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CONTENTS

Birds

Birds are warm-blooded vertebrates whose covering of feathers is the one major characteristic that distinguishes them from all other animals. Birds have a four-chambered heart (shared with all mammals), forelimbs modified into wings (shared with bats), a calcareous-shelled egg, and keen vision, the major sense relied upon by birds for information about their environment. Their sense of smell is not highly developed, and auditory range is limited. Most birds are diurnal in habit.

In the scheme of biological classification, birds constitute the class Aves. There are approximately 8,700 living species, and more than 1,000 extinct species have been identified from fossil remains. For coverage of related topics in the *Macropædia* and the *Micropædia,* see the *Propædia,* section 313, and the *Index.*

This article is divided into the following sections:

BIRDS: THE CLASS AVES

GENERAL FEATURES

The smallest living bird is generally acknowledged to be the bee hummingbird of Cuba, which is 6.3 centimetres (2.5 inches) long and weighs less than 3 grams (about 0.1 ounce). The largest living bird is the ostrich, which may stand 2.5 metres (8 feet) tall and weigh 135 kilograms (300 pounds). Some extinct birds were even larger: the largest of the moas of New Zealand and the elephant birds of Madagascar may have reached over 3 metres (10 feet) in height. Among flying birds, the wandering albatross has the greatest wingspan, up to 3.5 metres (11.5 feet), and the trumpeter swan perhaps the greatest weight, 17 kilograms (38 pounds). A Pleistocene condorlike bird, *Teratornis incredibilis,* had an estimated wingspan of about 5 metres (16.5 feet) and was by far the largest known flying bird.

The ability to fly has permitted an almost unlimited radiation of birds, so that they are now found virtually everywhere on earth, from occasional stragglers over the polar ice caps to complex communities in tropical forests. In general the number of species found breeding in a given area is directly proportional to the size of the area and the diversity of habitats available. The total number of species is also related to such factors as the position of the area with respect to migration routes and wintering grounds of species that nest outside the area. In the United States, Texas and California have both the largest number of species recorded (545 and 461, respectively, including both resident and migrant species) and the largest number breeding (300 and 286). Seven hundred and seventy-five species, 650 of them breeding, have been recorded from North America north of Mexico. The figures for Europe exclusive of the Soviet Union are 577 and 420, and the figures for the Soviet Union are 704 and 622. Costa Rica, with an area of only about 51,000 square kilometres (about 20,000 square miles) and a known avifauna of at least 758 species, probably has the most diversified group for its size of any country.

BIRD AND HUMAN RELATIONSHIPS

Wild birds and their eggs have been at least incidental sources of food for humans since their origin and still are in most societies. The eggs of some colonial seabirds, such as gulls, terns, and murres, or guillemots, and the young of some shearwaters (muttonbirds) are even now harvested in large quantities. With the development of agrarian human cultures, several species of birds became domesticated. Of these, chickens, ducks, geese, and pigeons, descended from the red jungle fowl (*Gallus gallus*), mallard duck (*Anas platyrhynchos*), greylag goose (*Anser anser*), and rock dove (*Columba livia*), respectively, were taken in early and have been selectively bred into many varieties. After the discovery of the New World, the turkey (*Meleagris gallopavo*), which had already been domesticated by the Indians, and the Muscovy duck (*Cairina moschata*) were brought to Europe and produced several varieties. Guinea fowl (*Numida meleagris*) from Africa were also widely exported and kept not only for food but because they are noisy when alarmed, thus warning of the approach of intruders. Besides being a food source, pigeons have long been bred and trained for carrying messages, and the ability of frigate birds to "home" to their nesting colonies has enabled inhabitants of the South Seas to send messages by these birds. For further information on domestication of birds, see FARMING: *Livestock farming* and *Poultry farming.*

Domestication

With the development of modern culture, hunting evolved from a foraging activity to a sport, in which the food value of the game became secondary. Large sums are now spent annually on hunting waterfowl, quail, grouse, pheasants, doves, and other game birds. Sets of rules and conventions have been set up for hunting, and in one elaborate form of hunting, falconry, there is not only a large body of specialized information on keeping and training falcons but also a complex terminology, much of it centuries old.

Feathers have been used for decoration since early times. Their use in the headdresses of American Indians and various peoples of New Guinea is well known. Feather robes were made by Polynesians and Eskimos; down quilts, mattresses, and pillows are part of traditional European folk culture. Large feathers have often been used in fans, thereby providing an example of an object put to opposite uses—for cooling as well as for conserving heat. Whereas most feathers used in decorating are now saved as by-products of poultry raising or hunting, until early in the 20th century, egrets, grebes, and other birds were widely shot for their plumes alone. Ostrich farms have been established to produce plumes. Large quills were once widely used for writing, and feathers have long been used on arrows and fishing lures.

Many birds are kept as pets. Small finches and parrots are especially popular and easy to keep. Of these, the canary (*Serinus canaria*) and the budgerigar of Australia (*Melopsittacus undulatus,* sometimes called parakeet) are widely kept and have been bred for a variety of colour types. On large parks and estates, ornamental species like peafowl (*Pavo*) and various exotic waterfowl and pheasants are often kept. Zoological parks in many cities import birds from many lands and are a source of recreation for millions of people each year.

Birds as pests

With the rise of agriculture, man's relationship with birds became more complex. In regions where grain and fruit are grown, depredations by birds may be a serious problem. In North America various species of blackbirds (family Icteridae) are serious pests in grainfields; while in Africa a grain-eating finch, the red-billed quelea (*Quelea quelea*), occurs, like locusts, in plague proportions so numerous that alighting flocks may break the branches of trees. The use of city buildings for roosts by large flocks of starlings and blackbirds is also a problem, as is the nesting of albatrosses on airplane runways on Pacific islands. As a result of these problems, conferences on the control of avian pests are held with increasing frequency.

Although birds are subject to a great range of diseases and parasites, few of these are known to be capable of infecting man. Notable exceptions are ornithosis (or psittacosis), caused by one or more viruses that are transmitted directly to man from pigeons, parrots, and a variety of other birds, a serious and sometimes fatal disease resembling virus pneumonia. Encephalitis, an inflammation of the brain, is also serious and is transmitted from birds to man and to his domestic animals by biting arthropods, including mosquitos. Wild birds may also act as reservoirs for diseases that adversely affect domesticated birds. Much work has been done recently on the ecology of viruses, with more and more of them being found in birds.

The study of birds has contributed much to both the theoretical and practical aspects of biology. Darwin's studies of the Galápagos finches and other birds during the voyage of the "Beagle" were important in his formulation of the idea of the origin of species through natural selection. Study collections of birds in research museums still provide the bases for important studies of geographic variation, speciation, and zoogeography, because birds are one of the best known of animal groups. Early work on the domestic fowl added to the development of both genetics and embryology. The study of animal behaviour (ethology) has been based to a large extent on studies of birds by Konrad Lorenz, Nikolaas Tinbergen, and their successors. Birds also have been the primary group in the study of migration and orientation and the effect of hormones on behaviour and physiology.

Birds feature prominently in mythology and the literature of many countries. Some of their attributes, real or imagined, have led to their symbolic use in art as in language. The aesthetic and recreational pleasures of birdwatching are increasingly being recognized.

Man's impact on bird populations has become increasingly strong. Since 1680, approximately 80 species of birds have become extinct, and an even larger number are seriously endangered. While pollution and pesticides are important factors in the decline of certain large species, such as the peregrine falcon, osprey, and brown pelican, the destruction of natural areas and introduction of exotic animals and diseases have probably been the most devastating. Concerted efforts are required to ensure the survival of rare species and to learn as much as possible about them. (R.W.St.)

NATURAL HISTORY

Locomotion. Because of their body structure and their feathery body covering, birds are the best fliers among animals, better than the insects and the flying mammals, the bats. There are, however, considerable differences in flying ability among various birds. Penguins cannot fly but spend much of their time in the water swimming with their paddlelike wings; such birds as ostriches and kiwis have rudimentary wings and are permanently afoot. At the other extreme are the long-winged swifts and frigate birds that move from their perches only to fly, never to walk. Most birds alternate some walking or swimming with their flying.

Birds usually fly when they have any considerable distance to travel; there are exceptions, however. The mountain quail of California make their annual migrations up and down the mountains by foot. The murres, or guillemots, of the Greenland coast migrate southward by swimming; they begin their journey before the young have grown their flight feathers and before some of the adults at least have regrown their recently molted ones. The Adélie penguins may ride northward on drifting ice floes; at the approach of nesting time they swim back to the Antarctic continent and then walk over the ice to their breeding grounds many miles inland.

Flight. Birds fly by flapping their wings, steering mainly with their tails. A goshawk, pursuing its prey through the forest, uses its long tail in making quick turns, and the barn swallow uses its deeply forked tail in making the involved patterns of its graceful flight. Ducks with their short tails have a swift but direct flight. There is, however, such great diversity in birds' tails that the precise size and shape probably is not of critical importance.

Comparing a bird to an airplane, a bird's wing is both wing and propeller. The basal part of the wing supplies most of the supporting surface, the wing tip most of the propelling force. A bird's wing has many adjustable features: it can be shortened or lengthened by flexion; the feathers of the tip can be spread or closed; the angle of the whole wing or its parts, on one side or the other or on both sides, can be altered. All these adjustments make the aerodynamics of a bird's wing much more complicated than those of the airplane; consequently, the flight of a bird is much more varied and adaptable.

Flying ability varies widely among birds, and different types of wings correlate with different types of flight. Many songbirds use their short, rounded wings mostly to move with quick wing beats from perch to perch or from ground to perch. Ducks have pointed wings that, beaten at high speed, provide rapid flight for long distances. Swallows, terns, and frigate birds have long, pointed wings that enable these birds to fly and manoeuvre gracefully for hours with leisurely wing beats. Large herons with long, broad wings travel far with slow, measured wing beats, while buzzards soar high in the sky on their long, broad wings. Gulls and albatrosses with long, narrow wings sail along the beaches or over the waves with infrequent wing strokes. A hummingbird can whir its tiny wings so rapidly that it can hover as it thrusts its long bill into a blossom; it can even fly backward as it leaves the bloom.

Speed

The speed with which birds fly varies greatly from species to species, and of course individual birds can vary their speed. The data on the speed of birds' flight are difficult to evaluate. One of the complicating factors is that a bird's speed in relation to the ground may depend on the force of the wind. A bird flying at an airspeed of 40 mph with a 60-mph wind behind it would travel at 100 mph in relation to the ground (1 mile = 1.61 kilometeres). The same bird flying into a 60-mph wind would be losing ground at the rate of 20 mph. Despite the variables involved in determining a bird's speed of flight, the following generalized speeds, based on level flight in calm air, appear to be sound:

10–20 mph—many small songbirds such as sparrows and wrens
20–30 mph—many medium-sized birds such as thrushes and grackles, and larger, long-winged birds such as herons, pelicans, and gulls
20–40 mph—many small- and medium-sized birds such as starlings, chimney swifts, and mourning doves
40–60 mph—the faster-flying birds such as falcons, ducks, geese, and domestic pigeons

There are many faster records, often disputed, such as that of 200 mph for an Indian spine-tailed swift in level flight and 170 mph for a golden eagle in a dive. A homing pigeon has been timed at 94.3 mph.

