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The Scientific Wonder of Birds

Course Guidebook

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Bruce E. Fleury is a Senior Professor of the Practice Emeritus in the Department of Ecology and Evolutionary Biology at Tulane University, where he taught more than 10,000 students before he retired. He earned his MS and PhD in Biology from Tulane, his BA in Psychology and General Science from the University of Rochester, and his MA in Library, Media, and Information Studies from the University of South Florida.

As a sophomore at the University of Rochester, Professor Fleury took an introductory class in biology and was hooked from the first lecture. He also discovered the art of birding and spent many pleasant hours pursuing warblers in a nearby abandoned cemetery.

While Professor Fleury was working at Tulane University as the head of the science and engineering division of the main library, he saw an opportunity to fulfill his dream of becoming a biologist and started taking classes at Tulane part-time. His first biology class there was Ornithology, taught by an inspiring professor, the late Dr. Alfred Smalley. Professor Fleury would someday teach that same class.

After receiving his PhD in Biology, Professor Fleury began a second career as a biology teacher. He won several teaching awards, and his classes were especially popular among nonmajors, who found that his approach assumed little or no prior knowledge of science.

Professor Fleury is the author of *Dinosaurs: A Guide to Research*, an award-winning reference book, and *How to Flunk Out of College*, a survival guide for students. He is also the author of three children's books—*Queen of the Cats*, *Queen of the Rats*, and *Moccasins in the Mist*—as well as numerous popular and professional articles.

Professor Fleury's other Great Course is *Mysteries of the Microscopic World*, which follows the history of infectious diseases and the coevolution of man and microbes. ■

Table of Contents

Introduction

Lecture Guides

Table of Contents

Supplementary Material

The Scientific Wonder of Birds

Birds are living, breathing dinosaurs, right in our backyards. This course will explore the origin, biology, and behavior of birds, starting with the discovery of *Archaeopteryx*. Birds evolved from theropods, a group of carnivorous dinosaurs that includes the ferocious *Velociraptor*. Thomas Henry Huxley first proposed a connection between birds and dinosaurs, and the course will review the evidence supporting his hypothesis. Recent fossil discoveries also suggest that some dinosaurs may have been capable of flight, and the course will contrast 2 competing theories for the origin of flight: the arboreal (trees to ground) and cursorial (ground to air) theories.

Flight seems almost magical, but the course's examination of lift—the force that keeps birds aloft—shows how it results from the dynamics of air moving past a shape called an airfoil, the asymmetrically curved surface of the wings of both birds and Boeings. The diverse styles of avian flight are shaped by the relationship between body weight and the size and shape of the wing. Feathers make flight possible as well as provide insulation, mechanical protection, and courtship plumage to attract a mate. Feathers are only one of the remarkable adaptations that helps birds soar through the skies, and the course's review of flight adaptations includes the efficient respiratory, digestive, and circulatory systems of birds, as well as their excellent senses.

Once in the air, birds have an uncanny ability to tell where they are and where they're going. The course's examination of navigation covers the way birds use the position of the Sun and stars, magnetic fields, and geographic features like rivers and mountains in the course of their annual migration. Birds know when it's time to migrate because their brains can track the changing length of days, keeping their annual cycles in sync with the changing seasons.

We have always underestimated the intelligence of birds, due to a fundamental misunderstanding of the structure of their brains and a belief that their behavior was mainly instinctual. Their use of tools, however, reveals their true genius and sets them apart from all other animals except humans. The course will offer several examples of tool use and many ways in which birds have turned our technology to their advantage.

Birds are both social and fiercely territorial. They form large roosts and breeding colonies and frequently forage in large flocks. Despite feeding side by side, birds have evolved many ways to minimize competition and actually catch more prey foraging as a group than by feeding alone. Like humans, birds are territorial animals, defending places to eat, nest, and mate. The course's survey of territorial behavior highlights the many advantages to territoriality, not the least of which is being able to attract a mate. The bluff and bluster that birds display to defend their territories provides a safe alternative to mortal combat.

