".

Some birds, such as pigeons, geese, and Red-crowned Cranes, remain with their mates for life and may produce offspring on a regular basis.

Scales

The scales of birds are composed of the same keratin as beaks, claws, and spurs. They are found mainly on the toes and metatarsus, but may be found further up on the ankle in some birds. Most bird scales do not overlap significantly, except in the cases of kingfishers and woodpeckers. The scales and scutes of birds are thought to be homologous to those of reptiles and mammals.

Bird embryos begin development with smooth skin. On the feet, the corneum, or outermost layer, of this skin may keratinize, thicken and form scales. These scales can be organized into;

1. Cancella – minute scales which are really just a thickening and hardening of the skin, crisscrossed with shallow grooves.
2. Reticula – small but distinct, separate, scales. Found on the lateral and medial surfaces (sides) of the chicken metatarsus. These are made up of alpha-keratin.
3. Scutella – scales that are not quite as large as scutes, such as those found on the caudal, or hind part, of the chicken metatarsus.
4. Scutes – the largest scales, usually on the anterior surface of the metatarsus and dorsal surface of the toes. These are made up of beta-keratin as in reptilian scales.

The rows of scutes on the anterior of the metatarsus can be called an acrometatarsium or acrotarsium.

Feathers can be intermixed with scales on some birds' feet. Feather follicles can lie between scales or even directly beneath them, in the deeper dermis layer of the skin. In this last case, feathers may emerge directly through scales, and be encircled at the plane of emergence entirely by the keratin of the scale.

Chapter- 5

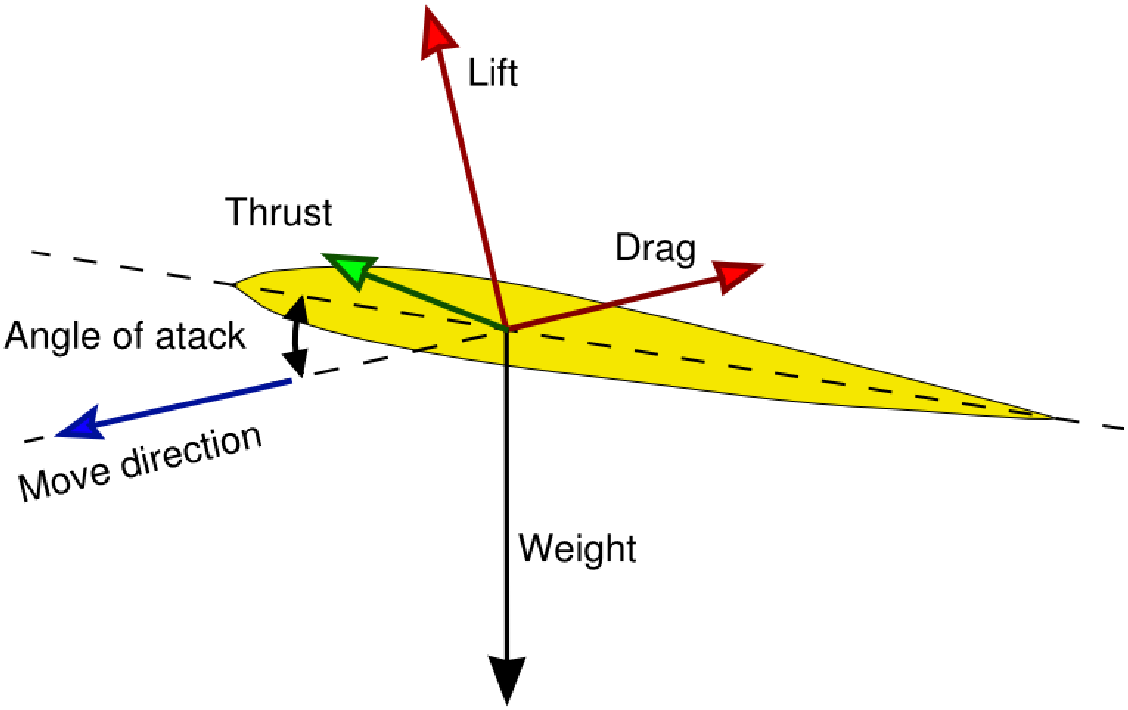
Bird Flight

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

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 that counteracts drag.

A flock of domestic pigeons each in a different phase of its flap.

Flapping

When a bird flaps, as opposed to gliding, its wings continue to develop lift as before, but the lift is rotated forward to provide 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.

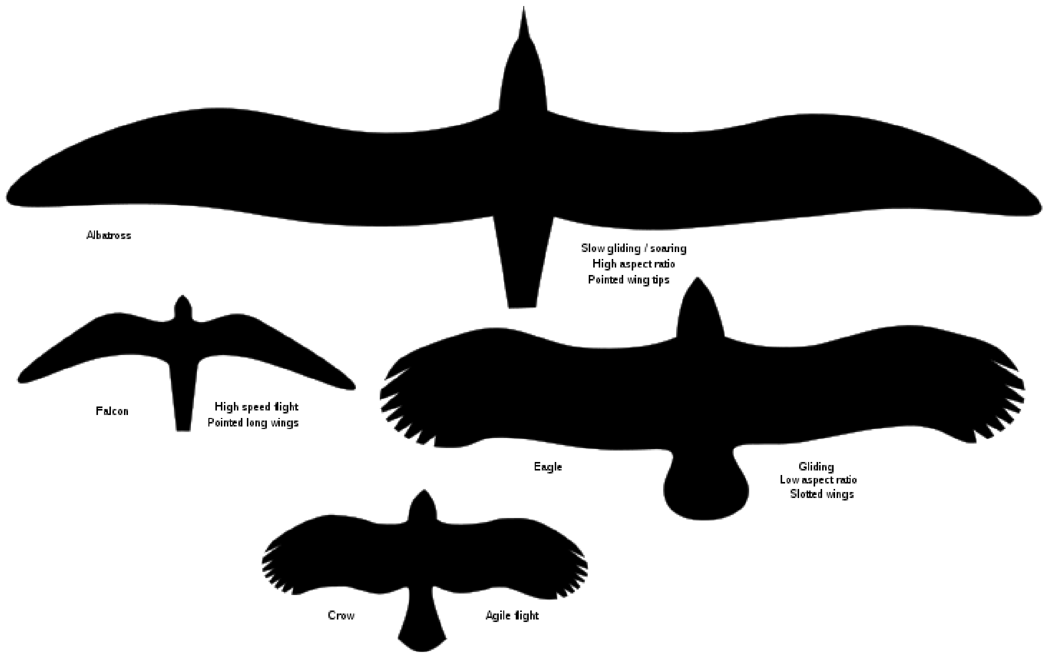
Wing

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), which serves 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, 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



Wing shapes

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.

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).

A Roseate Tern uses its low wing loading and high aspect ratio to achieve low speed flight

High aspect ratio wings

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. Low speed flight is important for birds that plunge dive for fish.

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 and wingtip vortices by "capturing" the energy in air flowing from the lower to upper wing surface 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

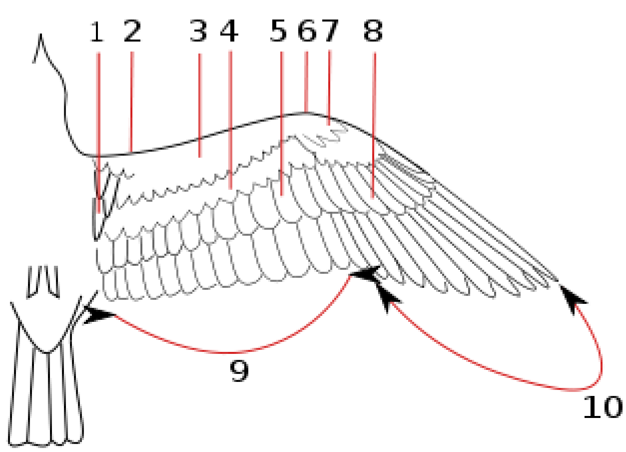
A male bufflehead runs atop the water while taking off

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



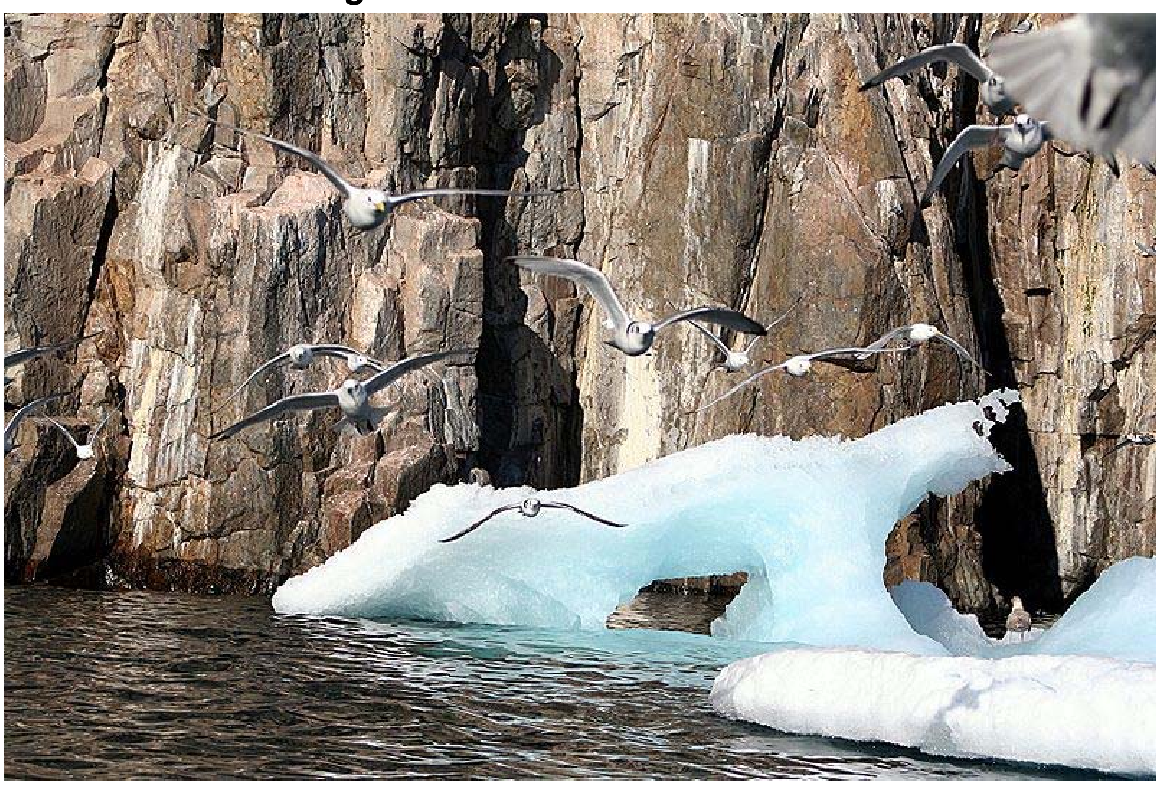
1 Axillaries; 2 Margin (Marginal underwing coverts); 3 Lesser underwing coverts; 4 Median underwing coverts (Secondary coverts); 5 Greater underwing coverts (Secondary

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.

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 that 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) as much as possible. 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.

Chapter- 6

Bird Vision

With forward facing eyes the Bald Eagle has a wide field of binocular vision.

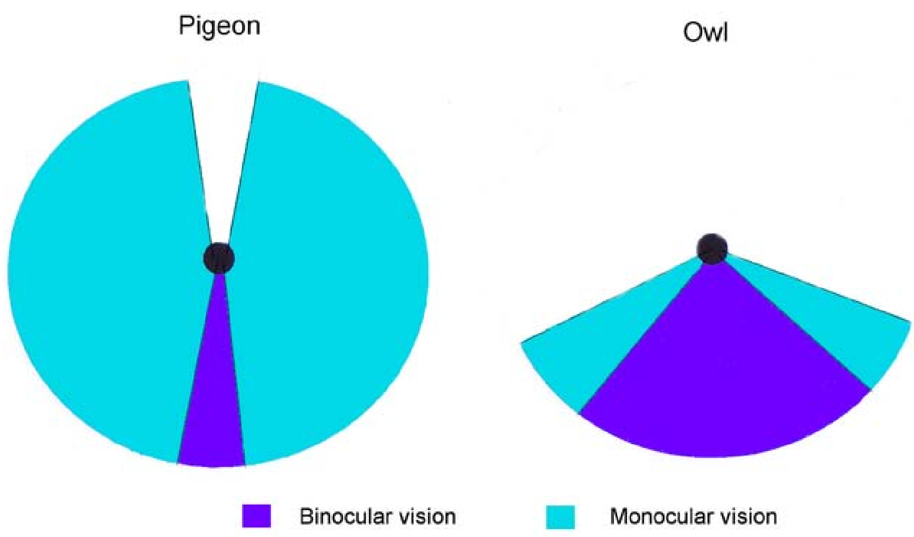
Vision is the most important sense for birds, since good eyesight is essential for safe flight, and this group has a number of adaptations which give visual acuity superior to that of other vertebrate groups; a pigeon has been described as "two eyes with wings". The avian eye resembles that of a reptile, with ciliary muscles that can change the shape of the lens rapidly and to a greater extent than in the mammals. Birds have the largest eyes relative to their size within the animal kingdom, and movement is consequently limited within the eye's bony socket. In addition to the two eyelids usually found in vertebrates, it is protected by a third transparent movable membrane. The eye's internal anatomy is similar to that of other vertebrates, but has a structure, the pecten oculi, unique to birds.

Birds, like fish, amphibians and reptiles, have four types of colour receptors in the eye. Most mammals have two types of receptors, although primates have three. This gives birds the ability to perceive not just the visible range but also the ultraviolet part of the spectrum, and other adaptations allow for the detection of polarised light or magnetic fields. Birds have proportionally more light receptors in the retina than mammals, and more nerve connections between the photoreceptors and the brain.

Some bird groups have specific modifications to their visual system linked to their way of life. Birds of prey have a very high density of receptors and other adaptations that maximise visual acuity. The placement of their eyes gives them good binocular vision enabling accurate judgement of distances. Nocturnal species have tubular eyes, low numbers of colour detectors, but a high density of rod cells which function well in poor light. Terns, gull and albatrosses are amongst the seabirds which have red or yellow oil drops in the colour receptors to improve distance vision especially in hazy conditions.

Extraocular anatomy

The eye of a bird most closely resembles that of the reptiles. Unlike the mammalian eye, it is not spherical, and the flatter shape enables more of its visual field to be in focus. A circle of bony plates, the sclerotic ring, surrounds the eye and hold it rigid, but an improvement over the reptilian eye, also found in mammals, is that the lens is pushed further forward, increasing the size of the image on the retina.



Fields of view for an owl and a pigeon

Most birds cannot move their eyes, although there are exceptions, such as the Great Cormorant. Birds with eyes on the sides of their heads have a wide visual field, useful for detecting predators, while those with eyes on the front of their heads, such as owls, have binocular vision and can estimate distances when hunting. The American Woodcock probably has the largest visual field of any bird, 360^o in the horizontal plane, and 180^o in the vertical plane.

The nictitating membrane of a Masked Lapwing

The eyelids of a bird are not used in blinking. Instead the eye is lubricated by the nictitating membrane, a third concealed eyelid that sweeps horizontally across the eye like a windscreen wiper. The nictitating membrane also covers the eye and acts as a contact lens in many aquatic birds when they are under water. When sleeping, the lower eyelid rises to cover the eye in most birds, with the exception of the horned owls where the upper eyelid is mobile.

The eye is also cleaned by tear secretions from the lachrymal gland and protected by an oily substance from the Harderian glands which coats the cornea and prevents dryness. The eye of a bird is larger compared to the size of the animal than for any other group of animals, although much of it is concealed in its skull. The Ostrich has the largest eye of any land vertebrate, with an axial length of 50 mm (2 in), twice that of the human eye.

Bird eye size is broadly related to body mass. A study of five orders (parrots, pigeons, petrels, raptors and owls) showed that eye mass is proportional to body mass, but as expected from their habits and visual ecology, raptors and owls have relatively large eyes for their body mass.

Behavioural studies show that many avian species focus on distant objects preferentially with their lateral and monocular field of vision, and birds will orient themselves sideways to maximise visual resolution. For a pigeon, resolution is twice as good with sideways monocular vision than forward binocular vision, whereas for humans the converse is true.