Range

The record long-range flight of a bird species in a single season is undoubtedly held by the Arctic terns that migrate from a summering ground in the Arctic to a wintering ground in the Antarctic, travelling more than 11,600 kilometres (7,200 miles) one way. Some long-range flights are made very quickly: a blue-winged teal banded in Canada was recovered 6,100 kilometres (3,800 miles) away in Venezuela only 30 days later; a Manx shearwater, trapped at its nest in Wales and transported 5,200 kilometres (3,200 miles) to Massachusetts and released, returned home in 12½ days. Some very small birds regularly make long water crossings in a single flight. Ruby-throated hummingbirds fly across the more than 500-mile-wide Gulf of Mexico, and many warblers fly from the American coast to Bermuda, a journey of about the same distance. For further information on bird migration, see BEHAVIOUR, ANIMAL: *Animal migration.*

Flightlessness. Flight, so characteristic of birds, is maintained during the molt in most species by a gradual replacement of the flight feathers. However, ducks and geese, some rails and loons (divers), and auks shed all of their flight feathers at one time, immediately after the nesting season. Not until these feathers are replaced are the birds able to fly again. Most of these are birds that find their food by walking or swimming, as would be expected. Some ducks living in the marshes become very shy and retiring at this season, skulking in the reeds, but geese nesting in the Arctic barrens continue to walk about over the tundra, feeding. In another group of birds, however, the hornbills of Africa and Asia, only the females lose both flight and tail feathers at once; they stay in the nest until the feathers grow out again, being fed during this period by the males.

Evolutionary flightlessness

Some birds have completely lost the power of flight during the course of evolution. The close similarity in basic structure of both flightless and flying birds indicates, however, that they all had a common flying ancestor. The rudimentary wings and the flightless condition of the ostrich-like birds and the penguins is a secondary, specialized condition. That flightlessness is a secondary condition is made still more apparent in other flightless birds that belong to families most of whose members are capable of flight. The extinct great auk of the North Atlantic is one of the best known examples of such a flightless bird; the rail family also is noted for having many flightless species living on islands in the Pacific and the South Atlantic. Loss of flight seems to occur most often on isolated islands where there are no mammal predators. In New Zealand, where there are no native land mammals, not only are there many species of extinct flightless moas but also flightless kiwis, penguins, and rails and a duck, an owl, and several songbirds that are nearly flightless. The ostrich-like birds of continental distribution present an apparent contradiction to this correlation of mammal-free island habitats with bird flightlessness. Another adaptation, however, their great size, has enabled these forms to escape the predation of mammals.

Walking, hopping, and swimming. Terrestrial birds such as pheasants tend to walk; arboreal songbirds tend to hop as they travel from branch to branch. Parrots often walk along branches, and house sparrows hop when they come to the ground, while palm warblers walk on the ground and some songbirds, such as American robins and European blackbirds, may both walk and hop. Some birds with small feet, such as swifts, hummingbirds, bee eaters, and many hornbills, use their feet only for perching and rarely walk at all. Other birds with robust feet, such as guinea fowl and rails, do most of their moving about on foot. Jacanas with their greatly elongated toes and nails walk over floating water weeds, and herons with long legs wade in shallow water. The ostrich is probably the fastest running bird; some investigators have credited it with a speed of 50 mph (80.5 kph), at which time the length of its stride was about 25 feet (7.6 metres).

The usual position of a bird's body in walking is more or less parallel to the ground. But the penguins, with their feet far to the rear of their bodies, stand upright as they waddle along. When the Adélie penguin, however, makes its trek of many miles over the snow-covered ice to its breeding grounds, it may vary its awkward waddle with periods of tobogganing; *i.e.*, sliding along on its breast and propelling itself with thrusts of its feet.

Some water birds have become so adapted to swimming that they are practically helpless on land. In this class are loons, which shuffle awkwardly the few feet from the water to their nests. Swimming in birds is usually correlated with webbed feet, but coots and grebes, with only lobes on their toes, also swim and dive, and gallinules, without either webs or lobes on their toes, commonly swim. On the other hand, frigate birds, with partly webbed feet, never swim. Penguins swim through the water with their wings and use their webbed feet only for steering. Auks use their wings and webbed feet in swimming underwater.

Some birds such as the mallard usually swim at the surface, feeding only as far underwater as they can reach by dipping their heads. Other ducks, such as scoters and pochards, commonly dive to the bottom for their food, and cormorants, auks, and loons pursue fish underwater. Sometimes loons are taken at remarkable depths in fishermen's nets and on set lines, indicating that they may dive as deep as 200 feet.

Pond ducks, such as mallards and teals, spring straight up from the water's surface into the air in flight, but many swimming birds—for example, coots, grebes, cormorants, and diving ducks—take off with a long spattering run along the surface. (Au.L.R.)

Behaviour. Birds depend to a great extent on innate behaviour, responding automatically to specific visual or auditory stimuli. Even much of their feeding and reproductive behaviour is stereotyped. Feather care is vital to keep the wings and tail in condition for flying and the rest of the feathers in place where they can act as insulation. Consequently preening, oiling, shaking, and stretching movements are well developed and regularly used. Some movements, like the simultaneous stretching of one wing, one leg, and half the tail (all on the same side) are widespread if not universal among birds. Stretching both wings upward, either folded or spread, is another common movement, as is a shaking of the whole body beginning at the posterior end. Other movements have evolved in connection with bathing, either in water or in dust. Such comfort movements have frequently become ritualized as components of displays.

Many birds maintain a minimum distance between themselves and their neighbours, as can be seen in the spacing of a flock of swallows perched on a wire. In the breeding season most species maintain territories, defended areas ranging from the immediate vicinity of the nest to extensive areas in which a pair not only nests but also forages. The frequency of actual fighting is in birds greatly reduced by ritualized threat and appeasement displays. Birds range from solitary (*e.g.*, many birds of prey) to highly gregarious, like the guanay cormorants of the Peru Current off the west coast of South America, which nest in enormous colonies of hundreds of thousands and feed in large flocks with boobies and pelicans.

Vocalization

Auditory signals, like visual ones, are almost universal among birds. The most familiar vocalization of birds is that usually referred to as "song." It is a conspicuous sound (not necessarily musical) that is used, especially early in the breeding season, to attract a mate, to warn off another bird of the same sex, or both. As such it is usually associated with establishing and maintaining territories. Individual variation in songs of many species is well known, and it is believed that some birds can recognize their mates and neighbours by this variation. Many other types of vocalizations are also known. Pairs or flocks may be kept together by series of soft location notes. Alarm notes alert other individuals to the presence of danger; in fact, the American robin (and probably many other species) uses one note when it sees a hawk overhead and another when it sees a predator on the ground. Begging calls are important in stimulating parents to feed their young. Other calls are associated with aggressive situations, courtship, and mating. Nonvocal sounds are not uncommon. Some snipe and hummingbirds have narrow tail feathers that produce loud sounds when the birds are in flight, as do the narrowed outer primaries of the American woodcock. The elaborate courtship displays of grouse include vocalizations as well as stamping of the feet and noises made with the wings. Bill clapping is a common part of courtship in storks, and bill snapping is a common threat of owls.

Drawing by R. Keane based on M.H. Clench

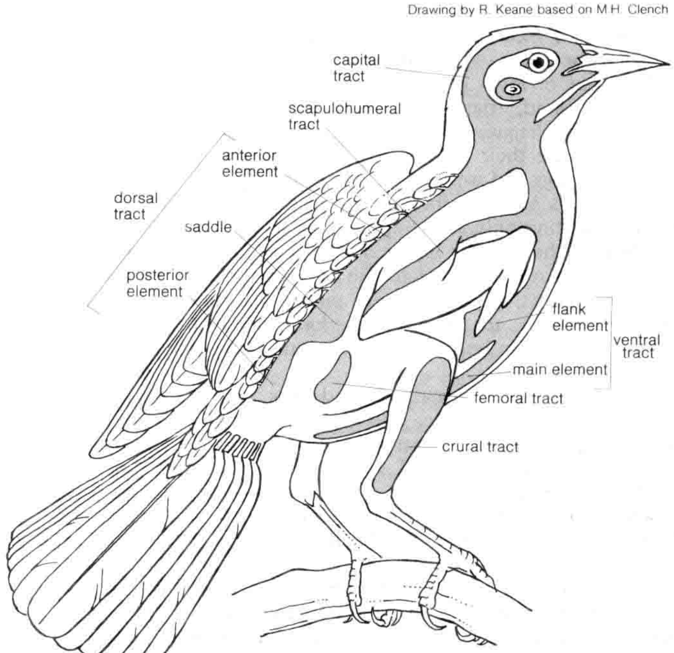

Figure 1: Basic body feather tracts on a generalized songbird. Shaded areas show the right half of each tract.

The nest

Most birds build nests in which the eggs are laid. Nests vary widely: they may be a scrape in the sand, a deep burrow, a hole in a tree or rock, an open cup, a globular or retort-shaped mass with a side entrance tube, or an elaborately woven hanging structure. The materials with which nests are made also vary widely. Some nests are lined with small stones, others are built of dirt or mud with or without plant material. Sticks, leaves, algae, rootlets, and other plant fibres are used alone or in combination. Some birds seek out animal materials such as feathers, horsehair, or snakeskin. The nest materials may be held together by weaving, sewing, or felting the materials themselves or with mud or spider webs. Swifts use saliva to glue nest materials together and to attach the nest to the supporting structure. In at least one species of swift, the entire nest is made of saliva and is the prized ingredient of birds' nest soup in the Orient. All birds incubate their eggs, except megapodes (mound builders), which depend on the heat generated by decaying vegetation or other external sources, and brood parasites, which lay their eggs in the nests of other species. Murres and the king and emperor penguins build no nest but incubate with the egg resting on top of the feet. In most birds a brood patch is developed. This bare area on the abdomen is edematous (fluid filled) and highly vascularized and is in direct contact with the eggs during incubation. Its development during the breeding season is under hormonal control. When the parent is off the nest, adjacent feathers are directed over the brood patch, and it is usually not apparent. A few birds (*e.g.*, boobies) keep their webbed feet over the eggs during incubation.

Incubation takes from 11 to 80 days, depending at least in part on the size of the bird and the degree of development at hatching. Most songbirds and members of some other groups are hatched nearly naked and helpless (altricial) and are brooded until well able to regulate their body temperature. They are fed by the parents until after they are capable of flight. The young of numerous other birds, such as chickens, ducks, and shorebirds, are hatched with a heavy coat of down and are capable of foraging for themselves almost immediately (precocial). Still others, such as the petrels and the auks are downy when hatched but remain in the nest and are fed by their parents.

The length of time parents care for young birds varies widely. Young megapodes can fly shortly after hatching and are entirely independent of their parents; young royal albatrosses may spend up to 243 days at the nest and in the area immediately around it before they can fly. The length of time needed to attain independence is related to size and condition at hatching. Ground-nesting birds tend to take less and hole-nesting birds more time than the average.

The number of eggs in a set varies from 1 to about 20. Some species invariably lay the same number per clutch (determinate laying), whereas in the majority the number is variable (indeterminate laying). In species of the latter category, clutch size tends to be smaller in tropical regions than in cold ones. There is also a tendency for birds in warm regions to make more nesting attempts in a given season. In the Arctic, where the season is very short, the cycle of breeding and the molt that follows it are telescoped into a minimum of time.