Birds announce their territories through songs and calls. Calls usually have a specific context, such as alarm calls to warn of predators or contact calls to help keep flocks together. Songs are more complex vocalizations. The syrinx, the vocal organ of birds, is even capable of making 2 songs at the same time, one from each side of the throat. You'll learn how songs develop and consider both innate and learned components. You'll also discover that birds, like humans, have distinct regional dialects. Songs are also used in courtship displays, and in several species the number of songs a bird can sing correlates with its ability to attract a mate.

Birds are mostly monogamous, although a small percentage are polygamous. Their mating systems are shaped by the ability of either sex to monopolize mates or critical resources that mates require. But as you'll discover, monogamy among birds is often superficial. Divorce is common, and mixed parentage due to extra-pair copulations occurs in many species. The course will review several examples of mating systems, ending with the bowerbirds, the master architects of romance.

Once the pair bond is formed, parents usually build a nest to hold their eggs. Nests come in many shapes and sizes and include many types of materials, both natural and manmade, including sticks, leaves, grass, and mud. Nests protect chicks from predators and bad weather and provide an ideal thermal environment for incubating eggs. Eggs are a marvelous innovation, keeping the embryo safe in a shell that encloses both food (egg yolk) and water (egg white). Some birds, however, can't be bothered with building nests and lay their eggs in the nests of other birds. These brood parasites have a devastating effect on many species of birds.

Raising baby birds is a formidable challenge. Parents must devote incredible amounts of energy to incubating eggs, brooding young, and protecting them from predators and may make thousands of feeding trips to fledge their demanding young. The course will contrast the 2 basic patterns of development in chicks: altricial (born naked and helpless) and precocial (born fully feathered and ready to leave the nest). The course concludes with a survey of cooperative breeders and the role of nest helpers in extended families of birds. ■

BIRDS AND DINOSAURS: THE ORIGIN OF FLIGHT

LECTURE 1

Birds are flying dinosaurs—not the distant relatives of dinosaurs, but actual living, breathing dinosaurs! This lecture follows a winding road of scientific discovery that led to this connection between birds and dinosaurs. The lecture also reviews competing theories for the origins of birds and dinosaurs and analyzes the evidence linking them together. Additionally, the lecture considers whether birds (and dinosaurs) first learned to fly by leaping from the ground, gliding from the treetops, or a combination of both.

Evidence of Birds in the Fossil Record

The first evidence of birds in the fossil record was a single feather that was imprinted on a slab of Solnhofen limestone that was so fine it was used to make lithographic plates. It was uncovered in a Bavarian quarry and acquired by Hermann von Meyer, who named it *Archaeopteryx lithographica*, meaning “ancient wing drawn in the rocks.”