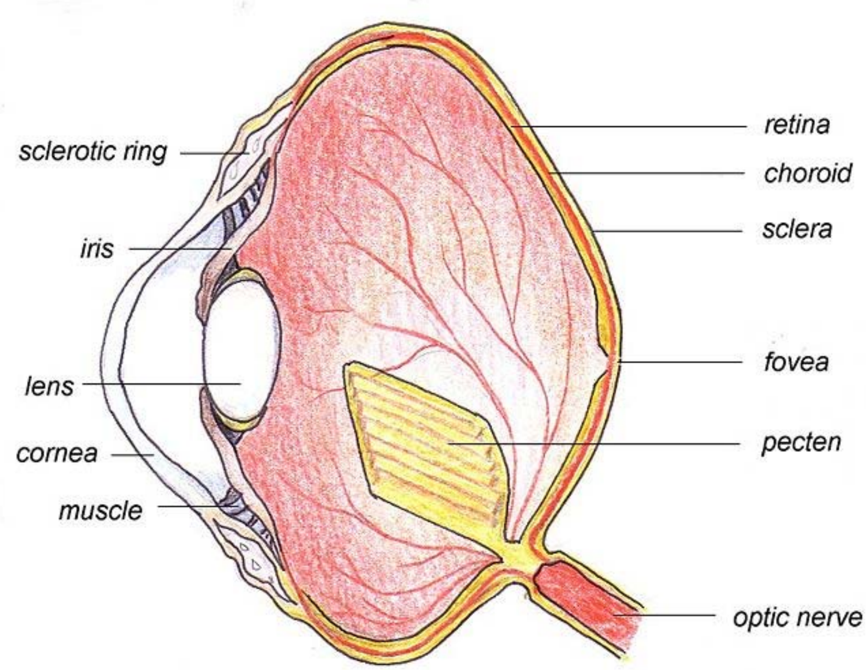
The European Robin has relatively large eyes, and starts to sing early in the morning.

The performance of the eye in low light levels depends on the distance between the lens and the retina, and small birds are effectively forced to be diurnal because their eyes are not large enough to give adequate night vision. Although many species migrate at night, they often collide with even brightly lit objects like lighthouses or oil platforms. Birds of prey are diurnal because, although their eyes are large, they are optimised to give maximum spatial resolution rather than light gathering, so they also do not function well in poor light. Many birds have an asymmetry in the eye's structure which enables them to keep the horizon and a significant part of the ground in focus simultaneously. The cost of this adaptation is that they have myopia in the lower part of their field of view.

Birds with relatively large eyes compared to their body mass, such as Common Redstarts and European Robins sing earlier at dawn than birds of the same size and smaller body mass. However, if birds have the same eye size but different body masses, the larger species sings later than the smaller. This may be because the smaller bird has to start the day earlier because of weight loss overnight.

Nocturnal birds have eyes optimised for visual sensitivity, with large corneas relative to the eye's length, whereas diurnal birds have longer eyes relative to the corneal diameter to give greater visual acuity. Information about the activities of extinct species can be deduced from measurements of the sclerotic ring and orbit depth. For the latter measurement to be made, the fossil must have retained its three-dimensional shape, so activity pattern cannot be determined with confidence from flattened specimens like *Archaeopteryx*, which has a complete sclerotic ring but no orbit depth measurement.

Anatomy of the eye



Anatomy of the avian eye

The main structures of the bird eye are similar to those of other vertebrates. The outer layer of the eye consists of the transparent cornea at the front, and two layers of sclera – a tough white collagen fibre layer which surrounds the rest of the eye and supports and protects the eye as a whole. The eye is divided internally by the lens into two main segments: the anterior segment and the posterior segment. The anterior chamber is filled with a watery fluid called the aqueous humour, and the posterior chamber contains the vitreous humour, a clear jelly-like substance.

The lens is a transparent convex or 'lens' shaped body with a harder outer layer and a softer inner layer. It focuses the light on the retina. The shape of the lens can be altered by ciliary muscles which are directly attached to lens capsule by means of the zonular fibres. In addition to these muscles, some birds also have a second set, Crampton's muscles, that can change the shape of the cornea, thus giving birds a greater range of accommodation than is possible for mammals. This accommodation can be rapid in some diving water birds such as in the mergansers. The iris is a coloured muscularly operated diaphragm in front of the lens which controls the amount of light entering the eye. At the centre of the iris is the pupil, the variable circular area through which the light passes into the eye.

Hummingbirds are amongst the many birds with two foveae

The retina is a relatively smooth curved multi-layered structure containing the photosensitive rod and cone cells with the associated neurons and blood vessels. The density of the photoreceptors is critical in determining the maximum attainable visual acuity. Humans have about 200,000 receptors per mm^2, but the House Sparrow has 400,000 and the Common Buzzard 1,000,000. The photoreceptors are not all individually connected to the optic nerve, and the ratio of nerve ganglia to receptors is important in determining resolution. This is very high for birds; the White Wagtail has 100,000 ganglion cells to 120,000 photoreceptors.

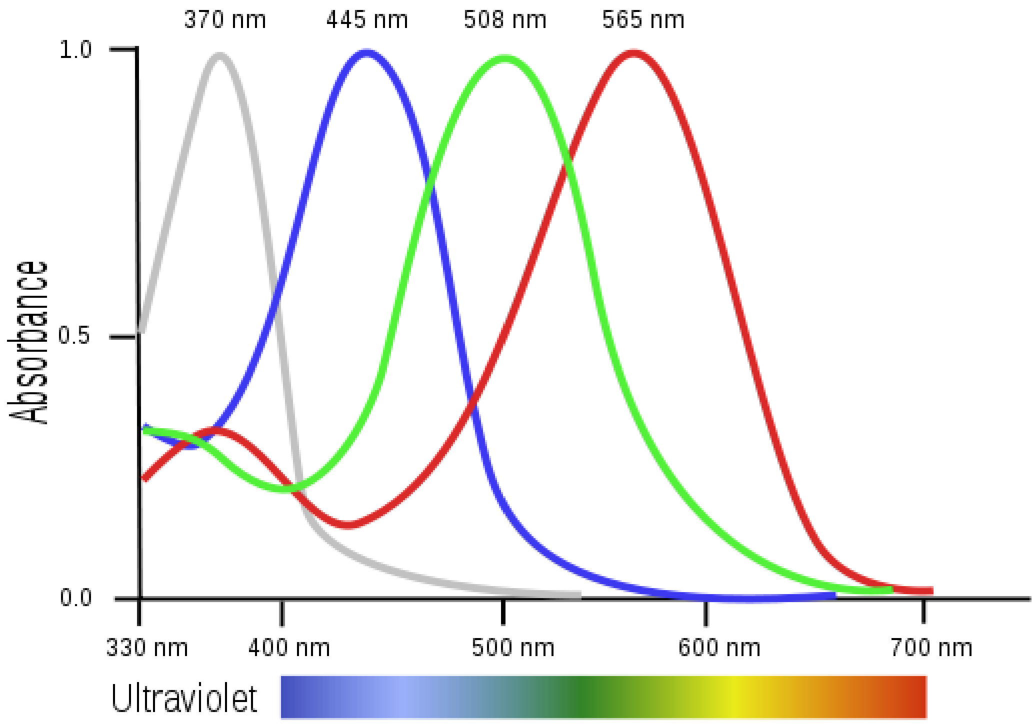
Rods are more sensitive to light, but give no colour information, whereas the less sensitive cones enable colour vision. In diurnal birds, 80% of the receptors may be cones (90% in some swifts) whereas nocturnal owls have almost all rods. As with other vertebrates except placental mammals, some of the cones may be double structures. These can amount to 50% of all cones in some species.

Towards the centre of the retina is the fovea which has a greater density of receptors and is the area of greatest forward visual acuity, i.e. sharpest, clearest detection of objects. In 54% of birds, including birds of prey, kingfishers, hummingbirds and swallows, there is second fovea for enhanced sideways viewing. The optic nerve is a bundle of nerve fibres which carry messages from the eye to the relevant parts of the brain and vice-versa. Like mammals, birds have a small blind spot without photoreceptors at the optic disc, under which the optic nerve and blood vessels join the eye.

The pecten is a poorly understood body consisting of folded tissue which projects from the retina. It is well supplied with blood vessels and appears to keep the retina supplied with nutrients, and may also shade the retina from dazzling light or aid in detecting moving objects.

The choroid is a layer situated behind the retina which contains many small arteries and veins. These provide arterial blood to the retina and drain venous blood. The choroid contains melanin, a pigment which gives the inner eye its dark colour, helping to prevent disruptive reflections.

Light perception



The four pigments in a bird's cones extend the range of colour vision into the ultraviolet.

There are two sorts of light receptors in a bird’s eye, rods and cones. Rods, which contain the visual pigment rhodopsin are better for night vision because they are sensitive to small quantities of light. Cones detect specific colours (or wavelengths) of light, so they are more important to colour-oriented animals such as birds. Most birds are tetrachromatic, possessing ultraviolet (UV) sensitive cone cells in the eye as well as those for red, green and blue, but pigeons have an additional pigment and are therefore pentachromatic.

The four spectrally distinct cone pigments are derived from the protein opsin, linked to a small molecule called retinal, which is closely related to vitamin A. When the pigment absorbs light the retinal changes shape and alters the membrane potential of the cone cell affecting neurones in the ganglia layer of the retina. Each neurone in the ganglion layer may processes information from a number of photoreceptor cells, and may in turn trigger a nerve impulse to relay information along the optic nerve for further processing in specialised visual centres in the brain. The more intense a light, the more photons are absorbed by the visual pigments, the greater the excitation of each cone, and the brighter the light appears.

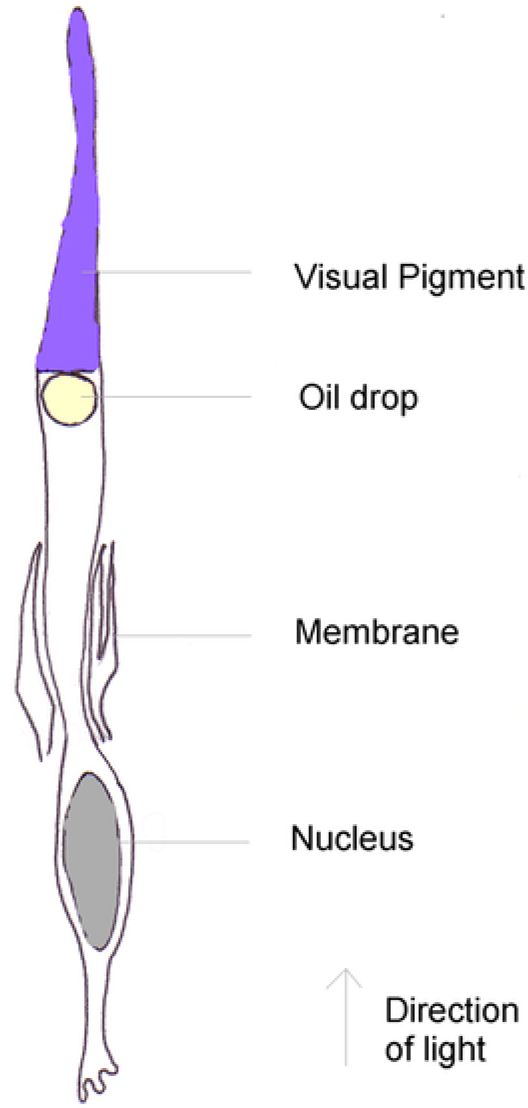


Diagram of a bird cone cell

By far the most abundant cone pigment in every bird species examined is the long-wavelength form of iodopsin, which absorbs at wavelengths near 570 nm. This is roughly the spectral region occupied by the red- and green-sensitive pigments in the primate retina, and this visual pigment dominates the colour sensitivity of birds. In penguins, this pigment appears to have shifted its absorption peak to 543 nm, presumably an adaptation to a blue aquatic environment.

The information conveyed by a single cone is limited: by itself, the cell cannot tell the brain which wavelength of light caused its excitation. A visual pigment may absorb two wavelengths equally, but even though their photons are of different energies, the cone cannot tell them apart, because they both cause the retinal to change shape and thus trigger the same impulse. For the brain to see colour, it must compare the responses of two or more classes of cones containing different visual pigments, so the four pigments in birds give increased discrimination.

Each cone of a bird or reptile contains a coloured oil droplet; these no longer exist in mammals. The droplets, which contain high concentrations of carotenoids, are placed so that light passes through before reaching the visual pigment. They act as filters, removing some wavelengths and narrowing the absorption spectra of the pigments. This reduces the response overlap between pigments and increases the number of colours that a bird can discern. Six types of cone oil droplets have been identified; five of these have carotenoid mixtures that absorb at different wavelengths and intensities, and the sixth type has no pigments.

The colours and distributions of retinal oil droplets vary considerably among species, and is more dependent on the ecological niche utilised (hunter, fisher, herbivore) than genetic relationships. As examples, diurnal hunters like the Barn Swallow and birds of prey have few coloured droplets, whereas the surface fishing Common Tern has a large number of red and yellow droplets in the dorsal retina. The evidence suggests that oil droplets respond to natural selection faster than the cone's visual pigments. Even within the range of wavelengths that are visible to humans, passerine birds can detect colour differences that humans do not register. This finer discrimination, together with the ability to see ultraviolet light, means that many species show sexual dichromatism that is visible to birds but not humans.

Migratory songbirds use the Earth’s magnetic field, stars, the Sun, and polarised light patterns to determine their migratory direction. An American study showed that migratory Savannah Sparrows used polarised light from an area of sky near the horizon to recalibrate their magnetic navigation system at both sunrise and sunset. This suggested that skylight polarisation patterns are the primary calibration reference for all migratory songbirds. However, it appears that birds may be responding to secondary indicators of the angle of polarisation, and may not be actually capable of directly detecting polarisation direction in the absence of these cues.

Ultraviolet

The Common Kestrel can detect the ultraviolet trail of its vole prey.

Birds can perceive ultraviolet light, which is involved in courtship. Many birds show plumage patterns in ultraviolet that are invisible to the human eye; some birds whose sexes appear similar to the naked eye are distinguished by the presence of ultraviolet reflective patches on their feathers. Male Blue Tits have an ultraviolet reflective crown patch which is displayed in courtship by posturing and raising of their nape feathers. Male Blue Grosbeaks with the most, brightest and most UV-shifted blue in their plumage are larger, hold the most extensive territories with abundant prey, and feed their offspring more frequently than other males do.

The bill’s appearance is important in the interactions of the Blackbird. Although the UV component seems unimportant in interactions between territory-holding males, where the degree of orange is the main factor, the female responds more strongly to males with bills with good UV-reflectiveness.

A UV receptor may give an animal an advantage in foraging for food. The waxy surfaces of many fruits and berries reflect UV light that might advertise their presence. Common Kestrels are able to locate the trails of voles visually. These small rodents lay scent trails of urine and faeces that reflect UV light, making them visible to the kestrels, particularly in the spring before the scent marks are covered by vegetation.

Perception

Movement

A hunting Common Kestrel needs a steady visual image

Birds can resolve rapid movements better than humans, for whom flickering at a rate greater than 50 Hz appears as continuous movement. Humans cannot therefore distinguish individual flashes of a fluorescent light bulb oscillating at 60Hz, but Budgerigars and chickens have flicker thresholds of more than 100 Hz. A Cooper's Hawk can pursue agile prey through woodland and avoid branches and other objects at high speed; to humans such a chase would appear as a blur.

Birds can also detect slow moving objects. The movement of the sun and the constellations across the sky is imperceptible to humans, but detected by birds. The ability to detect these movements allows migrating birds to properly orient themselves.

To obtain steady images while flying or when perched on a swaying branch, birds hold the head as steady as possible with compensating reflexes. Maintaining a steady image is especially relevant for birds of prey.

Edges and shapes

When an object is partially blocked by another, humans unconsciously tend to make up for it and complete the shapes. It has however been demonstrated that pigeons do not complete occluded shapes. A study based on altering the grey level of a perch that was coloured differently from the background showed that budgerigars do not detect edges based on colours.

Magnetic fields

The perception of magnetic fields by migratory birds has been suggested to be light dependent. Birds move their head to detect the orientation of the magnetic field, and studies on the neural pathways have suggested that birds may be able to "see" the magnetic fields. The right eye of a migratory bird contains photoreceptive proteins called cryptochromes. Light excites these molecules to produce unpaired electrons that interact with the Earth's magnetic field, thus providing directional information.