Feeding habits. The earliest birds were probably insectivorous, as are many modern ones, and the latter have evolved many specializations for catching insects: swifts, swallows, and nightjars have wide gapes for catching insects on the wing; some woodpeckers can reach wood-boring grubs while others can catch ants by probing anthills with their long, sticky tongues; thrashers dig in the ground with their bills; tree creepers and woodhewers probe bark crevices; and warblers glean insects from many kinds of vegetation. Raptorial birds have evolved talons and hooked bills for feeding on larger animals, and vultures have bare heads and tearing bills for feeding on carrion. Herons have spearlike bills and trigger mechanisms in the neck for catching fish, while kingfishers, terns, and boobies plunge into the water after similar prey. Long-billed waders probe for worms and other invertebrates. Of the many kinds of birds that feed on plant material, most use seeds, fruit, or nectar, which are high in food value; leaves and buds are eaten by fewer species. While some kinds of birds feed entirely on a single kind of food, others may take a wide range of foods, and many have seasonal changes.

FORM AND FUNCTION

Body proportions. Birds arose as warm-blooded, arboreal, flying animals with forelimbs adapted for flight and hindlimbs for perching. This basic plan has become so modified, through the course of evolution, that in some forms it is difficult to recognize. The maximum size attainable by flying birds is limited by the fact that wing area varies as the square of linear proportions, and weight or volume as the cube. On the other hand, the minimum size is probably governed by another aspect of the surface-volume ratio: the relative increase, with decreasing size, in surface through which heat can be lost. The largest flying birds have highly pneumatic skeletons (part of the bone is replaced by air cavities) and other adaptations for reducing weight; the small size of some hummingbirds may be facilitated by the decrease in heat loss resulting from their becoming torpid at night.

When birds lose the power of flight, the limit on their maximum size is lifted, as can be seen in the ostrich and other ratite birds. Some birds (auks, diving petrels, and certain ducks) use the wings for propulsion underwater as well as in the air. When birds that "fly" underwater lose the ability to fly in air, the wings become highly modified as paddles, as in the penguins.

Wing shape

The types of flight found in birds vary considerably. At least two major types of modifications for gliding or soaring are found. The albatrosses and some other seabirds have long, narrow wings and take advantage of winds over the oceans, whereas some vultures and hawks have broad wings with slotted tips and make more use of updrafts and winds deflected by hills. Short, broad wings are characteristic of chicken-like birds, which fly up with a rush of rapid wing beats. Birds like ducks, pigeons, and falcons, which fly rapidly with continuous wing beats, tend to have moderately long, pointed wings, while swifts and hummingbirds, with their narrow, curved wings fly rapidly and manoeuvre easily. The shape of a bird's tail also appears to be related to flight. Forms with deeply forked tails, such as frigate birds, terns, and some swallows, manoeuvre easily, whereas the opposite extreme, long, graduated tails, are often found in rapid, direct fliers such as some parrots and doves. Woodpeckers and some other climbing birds have strong tail feathers with stout shafts, which they use as props while on the trunks of trees.

The bipedal gait, dictated by modification of the forelimbs for flight, necessitates manipulating food by the bill and feet and poses problems in balance. The relative lengths of the segments of the legs must be such that as the bird shifts from a standing to a sitting position, its centre of gravity remains over the feet. As some birds moved out of the trees and became terrestrial or aquatic, their legs were accordingly modified. The toes became shorter and the opposable first toe was lost in rapidly running forms like rheas and ostriches, and the toes became very long in birds that walk on aquatic vegetation or soft ground. In very large, slow-moving birds such as moas, the leg bones became very heavy. Wading birds developed long legs, and climbing birds developed short legs with strongly curved, sharp claws. In swimming and diving birds, webs developed between the toes or lobes on the sides of the toes.

Feathers and molt. Feathers are unique to birds and characteristic of them. Like the scales of reptiles, and those on the feet of birds, feathers are made of keratin, a fibrous protein also found in hair. Feathers vary considerably in structure and function (Figure 2). Contour feathers form most of the surface of the bird, streamlining it for flight and often waterproofing it. The basal portion may be downy and thus act as insulation. The major contour feathers of the wing (remiges) and tail (rectrices) and their coverts function in flight. Contour feathers grow in tracts (pterylae) separated by bare areas (apteria) and develop from follicles in the skin.

Drawing by R. Keane

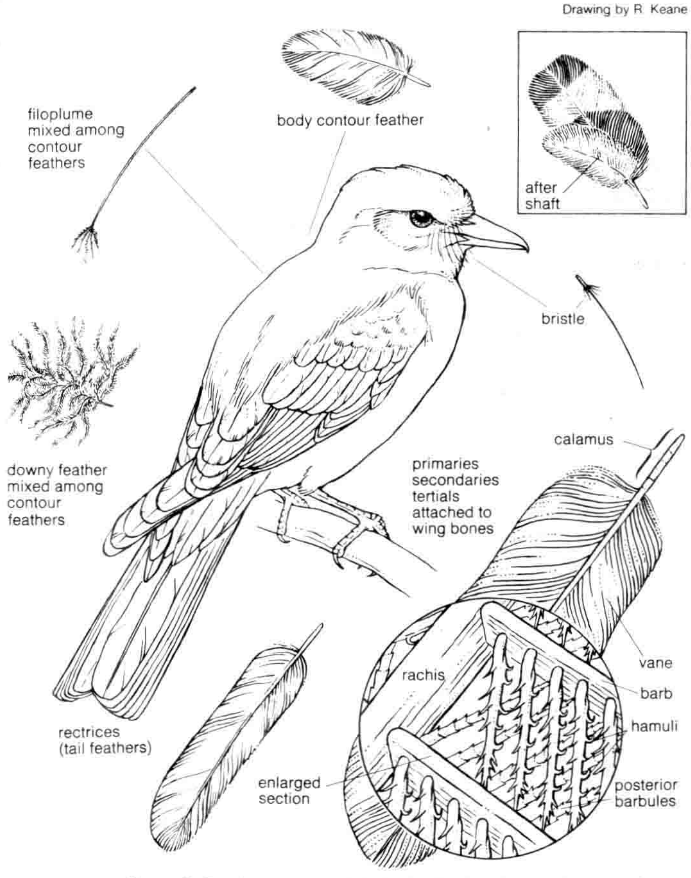

Figure 2: Feather types and their distribution on a typical perching bird.

Feather structure

The typical contour feather consists of a tapered central shaft, the rachis, with paired branches (barbs) on each side. An unbranched basal section of the rachis is called the calamus, part of which lies beneath the skin. The barbs, in turn, have branches, the barbules. The barbules on the distal side of each barb have hooks (hamuli) that engage the barbules of the next barb. The barbs at the base of the vane are often plumaceous; *i.e.*, lacking in hamuli and remaining free of each other. In many birds each contour feather on the body (but rarely on the wings) is provided with a complex branch, the aftershaft, or afterfeather, that arises at the base of the vane. The aftershaft has the appearance of a second, smaller feather, growing from the base of the first. Down feathers have loose-webbed barbs, all rising from the tip of a very short shaft. Their function is insulation, and they may be found in both pterylae and apteria in adult birds. They also constitute the first feather coat of most young birds. Filoplumes are hairlike feathers with a few soft barbs near the tip. They are associated with contour feathers and may be sensory or decorative in function. Bristle-like, vaneless feathers occur around the mouth, eyes, and nostrils of birds. They are especially conspicuous around the gape (corners of the mouth) of birds that catch insects in the air. Some bristles function as eyelashes on ground-dwelling birds, and the bristles over the nostrils may serve as filters.

The contour feathers are shed and replaced (molted) at least once a year, usually just after the breeding season. In addition, many birds have at least a partial molt before the breeding season. A typical series of molts and plumages would be juvenile plumage, postjuvenile (also called first prebasic) molt, first winter (or first basic) plumage, first prenuptial (or pre-alternate) molt, first nuptial (or alternate) plumage, first postnuptial (first annual, or second prebasic) molt, second winter (or basic) plumage, etc. Molt of the remiges and rectrices usually occurs as part of the annual molt and can be serial, from the innermost feather out (centrifugal), from the outermost in (centripetal), or simultaneous. Normally it is symmetrical between the right and left sides.

Coloration

Colour in birds is caused by pigments or structure. Buffs, red browns, dark browns, and blacks are caused by melanins, pigments synthesized by the bird and laid down in granules. Yellows, oranges, and reds come from carotenoid or lipochrome pigments; these originate at least in part from the food and are diffused in the skin and feathers. Porphyrin feather pigments occur in birds but less frequently than melanins and carotenoids. Blue colours in feathers are structural, based on a thin, porous layer of keratin overlying melanin pigment. Most greens result from the addition of yellow pigment to the structural blue colour. Iridescent colours result from thinly laminated structure of the barbules and are enhanced by underlying melanin deposits.

Birds' feet are covered with scales like those of reptiles. The scales are occasionally shed, but the timing of this molt is not known. The toes are tipped with claws, and vestigial claws are not infrequently found on the tips of the first two digits of the wing.

The bill is covered with a sheet of keratin, the rhamphotheca, which in petrels and a few other birds is divided into plates. In birds that probe for food (kiwis, woodcock, etc.), many sensory pores are found near the tip of the bill. Both melanins and carotenoids are found in the rhamphotheca and in the scales of the feet.

The skin of a bird is almost without glands. The important exception is the oil (uropygial) gland, which lies on the rump at the base of the tail. The secretion of

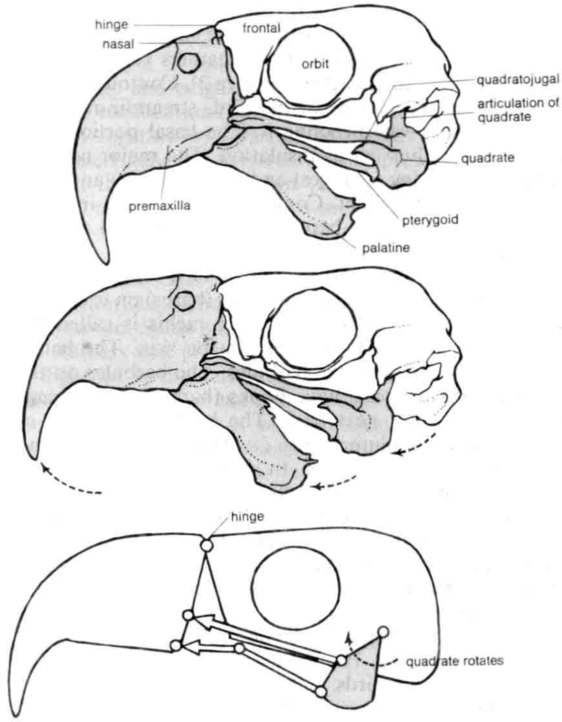

Figure 3: *Kinesis of the cranium of a macaw.*
(Top) With upper mandible lowered. (Centre) With upper mandible raised. (Bottom) Showing forces acting on mandible.

Drawing by R. Keane based on A. Bellairs and C.R. Jenkin, "The Skeleton of Birds," in J. Marshall (ed.), *Biology and Comparative Physiology of Birds*, vol. 1; Academic Press, Inc.

this gland contains approximately one-half lipids (fats) and is probably important in dressing and waterproofing the plumage. In a few birds, the secretion has a strong, offensive odour. Some birds, in which the oil gland is small or absent, have a specialized type of feather (powder down) that grows continuously and breaks down into a fine powder, believed to be used in dressing the plumage.