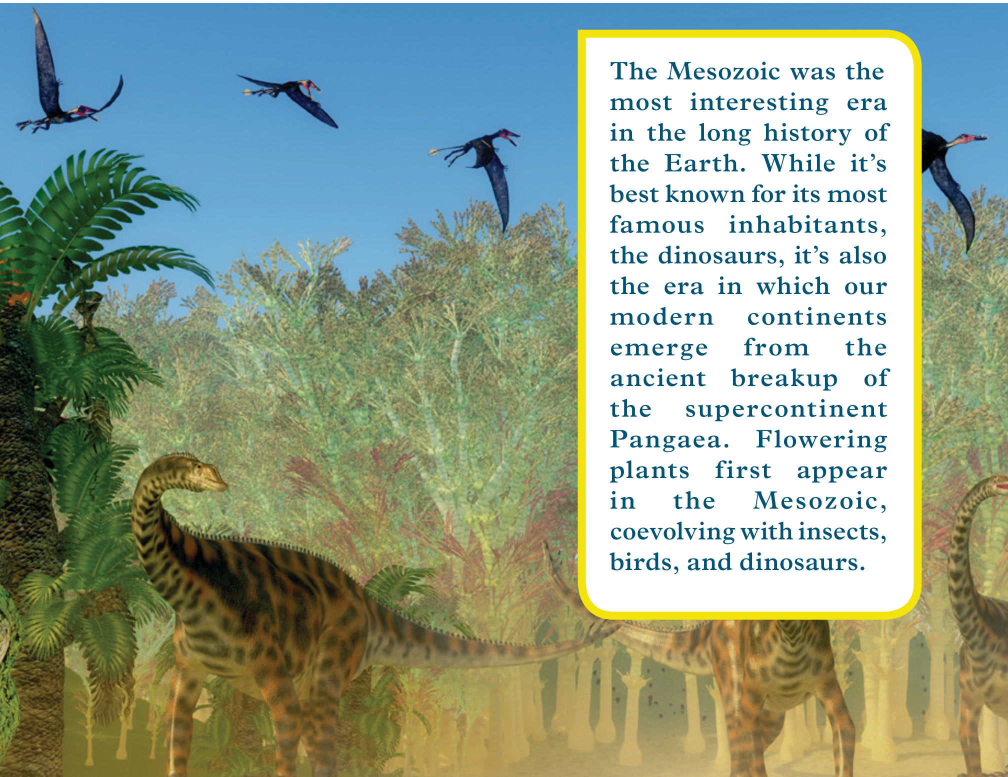
Soon after this feather was unearthed, a second specimen of *Archaeopteryx* was discovered—a nearly intact, beautifully preserved small fossil reptile covered in feathers.

Archaeopteryx

The discovery of *Archaeopteryx* in 1861 burst like a thunderbolt on the Victorian scientific community. It was just what Charles Darwin needed to defend his theory of evolution. The publication of Darwin's *On the Origin of Species* in 1859 had generated an intense debate among Victorian scientists over the nature of evolution. If Darwin was correct about the process of evolution, there should be intermediate stages—the so-called missing links—between different groups of animals.

Thomas Henry Huxley, known as Darwin's bulldog for his fierce defense of Darwin's ideas, seized on *Archaeopteryx* as proof that Darwin was correct. Huxley claimed that *Archaeopteryx* was a critical missing link between birds and reptiles. *Archaeopteryx* is probably not directly ancestral to modern birds—just another side branch in the tree that leads to modern birds.

Archaeopteryx dates back to the late Jurassic, about 150 million years ago. The Jurassic is one of 3 periods comprising the Mesozoic era, the others being the Triassic and the Cretaceous. The Mesozoic is best known for its most famous inhabitants, the dinosaurs. Most orders of modern birds are first found in the early Cenozoic, the current era.

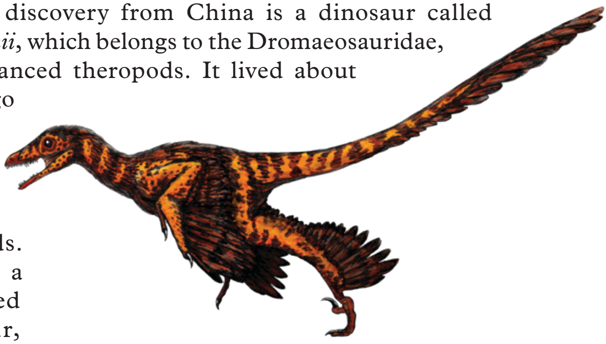


The Mesozoic was the most interesting era in the long history of the Earth. While it's best known for its most famous inhabitants, the dinosaurs, it's also the era in which our modern continents emerge from the ancient breakup of the supercontinent Pangaea. Flowering plants first appear in the Mesozoic, coevolving with insects, birds, and dinosaurs.

But an explosion of new discoveries, many of them in mainland China, has upset many theoretical apple carts. And the evidence continues to mount that birds are the direct descendants of dinosaurs—specifically, the suborder Theropoda, a clade of carnivorous dinosaurs that contains some of the most highly evolved, intelligent, and dangerous animals that ever lived.

Starting in the 1990s, several spectacular new discoveries were made in mainland China of birdlike feathered dinosaurs. Dinosaurs like *Sinosauropteryx* provide strong evidence that birds evolved from theropods.