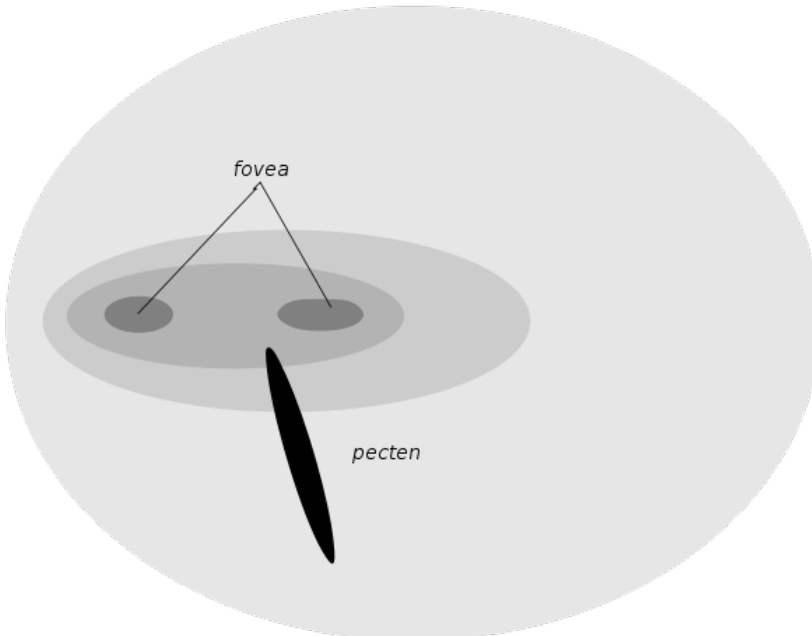
Variations across bird groups

Diurnal birds of prey

"Hawk-eyed" is a byword for visual acuity

The visual ability of birds of prey is legendary, and the keenness of their eyesight is due to a variety of factors. Raptors have large eyes for their size, 1.4 times greater than the average for birds of the same weight, and the eye is tube-shaped to produce a larger retinal image. The retina has a large number of receptors per square millimetre, which determines the degree of visual acuity. The more receptors an animal has, the higher its ability to distinguish individual objects at a distance, especially when, as in raptors, each receptor is typically attached to a single ganglion.

Many raptors have foveas with far more rods and cones than the human fovea (65,000/mm^2 in American Kestrel, 38,000 in humans) and this provides these birds with spectacular long distance vision. The fovea itself can also be lens-shaped, increasing the effective density of receptors further. This combination of factors gives *Buteo* buzzards distance vision 6 to 8 times better than humans.



Each retina of the Black-chested Buzzard-eagle has two fovea

The forward facing eyes of a bird of prey give binocular vision, which is assisted by a double fovea. The raptor's adaptations for optimum visual resolution (an American Kestrel can see a 2–mm insect from the top of an 18–m tree) has a disadvantage in that its vision is poor in low light level, and it must roost at night. Raptors may have to pursue mobile prey in the lower part of their visual field, and therefore do not have the lower field myopia adaptation demonstrated by many other birds. Scavenging birds like vultures do not need such sharp vision, so a condor has only a single fovea with about 35,000 receptors mm^2

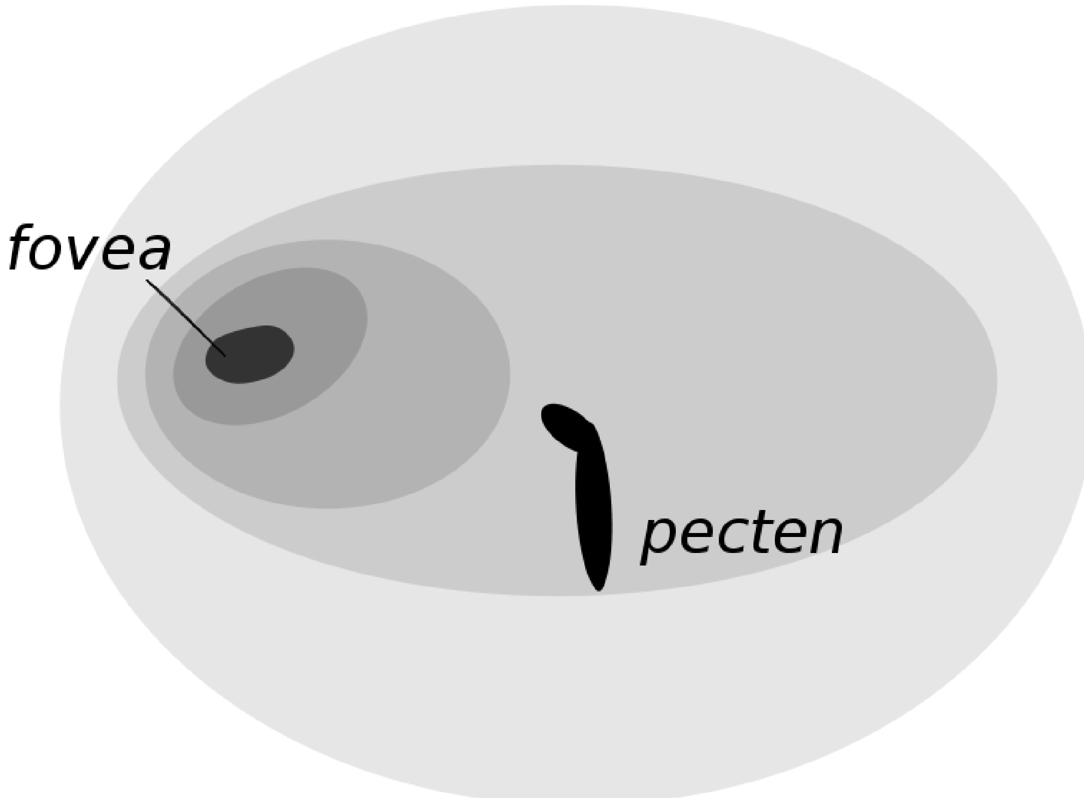
Raptors lack coloured oil drops in the cones, and probably have similar colour perception to humans, and lack the ability to detect polarised light. The generally brown, grey and white plumage of this group, and the absence of colour displays in courtship suggests that colour is relatively unimportant to these birds.

In most raptors a prominent eye ridge and its feathers extends above and in front of the eye. This "eyebrow" gives birds of prey their distinctive stare. The ridge physically protects the eye from wind, dust, and debris and shields it from excessive glare. The Osprey lacks this ridge, although the arrangement of the feathers above its eyes serves a similar function; it also possesses dark feathers in front of the eye which probably serve to reduce the glare from the water surface when the bird is hunting for its staple diet of fish.

Nocturnal birds

Eurasian Eagle-owl

Owls have very large eyes for their size, 2.2 times greater than the average for birds of the same weight, and positioned at the front of the head. The eyes have a field overlap of 50–70%, giving better binocular vision than for diurnal birds of prey (overlap 30–50%). The Tawny Owl's retina has about 56,000 light-sensitive rods per square millimetre (36 million per square inch); although earlier claims that it could see in the infrared part of the spectrum have been dismissed.



Each owl's retina has a single fovea

Adaptations to night vision include the large size of the eye, its tubular shape, large numbers of closely packed retinal rods, and an absence of cones, since colour vision is unnecessary at night. There are few coloured oil drops, which would reduce the light intensity, but the retina contains a reflective layer, the tapetum lucidum. This increases the amount of light each photosensitive cell receives, allowing the bird to see better in low light conditions. Owls normally have only one fovea, and that is poorly developed except in diurnal hunters like the Short-eared Owl.

Besides owls, bat hawks, frogmouths and nightjars also display good night vision. Some bird species nest deep in cave systems which are too dark for vision, and find their way to the nest with a simple form of echolocation. The Oilbird is the only nocturnal bird to echolocate, but several *Aerodramus* swiftlets also utilise this technique, with one species, Atiu Swiftlet, also using echolocation outside its caves.

Water birds

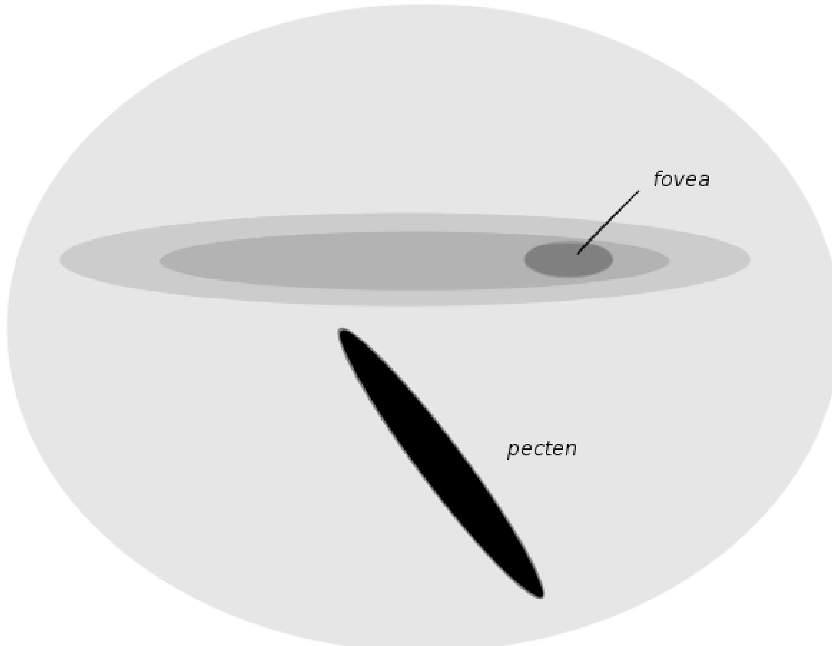
Terns have coloured oil droplets in the cones of the eye to improve distance vision

Seabirds such as terns and gulls that feed at the surface or plunge for food have red oil droplets in the cones of their retinas. This improves contrast and sharpens distance vision, especially in hazy conditions. Birds that have to look through an air/water interface have more deeply coloured carotenoid pigments in the oil drops than other species.

This helps them to locate shoals of fish, although it is uncertain whether they are sighting the phytoplankton on which the fish feed, or other feeding birds.

Birds that fish by stealth from above the water have to correct for refraction particularly when the fish are observed at an angle. Reef Herons and Little Egrets appear to be able to make the corrections needed when capturing fish and are more successful in catching fish when strikes are made at an acute angle and this higher success may be due to the inability of the fish to detect their predators.

Birds that pursue fish under water like auks and divers have far fewer red oil droplets, but they have special flexible lenses and use the nictitating membrane as an additional lens. This allows greater optical accommodation for good vision in air and water. Cormorants have a greater range of visual accommodation, at 50 dioptres, than any other bird, but the kingfishers are considered to have the best all-round (air and water) vision.



Each retina of the Manx Shearwater has one fovea and an elongated strip of high photoreceptor density

Tubenosed seabirds, which come ashore only to breed and spend most of their life wandering close to the surface of the oceans, have a long narrow area of visual sensitivity on the retina This region, the *area giganto cellularis*, has been found in the Manx Shearwater, Kerguelen Petrel, Great Shearwater, Broad-billed Prion and Common Diving-petrel. It is characterised by the presence of ganglion cells which are regularly arrayed and larger than those found in the rest of the retina, and morphologically appear similar to the cells of the retina in cats. The location and cellular morphology of this novel area suggests a function in the detection of items in a small binocular field projecting below and around the bill. It is not concerned primarily with high spatial resolution, but may assist in the detection of prey near the sea surface as a bird flies low over it.

The Manx Shearwater, like many other seabirds, visits its breeding colonies at night to reduce the chances of attack by aerial predators. Two aspects of its optical structure suggest that the eye of this species is adapted to vision at night. In the shearwater's eyes the lens does most of the bending of light necessary to produce a focused image on the retina. The cornea, the outer covering of the eye, is relative flat and so of low refractive power. In a diurnal bird like the pigeon, the reverse is true; the cornea is highly curved and is the principal refractive component. The ration of refraction by the lens to that by the cornea is 1.6 for the shearwater and 0.4 for the pigeon; the figure for the shearwater is consistent with that for a range of different nocturnal bird and mammal.

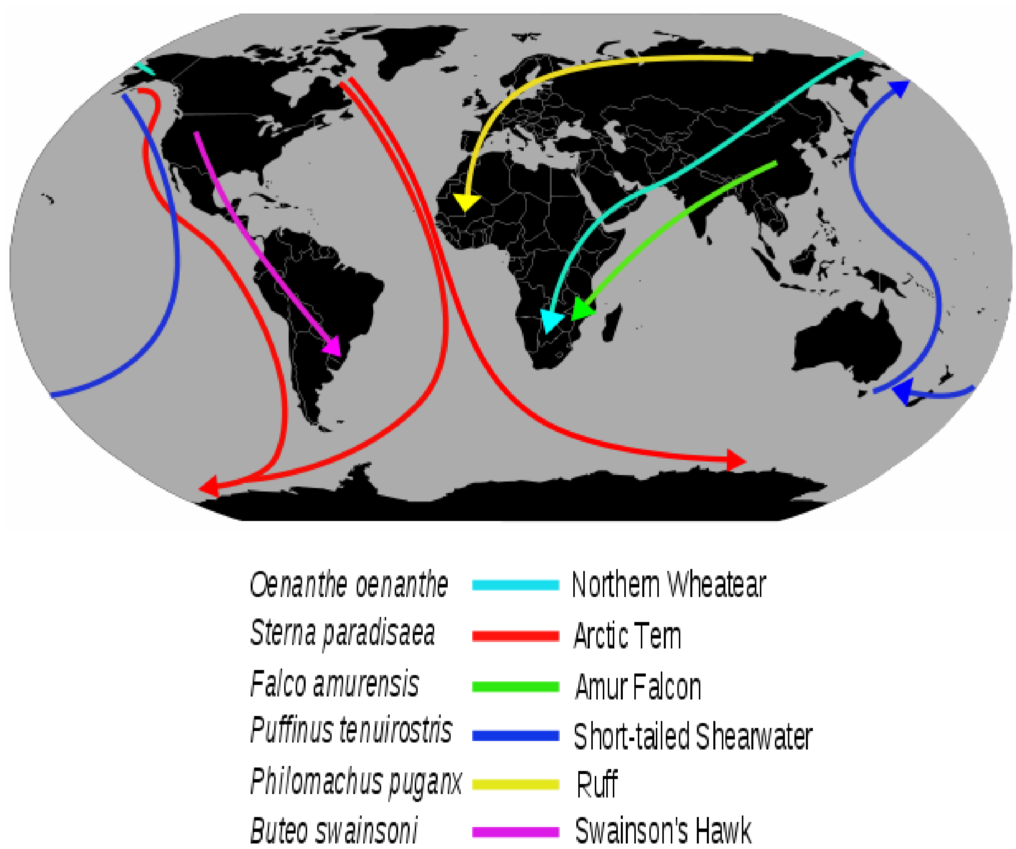
The shorter focal length of shearwater eyes give them a smaller, but brighter, image than is the case for pigeons, so the latter has sharper daytime vision. Although the Manx Shearwater has adaptations for night vision, the effect is small, and it is likely that these birds also use smell and hearing to locate their nests.

It used to be thought that penguins were short-sighted on land. Although the cornea is flat and adapted to swimming underwater, the lens is very strong and can compensate for the reduced corneal focusing when out of water. Almost the opposite solution is used by the Hooded Merganser which can bulge part of the lens through the iris when submerged.

Chapter- 7

Bird Migration

A flock of Barnacle Geese during autumn migration



Some migration routes

Bird migration is the regular seasonal journey undertaken by many species of birds. Bird movements include those made in response to changes in food availability, habitat or weather. Sometimes, journeys are not termed "true migration" because they are irregular (nomadism, invasions, irruptions) or in only one direction (dispersal, movement of young away from natal area). Migration is marked by its annual seasonality. In contrast, birds that are non-migratory are said to be resident or sedentary. Approximately 1800 of the world's 10,000 bird species are long-distance migrants.

General patterns

Many bird populations migrate long distances along a flyway. The most common pattern involves flying north in the spring to breed in the temperate or Arctic summer and returning in the fall to wintering grounds in warmer regions to the south. Of course, in the Southern Hemisphere the directions are reversed, but there is less land area in the far South to support long-distance migration.

The primary motivation for migration appears to be food; for example, some hummingbirds choose not to migrate if fed through the winter. Also, the longer days of the northern summer provide extended time for breeding birds to feed their young. This helps diurnal birds to produce larger clutches than related non-migratory species that remain in the tropics. As the days shorten in autumn, the birds return to warmer regions where the available food supply varies little with the season.

These advantages offset the high stress, physical exertion costs, and other risks of the migration such as predation. Predation can be heightened during migration: the Eleonora's Falcon, which breeds on Mediterranean islands, has a very late breeding season, coordinated with the autumn passage of southbound passerine migrants, which it feeds to its young. A similar strategy is adopted by the Greater Noctule bat, which preys on nocturnal passerine migrants. The higher concentrations of migrating birds at stopover sites make them prone to parasites and pathogens, which require a heightened immune response.

Within a species not all populations may be migratory; this is known as "partial migration". Partial migration is very common in the southern continents; in Australia, 44% of non-passerine birds and 32% of passerine species are partially migratory. In some species, the population at higher latitudes tends to be migratory and will often winter at lower latitude. The migrating birds bypass the latitudes where other populations may be sedentary, where suitable wintering habitats may already be occupied.

This is an example of *leap-frog migration*. Many fully-migratory species show leap-frog migration (birds that nest further North spend the winter further South), and many show the alternative, "chain migration" where populations 'slide' more evenly North and South without reversing order.

Within a population, it is common for different ages and/or sexes to have different patterns of timing and distance. Only the female Chaffinches in Scandinavia migrate, with the males staying resident. This has given rise to the latter's specific name of *coelebs*, a bachelor.