Skeleton. The avian skeleton (Figure 4) is notable for its strength and lightness, achieved by fusion of elements and by pneumatization (*i.e.*, presence of air cavities). The skull represents an advance over that of reptiles in the relatively larger cranium with fusion of elements, made possible by the fact that birds have a fixed adult size. Birds differ from mammals in being able to move the upper mandible, relative to the cranium. When the mouth is opened, both lower and upper jaws move: the former by a simple, hingelike articulation with the quadrate bone at the base of the jaw, the latter through flexibility provided by a hinge between the frontal and nasal bones. As the lower jaw moves downward, the quadrate rocks forward on its articulation with the cranium, transferring this motion through the bones of the palate and the bony bar below the eye to the maxilla, the main bone of the upper jaw.

Movable upper mandible

The number of vertebrae varies from 39 to 63, with remarkable variation (11 to 25) within the cervical (neck) series. The principal type of vertebral articulation is heterocoelous (saddle shaped). The three to 10 (usually five to eight) thoracic (chest) vertebrae each normally bear a pair of complete ribs consisting of a dorsal vertebral rib articulating with the vertebra and with the ventral sternal rib, which in turn articulates with the sternum (breastbone). Each vertebral rib bears a flat, backward-pointing spur, the uncinate process, characteristic of birds. The sternum, ribs, and their articulations form the structural basis for a bellows action, by which air is moved through the lungs. Posterior to the thoracic vertebrae is a series of 10 to 23 fused vertebrae, the synsacrum, to which the pelvic girdle is fused. Posterior to the synsacrum is a series of free caudal (tail) vertebrae and finally the pygostyle, which consists of several fused caudal vertebrae and supports the tail feathers. The sternum consists of a plate lying ventral to the thoracic cavity and a median keel extending ventrally from it. The plate and keel form the major area of attachment for the flight muscles. The bones of the pectoral girdle consist of the furcula (wishbone) and the paired coracoids and scapulas (shoulder blades). The sword-shaped scapula articulates with the coracoid and humerus (the bone of the upper "arm") and lies just dorsal to the rib basket. The coracoid articulates with the anterior (forward) edge of the sternum and with the scapula, humerus, and furcula. The furcula connects the shoulder joints with the anterior edge of the keel of the sternum. It consists of paired clavicles (collarbones) and, probably, the median, unpaired interclavicle.

The bones of the forelimb are modified for flight with feathers. Major modifications include restricting the motion of the elbow and wrist joints to one plane, reduction of the number of digits, loss of functional claws, fusion of certain bones of the "hand" (the metacarpals and most of the carpals) into a carpometacarpus, and modification of the elements, especially those toward the tip of the limb (distal), for the attachment of feathers. The wing bones are hollow, and the cavity in the humerus, at least, is connected with the air-sac system. As a general rule, large flying birds have proportionally greater pneumaticity in the skeleton than small ones. The highly pneumatic bones of large flying birds are reinforced with bony struts at points of stress. The humerus, radius, and ulna are well developed. The secondary flight feathers are attached to the ulna, which thus directly transmits force from the flight muscles to these feathers and is therefore relatively heavier than the radius. Two small wrist bones are present: the radiale, or scapholunar, and the ulnare, or cuneiform. The former lies between the distal end of the radius and the proximal part (the part toward the body) of the carpometacarpus. When the elbow joint is flexed (bent), the radius slides forward on the ulna and pushes the radiale against the carpometacarpus, which in turn flexes the wrist. Thus the two joints operate simultaneously. The U-shaped ulnare articulates with the ulna and the carpometacarpus. Anatomists differ on which bones of the reptilian "hand" are represented in the bird's wing. Embryological evidence suggests that the digits are II, III,

Wing skeleton

Drawing by R. Keane based on L. Darling and L. Darling, *Bird* (1962); Houghton Mifflin Company

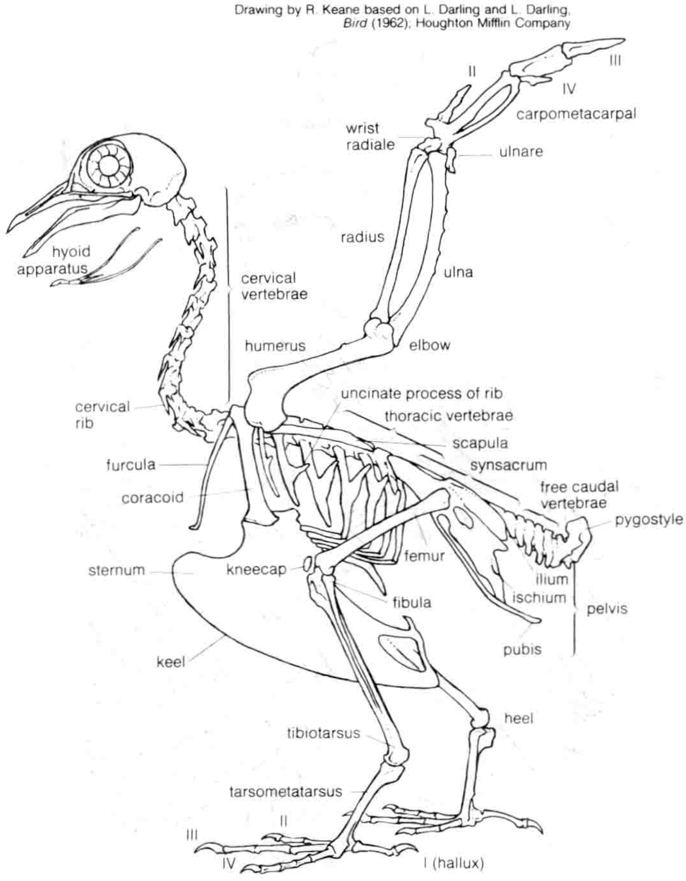

Figure 4: Pigeon skeleton, with the near wing raised and the far wing omitted.

and IV, but it is possible that they are actually I, II, and III. The carpometacarpus consists of fused carpals (bones of the wrist) and metacarpals (bones of the palm), metacarpals II and III (or III and IV) contributing the greater part of the bone. The phalanges (bones of the "fingers") are reduced to one each on the outer and inner digits and two on the middle one. The primary flight feathers are attached to the carpometacarpus and digits, the number attached to each being characteristic of the various major groups of birds.

Pelvis and leg

The pelvic girdle consists of three paired elements, the ilia, ischia, and pubes, which are fused into a single piece with the synsacrum. The ilium is the most dorsal element and the only one extending forward of the acetabulum

Drawing by R. Keane based on L. Darling and L. Darling, *Bird* (1962); Houghton Mifflin Company

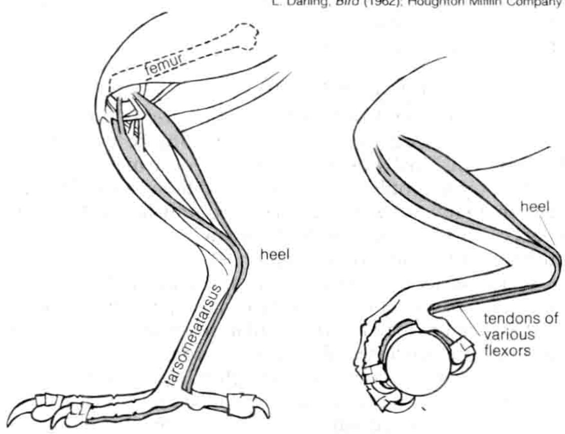

Figure 5: Perching mechanism of a pigeon with the leg extended and flexed.

(the socket of the leg). The ilium is fused with the synsacrum and the ischium, the latter of which is fused with the pubis. All three serve as attachments for leg muscles and contribute to the acetabulum, which forms the articulation for the femur. The leg skeleton consists of the femur (thighbone), tibiotarsus (main bone of the lower leg), fibula, tarsometatarsus (fused bones of the ankle and middle foot), and phalanges (toes). The fibula is largest at its proximal (upper) end, where it forms part of the knee joint and tapers to a point distally, never forming part of the ankle joint. The latter joint is simplified, there being but two bones involved: the tibiotarsus, consisting of the tibia (the so-called shinbone in man) fused with the three proximal tarsals (upper ankle bones), and the tarsometatarsus, resulting from the fusion of metatarsals I through IV and the distal row of tarsals. Metatarsals II through IV contribute most to the tarsometatarsus. The basic number of phalanges (sections) on the toes is two, three, four, and five, respectively; *i.e.*, one more than the number of the toe. Most birds have four toes, the fifth being always absent, but there are many variations in the number of digits, or phalanges, representing reductions of the basic arrangement.

The basic avian foot is adapted for perching. The first, or hind, toe (hallux) opposes the other three, and the tendons for the muscles that bend the toes pass behind the ankle joint in such a way that when the ankle is bent the toes are also. The weight of a crouched bird thus keeps the toes clasped around the perch.

Muscles

Internal organs. The cardiac (heart) muscles and smooth muscles of the viscera of birds resemble those of reptiles and mammals. The smooth muscles in the skin include a series of minute feather muscles, usually a pair running from a feather follicle to each of the four surrounding follicles. Some of these muscles act to raise the feathers, others to depress them. The striated (striped) muscles that move the limbs are concentrated on the girdles and the proximal parts of the limbs. Two pairs of large muscles move the wings in flight: the pectoralis, which lowers the wing, and the supracoracoideus, which raises it. The latter lies in the angle between the keel and the plate of the sternum and along the coracoid. It achieves a pulley-like action by means of a tendon that passes through the canal

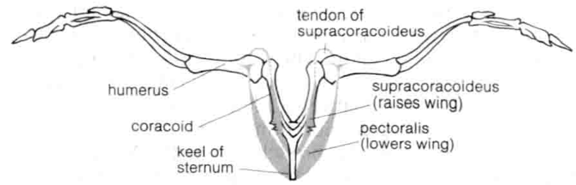

Figure 6: Pectoral girdle of a generalized bird.

Drawing by R. Keane based on L. Darling and L. Darling, *Bird* (1962); Houghton Mifflin Company

at the junction of the coracoid, furcula, and scapula and attaches to the dorsal side of the head of the humerus. The pectoralis lies over the supracoracoideus and attaches directly to the head of the humerus. In most birds the supracoracoideus is much smaller than the pectoralis, weighing as little as one-twentieth as much; in the few groups that use a powered upstroke of the wings (penguins, auks, swifts, hummingbirds, and a few others), the supracoracoideus is relatively large. Avian striated muscles contain a respiratory pigment, myoglobin. There are relatively few myoglobin-containing cells in "white meat," whereas "dark meat" derives its characteristic colour from their presence. The former type of muscle is used in short, rapid bursts of activity, whereas the latter is characteristic of muscles used continuously for long periods and especially in muscles used during diving.

Circulatory features

The circulatory system of birds is advanced over that of reptiles in several ways: (1) there is a complete separation between the pulmonary (lung) and systemic (body) circulations, as in the mammals; (2) the left systemic arch (aortic artery) is lost, blood passing from the heart to the dorsal aorta via the right arch; (3) the postcaval vein is directly connected with the renal portal that connects the kidneys with the liver; and (4) the portal circulation through the kidneys is greatly reduced. Birds' hearts are large—0.2 to over 2.4 percent of body weight, as opposed to 0.24 to 0.79 percent in most mammals.