Another remarkable discovery from China is a dinosaur called *Sinornithosaurus millenii*, which belongs to the Dromaeosauridae, a family of very advanced theropods. It lived about 125 million years ago and was covered from head to toe with feathers—as were many, if not most, theropods. It is definitely not a bird, but a feathered theropod dinosaur, much like *Velociraptor*.

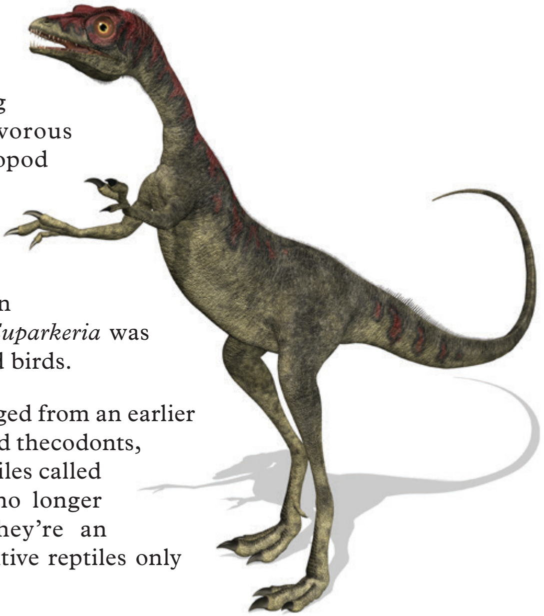


S. millenii is one of the smallest dromaeosaurs. Miniaturization in the dromaeosaur lineage was a significant factor in early avian evolution, because flight would prove especially useful for a small, lightweight animal trying to escape predators.

Our knowledge of the earliest evolution of birds is extremely sketchy, and the ultimate origin of birds is still a bit of a mystery. And it doesn't help that avian taxonomy—the scientific classification of birds—is a very challenging subject, because all birds are basically built the same way. It's what evolutionary biologists call a design restraint.

It's interesting that something as infinitely diverse as evolution should be constrained to run in narrow channels; in this case, it's imposed by the nature of flight. The structural demands of flight are so great that they impose a structural uniformity on all birds.

Avian Evolution



Huxley was struck by the fact that *Archaeopteryx*, in many respects, resembled nothing more than a small carnivorous dinosaur, similar to the theropod *Compsognathus*. His theory that birds evolved from dinosaurs held sway until 1913, when Robert Broom unearthed *Euparkeria*, a South African reptile. Broom claimed that *Euparkeria* was ancestral to both dinosaurs and birds.

Both dinosaurs and birds diverged from an earlier group of primitive reptiles called thecodonts, which belong to a group of reptiles called archosaurs. Thecodonts are no longer considered a valid clade; they're an evolutionary grab bag of primitive reptiles only loosely related to one another.

There's little doubt that dinosaurs evolved from thecodonts. Most debates over dinosaur ancestry hinge on which group of thecodonts dinosaurs evolved from, and the jury is still out on that argument.

Dinosaurs diverged very early on into 2 main lines separated primarily by differences in their pelvic structure—their hips.

> Ornithischia, or bird-hipped dinosaurs, include the duck-billed hadrosaurs, the horned ceratopsians, ankylosaurs, and stegosaurs.
>
> Saurischia, or lizard-hipped dinosaurs, include the herbivorous sauropods and the carnivorous theropods. It is from this group that birds are thought to have evolved—specifically from the family of theropods called the Dromaesauridae.

The thecodont ancestry hypothesis was championed by Gerhard Heilmann in his classic 1926 book *The Origin of Birds*. One of his central arguments was that theropods lacked a special bone called the clavicle, or collarbone. The 2 clavicles of reptiles become fused to form the furcula, or wishbone, which is very important for a flying bird; it spreads apart during the downstroke of the wing and springs back to add power to the upstroke. Heilmann claimed that lacking this bone meant that dinosaurs could not have given rise to birds and that birds and dinosaurs diverged independently from the more primitive thecodonts.