Most migrations begin with the birds starting off in a broad front. Often, this front narrows into one or more preferred routes termed flyways. These routes typically follow mountain ranges or coastlines, sometimes rivers, and may take advantage of updrafts and other wind patterns or avoid geographical barriers such as large stretches of open water. The specific routes may be genetically programmed or learned to varying degrees. The routes taken on forward and return migration are often different. A common pattern in North America is clockwise migration, where birds flying North tend to be further West, and flying South tend to shift Eastwards.

Many, if not most, birds migrate in flocks. For larger birds, flying in flocks reduces the energy cost. Geese in a V-formation may conserve 12–20 % of the energy they would need to fly alone. Red Knots *Calidris canutus* and Dunlins *Calidris alpina* were found in radar studies to fly 5 km per hour faster in flocks than when they were flying alone.

Birds fly at varying altitudes during migration. An expedition to Mt. Everest found skeletons of Pintail and Black-tailed Godwit at 5000 m (16,400 ft) on the Khumbu Glacier. Bar-headed Geese have been seen flying over the highest peaks of the Himalayas above 8000 m (29000 ft) even when low passes of 3000 m (10000 ft) were nearby. Seabirds fly low over water but gain altitude when crossing land, and the reverse pattern is seen in landbirds. However most bird migration is in the range of 150 m (500 ft) to 600 m (2000 ft). Bird-hit aviation records from the United States show most collisions occur below 600 m (2000 ft) and almost none above 1800 m (6000 ft).

Bird migration is not limited to birds that can fly. Most species of penguin migrate by swimming. These routes can cover over 1000 km. Blue Grouse *Dendragapus obscurus* perform altitudinal migration mostly by walking. Emus in Australia have been observed to undertake long-distance movements on foot during droughts.

Historical views

The earliest recorded observations of bird migration were 3000 years ago, as noted by Hesiod, Homer, Herodotus, Aristotle and others. The Bible also notes migrations, as in the Book of Job (39:26), where the inquiry is made: "Doth the hawk fly by Thy wisdom and stretch her wings toward the south?" The author of Jeremiah (8:7) wrote: "The stork in the heavens knoweth her appointed time; and the turtledove, and the crane, and the swallow, observe the time of their coming."

Aristotle noted that cranes traveled from the steppes of Scythia to marshes at the headwaters of the Nile. Pliny the Elder, in his *Historia Naturalis*, repeats Aristotle's observations. Aristotle however suggested that swallows and other birds hibernated. This belief persisted as late as 1878, when Elliott Coues listed the titles of no less than 182 papers dealing with the hibernation of swallows. It was not until early in the nineteenth century that migration as an explanation for the winter disappearance of birds from northern climes was accepted.

Long-distance migration

Swainson's Thrush

Northern Pintail

The typical image of migration is of northern landbirds, such as swallows and birds of prey, making long flights to the tropics. Many northern-breeding ducks, geese and swans are also long-distance migrants, but need only to move from their Arctic breeding grounds far enough south to escape frozen waters. Most Holarctic wildfowl species remain in the Northern Hemisphere, but in countries with milder climates. For example, the pink-footed goose migrates from Iceland to Britain and neighbouring countries. Migratory routes and wintering grounds are traditional and learned by young during their first migration with their parents. Some ducks, such as the Garganey, move completely or partially into the tropics.

The same considerations about barriers and detours that apply to long-distance land-bird migration apply to water birds, but in reverse: a large area of land without bodies of water that offer feeding sites is a barrier to a water bird. Open sea may also be a barrier to a bird that feeds in coastal waters. Detours avoiding such barriers are observed: for example, Brent Geese migrating from the Taymyr Peninsula to the Wadden Sea travel via the White Sea coast and the Baltic Sea rather than directly across the Arctic Ocean and northern Scandinavia.

Bar-tailed Godwit

A similar situation occurs with waders (called "shorebirds" in North America). Many species, such as Dunlin and Western Sandpiper, undertake long movements from their Arctic breeding grounds to warmer locations in the same hemisphere, but others such as Semipalmated Sandpiper travel longer distances to the tropics in the Southern Hemisphere. Like the large and powerful wildfowl, the waders are strong fliers. This means that birds wintering in temperate regions have the capacity to make further shorter movements in the event of particularly inclement weather.

For some species of waders, migration success depends on the availability of certain key food resources at stopover points along the migration route. This gives the migrants an opportunity to "refuel" for the next leg of the voyage. Some examples of important stopover locations are the Bay of Fundy and Delaware Bay.

Some Bar-tailed Godwits have the longest known non-stop flight of any migrant, flying 11,000 km from Alaska to their New Zealand non-breeding areas. Prior to migration, 55 percent of their bodyweight is stored fat to fuel this uninterrupted journey.

Arctic Terns

Seabird migration is similar in pattern to those of the waders and waterfowl. Some, such as the Black Guillemot and some gulls, are quite sedentary; others, such as most terns and auks breeding in the temperate northern hemisphere, move varying distances south in winter. The Arctic Tern has the longest-distance migration of any bird, and sees more daylight than any other, moving from its Arctic breeding grounds to the Antarctic non-breeding areas. One Arctic Tern, ringed (banded) as a chick on the Farne Islands off the British east coast, reached Melbourne, Australia in just three months from fledging, a sea journey of over 22,000 km (14,000 miles). A few seabirds, such as Wilson's Petrel and Great Shearwater, breed in the southern hemisphere and migrate north in the southern winter. Seabirds have the additional advantage of being able to feed during migration over open waters.

The most pelagic species, mainly in the 'tubenose' order Procellariiformes, are great wanderers, and the albatrosses of the southern oceans may circle the globe as they ride the "roaring forties" outside the breeding season. The tubenoses spread widely over large areas of open ocean, but congregate when food becomes available. Many are also among the longest-distance migrants; Sooty Shearwaters nesting on the Falkland Islands migrate 14,000 km (9,000 miles) between the breeding colony and the North Atlantic Ocean off Norway. Some Manx Shearwaters do this same journey in reverse. As they are long-lived birds, they may cover enormous distances during their lives; one record-breaking Manx Shearwater is calculated to have flown 8 million km (5 million miles) during its over-50 year lifespan.

Griffon Vulture soaring

Some large broad-winged birds rely on thermal columns of rising hot air to enable them to soar. These include many birds of prey such as vultures, eagles, and buzzards, but also storks. These birds migrate in the daytime. Migratory species in these groups have great difficulty crossing large bodies of water, since thermals only form over land, and these birds cannot maintain active flight for long distances. The Mediterranean and other seas present a major obstacle to soaring birds, which must cross at the narrowest points. Massive numbers of large raptors and storks pass through areas such as Gibraltar, Falsterbo, and the Bosphorus at migration times. More common species, such as the Honey Buzzard, can be counted in hundreds of thousands in autumn. Other barriers, such as mountain ranges, can also cause funnelling, particularly of large diurnal migrants. This is a notable factor in the Central American migratory bottleneck.

Ruby-throated Hummingbird

Many of the smaller insectivorous birds including the warblers, hummingbirds and flycatchers migrate large distances, usually at night. They land in the morning and may feed for a few days before resuming their migration. The birds are referred to as *passage migrants* in the regions where they occur for short durations between the origin and destination.

Nocturnal migrants minimize predation, avoid overheating, and feed during the day. One cost of nocturnal migration is the loss of sleep. Migrants may be able to alter their quality of sleep to compensate for the loss.

Short-distance and altitudinal migration

Cedar Waxwing

Many long-distance migrants appear to be genetically programmed to respond to changing day length. Species that move short distances, however, may not need such a timing mechanism, and may move in response to local weather conditions.

Thus mountain and moorland breeders, such as Wallcreeper and White-throated Dipper, may move only altitudinally to escape the cold higher ground. Other species such as Merlin and Skylark will move further to the coast or to a more southerly region. Species like the Chaffinch are not migratory in Britain, but will move south or to Ireland in very cold weather.

Short-distance passerine migrants have two evolutionary origins. Those that have long-distance migrants in the same family, such as the Chiffchaff, are species of southern hemisphere origins that have progressively shortened their return migration to stay in the northern hemisphere.

Species that have no long-distance migratory relatives, such as the waxwings, are effectively moving in response to winter weather, rather than enhanced breeding opportunities.

Woodland Kingfisher

In the tropics there is little variation in the length of day throughout the year, and it is always warm enough for a food supply (although because of competition, there may not be enough food for every bird). Migration within the tropics has been far less studied than in the temperate zones. It was once assumed that tropical birds were mostly sedentary; however, altitudinal migration and other within-tropics movements appear to be surprisingly common. Many tropical regions have wet and dry seasons, inducing some birds to migrate or wander widely to find food. Indeed, the monsoons of India are preceded by the arrival of the Jacobin Cuckoo, the "harbinger of the monsoon". Other examples include the Woodland Kingfisher of west Africa and many Australian birds.

There are a few species, notably cuckoos, which are genuine long-distance migrants within the tropics. An example is the Lesser Cuckoo, which breeds in India and spends the non-breeding season in Africa. Such examples help make the case that food supplies, not weather per se, drive migration patterns.

Altitudinal migration is common on mountains worldwide, such as in the Himalayas and the Andes. Quite often, altitudinal migration is combined with distance migration; for example, the Himalayan Kashmir Flycatcher and Pied Thrush both move as far south as the highlands of Sri Lanka. Altitudinal migration may even be important to birds living on relatively small islands, such as the Hawaiian Islands, which have high mountains.

Irruptions and dispersal

Sometimes circumstances such as a good breeding season followed by a food source failure the following year lead to irruptions in which large numbers of a species move far beyond the normal range. Bohemian Waxwing and Common Crossbills show this unpredictable variation in annual numbers.

The temperate zones of the southern continents have extensive arid areas, particularly in Australia and western southern Africa, and weather-driven movements are common but not always predictable. A couple of weeks of heavy rain in one part or another of the usually dry centre of Australia, for example, causes dramatic plant and invertebrate growth, attracting birds from all directions. This can happen at any time of year, and, in any given area, may not happen again for a decade or more, depending on the frequency of El Niño and La Niña periods.

Rainbow Bee-eater

Bird migration is primarily, but not entirely, a Northern Hemisphere phenomenon. In the Southern Hemisphere, seasonal migration tends to be much less obvious. There are several reasons for this.

First, the largely uninterrupted expanses of land mass or ocean tend not to funnel migrations into narrow and obvious pathways, making them less obvious to the human observer. Second, at least for terrestrial birds, climatic regions tend to fade into one another over a long distance rather than be entirely separate: this means that rather than make long trips over unsuitable habitat to reach particular destinations, migrant species can usually travel at a relaxed pace, feeding as they go. Short of banding studies it is often not obvious that the birds seen in any particular locality as the seasons change are in fact different members of the same species passing through, gradually working their way north or south.

Many species do in fact breed in the temperate southern hemisphere regions and winter further north in the tropics. The southern African Greater Striped Swallow, and the Australian Satin Flycatcher, Dollarbird, and Rainbow Bee-eater for example, winters well north of their breeding range.

Physiology and control

The control of migration, its timing and response are genetically controlled and appear to be a primitive trait that is present even in non-migratory species of birds. The ability to navigate and orient themselves during migration is a much more complex phenomenon that may include both endogenous programs as well as learning.

Timing

The primary physiological cue for migration are the changes in the day length. These changes are also related to hormonal changes in the birds.

In the period before migration, many birds display higher activity or Zugunruhe (German: *migratory restlessness*) as well as physiological changes such as increased fat deposition. The occurrence of Zugunruhe even in cage-raised birds with no environmental cues (e.g. shortening of day and falling temperature) has pointed to the role of circannual endogenous programs in controlling bird migrations. Caged birds display a preferential flight direction that corresponds with the migratory direction they would take in nature, even changing their preferential direction at roughly the same time their wild conspecifics change course.

In species where there is polygyny and with considerable sexual dimorphism, there is a tendency for males to return earlier to the breeding sites than their females. This is termed as protandry.

Orientation and navigation

The routes of satellite tagged Bar-tailed Godwits migrating north from New Zealand. This species has the longest known non-stop migration of any species, up to 10,200 km (6,300 mi).

Navigation is based on a variety of senses. Many birds have been shown to use a sun compass. Using the sun for direction involves the need for making compensation based on the time. Navigation has also been shown to be based on a combination of other abilities including the ability to detect magnetic fields (magnetoception), use visual landmarks as well as olfactory cues.

Long distance migrants are believed to disperse as young birds and form attachments to potential breeding sites and to favourite wintering sites. Once the site attachment is made they show high site-fidelity, visiting the same wintering sites year after year.

The ability of birds to navigate during migrations cannot be fully explained by endogenous programming, even with the help of responses to environmental cues. The ability to successfully perform long-distance migrations can probably only be fully explained with an accounting for the cognitive ability of the birds to recognize habitats and form mental maps. Satellite tracking of day migrating raptors such as Ospreys and Honey Buzzards has shown that older individuals are better at making corrections for wind drift.

As the circannual patterns indicate, there is a strong genetic component to migration in terms of timing and route, but this may be modified by environmental influences. An interesting example where a change of migration route has occurred because of such a geographical barrier is the trend for some Blackcaps in central Europe to migrate west and winter in Britain rather than cross the Alps.

Migratory birds may use two electromagnetic tools to find their destinations: one that is entirely innate and another that relies on experience. A young bird on its first migration flies in the correct direction according to the Earth's magnetic field, but does not know how far the journey will be. It does this through a radical pair mechanism whereby chemical reactions in special photo pigments sensitive to long wavelengths are affected by the field. Note that although this only works during daylight hours, it does not use the position of the sun in any way. At this stage the bird is similar to a boy scout with a compass but no map, until it grows accustomed to the journey and can put its other facilities to use. With experience they learn various landmarks and this "mapping" is done by magnetites in the trigeminal system, which tell the bird how strong the field is. Because birds migrate between northern and southern regions, the magnetic field strengths at different latitudes let it interpret the radical pair mechanism more accurately and let it know when it has reached its destination. More recent research has found a neural connection between the eye and "Cluster N", the part of the forebrain that is active during migrational orientation, suggesting that birds may actually be able to *see* the magnetic field of the earth.

Vagrancy

Migrating birds can lose their way and occur outside their normal ranges. These can be due to flying past their destinations as in the "spring overshoot" in which birds returning to their breeding areas overshoot and end up further north than intended. Reverse migration, where the genetic programming of young birds fails to work properly, can lead to great rarities turning up as vagrants thousands of kilometres out of range. Certain areas, because of their location, have become famous as watchpoints for migrating birds. Examples are the Point Pelee National Park in Canada, and Spurn in England. Drift migration of birds blown off course by the wind can result in "falls" of large numbers of migrants at coastal sites.

Migration conditioning

It has been possible to teach a migration route to a flock of birds, for example in re-introduction schemes. After a trial with Canada Geese, microlight aircraft were used in the US to teach safe migration routes to reintroduced Whooping Cranes.

Adaptations

Birds need to alter their metabolism in order to meet the demands of migration. The storage of energy through the accumulation of fat and the control of sleep in nocturnal migrants require special physiological adaptations. In addition, the feathers of a bird suffer from wear-and-tear and require to be molted. The timing of this molt - usually once a year but sometimes two - varies with some species molting prior to moving to their winter grounds and others molting prior to returning to their breeding grounds. Apart from physiological adaptations, migration sometimes requires behavioural changes such as flying in flocks to reduce the energy used in migration or the risk of predation.

Evolutionary and ecological factors

Whether a particular species migrates depends on a number of factors. The climate of the breeding area is important, and few species can cope with the harsh winters of inland Canada or northern Eurasia. Thus the partially migratory Blackbird *Turdus merula* is migratory in Scandinavia, but not in the milder climate of southern Europe. The nature of the staple food is also significant. Most specialist insect eaters outside the tropics are long-distance migrants, and have little choice but to head south in winter.

Sometimes the factors are finely balanced. The Whinchat *Saxicola rubetra* of Europe and the Siberian Stonechat *Saxicola maura* of Asia are long-distance migrants wintering in the tropics, whereas their close relative, the European Stonechat *Saxicola rubicola* is a resident bird in most of its range, and moves only short distances from the colder north and east. A possible factor here is that the resident species can often raise an extra brood.

Recent research suggests that long-distance passerine migrants are of South American and African, rather than northern hemisphere, evolutionary origins. They are effectively southern species coming north to breed rather than northern species going south to winter.

Theoretical analyses, summarized by Alerstam (2001), show that detours that increase flight distance by up to 20% will often be adaptive on aerodynamic grounds - a bird that loads itself with food to cross a long barrier flies less efficiently. However some species show circuitous migratory routes that reflect historical range expansions and are far from optimal in ecological terms. An example is the migration of continental populations of Swainson's Thrush, which fly far east across North America before turning south via Florida to reach northern South America; this route is believed to be the consequence of a range expansion that occurred about 10,000 years ago. Detours may also be caused by differential wind conditions, predation risk, or other factors.

Climate change

Large scale climatic changes, as have been experienced in the past, are expected to have an effect on the timing of migration. Studies have shown a variety of effects including timing changes in migration, breeding as well as population variations.