The avian lung differs from the type found in other land vertebrates, in containing fine tubes (capillaries) through which air passes and through the walls of which gas ex-

Drawing by R. Keane based on A.L. Thomson (ed.), *A New Dictionary of Birds*, British Ornithologists' Union and J. Marshall (ed.), *Biology and Comparative Physiology of Birds* (1961); Academic Press

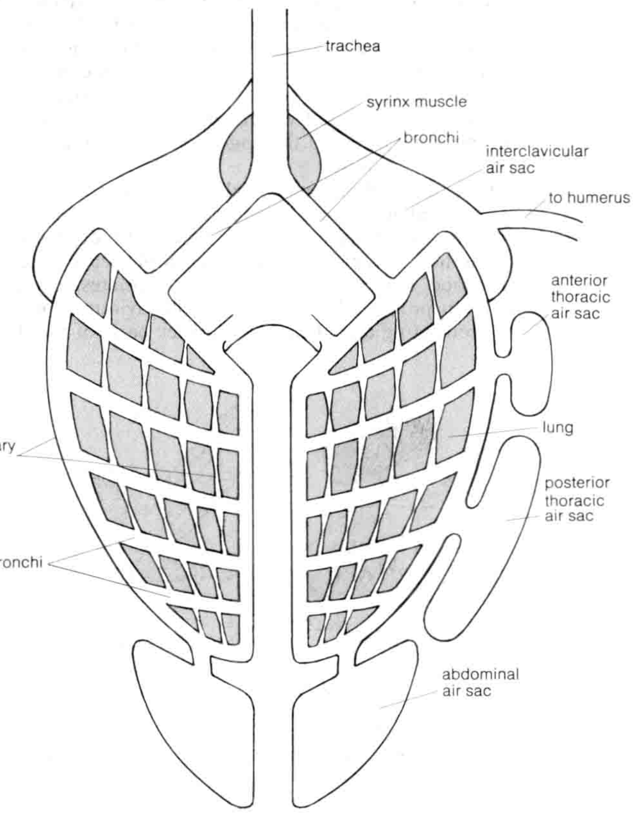

Figure 7: Avian lung and air sac system in a generalized bird.

change takes place. Several pairs of nonvascular air sacs are connected with the lungs and extend into the pneumatic parts of the skeleton. The sound-producing organ in birds is the syrinx, located where the trachea (windpipe) divides into the bronchial tubes. The sounds are made by the flow of air setting up vibrations in membranes formed from part of the trachea, bronchi, or both. Muscles between the sternum and trachea or along the trachea and bronchi vary tension on the membranes.

The avian digestive system shows adaptations for a high metabolic rate and flight. Enlargements (collectively called the crop) of parts of the esophagus permit the temporary storage of food prior to digestion. The stomach is typically divided into a glandular proventriculus and a muscular gizzard, the latter lying near the centre of gravity of the bird and compensating for the lack of teeth and the generally weak jaw musculature. Otherwise, the digestive system does not vary markedly from the general vertebrate type.

Like reptiles, birds possess a cloaca, a chamber that receives digestive and metabolic wastes and reproductive products. A dorsal outpocketing of the cloaca, the bursa of Fabricius, controls antibody-mediated immunity in young birds. The bursa regresses with age, and thus its presence or absence may be used to determine age.

The testes of the male bird are internal, like those of reptiles. Intromittent organs are found in only a few groups (waterfowl, cracids, tinamous, ratites). The distal part of the vas deferens (the seminal sac) becomes enlarged and convoluted in the breeding season and takes on both secretory and storage functions. In passerine birds, at least, this enlargement and the adjacent part of the cloaca form a cloacal protuberance, a swelling visible on the outside of the bird. Usually only the left ovary and oviduct are functional. The albumen, membranes, and shell are laid down in the oviduct as the egg moves down it. The gonads and accessory sexual organs of both sexes enlarge and regress seasonally. In the breeding season, the testes of finches may increase over 300-fold in volume over their winter size.

Temperature control

Birds are homeothermic (warm-blooded) and maintain a body temperature of approximately 41° C (106° F). This temperature may be 1–1.7° C less during periods of sleep and up to 2° C higher at times of great activity. Feathers, including down, provide effective insulation. In addition, layers of subcutaneous fat add further insulation in penguins and in some other water birds. Reduction of heat loss from the feet in cold weather is accomplished by reducing blood flow to the feet and by a heat-exchange network in the blood vessels of the upper leg, so that the temperature of blood flowing into the unfeathered part of the leg is very low.

Birds differ from mammals in lacking sweat glands, hence heat loss is accomplished by rapid panting, which reaches 300 respirations per minute in domestic hens. Some heat dissipation can be accomplished by regulation of blood flow to the feet. In hot climates, overheating is often prevented or reduced by behavioural means—by concentrating activities in the cooler parts of the day and seeking shade during the hot periods. Temporary hypothermia (lowered body temperature) and torpor are known for several species of nightjars, swifts, and hummingbirds. Torpor at night is believed to be widespread among hummingbirds. The heart rate of birds varies widely—from 60 to 70 beats per minute in the ostrich to more than 1,000 in some hummingbirds.

The kidneys lie in depressions that are located on the underside of the pelvis. The malpighian bodies, which are the active tubules of the kidney, are very small in comparison to those of mammals, ranging from 90 to 400 per cubic millimetre. More than 60 percent of the nitrogen is excreted as uric acid or its salts. There is some resorption of water from the urine in the cloaca, with uric acid remaining. There is no urinary bladder, the urine being voided with the feces. In marine birds, salt is excreted in a solution from glands lying above the eyes through ducts leading to the nasal cavity.

EVOLUTION AND PALEONTOLOGY

Archaeopteryx

The earliest known fossil bird is *Archaeopteryx lithographica*, which was discovered in Upper Jurassic deposits in Bavaria. This bird was about the size of a magpie. It resembled some reptiles, however, and differed from Recent birds in many ways: (1) the jaws contained teeth set in sockets; (2) the articulations between the vertebrae were amphicoelous (concave at both ends); (3) there were only six sacral vertebrae; (4) the long tail was made up of a series of free vertebrae each bearing a pair of rectrices; (5) the slender ribs lacked articulations with the sternum and uncinate processes (flat upward projections); (6) ventral ribs (gastralia) were present behind (posterior to) the sternum; (7) the sternum was short and not keeled; (8) the bones were not pneumatic; (9) the third metacarpal bone in the wing was fused to the carpals, but the first two metacarpals were free, resulting in three movable digits of the "hand," all with functional claws; (10) the fibula was as long as the tibia; (11) the metatarsal bones were free; (12) the cerebral hemispheres were elongated and slender, and the cerebellum lay behind the midbrain, not overlapping it from behind or crowding it downward. The avian characteristics of *Archaeopteryx* included the possession of feathers, the elongated, backward-directed pubis, the furcula, and the opposable hallux. In the structure of the beak, eye, and jaw articulation, in the fusion of the third metacarpal with the carpals, and in the fusion of each of the distal tarsals with the corresponding metatarsal, *Archaeopteryx* represented an intermediate stage between reptiles and modern birds.

The absence of a keel on the short sternum indicates that *Archaeopteryx* did not fly but glided. The opposable hallux, indicative of the perching type of foot, and the clawed digits of the hand point to an arboreal existence. From the arrangement of feathers on the wing and the number and arrangement of bones in the limbs, it appears that *Archaeopteryx* was near the main line of avian evolution. From the fact that the skull was diapsid (*i.e.*, had two "windows") and from certain features of the limb bones,

Drawing by R. Keane

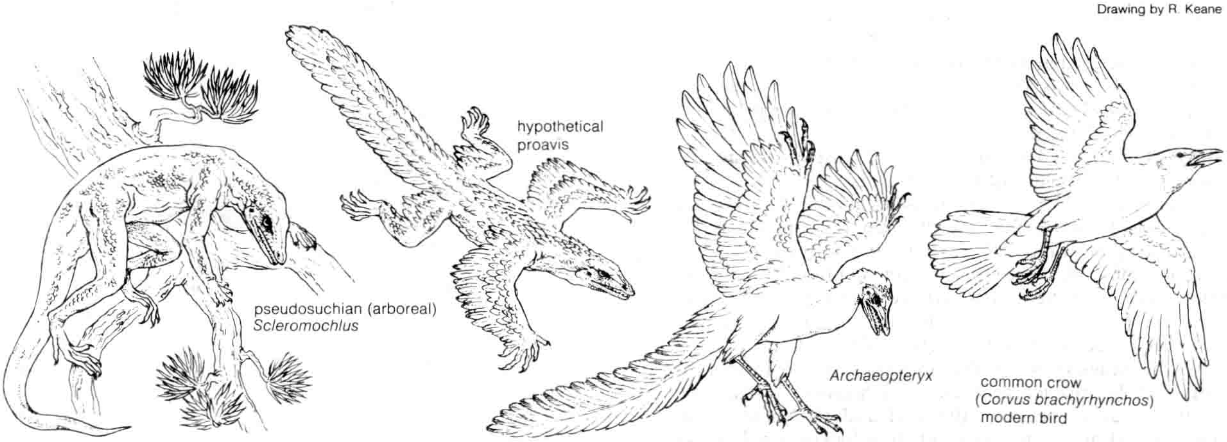

Figure 8: Four stages in the evolution of modern birds.

it appears that *Archaeopteryx* was descended from reptiles of the Triassic order Thecodontia.

The origins of flight

By the Triassic Period (225,000,000 years ago) a group of small bipedal reptiles, the pseudosuchians, were well established. Their skulls had much in common with that of *Archaeopteryx,* although they had heavier jaws and smaller eyes. It is likely that one group of pseudosuchians became arboreal. The advantages of such a life would be safety from large terrestrial predators and an abundance of insect food. Once these reptiles were in the trees, selective pressures would favour mutations leading to many avian features. The swaying of branches would favour the evolution of the grasping foot. Use of the forelimbs in climbing from branch to branch would favour enlargement of the claws and elongation of the forelimb, which was short in the bipedal ancestors. Greater visual acuity and more effective coordination are of special advantage in arboreal animals. Natural selection thus favoured larger eyes, narrower snouts (permitting better forward vision), and greater development of the cerebral lobes and cerebellum of the brain. The smaller jaws may also indicate the advantages of lightness, balance, and a specialization for feeding on insects as opposed to the apparently more general carnivorous diet of the terrestrial ancestors. Perhaps most important was the development of homeothermy (internal temperature control). A warm-blooded insect eater has an enormous advantage in being able to capture insects when they are cold and slow to react. It is also advantageous in the wind-moved environment of the treetops. In addition to increased food intake and advanced respiratory and circulatory systems, however, homeothermy requires effective insulation. It is likely that feathers evolved to fill this requirement, although many authorities believe the origin of feathers was directly connected with flight. Just how feathers evolved from reptilian scales is unknown, but it is known that the two are similar in chemical composition and that some pseudosuchians had scales bearing an imprint of a feather-like pattern on their surface. Elongated feathers on the forelimb and tail may have evolved for balancing and for gliding to produce the *Archaeopteryx* stage.

In the evolution of modern birds from an *Archaeopteryx*-like form, the development of active flight must have occurred early. This meant an increase in size of the muscles moving the wing and the development of a keel on the sternum as an added area of attachment for these muscles. As the tail took on more of a steering function and less of a supportive one, it became shorter and more readily moved as a unit. Feathers became increasingly specialized for different functions, and at the same time, the trends in the development of the eyes, brain, and respiratory and circulatory systems associated with the evolution of the homeothermic, arboreal, gliding types continued. By the time birds became strong fliers, they were ready to radiate out into many new environments; and by the Cretaceous Period (136,000,000 to 65,000,000 years ago), they had begun to do so. This radiation has produced the large array of adaptive types known today.