Ecological effects

The migration of birds also aids the movement of other species, including those of ectoparasites such as ticks and lice, which in turn may carry micro-organisms including those of concern to human health. Considerable interest has been taken due to the global spread of avian influenza, however migrant birds have not been found to be a special risk, with import of pet and domestic birds being a greater threat. Some viruses that are maintained in birds without lethal effects, such as the West Nile Virus may however be spread by migrating birds. Birds may also have a role in the dispersal of propagules of plants and plankton.

Some predators take advantage of the concentration of birds during migration. Greater Noctule bats feed on nocturnal migrating passerines. Some birds of prey specialize on migrating waders.

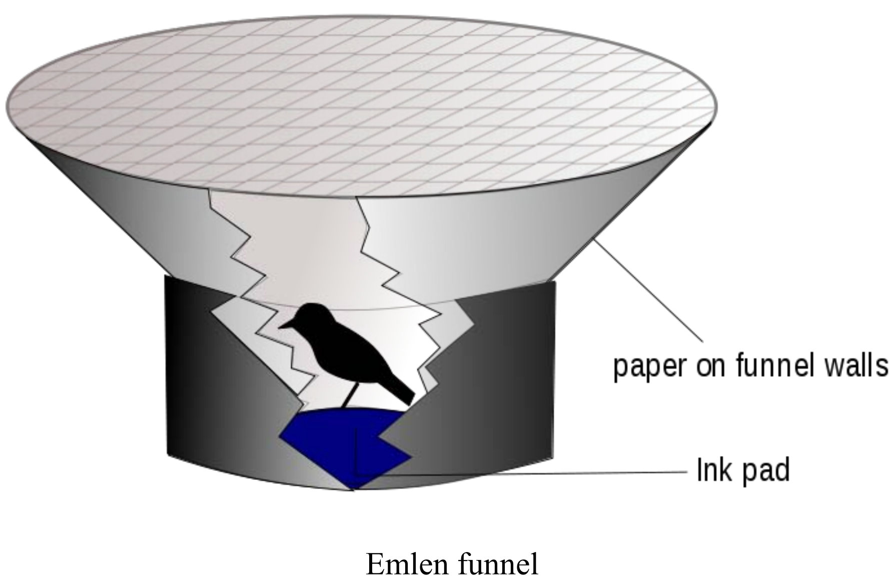
Study techniques

Early studies on the timing of migration began in 1749 in Finland, with Johannes Leche of Turku collecting the dates of arrivals of spring migrants.

Bird migration routes have been studied by a variety of techniques of which ringing is the oldest. Color marking and use of radar, satellite tracking are some of the other techniques.

Stable isotopes of hydrogen, oxygen, carbon, nitrogen, and sulphur have also been used to establish avian migratory connectivity between wintering sites and breeding grounds. Stable isotopic methods to establish migratory linkage rely on spatial isotopic differences in bird diet that are incorporated into inert tissues like feathers, or into growing tissues such as claws and muscle or blood.

An approach to identify migration intensity makes use of upward pointing microphones to record the nocturnal contact calls of flocks flying overhead. These are then analyzed in a laboratory to measure time, frequency and species.



Emlen funnel

An older technique to quantify migration involves observing the face of the moon towards full moon and counting the silhouettes of flocks of birds as they fly at night.

Orientation behaviour studies have been traditionally carried out using variants of a setup known as the **Emlen funnel**, which consists of a circular cage with the top covered by glass or wire-screen so that either the sky is visible or the setup is placed in a planetarium or with other controls on environmental cues. The orientation behaviour of the bird inside the cage is studied quantitatively using the distribution of marks that the bird leaves on the walls of the cage. Other approaches used in pigeon homing studies make use of the direction in which the bird vanishes on the horizon.

Threats and conservation

Human activities have threatened many migratory bird species.The distances involved in bird migration mean that they often cross political boundaries of countries and conservation measures require international cooperation. Several international treaties have been signed to protect migratory species including the Migratory Bird Treaty Act of 1918 of the US and the African-Eurasian Migratory Waterbird Agreement.

The concentration of birds during migration can put species at risk. Some spectacular migrants have already gone extinct, the most notable being the Passenger Pigeon (*Ectopistes migratorius*). During migration the flocks were a mile (1.6 km) wide and 300 miles (500 km) long, taking several days to pass and containing up to a billion birds.

Other significant areas include stop-over sites between the wintering and breeding territories. A capture-recapture study of passerine migrants with high fidelity for breeding and wintering sites did not show similar strict association with stop-over sites.

Hunting along the migratory route can also take a heavy toll. The populations of Siberian Cranes that wintered in India declined due to hunting along the route, particularly in Afghanistan and Central Asia. Birds were last seen in their favourite wintering grounds in Keoladeo National Park in 2002.

Structures such as power lines, wind farms and offshore oil-rigs have also been known to affect migratory birds. Habitat destruction by land use changes is the biggest threat, and shallow wetlands that are stopover and wintering sites for migratory birds are particularly threatened by draining and reclamation for human use.

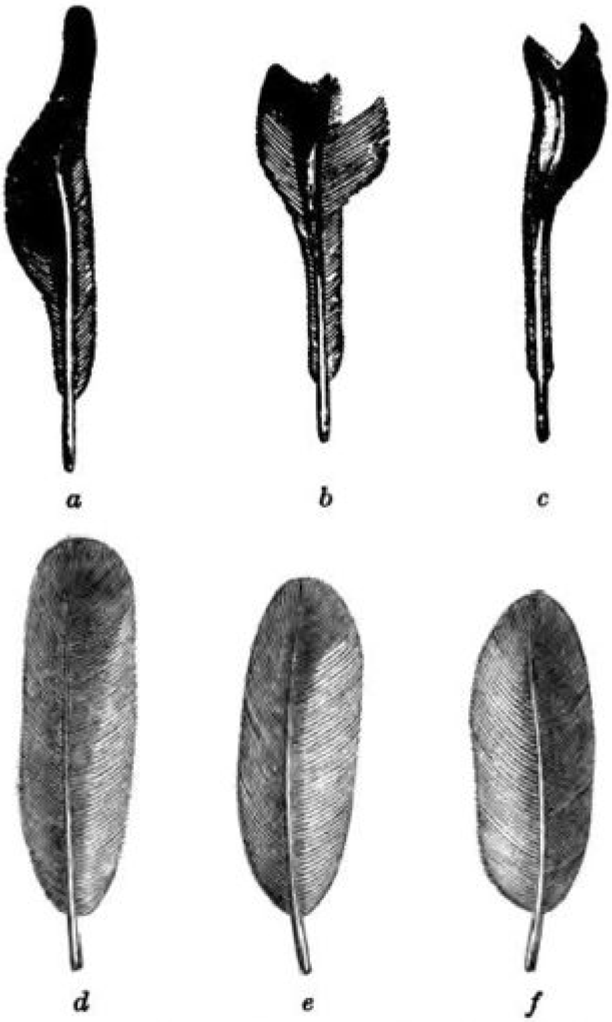
Chapter- 8

Bird Vocalization

A male Blackbird (*Turdus merula*) singing. Bogense havn, Funen, Denmark.

Bird vocalization includes both bird calls and bird songs. In non-technical use, bird songs are the bird sounds that are melodious to the human ear. In ornithology and birding, (relatively complex) songs are distinguished by function from (relatively simple) calls.

Definition



Secondary wing-feathers of *Pipra deliciosa* (from Mr. Sclater, in Proc. Zool. Soc. 1860). The three upper feathers, *a*, *b*, *c*, from the male; the three lower corresponding feathers, *d*, *e*, *f*, from the female.

a. and *d*. Fifth secondary wing-feather of male and female, upper surface. *b* and *e*. Sixth secondary, upper surface. *c* and *f*. Seventh secondary, lower surface.

Wing feathers of a male Club-winged Manakin, with the modifications noted noted by P L Sclater in 1860 and discussed by Charles Darwin in 1871

The distinction between songs and calls is based upon complexity, length, and context. Songs are longer and more complex and are associated with courtship and mating, while calls tend to serve such functions as alarms or keeping members of a flock in contact. Other authorities such as Howell and Webb (1995) make the distinction based on function, so that short vocalizations such as those of pigeons and even non-vocal sounds such as the drumming of woodpeckers and the "winnowing" of snipes' wings in display flight are considered songs. Still others require song to have syllabic diversity and temporal regularity akin to the repetitive and transformative patterns which define music.

It is generally agreed upon in birding and ornithology which sounds are songs and which are calls, and a good field guide will differentiate between the two.

Bird song is best developed in the order Passeriformes. Most song is emitted by male rather than female birds. Song is usually delivered from prominent perches although some species may sing when flying. Some groups are nearly voiceless, producing only percussive and rhythmic sounds, such as the storks, which clatter their bills. In some manakins (Pipridae), the males have evolved several mechanisms for mechanical sound production, including mechanisms for stridulation not unlike those found in some insects.

The production of sounds by mechanical means as opposed to the use of the syrinx has been termed variously *instrumental music* by Charles Darwin, *mechanical sounds* and more recently *sonation*. The term *sonate* has been defined as the act of producing non-vocal sounds that are intentionally modulated communicative signals, produced using non-syringeal structures such as the bill, wings, tail, feet and body feathers.

Anatomy

The avian vocal organ is called the syrinx; it is a bony structure at the bottom of the trachea (unlike the larynx at the top of the mammalian trachea). The syrinx and sometimes a surrounding air sac resonate to sound waves that are made by membranes past which the bird forces air. The bird controls the pitch by changing the tension on the membranes and controls both pitch and volume by changing the force of exhalation. It can control the two sides of the trachea independently, which is how some species can produce two notes at once.

Function

Scientists hypothesize that bird song has evolved through sexual selection, and experiments suggest that the quality of bird song may be a good indicator of fitness. Experiments also suggest that parasites and diseases may directly affect song characteristics such as song rate, which thereby act as reliable indicators of health. The song repertoire also appears to indicate fitness in some species. The ability of male birds to hold and advertise territories using song also demonstrates their fitness.

Communication through bird calls can be between individuals of the same species or even across species. Birds communicate alarm through vocalizations and movements that are specific to the threat, and bird alarms can be understood by other animal species, including other birds, in order to identify and protect against the specific threat. Mobbing calls are used to recruit individuals in an area where an owl or other predator may be present. These calls are characterized by wide frequency spectra, sharp onset and termination, and repetitiveness which are common across species and are believed to be helpful to other potential "mobbers" by being easy to locate. The alarm calls of most species, on the other hand, are characteristically high-pitched making the caller difficult to locate.

Individual birds may be sensitive enough to identify each other through their calls. Many birds that nest in colonies can locate their chicks using their calls. Calls are sometimes distinctive enough for individual identification even by human researchers in ecological studies.

Many birds engage in duet calls. In some cases the duets are so perfectly timed as to appear almost as one call. This kind of calling is termed antiphonal duetting. Such duetting is noted in a wide range of families including quails, bushshrikes, babblers such as the scimitar babblers, some owls and parrots. In territorial songbirds, birds are more likely to countersing when they have been aroused by simulated intrusion into their territory. This implies a role in intraspecies aggressive competition.

Some birds are excellent vocal mimics. In some tropical species, mimics such as the drongos may have a role in the formation of mixed-species foraging flocks. Vocal mimicry can include conspecifics, other species or even man-made sounds. Many hypotheses have been made on the functions of vocal mimicry including suggestions that they may be involved in sexual selection by acting as an indicator of fitness, help brood parasites, protect against predation but strong support is lacking for any function. Many birds, and especially those that nest in cavities, are known to produce a snake like hissing sound that may help deter predators at close range.

Some cave-dwelling species, including Oilbird and Swiftlets (*Collocalia* and *Aerodramus* spp.), use audible sound (with the majority of sonic location occurring between 2 and 5 kHz) to echolocate in the darkness of caves. The only bird known to make use of infrasound (at about 20 Hz) is the western capercaillie.

The hearing range of birds is from below 50 Hz (infrasound) to above 20 kHz (ultrasound) with maximum sensitivity between 1 and 5 kHz. The range of frequencies at which birds call in an environment varies with the quality of habitat and the ambient sounds. It has been suggested that narrow bandwidths, low frequencies, low-frequency modulations, and long elements and inter-element intervals should be found in habitats with complex vegetation structures (which would absorb and muffle sounds) while high frequencies, broad bandwidth, high-frequency modulations (trills), and short elements and inter-elements may be expected in habitats with herbaceous cover. It has been hypothesized that the available frequency range is partitioned and birds call so that overlap between different species in frequency and time is reduced. This idea has been termed the "acoustic niche". Birds sing louder and at a higher pitch in urban areas, where there is ambient low-frequency noise.

Bird Language

The language of the birds has long been a topic for anecdote and speculation. That calls have meanings that are interpreted by their listeners has been well demonstrated. Domestic chickens have distinctive alarm calls for aerial and ground predators, and they respond to these alarm calls appropriately. However a language has, in addition to words, structures and rules. Studies to demonstrate the existence of language have been difficult due to the range of possible interpretations. Research on parrots by Irene Pepperberg is claimed to demonstrate the innate ability for grammatical structures, including the existence of concepts such as nouns, adjectives and verbs. Studies on starling vocalizations have also suggested that they may have recursive structures.

The term "bird language" may also more informally refer to patterns in bird vocalizations that communicate information to other birds or other animals in general. Wilderness Awareness School groups bird vocalizations into 5 different classes, sometimes called "voices," each of which communicates different information. Companion calling is a short vocalization made between mates, parent and young, or members of a flock to maintain contact when out of visual range. Juvenile begging is a strident, loud vocalization often made by young to a parent when begging for food. Intraspecific aggression can consist of loud, alarmed-sounding vocalizations or of energetic song, and may be heard when members of the same species behave aggressively toward each other. Alarm may be heard when birds are startled, frightened, or terrified for their lives, and can take many forms. Mobbing is one example of alarm, while a high-pitched alarm call is another.

Of the 5 voices of the birds, four of them communicate the message that the bird feels safe. Birds that engage in song, companion calling, juvenile begging, and intraspecific aggression all display what Jon Young calls "baseline" behavior, or a relaxed state free of the fear of predation. Alarm communicates the presence of a predator, or an influence that the bird may see as predatory such as a human hiker. Alarms have distinct sounds and shapes, each of which is specific to the source of the disturbance. For example, ravens mobbing a hawk or owl in a tree will clump around the predator in a loose ball, calling and diving. If the ravens rise off the tree and fly higher, the predator was a hawk and has flown up to escape, as is typical of hawks. If the ravens drop out of the tree and fly low and away, the predator was an owl and has dropped low off its perch to escape, as is typical of owls.

Neurophysiology

The main brain areas involved in bird song are:

- Anterior forebrain pathway (vocal learning): composed of the lateral part of the magnocellular nucleus of anterior neostriatum (LMAN), which is a homologue to mammalian basal ganglia); Area X, which is part of the basal ganglia; and the Dorso-Lateral division of the Medial thalamus (DLM).
- Song production pathway: composed of the HVC (sometimes, inaccurately, called the Hyperstriatum Ventralis pars Caudalis); robust nucleus of the arcopallium (RA); and the tracheosyringeal part of the hypoglossal nucleus (nXIIts).

Both pathways show sexual dimorphism, with the male producing song most of the time. It has been noted that injecting testosterone in non-singing female birds can induce growth of the HVC and thus production of song.

Birdsong production is generally thought to start at the nucleus uvaeformis of the thalamus with signals emanating along a pathway that terminates at the syrinx. The pathway from the thalamus leads to the interfacial nucleus of the nidopallium to the HVC, and then to RA, the dorso-lateral division of the medial thalamus and to the tracheosyringeal nerve.