The lightness and pneumaticity of bird bones makes them poor candidates for fossilization. As might be expected, heavyboned diving birds and large flightless birds are disproportionally represented in the record.

Cretaceous birds

One of the best known groups of fossil birds consists of *Hesperornis* and its relatives. These birds were highly specialized foot-propelled divers of the Upper Cretaceous. The known species of *Hesperornis* were up to six feet (1.8 metres) long and had completely lost the power of flight. The sternum lacked a keel; the humerus was small and weak; and the other, more distal, elements of the wing were missing. The pelvis and hindlimb had a strong but superficial resemblance to those of modern loons and grebes—the pelvis was narrow; the femur short and stout with a hingelike articulation with the pelvis; the tibiotarsus long, with a long cnemial crest (a projection at its upper end); and the tarsometatarsus laterally compressed. Two major features (and several less obvious ones) indicate, however, that the resemblance was the result of convergent evolution: the ischia and pubes were free for most of their length, and the cnemial process was made up entirely of the patella; in the loon, this process is derived from the tibiotarsus. *Hesperornis* was remarkable for three features: it had teeth set in grooves, not sockets, in the maxilla and mandible; the phalanges of the stout fourth toe had a unique rotary ball-and-flange type of articulation; and the free tail vertebrae had broad lateral projections and limited vertical motion, indicating that the tail was somewhat beaver-like in its action. *Baptornis,* a contemporary relative of *Hesperornis,* was smaller and less strongly modified. While flightless, it had less reduced wings than *Hesperornis,* and it lacked the peculiar modifications of the fourth toe and caudal vertebrae.

Living on the same seas as *Hesperornis* and *Baptornis* was a group of flying birds known as *Ichthyornis* and *Apatornis.* Although not related to gulls, these birds resembled them superficially and may well have been their ecological counterparts. It was long believed that *Ichthyornis* had teeth, like *Hesperornis;* but it is now thought that the toothed jaws formerly thought to belong to *Ichthyornis* were really those of a small mosasaur, a marine reptile.

Large flightless predators

After the extinction of the dinosaurs and before large carnivorous mammals evolved, two groups of large flightless birds evolved to fill a similar niche. From the upper Paleocene to the middle Eocene, *Diatryma* and its relatives were major predators in the Northern Hemisphere. The largest species stood over two metres (seven feet) tall and had stout hooked beaks. They are of uncertain relationships but may have been distantly related to cranes and rails. The second group, that of *Phororhacos* and related genera, had a long history (from the lower Oligocene to the middle Pliocene) in South America, which was without large carnivores until relatively late. Fragmentary Pleistocene material from Florida has also been assigned to this group. The *Phororhacos* line evidently evolved from cariama-like stock and radiated into numerous genera and species, the largest of them (*Onactornis*) standing 2.5 metres (eight feet) tall and having a skull 80 centimetres (31 inches) long and 40 centimetres (16 inches) high.

Large grazing or browsing birds appear to have evolved several times. On continents where there are large predators, these birds have always been rapid runners (ostriches, rheas, emus), but on islands lacking such predators, they were slow-moving, heavy-bodied birds. Two such groups were the elephant birds of Madagascar and the moas of New Zealand, the largest in each group approaching 10 feet in height. Fragmentary fossil material from Eocene and Oligocene deposits in Egypt indicates that similarly adapted birds occurred there before the advent of large carnivores.

Except for the *Hesperornis* line, teeth appear to have been lost very early in the history of birds, but fish-eating birds have evolved several toothlike structures for grasping their prey. Perhaps the most remarkable adaptation was that of *Osteodontornis* and its relatives, large, flying marine birds that flourished from the lower Eocene to the Miocene. In these birds, there were bony projections of the upper and lower jaws, which were covered by the ramphotheca, forming sharp, toothlike structures.

The fact that fewer bird fossils are found in earlier deposits is well illustrated by expressing the number of known species in a given geological period in terms of the duration of the period. About 35 species of birds are known from Cretaceous deposits, which were laid down over an estimated 71,000,000 years, giving a figure of 0.5 species per 1,000,000 years. The corresponding figure for the Paleocene is 1.2 (12 species in 10,000,000 years) and that for the Eocene, 5.4 (87 species in 16,000,000 years). Up-to-date figures for the later periods are not available, but estimates based on several recent sources are 7.9 per 1,000,000 years in the Oligocene, 12.3 in the Miocene, and 21.8 in the Pliocene. The Pleistocene, which lasted approximately 2,500,000 years, has yielded nearly a thousand species of fossil birds. From this it is evident that very little is known about the early avifaunas. It is known, however, that, as might be expected, the birds in the earlier periods differ more from Recent species than do those of the later periods. Of the 12 families of birds recorded from Cretaceous deposits, only two are still extant, whereas the majority of species recorded from the Pleistocene were structurally little, if at all, different from living forms. Thus the absence of a group in the fossil record, especially in the earlier periods, is rarely significant.

The major diversification of birds probably took place in the Cretaceous, which lasted longer than the sum of all subsequent periods, and it must have started early in that period because fragmentary material of foot-propelled divers (*Enaliornis*) and of an early relative of the flamingos (*Gallornis*) are known from Lower Cretaceous deposits of Europe. Upper Cretaceous deposits have yielded, besides *Hesperornis* and *Ichthyornis* and their relatives, diving birds similar to *Enaliornis* (*Lonchodytes*), other early flamingo-like birds, and species in the same suborders as gannets, ibises, rails, and shorebirds.

Paleocene deposits have yielded the earliest known loons, cormorants, New World vultures, and gulls. In addition, the large, flightless predatory birds culminating in *Diatryma* first made their appearance during this period. From the far richer Eocene deposits have come the earliest known rheas, penguins, albatrosses, tropic birds, anhingas, true flamingos, herons, storks, secretary birds, hawks, curassows, cranes, bustards, avocets, auks, sand grouse, cuckoos, owls, swifts, trogons, rollers, hornbills, and songbirds. Almost certainly all living orders and most living families of birds were in existence by the end of the Eocene period. One of the most interesting finds from this period was fossils of *Neocathartes,* a long-legged bird allied to the New World vultures. There are several anatomical similarities between this group of vultures and the storks, and the existence of this fossil lends support to the idea that the storks and New World vultures are more closely related to each other than each family is to the birds with which it is usually grouped.

Important Oligocene fossils include the earliest phororhacoids, one of the few groups of fossil birds that is known from enough material from over a long enough time span to show evolutionary trends, in this case, both in size and in bill form.

Fossils of Miocene birds are numerous. Several early groups of pelecaniform, cranelike, and flamingo-like birds are known last from this period, and the first of the Mancallidae, superficially penguin-like auks, appeared. Otherwise, the avifauna was essentially modern.

By Pliocene times, most modern genera were probably in existence. The Mancallidae continued on the California coast at least until the middle of the period.

The appearance and extinction of large birds as well as mammals was a feature of the Pleistocene. Perhaps most notable were the teratorns, "super condors," which were found in North America. These included *Teratornis incredibilis,* the largest known flying bird.

CLASSIFICATION

Distinguishing taxonomic features. In classifying birds, most systematists rely primarily on structural characters. Plumage characters include the number of remiges and rectrices; the presence or absence of down on the feather tracts, on apteria, and on the oil gland; and the presence or absence of an aftershaft. Characteristics of the bill and feet are useful, as is the arrangement of bones in the palate and around the nostrils. The presence or absence of certain thigh muscles and the arrangement of the carotid arteries, the syrinx, and the deep flexor tendons of the toes are employed, as is the condition of the young when hatched. Advances in the study of protein structure and of chromosomes have provided new means of determining taxonomic relationships.

Annotated classification. This classification is based primarily on that of the American ornithologist Alexander Wetmore but includes the ideas of a number of other authorities. It is unlikely that most avian systematists would agree on all aspects of one arrangement, but the one presented below will satisfy many. The dagger (†) indicates extinct groups, known only from fossils.

CLASS AVES

Vertebrate (backboned) animals primarily adapted for flight with feathers. Warm-blooded, 4-chambered heart, left systemic arch lost. Lower jaw articulates with cranium via the quadrate; teeth absent in living forms. Reproduction by hard-shelled eggs, nearly always incubated by one or both parents. About 8,600 living species.

†Subclass Archaeornithes

†*Order Archaeopterygiformes (Archaeopteryx).* Upper Jurassic; Europe. Teeth set in sockets; long, unfused caudal vertebrae, each bearing a pair of rectrices; keelless sternum; functional claws on digits of hand. Gliding birds, about 50 cm long.

Subclass Neornithes

†*Superorder Odontognathae*

†*Order Hesperornithiformes (Hesperornis, Baptornis).* Upper Cretaceous; North and South America. Teeth set in groove in jaws. Flightless, foot-propelled diving birds, 1 to 2 m long.

Superorder Neognathae

Order Tinamiformes (tinamous). Upper Pliocene to present; Central and South America. Superficially quaillike or grouselike ground-dwelling birds with flat, elongated, and rather weak bills and very small tails. Size 15–50 cm.

Order Rheiformes (rheas). Lower Eocene to present; South America. Ostrich-like cursorial birds with very small tails and no aftershaft on the feathers. Sexes alike. Length 90–130 cm.

Order Struthioniformes (ostrich). Lower Pliocene to present (the Eocene *Eleutherornis* may belong here); southwestern Asia and Africa (fossils from southern Europe and southeastern Asia). 2-toed (3rd and 4th) running birds. Males black and white, females brown. Aftershafts, down, and filoplumes absent. Largest living bird; length to 180 cm, height 260 cm, weight 136 kg, egg 1.6 kg.

Order Casuariiformes (emus, cassowaries). Pleistocene to present; Australia, New Guinea, adjacent islands. Very large, cursorial (running) birds. Sexes alike, brown (emus) or blackish with brightly coloured wattles and skin on head (cassowaries). Aftershaft very large. Length 130–190 cm.

†*Order Aepyornithiformes* (elephant birds). Pleistocene; Madagascar (upper Eocene and lower Oligocene fossils from Egypt have been placed here). Very large and graviportal (heavy bodied); height to 3 m; egg weight estimated at 10 kg.

Order Dinornithiformes (moas, kiwis). Upper Miocene or lower Pliocene to present; New Zealand. Very large (to 3 m tall) and graviportal birds (moas) or smaller (length 30–80 cm); almost wingless, nocturnal, probing birds (kiwis).

Order Podicipediformes (grebes). Lower Miocene to present; worldwide. Foot-propelled diving birds with lobed toes, minute tails, and silky plumage. Length 21–66 cm.

Order Procellariiformes (albatrosses, shearwaters, fulmars, prions, petrels). Middle Eocene to present; all oceans, but most numerous in Southern Hemisphere. Web-footed marine birds with tubular nostrils; rhamphotheca divided into plates; possess a musky smell. Most have narrow wings and stiff, gliding flight. Length 14–135 cm.

Order Sphenisciformes (penguins). Upper Eocene to present; oceans of Southern Hemisphere. Wings flipper-like, for propulsion underwater; webbed feet short and stout; stance upright. Feathers short and dense, molted in patches. Length 40–120 cm (fossil forms to 180 cm).