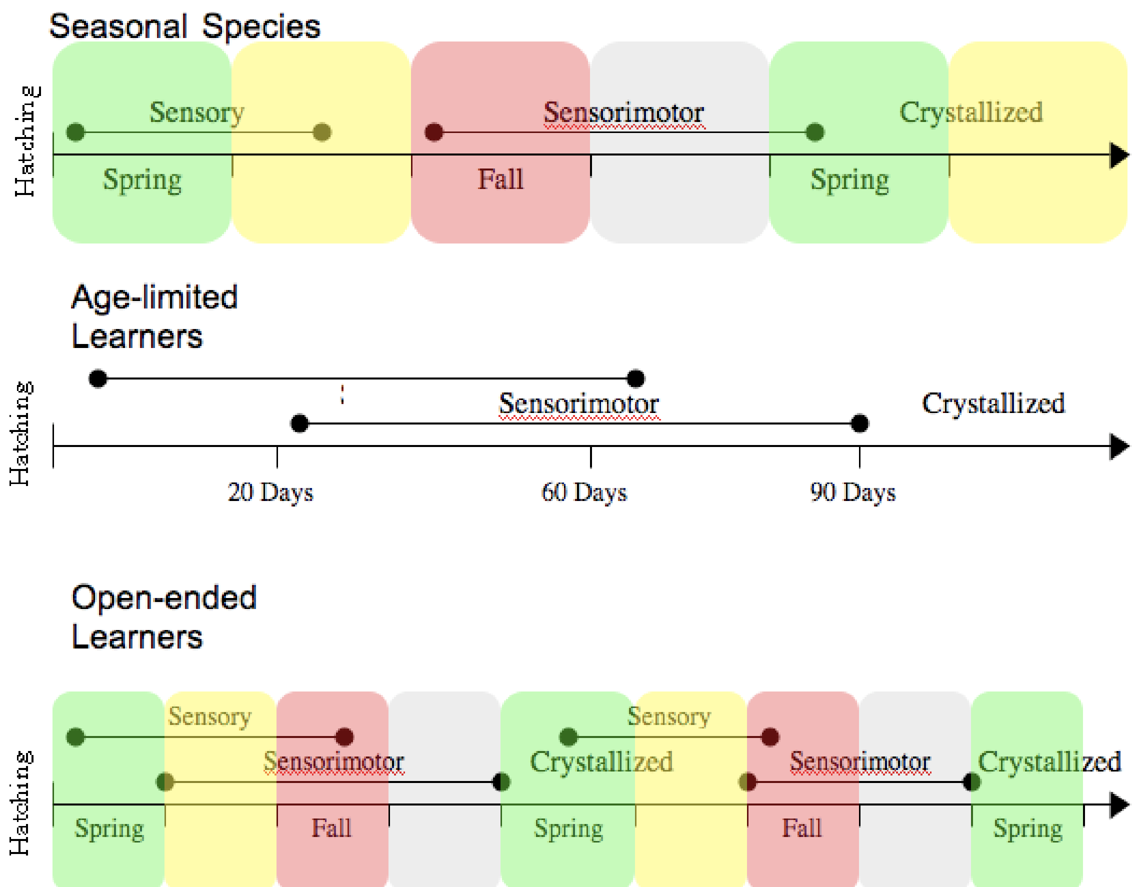
The gene FOXP2, defects of which affect both speech and comprehension of language in humans, becomes more active in the striatal region of songbirds during the time of song learning.

Recent research in birdsong learning has focused on the Ventral Tegmental Area (VTA), which sends a dopamine input to the para-olfactory lobe and Area X, LMAN and the ventrolateral medulla. Other researchers have explored the possibility that HVc is responsible for syllable production, while the robust nucleus of the arcopallium, the primary song output nucleus, may be responsible for syllable sequencing and production of notes within a syllable.

Learning

The songs of different species of birds vary, and are more or less characteristic of the species. In modern-day biology, bird song is typically analysed using acoustic spectroscopy. Species vary greatly in the complexity of their songs and in the number of distinct kinds of song they sing (up to 3000 in the Brown Thrasher); in some species, individuals vary in the same way. In a few species such as starlings and mockingbirds, songs imbed arbitrary elements learned in the individual's lifetime, a form of mimicry (though maybe better called "appropriation" [Ehrlich *et al.*], as the bird does not pass for another species). As early as 1773 it was established that birds learnt calls and cross-fostering experiments were able to force a Linnet *Acanthis cannabina* to learn the song of a skylark *Alauda arvensis*. In many species it appears that although the basic song is the same for all members of the species, young birds learn some details of their songs from their fathers, and these variations build up over generations to form dialects.

Birds learn songs early in life with sub-vocalizations that develop into renditions of adult songs. Zebra Finches, the most popular species for birdsong research, develop a version of a familiar adult's song after 20 or more days from hatch. By around 35 days, the chick will have learned the adult song. The early song is "plastic" or variable and it takes the young bird two or three months to perfect the "crystallized" song (which is less variable) of sexually mature birds.



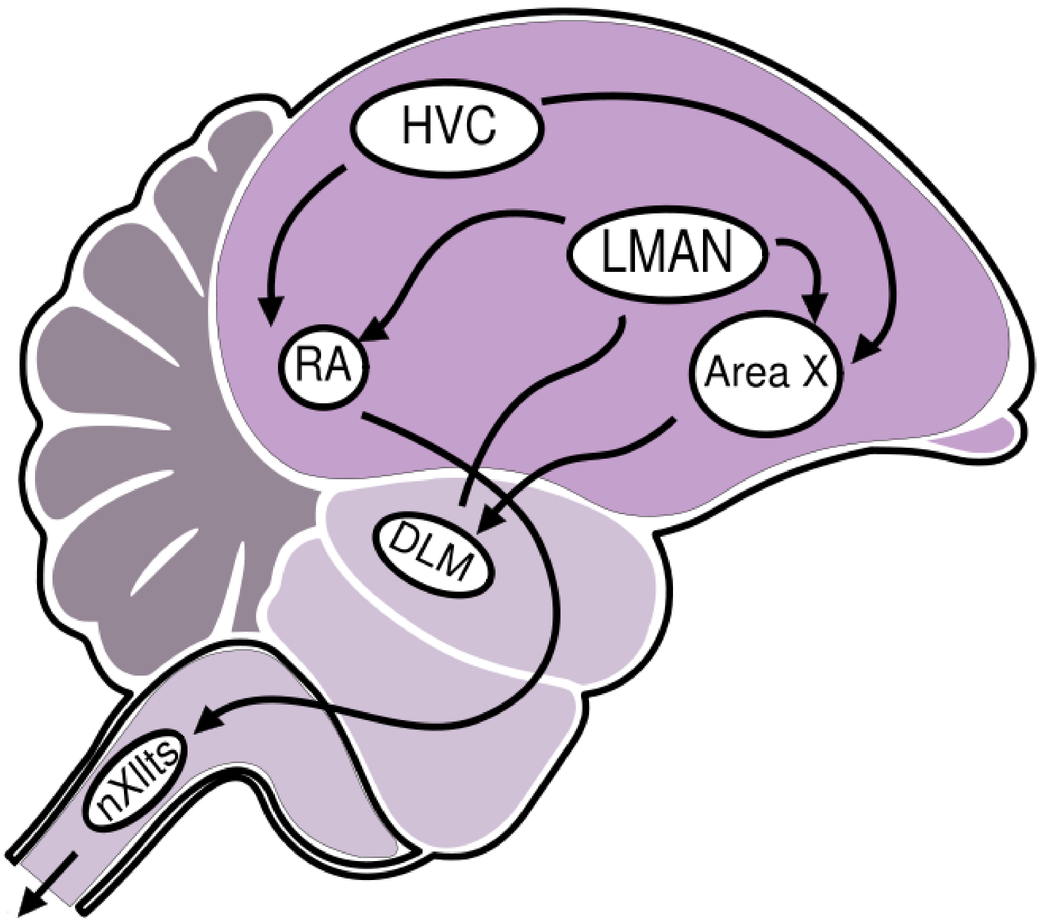
Timeline for song learning in different species. Diagram adapted from Brainard & Doupe, 2002.

Research indicates birds' acquisition of song is a form of motor learning that involves regions of the basal ganglia. Models of bird-song motor learning are sometimes used as models for how humans learn speech. In some species such as zebra finches, learning of song is limited to the first year; they are termed 'age-limited' or 'close-ended' learners. Other species such as the canaries can develop new songs even as sexually mature adults; these are termed 'open-ended' learners.

Researchers have hypothesized that learned songs allow the development of more complex songs through cultural interaction, thus allowing intraspecies dialects that help birds stay with their own kind within a species, and it allows birds to adapt their songs to different acoustic environments.

Auditory feedback in bird song learning

Early experiments by Thorpe in 1954 showed the importance of a bird being able to hear a tutor's song. When birds are raised in isolation, away from the influence of conspecific males, they still sing. While the song they produce resembles the song of a wild bird, it lacks the complexity and sounds distinctly different. The importance of the bird being able to hear himself sing in the sensorimotor period was later discovered by Konishi. Birds deafened before the song crystallization period went on to produce very different songs from the wild type. These findings lead scientists to believe there could be a specific part of the brain dedicated to this specific type of learning.



Song learning pathway in birds (Based on Nottebohm, 2005)

The main focus in the search for the neuronal aspect of bird song learning was guided by the song template hypothesis. This hypothesis is the idea that when a bird is young he memorizes the song of his tutor. Later, during the development phase as an adult, he matches his own trial vocalizations using auditory feedback to an acoustic template in the brain. Based on this information, he adjusts his song if needed. To find this "song template," experimenters lesioned certain parts of the brain and observed the effects.

- Lesioning the song production pathway (RA, xXII or HVc) in the brain creates serious effects on song production in all birds.
- Lesions parts of the anterior forebrain pathway, or vocal learning pathway, DLM and area X, result in deficits in learning in all birds.

- Lesioning LMAN, located in the anterior forebrain pathway in young birds disrupts song production.
- Lesioning LMAN on an adult bird shows no effect.
- Lesioning LMAN on an adult canary (an "open-ended learner" species, which can learn songs later in life) shows a progressive deterioration of song.

These results show that the area known as LMAN is the only brain area in the pathway that shows some plasticity and further studies have shown that this area of the brain responds best to the bird's own song. This neuroplasticity is vital for a bird being able to learn a song. The ability to make small adjustments based on auditory feedback is needed for the complexity of these beautiful songs. Just like any musician, birds need to practice and be able to evaluate what their song sounds like and what it's supposed to sound like in order to get it right.

To complete the picture on bird song learning, experimenters needed to discover the true plasticity of the brain. While deafening and creating auditory isolation were good techniques for discovering basic characteristics about the brain, a reversible procedure was needed to investigate further. The solution was found in disruption of the auditory feedback, or what a bird hears. A computer is able to capture the song of a singing bird and play back portions of its song, or selectively play back a certain syllable while the bird is singing. The computer is basically playing the age old trick of repeating whatever the bird sings, the "stop copying me" game. This creates such a disruption that an adult bird will start to decrystallize its song, which includes a loss of spectral and temporal rigidity characteristic of adult song. It reverts back to the song it started singing with, before any learning took place. Furthermore, when the feedback was stopped, the birds slowly recovered their original song, something that was unheard of. These results show that there is a fair amount of plasticity retained in the brain, even for close-ended learners. This new found plasticity in adult birds and the results on the plasticity of LMAN (shown above) combine into a model for bird song learning (diagram coming soon).

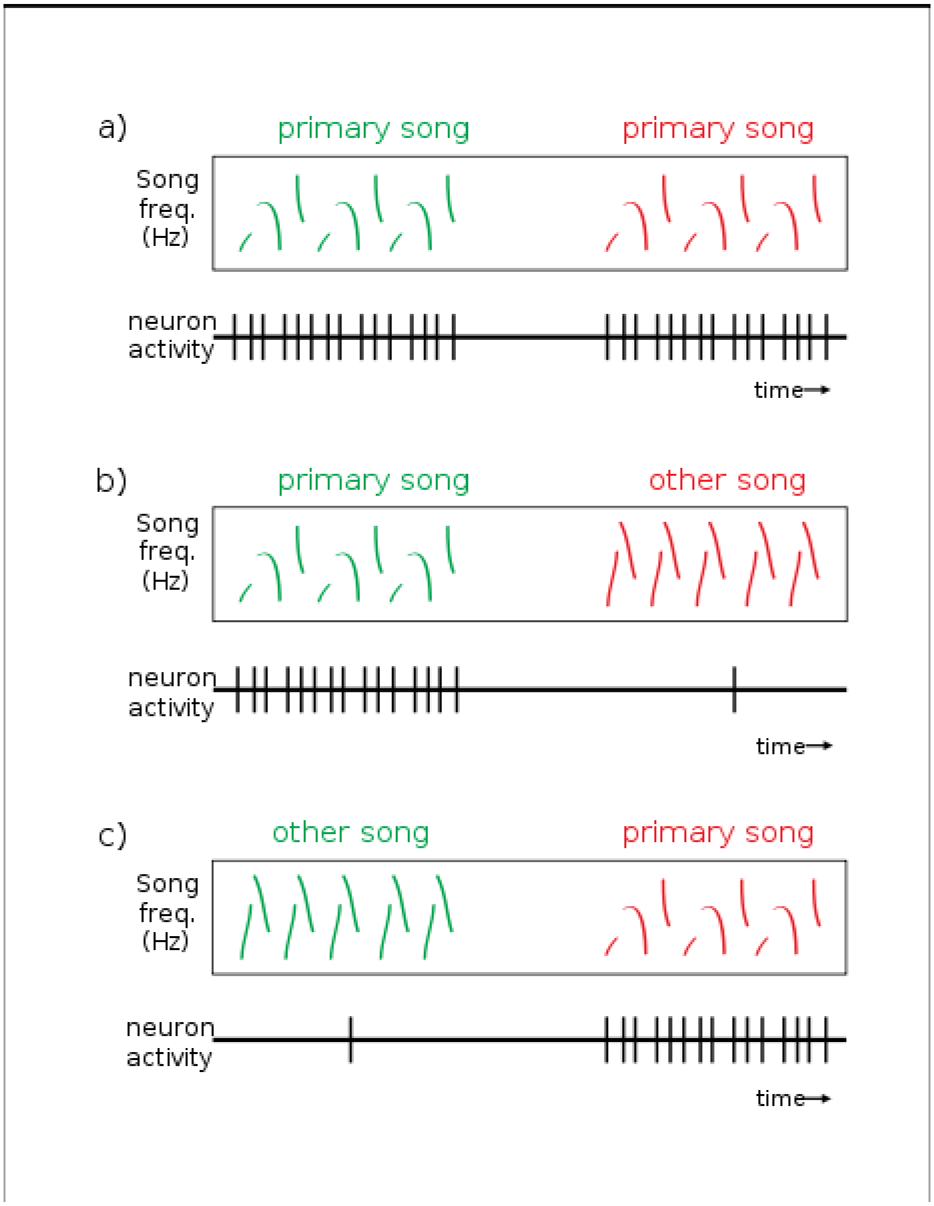
Mirror neurons and vocal learning

A mirror neuron is a neuron that discharges both when an individual performs an action, and when he perceives that same action being performed by another. These neurons were first discovered in macaque monkeys, but recent research suggests that mirror neuron systems may be present in other animals including humans.

Mirror neurons have the following characteristics:

- They are located the premotor cortex
- They exhibit both sensory and motor properties
- They are action-specific – mirror neurons are only active when an individual is performing or observing a certain type of action (e.g.: grasping an object).

Because mirror neurons exhibit both sensory and motor activity, some researchers have suggested that mirror neurons may serve to map sensory experience onto motor structures. This has implications for birdsong learning– many birds rely on auditory feedback to acquire and maintain their songs. Mirror neurons may be mediating this comparison of what the bird hears and what he produces.



Song selectivity in HVCx neurons: neuron activity in response to calls heard (green) and calls produced (red). **a.** Neurons fire when the primary song type is either heard or sung. **b,c.** Neurons do not fire in response to the other song type, regardless of whether it is heard or sung. Sketch based on figure from Prather et al. (2008)

In search of these auditory-motor neurons, Jonathan Prather and other researchers at Duke University recorded the activity of single neurons in the HVCs of swamp sparrows. They discovered that the neurons that project from the HVC to Area X (HVC_X neurons) are highly responsive when the bird is hearing a playback of his own song. These neurons also fire in similar patterns when the bird is singing that same song. Swamp sparrows employ 3-5 different song types, and the neural activity differs depending on which song is heard or sung. The HVC_X neurons only fire in response to the presentation (or singing) of one of the songs, the primary song type. They are also temporally selective, firing at a precise phase in the song syllable.

Because the timing of the neural response is identical regardless of whether the bird was listening or singing, how can we be sure that the bird isn't just hearing himself? Prather et al. found that during the short period of time before and after the bird sings, his HVC_X neurons become insensitive to auditory input. In other words, the bird becomes "deaf" to his own song. This suggests that these neurons are producing a corollary discharge, which would allow for direct comparison of motor output and auditory input. This may be the mechanism underlying learning via auditory feedback.

Overall, the HVC_X auditory-motor neurons in swamp sparrows are very similar to the visual-motor mirror neurons discovered in primates. Like mirror neurons, the HVC_X neurons:

- Are located in a premotor brain area
- Exhibit both sensory and motor properties
- Are action-specific – a response is only triggered by the 'primary song type'

The function of the mirror neuron system is still unclear. Some scientists speculate that mirror neurons may play a role in understanding the actions of others, imitation, theory of mind and language acquisition, though there is currently insufficient neurophysiological evidence in support of these theories. Specifically regarding birds, it is possible that the mirror neuron system serves as a general mechanism underlying vocal learning, but further research is needed. In addition to the implications for song learning, the mirror neuron system could also play a role in territorial behaviors such as song-type matching and countersinging.

Identification and systematics

The specificity of bird calls has been used extensively for species identification. The calls of birds have been described using words or nonsense syllables, or line diagrams. Common terms in English include words such as *quack*, *chirp* and *chirrup*. These are subject to imagination and vary greatly; a well-known example is the White-throated Sparrow's song, given in Canada as *O sweet Canada Canada Canada* and in New England as *Old Sam Peabody Peabody Peabody* (also *Where are you Frederick Frederick Frederick?*). In addition to nonsense words, grammatically correct phrases have been constructed as likenesses of the vocalizations of birds. For example, the Barred

Owl produces a motif which some bird guides describe as *Who cooks for you? Who cooks for you all?* with the emphasis placed on *you*.