Order Pelecaniformes (pelicans, boobies, tropic birds, cormorants, frigate birds). Paleocene to present; worldwide. Water birds with all 4 toes webbed; bill hooked or straight and sharply pointed. Length 50–180 cm.

Order Anseriformes (screamers, waterfowl). Middle Eocene to present. Web-footed birds with broad bills containing fine plates or lamellae (waterfowl); or large-footed marsh birds with chicken-like bills (screamers). Length 29–160 cm.

Order Phoenicopteriformes (flamingos). Cretaceous to present; discontinuously distributed in warm regions except Australasia. More varied and widely distributed as fossils. Web-footed birds with long legs, long necks, bent bills with lamellae, and much pink or red in the plumage. Share characters with both Anseriformes and Ciconiiformes, but evidently closer to the latter, with which they are sometimes grouped. Length 91–122 cm (some fossil forms smaller).

Order Ciconiiformes (herons, storks, ibises, spoonbills). Upper Cretaceous to present; worldwide except in extreme north. Long-legged wading birds with long bills; feet not webbed. Although usually grouped together, herons and storks may prove to belong to different orders. Length 28–152 cm.

Order Falconiformes (diurnal birds of prey). Upper Paleocene to present; worldwide. Diurnal raptors with hooked beaks, long talons, and short (hawks, falcons) or very long (secretary bird) legs or carrion-eating birds with weaker claws and tearing bills (vultures, condors). Length 15–150 cm (some fossil forms larger).

Order Galliformes (grouse, pheasants, quail, turkeys). Middle Eocene to present; nearly worldwide, except southern South America. Terrestrial or arboreal chicken-like birds; strong, scratching feet; short, rounded wings; feathers with long aftershafts. Length 13–198 cm.

Order Gruiformes (cranes, rails, coots, cariamas, bustards). Upper Cretaceous to present; worldwide. Diverse group, ranging from small quail-like hemipodes to large long-legged cranes, marsh-inhabiting rails, swimming coots and fin-foots, and cursorial bustards. The Tertiary phororhacoids belong here, as may the very large *Diatryma* and its relatives. Length 11–152 cm (fossils to 200 cm tall).

†*Order Ichthyornithiformes (Ichthyornis, Apatornis).* Upper Cretaceous; North America. Superficially gull- or ternlike water birds of uncertain affinities. Length approximately 21 to 26 cm (estimated from reconstruction of fossils).

Order Charadriiformes (plovers, sandpipers, gulls, terns, auks). Upper Cretaceous to present; worldwide. 3 basic body plans: Suborder Charadrii—waders (shorebirds), usually feeding on small animals in mud or water, bill variable but often long and used for probing; Lari—web-footed, dense-plumaged water birds feeding by plunging into water for fish, robbing other birds, or scavenging; Alcae—dense-plumaged, web-footed, marine, wing-propelled divers, feeding on fish or invertebrates. Length 13–76 cm.

Order Gaviiformes (loons or divers). Upper Paleocene to present; Holarctic. Foot-propelled diving birds with webbed feet and pointed bills. Cnemial crest an extension of the tibia. Length 66–95 cm.

Order Columbiformes (sand grouse, pigeons, doves, dodoes). Upper Eocene or lower Oligocene to present; worldwide except in extreme north. Fast-flying birds with pointed wings and weak bills; feed on seeds and fruit. Length 15–84 cm.

Order Psittaciformes (parrots, lories, cockatoos). Upper Oligocene to present; throughout tropics, with some temperate-zone species. Often brightly coloured. Strong-flying, seed-, fruit-, or nectar-eating birds with very stout, hooked bills and zygodactyl feet (*i.e.,* outer toe reversed). Length 9.5–99 cm.

Order Cuculiformes (turacos, cuckoos, roadrunners). Upper Eocene or lower Oligocene to present; worldwide except in extreme north. Long-tailed birds with zygodactyl or semizygodactyl feet. Feed on both fruits and small animals. Most arboreal, a few terrestrial. Some brood parasites. Length 16–70 cm.

Order Strigiformes (owls). Eocene to present; worldwide. Nocturnal raptorial birds with hooked beaks, strong talons, and soft plumage. Length 13–69 cm.

Order Caprimulgiformes (nightjars, frogmouths, oilbird). Pliocene to present; worldwide except in extreme north. Concealingly coloured, soft-plumaged, nocturnal birds with weak feet and very large mouths. Most feed on insects caught in flight. Length 19–53 cm.

Order Apodiformes (swifts, hummingbirds). Upper Eocene or lower Oligocene to present; worldwide except in extreme north; hummingbirds limited to New World. Rapid-flying birds that feed on the wing on insects and nectar. "Hand" and primaries constitute a relatively great proportion of the wing; feet weak. Length 6.3 to 23 cm.

Order Coliiformes (colies or mousebirds). Unknown as fossils. Africa south of the Sahara. Soft-plumaged birds with long, pointed tails and all 4 toes directed forward. Food largely vegetable, some insects. Length 29 to 36 cm.

Order Trogoniformes (trogons). Pantropical, except Australasia; upper Eocene or lower Oligocene to present. Extremely soft-plumaged arboreal birds; underparts yellow to red, head and neck often iridescent, tail long, black and white. Feet weak; 1st and 2nd toes directed backward. Food insects and small fruit. Length 23 to 34 cm.

Order Coraciiformes (kingfishers and allies). Eocene to present; worldwide except in extreme north. A heterogeneous group of hole-nesting birds. Many with long, pointed bills and blue or green in plumage. All have 2nd and 3rd or 3rd and 4th toes joined at base. Food largely animal, except hornbills, which eat much fruit. Length 9 to 160 cm.

Order Piciformes (woodpeckers, barbets, honey guides, toucans). Upper Oligocene (possibly upper Eocene) to present. Zygodactyl (rarely 3-toed) hole-nesting birds. Food insects and fruit. Woodpeckers are modified for climbing. Honey guides are brood parasites. Length 9 to 61 cm.

Order Passeriformes (perching birds). Upper Eocene to present; worldwide. The large complex assemblage of perching birds, containing more than half of the known species of birds. Bill, plumage, and habits highly varied. Length 7.5 to 102 cm.

Critical appraisal. It has frequently been stated that birds are one of the best known of animal groups. This is true, in the sense that most of the living species and subspecies in the world have probably been described; but because of inadequacies in the fossil record and repeated cases of convergent evolution within the group, our knowledge of the phylogenetic relationships between orders, suborders, and families of birds is inferior to that of mammals and reptiles.

The taxonomic positions of several bird groups remain open to question. The hoatzin, included above in the Galliformes, is often given its own order, Opisthocomiformes. The turacos, here included in the Cuculiformes, are considered by many authors to warrant separation as Musophagiformes. *Diatryma* and several related genera of extinct flightless predators are often placed in a distinct order, Diatrymiformes, near Gruiformes. The flamingos, which constitute the order Phoenicopteriformes above, are placed in the Ciconiiformes in many classifications. The sand grouse, family Pteroclidae, are believed by some to be more closely related to the shorebirds (order Charadriiformes) than to the pigeons (order Columbiformes), with which they are usually grouped.

Relationships among the ratites

One area particularly in need of study is the relationships among the various groups of ratites (ostriches, rheas, emus, moas, etc.). Formerly, some authorities argued that these birds and the penguins arose independently from cursorial reptiles, but it is now generally agreed that all of them passed through a flying stage in the course of their evolution. The ratite groups differ greatly in morphology and yet show remarkable similarities in palate and bill characters. The principal unanswered questions are how many different flightless lines evolved from flying ancestors and from how many different groups were the flying ancestors evolved. On zoogeographic grounds, it is likely that the isolated kiwi-moa, elephant bird, and emu-cassowary lines arose independently from each other and from ratites on the other continents. But the ostriches and rheas could be descended from a common flightless ancestor because of the known former land connections from Asia to North and South America.

Before organic evolution was understood and accepted, animals were grouped on the basis of general similarity. It is now known that many such groupings were unnatural from a phylogenetic standpoint but were instead the result of convergent evolution from different parental stocks. Examples are *Hesperornis,* loons, and grebes, and diving petrels and auks. It is likely that many more examples are not recognized or generally accepted. At least the following groups should be studied with this in mind: herons and storks, *Diatryma* and the phororhacoids, New World vultures and other falconiforms, sand grouse and pigeons, touracos and cuckoos, and swifts and hummingbirds. These examples are all from the ordinal or subordinal level; examples at lower levels would be far more numerous. (R.W.St.)

MAJOR BIRD ORDERS

The remainder of this article consists of a review of each of the major groups of birds, identified at the order level of biological classification and arranged in accordance with the annotated classification above.

There are some omissions, however. The extinct groups (designated in the annotated classification by the dagger [†]) are treated throughout this article under the heading *Evolution and paleontology.* Additional information on extinct birds and on avian evolution may be found in GEOCHRONOLOGY: *Fossil record.* Also omitted are the following orders: Rheiformes (rheas); Struthioniformes (ostriches); Dinornithiformes (moas and kiwis); Gaviiformes (loons, also called divers); Coliiformes (colies, also called mousebirds); and Trogoniformes (trogons). These groups are represented by *Micropædia* entries under their common rather than scientific names. Finally, the flamingos (Phoenicopteriformes) are treated in the section on Ciconiiformes.

Tinamiformes (tinamous)

The Tinamiformes, or tinamous, are a group of ground-dwelling, chicken-like birds of Central and South America. They have a superficial resemblance to partridges and quail (gallinaceous birds) but are placed in a distinct order related to the much larger rheas. Tinamous long have interested scientists because of many peculiar features of their skeleton and biology that link them to the large flightless birds or ratites: the ostriches, emus, cassowaries, and rheas.

Predation by man

Tinamous, considered by hunters to be among the finest game birds in terms of sport as well as palatability, are heavily hunted in many parts of South America. Market hunting has been curtailed by law; however, it is still practiced in some countries. Frozen tinamous from Argentina were formerly sold in the United States under the name South American quail. Although by the early 1980s only one species of tinamou was listed as endangered by the International Union for the Conservation of Nature, habitat destruction and heavy hunting have reduced a large number of populations.

GENERAL FEATURES

The 46 species of tinamous range in size from that of a small quail, about 15 centimetres (six inches) long and 150 grams (five ounces) in weight, to that of a large grouse, about 50 centimetres long and two kilograms (four pounds) in weight. Tinamous are rather uniform in body proportions and stance, resembling guinea fowl (Numididae). The head is small and the bill medium sized, relatively thin, and slightly downcurved. The long, slender neck is clothed in short feathers. The body is quite heavy, with a high rump outline from the enormous development of rump feathers, which generally hide the extremely short or even rudimentary tail. The short, rounded wings are inconspicuous on the standing bird, and the primary flight feathers are hidden by the full plumage of the flanks. The bare legs are typically rather thick and of medium length. There are three short front toes, with the hind toe either elevated or absent.

The sexes are alike, except that the female is generally slightly heavier and has brighter coloration. The plumage coloration is highly concealing, in spotted or barred patterns of brown, gray, rufous, or tan. The variation in coloration is dependent upon the environment. The crested tinamous of the genus *Eudromia* have a long and slender crest that the bird directs forward when it is excited. The colour of the legs or of the bill is vivid and diagnostic in several species, as for example in the yellow-legged tinamous (*Crypturellus noctivagus zabele*).