The use of spectrograms to visualize bird song was first introduced by W. H. Thorpe. These visual representations are also called sonograms or sonagrams. Some recent field guides for birds use sonograms to document the calls and songs of birds. The sonogram is objective, unlike descriptive phrases, but proper interpretation requires experience. Sonograms can also be roughly converted back into sound.

Bird song is an integral part of bird courtship and is a pre-zygotic isolation mechanism involved in the process of speciation. Many allopatric sub-species show differences in calls. These differences are sometimes minute, often detectable only in the sonograms. Song differences in addition to other taxonomic attributes have been used in the identification of new species. The use of calls has led to proposals for splitting of species complexes such as those of the *Mirafra* Bushlarks.

Bird song and music

Some musicologists believe that birdsong has had a large influence on the development of music. Although the extent of this influence is impossible to gauge, it is sometimes easy to see some of the specific ways composers have integrated birdsong with music.

There seem to be three general ways musicians or composers can be affected by birdsong: they can be influenced or inspired (consciously or unconsciously) by birdsong, they can include intentional imitations of bird song in a composition, or they can incorporate recordings of birds into their works.

One early example of a composition that imitates birdsong is Janequin's "Le Chant Des Oiseaux", written in the 16th century. Other composers who have quoted birds or have used birdsong as a compositional springboard include Vivaldi (*Spring* from the *Four Seasons*)), Biber (*Sonata Representativa*), Beethoven (*Sixth Symphony*), Wagner (*Siegfried*) and the jazz musicians Paul Winter (*Flyway*) and Jeff Silverbush (*Grandma Mickey*).

The twentieth-century French composer Olivier Messiaen composed with birdsong extensively. His Catalogue d'Oiseaux is a seven-book set of solo piano pieces based upon birdsong. His orchestral piece *Réveil des Oiseaux* is composed almost entirely of birdsong. Many of his other compositions, including *Quatuor pour la fin du temps*, similarly integrate birdsong.

The Italian composer Ottorino Respighi, with his *The Pines of Rome* (1923–1924), may have been the first to compose a piece of music that calls for pre-recorded birdsong. A few years later, Respighi wrote *Gli Uccelli* ("The birds"), based on Baroque pieces imitating birds.

The Finnish composer Einojuhani Rautavaara in 1972 wrote an orchestral piece of music called *Cantus Arcticus* (Opus 61, dubbed *Concerto for Birds and Orchestra*) making extensive use of pre-recorded birdsongs from Arctic regions, such as migrating swans.

The American jazz musician Eric Dolphy sometimes listened to birds while he practiced flute. He claimed to have incorporated bird song into some of his improvisational music.

In the psychedelic era of the 1960s and 1970s, many rock bands included sound effects in their recordings. Birds were a popular choice. The English band Pink Floyd included bird sound effects in many of the songs from their 1969 albums *Soundtrack from the Film More* and *Ummagumma* (for example, Grantchester Meadows). Similarly, the English singer Kate Bush incorporated bird sound effects into much of the music on her 2005 album, Aerial.

The Music hall artist Ronnie Ronalde has gained notoriety for his whistling imitations of birds and for integrating birdsong with human song. His songs 'In A Monastery Garden' and 'If I Were A Blackbird' include imitations of the blackbird, his "signature bird."

The French composer François-Bernard Mâche has been credited with the creation of zoomusicology, the study of the music of animals. His essay *Musique, mythe, nature, ou les Dauphins d'Arion* (1983) includes a study of "ornitho-musicology", in which he speaks of "animal musics" and a longing to connect with nature.

The German DJ, techno music producer and naturalist Dominik Eulberg is an avid bird watcher, and several tracks by him prominently feature sampled bird sounds and even are titled after his favourite specimens.

The productions of The Jewelled Antler Collective often use field recordings featuring birdsong.

In 2007, The CT Collective issed two free albums devoted to music made using bird songs (one with human interaction, one without). The project was co-ordinated by looping musician Nick Robinson

Bird song and poetry

Bird song is a popular subject in poetry. Famous poems inspired by bird song include Percy Bysshe Shelley's To a Skylark ("Hail to thee, blithe Spirit!/Bird thou never wert") and Gerard Manley Hopkins' Sea and Skylark. Birdsongs and their relations to Middle-earth inhabitants are a common motif in J. R. R. Tolkien's literary work. The Grateful Dead performed a song called "Bird Song" that Jerry Garcia wrote and dedicated to Janis Joplin.

Chapter- 9

Bird Nest

Deep cup nest of the Great Reed-warbler

A **bird nest** is the spot in which a bird lays and incubates its eggs and raises its young. Although the term is popular in reference to a specific structure made by the bird itself—such as the grassy cup nest of the American Robin or Eurasian Blackbird, or the elaborately woven hanging nest of the Montezuma Oropendola, the Village Weaver or the Red-browed Pardalote—that is too restrictive a definition. For some species, a nest is simply a shallow depression made in sand; for others, it is the knot-hole left by a broken branch, a burrow dug into the ground, a chamber drilled into a tree, an enormous rotting pile of vegetation and earth, or a mud dome with an entrance tunnel. Some species of cave swiftlets of the genus *Collocalia* make their nests entirely from their saliva, which dries and hardens to form a bracket on the cave wall into which the birds lay their eggs. The smallest bird nests are those of some hummingbirds, tiny cups which can be a mere 2 cm (less than one inch) across and 2–3 cm (about one inch) high. At the other extreme, some nest mounds built by the Dusky Scrubfowl measure more than 11 m (34 ft) in diameter and stand nearly 5 m (15 ft) tall. Although nests are primarily used for breeding they may also be reused in the non-breeding season for roosting and some species build special *dormitory nests* or *roost nests* (or *winter-nest*) that are used only for roosting.

Nests are built each year in most species but some birds refurbish their old nests. The large **eyries** (or **aeries**) of some eagles are platform nests that have been used and refurbished for several years.

In yet another extreme, brood parasites have evolved to manipulate and use host individuals either of the same or different species to raise the young of the brood-parasite, which relieves the parasitic parent from the building of nests and the investment of rearing young.

In most species, the female does all or most of the nest construction, though the male often helps. In some polygynous species, however, the male may do most or all of the nest building. The nest may also form a part of their courtship display such as in bowerbirds and weaver birds. The ability to choose and maintain good nest sites and build high quality nests may be selected for by females in these species. In some species the young from previous broods may also act as helpers for the adults.

Nest types

Thick-billed Murres lay their single eggs directly onto rock ledges.

Not every bird species builds or uses a nest. Some auks, for instance—including Common Murre, Thick-billed Murre and Razorbill—lay their eggs directly onto the narrow rocky ledges they use as breeding sites. The eggs of these species are dramatically pointed at one end, so that they roll in a circle when disturbed. This is critical for the survival of the developing eggs, as there are no nests to keep them from rolling off the side of the cliff. Presumably because of the vulnerability of their unprotected eggs, parent birds of these auk species rarely leave them unattended.

King and Emperor Penguins also do not build nests; instead, they tuck their eggs and chicks between their feet and folds of skin on their lower bellies. They are thus able to move about while incubating, though in practice only the Emperor Penguin regularly does so. Emperor Penguins breed during the harshest months of the Antarctic winter, and their mobility allows them to form huge huddled masses which help them to withstand the extremely high winds and low temperatures of the season. Without the ability to share body heat (temperatures in the center of tight groups can be as much as 10C above the ambient air temperature), the penguins would expend far more energy trying to stay warm, and breeding attempts would probably fail.

Some crevice-nesting species, including Ashy Storm-petrel, Pigeon Guillemot, Eurasian Eagle-Owl and Hume's Tawny Owl, lay their eggs in the relative shelter of a crevice in the rocks or a gap between boulders, but provide no additional nest material. Potoos lay their single egg directly atop a broken stump, or into a shallow depression on a branch—typically where an upward-pointing branch died and fell off, leaving a small scar or knot-hole. Brood parasites, such as the New World cowbirds, the honeyguides, and many of the Old World and Australasian cuckoos, lay their eggs in the active nests of other species.

Scrape

Shell-lined scrape nest of a *Charadrius* plover

The simplest nest construction is the **scrape**, which is merely a shallow depression in soil or vegetation. This nest type, which typically has a rim deep enough to keep the eggs from rolling away, is sometimes lined with bits of vegetation, small stones, shell fragments or feathers. These materials may help to camouflage the eggs or may provide some level of insulation; they may also help to keep the eggs in place, and prevent them from sinking into muddy or sandy soil if the nest is accidentally flooded. Ostriches, most tinamous, many ducks, most shorebirds, most terns, some falcons, pheasants, quail, partridges, bustards and sandgrouse are among the species that build scrape nests.

Eggs and young in scrape nests — and the adults that brood them — are more exposed to predators and the elements than those in more sheltered nests; they are on the ground and typically in the open, with little to hide them. The eggs of most ground-nesting birds (including those that use scrape nests) are cryptically colored to help camouflage them when the adult is not covering them; the actual color generally corresponds to the substrate on which they are laid. Brooding adults also tend to be well camouflaged, and may be difficult to flush from the nest. Most ground-nesting species have well-developed distraction displays, which are used to draw (or drive) potential predators from the area around the nest. Most species with this type of nest have precocial young, which quickly leave the nest upon hatching.

In cool climates (such as in the high Arctic or at high elevations), the depth of a scrape nest can be critical to both the survival of developing eggs and the fitness of the parent bird incubating them. The scrape must be deep enough that eggs are protected from the convective cooling caused by cold winds, but shallow enough that they and the parent bird are not too exposed to the cooling influences of ground temperatures, particularly where the permafrost layer rises to mere centimeters below the nest. Studies have shown that an egg within a scrape nest loses heat 9% more slowly than an egg placed on the ground beside the nest; in such a nest lined with natural vegetation, heat loss is reduced by an additional 25%. The insulating factor of nest lining is apparently so critical to egg survival that some species — including Kentish Plovers — will restore experimentally-altered levels of insulation to their pre-adjustment levels (adding or subtracting material as necessary) within 24 hours.

Lichen-lined scrape nest of the American Golden-Plover

In warm climates, such as deserts and salt flats, heat rather than cold can kill the developing embryos. In such places, scrapes are shallower and tend to be lined with non-vegetative material (including shells, feathers, sticks and soil), which allows convective cooling to occur as air moves over the eggs. Some species, such as the Lesser Nighthawk and the Red-tailed Tropicbird, help reduce the nest's temperature by placing it in partial or full shade. Others, including some shorebirds, cast shade with their bodies as they stand over their eggs. Some shorebirds also soak their breast feathers with water and then sit on the eggs, providing moisture to enable evaporative cooling. Parent birds keep from overheating themselves by gular panting while they are incubating, frequently exchanging incubation duties, and standing in water when they are not incubating.

The technique used to construct a scrape nest varies slightly depending on the species. Beach-nesting terns, for instance, fashion their nests by rocking their bodies on the sand in the place they have chosen to site their nest, while skimmers build their scrapes with their feet, kicking sand backwards while resting on their bellies and turning slowly in circles. The Ostrich also scratches out its scrape with its feet, though it stands while doing so. Many tinamous lay their eggs on a shallow mat of dead leaves they have collected and placed under bushes or between the root buttresses of trees, and Kagus lay theirs on a pile of dead leaves against a log, tree trunk or vegetation. Marbled Godwits stomp a grassy area flat with their feet, then lay their eggs, while other grass-nesting waders bend vegetation over their nests so as to avoid detection from above. Many female ducks, particularly in the northern latitudes, line their shallow scrape nests with down feathers plucked from their own breasts, as well as with small amounts of vegetation. Among scrape-nesting birds, the Three-banded Courser and Egyptian Plover are unique in their habit of partially burying their eggs in the sand of their scrapes.

Mound

Mound nest of the Malleefowl

Burying eggs as a form of incubation reaches its zenith with the Australasian megapodes. Several megapode species construct enormous **mound** nests made of soil, branches, sticks, twigs and leaves, and lay their eggs within the rotting mass. The heat generated by these mounds, which are in effect giant compost heaps, warms and incubates the eggs. Recent research has shown that much of the nest's heat results from the respiration of thermophilic fungi and other microorganisms rather than fermentation, as had been previously believed. The size of some of these mounds can be truly staggering; several of the largest—which contain more than 100 cubic metres (130 cu yd) of material, and probably weigh more than 50 tons (45,000 kg)—were initially thought to be Aboriginal middens.

In most mound-building species, males do most or all of the nest construction and maintenance. Using his strong legs and feet, the male scrapes together material from the area around his chosen nest site, gradually building a conical or bell-shaped pile. This process can take five to seven hours a day for more than a month. While mounds are typically reused for multiple breeding seasons, new material must be added each year in order to generate the appropriate amount of heat. A female will begin to lay eggs in the nest only when the mound's temperature has reached an optimal level.

Chilean Flamingos with mound nests

Both the temperature and the moisture content of the mound are critical to the survival and development of the eggs, so both are carefully regulated for the entire length of the breeding season (which may last for as long as eight months), principally by the male. Ornithologists believe that megapodes may use sensitive areas in their mouths to assess mound temperatures; each day during the breeding season, the male digs a pit into his mound and sticks his head in. If the mound's core temperature is a bit low, he adds fresh moist material to the mound, and stirs it in; if it is too high, he opens the top of the mound to allow some of the excess heat to escape. This regular monitoring also keeps the mound's material from becoming compacted, which would inhibit oxygen diffusion to the eggs and make it more difficult for the chicks to emerge after hatching. The Malleefowl, which lives in more open forest than do other megapodes, uses the sun to help warm its nest as well—opening the mound at midday during the cool spring and autumn months to expose the plentiful sand incorporated into the nest to the sun's warming rays, then using that warm sand to insulate the eggs during the cold nights. During hot summer months, the Malleefowl opens its nest mound only in the cool early morning hours, allowing excess heat to escape before recovering the mound completely. One recent study showed that the sex ratio of Australian Brush-turkey hatchlings correlated strongly with mound temperatures; females hatched from eggs incubated at higher mean temperatures.

Flamingos make a different type of mound nest. Using their beaks to pull material towards them, they fashion a cone-shaped pile of mud between 15–46 cm (6–18 in) tall, with a small depression in the top to house their single egg. The height of the nest varies with the substrate upon which it is built; those on clay sites are taller on average than those on dry or sandy sites. The height of the nest and the circular, often water-filled trench which surrounds it (the result of the removal of material for the nest) help to protect the egg from fluctuating water levels and excessive heat at ground level. In East Africa, for example, temperatures at the top of the nest mound average some 20°C (40°F) cooler than those of the surrounding ground.

The base of the Horned Coot's enormous nest is a mound built of stones, gathered one at a time by the pair, using their beaks. These stones, which may weigh as much as 450 g (about a pound) each, are dropped into the shallow water of a lake, making a cone-shaped pile which can measure as much as 4 m^2 (43 sq ft) at the bottom and 1 m^2 (11 sq ft) at the top, and 0.6 m (2.0 ft) in height. The total combined weight of the mound's stones may approach 1.5 tons (1,400 kg). Once the mound has been completed, a sizable platform of aquatic vegetation is constructed on top. The entire structure is typically reused for many years.

Burrow

Sand Martin at the entrance of its burrow nest

Soil plays a different role in the **burrow** nest; here, the eggs and young—and in most cases the incubating parent bird—are sheltered under the earth. Most burrow-nesting birds excavate their own burrows, but some use those excavated by other species; Burrowing Owls, for example, sometimes use the burrows of prairie dogs, ground squirrels, badgers or tortoises, China's endemic White-browed Tits use the holes of ground-nesting rodents and Common Kingfishers occasionally nest in rabbit burrows. Burrow nests are particularly common among seabirds at high latitudes, as they provide protection against both cold temperatures and predators. Puffins, shearwaters, some megapodes, motmots, todies, most kingfishers, the Crab Plover, miners and leaftossers are among the species which use burrow nests.

Most burrow nesting species dig a horizontal tunnel into a vertical (or nearly vertical) dirt cliff, with a chamber at the tunnel's end to house the eggs. The length of the tunnel varies depending on the substrate and the species; Sand Martins make relatively short tunnels ranging from 50–90 cm (20–35 in), for example, while those of the Burrowing Parakeet can extend for more than three meters (nearly 10 ft). Some species, including the ground-nesting puffbirds, prefer flat or gently sloping land, digging their entrance tunnels into the ground at an angle. In a more extreme example, the D'Arnaud's Barbet digs a vertical tunnel shaft more than a meter (39 in) deep, with its nest chamber excavated off to the side at some height above the shaft's bottom; this arrangement helps to keep the nest from being flooded during heavy rain. Buff-breasted Paradise-kingfishers dig their nests into the compacted mud of active termite mounds, either on the ground or in trees.

Burrow entrances in European Bee-eater colony

Birds use a combination of their beaks and feet to excavate burrow nests. The tunnel is started with the beak; the bird either probes at the ground to create a depression, or flies toward its chosen nest site on a cliff wall and hits it with its bill. The latter method is not without its dangers; there are reports of kingfishers being fatally injured in such attempts. Some birds remove tunnel material with their bills, while others use their bodies or shovel the dirt out with one or both feet. Female paradise-kingfishers are known to use their long tails to clear the loose soil.

Some crepuscular petrels and prions are able to identify their own burrows within dense colonies by smell. Sand Martins learn the location of their nest within a colony, and will accept any chick put into that nest until right before the young fledge.

Not all burrow-nesting species incubate their young directly. Some megapode species bury their eggs in sandy pits dug where sunlight, subterranean volcanic activity, or decaying tree roots will warm the eggs. The Crab Plover similarly makes use of a burrow nest, the warmth of which allows it to forage away from the nest.

Predation levels on some burrow-nesting species can be quite high; on Alaska's Wooded Islands, for example, river otters munched their way through some 23 percent of the island's Fork-tailed Storm-Petrel population during a single breeding season in 1977. There is some evidence that increased vulnerability may lead some burrow-nesting species to form colonies, or to nest closer to rival pairs in areas of high predation than they might otherwise do.

Cavity

A Northern Flicker protruding from its cavity nest

The **cavity** nest is a chamber, typically in living or dead wood, but sometimes in the trunks of tree ferns or large cacti, including saguaro. In tropical areas, cavities are sometimes excavated in arboreal insect nests. A relatively small number of species, including woodpeckers, trogons, some nuthatches and many barbets, can excavate their own cavities. Far more species—including parrots, tits, bluebirds, most hornbills, some kingfishers, some owls, some ducks and some flycatchers—use natural cavities, or those abandoned by species able to excavate them; they also sometimes usurp cavity nests from their excavating owners. Those species that excavate their own cavities are known as "primary cavity nesters", while those that use natural cavities or those excavated by other species are called "secondary cavity nesters". Both primary and secondary cavity nesters can be enticed to use nest boxes (also known as bird houses); these mimic natural cavities, and can be critical to the survival of species in areas where natural cavities are lacking.

Woodpeckers use their chisel-like bills to excavate their cavity nests, a process which takes, on average, about two weeks. Cavities are normally excavated on the downward-facing side of a branch, presumably to make it more difficult for predators to access the nest, and to reduce the chance that rain floods the nest. There is also some evidence that fungal rot may make the wood on the underside of leaning trunks and branches easier to excavate. Most woodpeckers use a cavity for only a single year. The endangered Red-cockaded Woodpecker is an exception; it takes far longer—up to two years—to excavate its nest cavity, and may reuse it for more than two decades. The typical woodpecker nest has a short horizontal tunnel which leads to a vertical chamber within the trunk. The size and shape of the chamber depends on species, and the entrance hole is typically only as large as is needed to allow access for the adult birds. While wood chips are removed during the excavation process, most species line the floor of the cavity with a fresh bed of them before laying their eggs.

Black Woodpecker youngsters in their cavity nest

Trogons excavate their nests by chewing cavities into very soft dead wood; some species make completely enclosed chambers (accessed by upward-slanting entrance tunnels), while others—like the extravagantly-plumed Resplendent Quetzal—construct more open niches. In most trogon species, both sexes help with nest construction. The process may take several months, and a single pair may start several excavations before finding a tree or stump with wood of the right consistency.

Species which use natural cavities—or old woodpecker nests—sometimes line the cavity with soft material such as grass, moss, lichen, feathers or fur. Though a number of studies have attempted to determine whether secondary cavity nesters preferentially choose cavities with entrance holes facing certain directions, the results remain inconclusive. While some species appear to preferentially choose holes with certain orientations, studies (to date) have not shown consistent differences in fledging rates between nests oriented in different directions.

Cavity-dwelling species have to contend with the danger of predators accessing their nest, catching them and their young inside and unable to get out. They have a variety of methods for decreasing the likelihood of this happening. Red-cockaded Woodpeckers peel bark around the entrance, and drill wells above and below the hole; since they nest in live trees, the resulting flow of resin forms a barrier that prevents snakes from reaching the nests. Red-breasted Nuthatches smear sap around the entrance holes to their nests, while White-breasted Nuthatches rub foul-smelling insects around theirs. Eurasian Nuthatches wall up part of their entrance holes with mud, decreasing the size and sometimes extending the tunnel part of the chamber. Most female hornbills seal themselves into their cavity nests, using a combination of mud (in some species brought by their mates), food remains and their own droppings to reduce the entrance hole to a narrow slit.

Cup

Cup nest of a Common Blackbird

Cup nest of a Redwing, with newly hatched chicks

The **cup** nest is smoothly hemispherical inside, with a deep depression to house the eggs. Most are made of pliable materials—including grasses—though a small number are made of mud. Many passerines and a few non-passerines, including some hummingbirds and some swifts, build this type of nest.

Small bird species in more than 20 passerine families, and a few non-passerines—including most hummingbirds, kinglets and crests in the genus *Regulus*, some tyrant flycatchers and several New World warblers—use considerable amounts of spider silk in the construction of their nests. The lightweight material is strong and extremely flexible, allowing the nest to mold to the adult during incubation (reducing heat loss), then to stretch to accommodate the growing nestlings; as it is sticky, it also helps to bind the nest to the branch or leaf to which it is attached.

Saucer or plate

The **saucer** or **plate** nest, though superficially similar to a cup nest, has at most only a shallow depression to house the eggs.

Platform

The huge platform nest of the Osprey

The **platform** nest is a large structure, often many times the size of the (typically large) bird which has built it. Depending on the species, these nests can be on the ground or elevated. In the case of raptor nests, or **eyries** (also spelt **aerie**), these are often used for many years, with new material added each breeding season. In some cases, the nests grow large enough to cause structural damage to the tree itself, particularly during bad storms where the weight of the nest can cause additional stress on wind-tossed branches.

Pendant

Taveta Golden Weaver building pendant nest

The **pendant** nest is an elongated sac woven of pliable materials such as grasses and plant fibers and suspended from a branch. Oropendolas, caciques, orioles, weavers and sunbirds are among the species that weave pendant nests.

Sphere

The **sphere** nest is a roundish structure; it is completely enclosed, except for a small opening which allows access.

Nest protection and sanitation

Many species of bird conceal their nests to protect them from predators. Some species may choose nest sites that are inaccessible. Some may make specific modifications to keep predators at bay. Bird nests can also act as habitats for other inquiline species which may not affect the bird directly. Birds have also evolved nest sanitation measures to reduce the effects of parasites and pathogens on nestlings.

Some aquatic species such as grebes are very careful when approaching and leaving the nest so as not to reveal the location. Some species will use leaves to cover up the nest prior to leaving.

Ground birds such as plovers may use *broken wing* or *rodent run* displays to distract predators from nests.

Many species attack predators or apparent predators near their nests. Kingbirds attack other birds that come too close. In North America, Northern Mockingbirds, Blue Jays, and Arctic Terns can peck hard enough to draw blood. In Australia, a bird attacking a person near its nest is said to *swoop* the person. The Australian Magpie is particularly well-known for this behavior.

Nests can become home to many other organisms including parasites and pathogens. The excreta of the fledglings also pose a problem. In most passerines, the adults actively dispose the fecal sacs of young at a distance or consume them. This is believed to help prevent ground predators from detecting nests. Young birds of prey however usually void their excreta beyond the rims of their nests. Blowflies of the genus *Protocalliphora* have specialized to become obligate nest parasites with the maggots feeding on the blood of nestlings.

Some birds have been shown to choose aromatic green plant material for constructing nests that may have insecticidal properties, while others may use materials such as carnivore scat to repel smaller predators.

Nesting colony of Montezuma Oropendolas

Some birds use pieces of snake slough in their nests. It has been suggested that these may deter some nest predators such as squirrels.

Colonial nesting

Though most birds nest individually, some species—including seabirds, penguins, flamingos, many herons, gulls, terns, weaver, some corvids and some sparrows—gather together in sizeable colonies. Birds that nest colonially may benefit from increased protection against predation. They may also be able to better utilize food supplies, by following more successful foragers to their foraging sites.

In human culture

Many birds nest close to human habitations and some have been specially encouraged. Nesting White Storks have been protected and held in reverence in many cultures. Nest boxes are often used to encourage cavity nesting birds. The nesting of Peregrine Falcons on tall buildings has captured popular interest. Colonial breeders produce guano which is a valuable fertilizer. The saliva nests of Cave Swiftlets are used to make Bird's nest soup in parts of Southeast Asia.

Some species of birds are also considered nuisances when they nest in the proximity of human habitations. Feral pigeons are often unwelcome and sometimes also considered as a health risk.

The Beijing National Stadium, principal venue of the 2008 Summer Olympics, has been nicknamed "The Bird Nest" because of its architectural design, which its designers likened to a bird's woven nest.

Chapter- 10

Bird Conservation

The extinction of the Dusky Seaside Sparrow was caused by habitat loss.

Bird conservation is a field in the science of conservation biology related to threatened birds. Humans have had a profound effect on many bird species. Over one hundred species have gone extinct in historical times, although the most dramatic human-caused extinctions occurred in the Pacific Ocean as humans colonised the islands of Melanesia, Polynesia and Micronesia, during which an estimated 750-1800 species of bird went extinct. According to Worldwatch Institute, many bird populations are currently declining worldwide, with 1,200 species facing extinction in the next century. The biggest cited reason surrounds habitat loss. Other threats include overhunting, accidental mortality due to structural collisions, long-line fishing bycatch, pollution, competition and predation by nonnative invasive species, oil spills and pesticide use and climate change. Governments, along with numerous conservation charities, work to protect birds in various ways, including legislation, preserving and restoring bird habitat, and establishing captive populations for reintroductions.

Threats to birds

Habitat loss

The most critical threat facing threatened birds is the destruction and fragmentation of habitat. The loss of forests, plains and other natural systems into agriculture, mines, and urban developments, the draining of swamps and other wetlands, and logging reduce potential habitat for many species. In addition the remaining patches of habitat are often too small or fragmented by the construction of roads or other such barriers that cause populations in these fragmented *islands* to become vulnerable to localised extinction. In addition many forest species show limited abilities to disperse and occupy new forest fragments. The loss of tropical rainforest is the most pressing problem, as these forests hold the highest number of species yet are being destroyed quickly. Habitat loss has been implicated in a number of extinctions, including the Ivory-billed Woodpecker (disputed because of "rediscovery"), Bachman's Warbler and the Dusky Seaside Sparrow.

Introduced species

Arctic Foxes introduced to the Aleutian Islands devastated populations of auks; here a Least Auklet has been taken.

Historically the threat posed by introduced species has probably caused the most extinctions of birds, particularly on islands. Ninety percent of historical extinctions have occurred on islands, and most prehistoric human caused extinctions were insular as well. Many island species evolved in the absence of predators and consequently lost many anti-predator behaviours. As humans traveled around the world they brought with them many foreign animals which disturbed these island species. Some of these were unfamiliar predators, like rats, feral cats, and pigs; others were competitors, such as other bird species, or herbivores that degraded breeding habitat. Disease can also play a role; introduced avian malaria is thought to be a primary cause of many extinctions in Hawaii. The Dodo is the most famous example of a species that was probably driven to extinction by introduced species (although human hunting also played a role), other species that were victims of introduced species were the Stephens Island Wren, Poʻo -uli and the Laysan Millerbird. Many species currently threatened with extinction are vulnerable to introduced species, such as the Kōkako, Black Robin, Mariana Crow, and the Hawaiian Duck.

Hunting and exploitation

Humans have exploited birds for a very long time, and sometimes this exploitation has resulted in extinction. Overhunting occurred in some instances with naive species unfamiliar with humans, such as the moa of New Zealand, in other cases it was an industrial level of hunting that led to extinction. The Passenger Pigeon was once the most numerous species of bird alive (possibly ever), overhunting reduced a species that once numbered in the billions to extinction. Hunting pressure can be for food, sport, feathers, or even come from scientists collecting museum specimens. Collection of Great Auks for museums pushed the already rare species to extinction.

The harvesting of parrots for the pet trade has led to many species becoming endangered. Between 1986 and 1988 two million parrots were legally imported into the US alone. Parrots are also illegally smuggled between countries, and rarer species can command high prices.

Hybridisation

Hybridisation may also endanger birds, damaging the gene stock. For example, the American Black Duck has been often reported hybridising with the Mallard, starting a slow decline.

Gamebird hybrids are particularly common and many breeders produce hybrids that may be accidentally or intentionally introduced into the wild.

Other threats

This Black-browed Albatross has been hooked on a long-line.

Birds face a number of other threats. Pollution has led to serious declines in some species. The pesticide DDT was responsible for thinning egg shells in nesting birds, particularly seabirds and birds of prey that are high on the food chain. Seabirds are also vulnerable to oil spills, which destroy the plumage's waterproofing causing the bird to drown or die of hypothermia. Light pollution can also have a damaging effect on some species, particularly nocturnal seabirds such as petrels.

Seabirds face another threat in the form of bycatch; where birds in the water become tangled in fishing nets or hooked on lines set out by long-line fisheries. As many as 100,000 albatrosses are hooked and drown each year on tuna lines set out by long-line fisheries.

Birds are also threatened by high rise buildings, communications towers, and wind farms; an estimated 975 million birds a year are killed this way in the North America alone, according to the American Bird Conservancy. The largest source of human-related bird death is due to glass windows, which kill 100-900 million birds a year. The next largest sources of human caused death are hunting (100+ million), house cats (100 million), cars and trucks (50 to 100 million), electric power lines (174 million), and pesticides (67 million). Birds are also killed in large quantities by flying into communication tower guidelines, usually after being attracted by tower lights. This phenomena is called towerkill and is responsible for 5-50 million birds deaths a year. The presence of towers may seriously impact endangered species living in the vicinity.

Conservation techniques

Scientists and conservation professionals have developed a number of techniques to protect bird species. These techniques have had varying levels of success.

Captive breeding

Captive breeding, or *ex-situ* conservation, has been used in a number of instances to save species from extinction. The principal is to create a viable population of a species in either zoos or breeding facilities, for later reintroduction back into to the wild. As such a captive population can either serve as an insurance against the species going extinct in the wild or as a last ditch effort in situations where conservation in the wild is impossible. Captive breeding has been used to save several species from extinction, the most famous example being the California Condor, a species that declined to less than thirty birds. In order to save the California Condor the decision was made to take every individual left in the wild into captivity. From these 22 individuals a breeding programme began that brought the numbers up to 273 by 2005. An even more impressive recovery was that of the Mauritius Kestrel, which by 1974 had dropped to only four individuals, yet by 2006 the population was 800.

Reintroduction and translocations

Reintroductions of captive bred populations can occur to replenish wild populations of an endangered species, to create new populations or to restore a species after it has become extinct in the wild. Reintroductions helped bring the wild populations of Hawaiian Geese from 30 birds to over 500. The Mauritius Kestrel was successfully reintroduced into the wild after its captive breeding programme. Reintroductions can be very difficult and often fail if insufficient preparations are made, as species born in captivity may lack the skills and knowledge needed for life in the wild after living in captivity. Reintroductions can also fail if the causes of a birds decline have not been adequately addressed. Attempts to reintroduce the Bali Starling into the wild failed due to continued poaching of reintroduced birds.

The introduction of captives of unknown pedigree can pose a threat to native populations. Domestic fowl have threatened endemic species such as *Gallus g. bankiva* while pheasants such as the Ring-necked Pheasant and captive Cheer pheasants of uncertain origin have escaped into the wild or have been intentionally introduced. Green peafowl of similar mixed origins confiscated from local bird dealers have been released into areas with native wild birds.

Translocations involve moving populations of threatened species into areas of suitable habitat currently unused by the species. There are several reasons for doing this; the creation of secondary populations that act as an insurance against disaster, or in many cases threats faced by the original population in its current location. One famous translocation was of the Kakapo of New Zealand. These large flightless parrots were unable to cope with introduced predators in their remaining habitat on Stewart Island, so were moved to smaller offshore islands that had been cleared of predators. From there a recovery programme has managed to maintain and eventually increase their numbers.

Habitat protection

As the loss and destruction of habitat is the most serious threat facing many bird species, conservation organisations and government agencies tasked with protecting birds work to protect areas of natural habitat. This can be achieved through purchasing land of conservation importance, setting aside land or gazetting it as a national park or other protected area, and passing legislation preventing landowners from undertaking damaging land use practices, or paying them not to undertake those activities. The goals of habitat protection for birds and other threatened animals and plants often conflicts with other stakeholders, such as landowners and businesses, who can face economically damaging restrictions on their activities. Plans to protect crucial habitat for the Spotted Owl of North America required the protection of large areas of old growth forest in the western United States; this was opposed by logging companies who claimed it would cause job losses and reduced profits.