Protective coloration in spotted or barred patterns

NATURAL HISTORY

Locomotion. Highly adapted for ground dwelling, tinamous normally walk rapidly (especially the savanna species) and can run with amazing swiftness. If forced into extended running, however, as when chased by men or dogs, they tire quickly and are likely to stumble and fall. They are best able to escape notice by standing motionless with the neck extended or by quietly slipping away, making use of all available cover. Some species of tinamous may crouch or even feign death. They rise in flight only when almost stepped upon. Small tinamous that live in open terrain sometimes hide in animal holes, such as the burrows of armadillos.

The flight of tinamous is clumsy but swift and accompanied by an easily audible rumbling or whistling noise produced by the stiff, curved primaries. The elegant crested tinamou (*Eudromia elegans*) of the open tableland of Argentina alternates periods of flapping with short glides. When flushed, forest species sometimes collide with branches and tree trunks and may injure themselves. If forced to make several flights in short succession, tinamous soon become exhausted, apparently because of a low circulation rate, related in turn to the surprisingly small size of the heart and lungs. The flight muscles are well developed, but the circulatory system seems to be insufficient for sustained activity.

Unlike the gallinaceous birds, tinamous sleep on the ground at night. Exceptions are members of the genus *Tinamus*, which roost in trees, choosing horizontal branches or tangled lianas and perching on their rasplike feet without using the toes.

Vocalizations. The voices of tinamous are among the strongest and most pleasant of any in the neotropics. They consist of loud, stereotyped, but melodious whistles, varying from the long and astonishingly songlike sequence of the brown tinamou (*Crypturellus obsoletus*)—astonishing because most relatives of the tinamous do not produce elaborate vocalizations—to the monosyllabic call of the cinereous tinamou (*C. cinereus*). The calls of the male and female are similar but discernibly different to the human ear. The female solitary tinamou (*Tinamus solitarius*) has a special call given during the time before egg laying, and another call is uttered by both sexes of this species after perching at dusk.

Habitat selection and food habits. Collectively, tinamous are adapted to a wide variety of environments, including dense woodland, thickets, open woodland, savanna, and even to the bunchgrass-covered plateaus of the high Andes, where they occupy the ecological niche generally held by the grouse in other parts of the world. In some forest regions as many as five species of tinamous have been found to coexist, inhabiting slightly different types of plant communities. The grassland tinamous do not occur north of the Amazon River; there the tinamou niche is occupied by the crested bobwhite (*Colinus cristatus*), a species of quail.

Seasonal variation in feeding

The food taken by tinamous varies with the season and habitat. In summer the red-winged tinamou (*Rhynchotus rufescens*), for example, eats mainly animal material—largely insects, but its mouth is large enough to swallow mice. In the stomach of one bird 707 termites were counted. In winter the red-winged tinamou shifts over to vegetable food. It occasionally becomes a pest in agricultural areas, using its strong bill to dig up the roots of manioc, or cassava (*Manihot esculenta*). The small tinamous of the genus *Nothura* feeds primarily on seeds, but the spotted tinamou (*Nothura maculosa*) occasionally eats ticks in pastures. The forest-inhabiting solitary tinamou generally prefers small fruits and berries, collected on the ground. It might, however, also devour a frog when it finds one. The members of the genus *Nothoprocta* are considered beneficial to agriculture because of their large consumption of insect pests. Young tinamous of all species are more dependent upon insects than are the adults. Unlike the gallinaceous birds, tinamous do not scratch for food, as is evident by their weak toes and short nails; instead, they either turn over leaves and other debris with the bill or dig with it.

Reproduction. Courtship behaviour has been described for only a few species of tinamous. Certain species have well-defined breeding periods, and others breed throughout the year. Investigators have reported that courting birds raise the thickly feathered rump and display the brightly coloured undertail coverts. A similar display has been observed in a frightened *Crypturellus:* the bird presses the breast to the ground, raises the rump, spreads the terminal feathers like a fan, and exhibits the sharply marked undercoverts. Courting birds also have been observed to chase each other around on the ground.

Multiple mating is the rule among tinamous, although a few species such as the ornate tinamou (*Nothoprocta ornata*) maintain stable pairs. All forms of polygamy exist, the conditions varying between and even within species. Many species have uneven sex ratios; preponderance of males seems to be more frequent, the ratio reaching four to one in the variegated tinamou (*Crypturellus variegatus*). The ratio in the ornate tinamou is about one to one.

Parental behaviour by the male

The nest, a shallow depression in the ground, is constructed and defended by the male. The eggs are among the most beautiful of all bird eggs, always monochromatic and highly glazed. The colours include light chocolate brown, near black, purple, dark bluish green, light yellowish green, and gray when laid, but the shell pigments fade when exposed to light. One hen, or more, places her eggs in the nest of a male; when several females provide the eggs, the clutch may become quite large, eight to 16 eggs. Incubation, which lasts 17 to 21 days, is done entirely by the male, who broods and guides the chicks for several weeks after hatching. The chicks, blotched and streaked like the young of the rheas, are able to run as soon as they are hatched. When frightened, they squat and freeze, becoming almost invisible.

PALEONTOLOGY AND CLASSIFICATION

There is no doubt that the tinamous represent one of the oldest stocks of birds on the South American continent. To date, three genera of fossil tinamous, of one species each, have been described from a single deposit from the Miocene of Argentina (about 10,000,000 years ago). The majority of other fossil tinamous, mostly representing species still extant, has been discovered at scattered sites from the upper Pleistocene (less than 1,000,000 years ago) of South America.

Many authors have noted anatomical and biological resemblances between the tinamous and rheas, or nandus (Rheidae). The structure of the bony palate, an important feature in the taxonomy of ratite birds, quite clearly links the two groups, but most authorities prefer to maintain them as separate orders, Rheiformes and Tinamiformes, each with a single family, respectively, Rheidae and Tinamidae.

(H.S.)

Casuariiformes (emus, cassowaries)

The order Casuariiformes includes two families of large flightless birds: Dromaiidae for the emu (*Dromaius novaehollandiae*), found only in Australia; and Casuariidae for three species of cassowaries (*Casuarius*), restricted to northern Australia, New Guinea, and nearby islands. Of the two groups, the emu is far better known, both biologically and popularly, being exhibited in zoos around the world.

The emu was first identified by European explorers in 1788, more than a century after the first cassowaries had been seen by Europeans; in 1697 a Dutch navigator, Willem de Vlamingh, had seen the emu's footprints in western Australia and had attributed them to a "Kasuarius." Cassowaries first became known to Europeans in the 17th century—there was a published reference to a "Casoaris" in 1658—when the Portuguese and Dutch colonized the East Indies. Both names, emu and cassowary, were originally applied to cassowaries; the emu was known as the New Holland or New South Wales cassowary until the early 19th century, when the name emu was gradually transferred to it. By the late 19th century about 11 species of cassowaries were recognized, but greater understanding of variation within species has reduced the number to three: the double-wattled, or Australian, cassowary (*Casuarius casuarius*), the single-wattled, or one-wattled, cassowary (*C. unappendiculatus*), and the dwarf, or Bennett's, cassowary (*C. bennetti*).

IMPORTANCE TO MAN

The emu and cassowaries are important foods for the indigenous peoples of both New Guinea and Australia; the flesh of the thigh muscles somewhat resembles beef. In New Guinea cassowaries are captured as chicks and held in enclosures until they are large enough to eat. The feathers are frequently used for personal adornment. In Australia cassowary feathers formerly were used for the notorious *kurdaitcha* shoes, or "shoes of silence," worn by Aboriginal executioners on nocturnal missions of tribal vengeance or punishment. During World War I members of the Australian cavalry regiments wore tufts of emu plumes on their slouch hats.

Since the time of European settlement in southeastern Australia, the emu has become much less abundant, and three island forms have been exterminated by hunting. In Western Australia, however, the bird has remained common and has become a pest in the wheat-farming areas, breaking fences and trampling and eating crops. In 1932 members of an army machine-gun unit were employed in a campaign against a concentration of emus, estimated to be about 20,000, in the vicinity of the wheat-belt centre of Campion.

The Emu War in Australia

The outcome of this bizarre Emu War, as it was called, has been summarized by the ornithologist D.L. Serventy as follows:

> . . . the machine-gunners' dreams of point blank fire into serried masses of Emus were soon dissipated. The Emu command had evidently ordered guerrilla tactics, and its unwieldy army soon split up into innumerable small units that made use of the military equipment uneconomic. A crestfallen field force therefore withdrew from the combat area after about a month.

Yearly kills of emus in Western Australia for bounty payments vary from about 5,000 to nearly 40,000 birds. The emus, however, remain plentiful, and small parties may be seen within 15 or 20 kilometres (9 or 12 miles) of Perth, the capital of the state.

NATURAL HISTORY

Reproduction. Throughout its climatically varied range the emu is a winter breeder; egg laying begins at the end of April. The nest is a flattened bed of bark, grasses, and leaves near a tree or bush and is so situated that the sitting bird (always the male) has a good view of its surroundings. Despite their size, nests are extremely difficult to find. The large green eggs, with granulated shells, average about 130 millimetres (slightly over five inches) in length and 87 millimetres (3.4 inches) in width and weigh 450 to 800 grams (16 to 28 ounces). They are laid at intervals of about four days, and the male starts incubation when the hen has laid five to nine. The normal clutch size is eight, nine, or 10 eggs, with large clutches up to 16. In exceptionally good seasons as many as 20 eggs may be laid, in poor seasons as few as four or five. Incubation varies from about 58 to 61 days, during which the male seldom leaves the nest, even to feed.

Eggs

The newly hatched chicks, which are concealingly streaked

Drawing by R. Keane

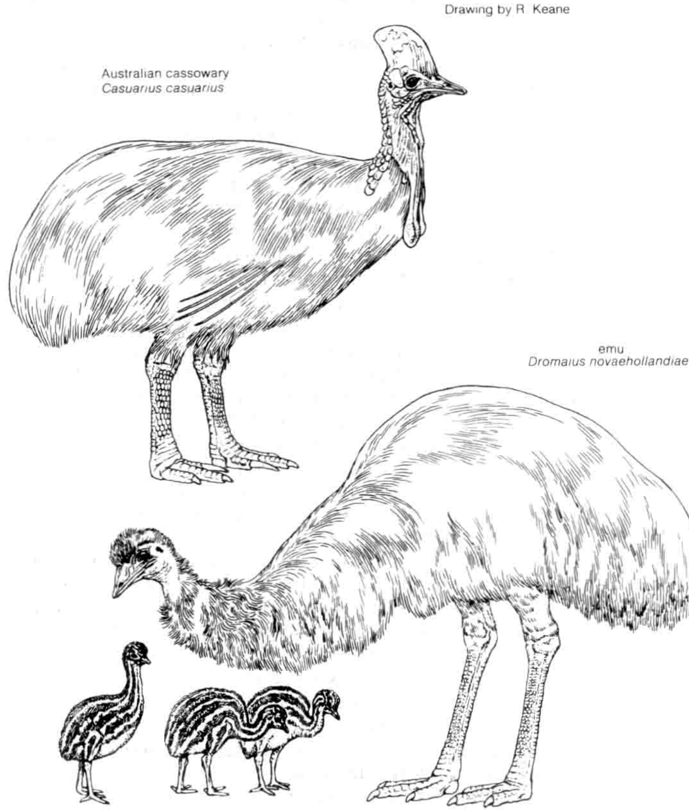

Figure 9: Emu and cassowary.