The thecodont hypothesis, kept alive by Alan Feduccia, claims that theropods are too specialized or too late in time to have given rise to birds. Feduccia, like Heilmann, claimed that birds and dinosaurs must have arisen independently from the earlier and less-specialized thecodonts.

A big problem with this theory is that it relies on an unknown thecodont ancestor, which makes it impossible to prove or disprove. Also, clavicles have since been discovered in small theropods, which refutes Heilmann's original evidence for an independent origin of birds and dinosaurs.

Starting in the 1960s, John Ostrom began to assemble an impressive amount of evidence to demonstrate that Huxley was correct. Birds are most closely related to theropod dinosaurs—specifically, as Huxley claimed, to a group of theropods called coelurosaurs.

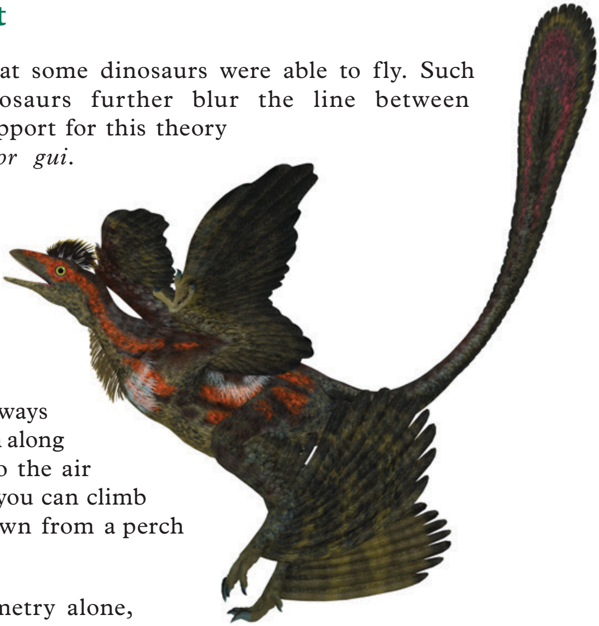
Jacques Gauthier, a leading expert on dinosaur taxonomy, places the birds within the Coelurosauria, a diverse group of small, agile bipedal carnivorous dinosaurs. Gauthier says that birds are not distant descendants of theropod dinosaurs, but actually *are* theropod dinosaurs.

Gauthier offers an impressive list of 83 shared characteristics, called synapomorphies, that unite dinosaurs and birds, including 17 characters originally proposed by Huxley. Synapomorphies are traits held in common between groups of organisms—traits that are different from those of the ancestral species. Thirty of Gauthier's synapomorphies define the taxon Coelurosauria, which now contains the birds. Gauthier claims birds evolved from the Dromaeosaurs, a group of agile carnivores that includes *Velociraptor.*

The most important evidence linking birds and dinosaurs comes from molecular analysis of protein fragments gleaned from a fragment of bone. In 2000, Bob Harmon discovered a large *Tyrannosaurus rex* bone, in which Mary Schweitzer found small fragments of 68-million-year-old soft tissue. In 2007, John Asara examined the samples and extracted segments of 7 proteins. Comparing them with other vertebrate animals, he discovered that the collagen of *T. rex* was closest to that of chickens—solid molecular evidence linking birds and dinosaurs.

Theories of Flight

Gregory Paul claims that some dinosaurs were able to fly. Such airborne, birdlike dinosaurs further blur the line between dinosaurs and birds. Support for this theory comes from *Microraptor gui*. This small feathered dinosaur had 2 pairs of feathered wings. The feather vanes are also asymmetric, suggesting that this was a flying animal.



Basically, there are only 2 ways to learn to fly: You can run along the ground and leap into the air (the cursorial theory) or you can climb to a height and glide down from a perch (the arboreal theory).

Based on feather asymmetry alone, *Archaeopteryx* was at least a weak flyer. But did it launch itself from the ground, as do modern birds, or did it need to climb a tree and launch itself from a height to get into the air?

The arboreal theory claims that ancestral birds were tree dwellers who leapt from branch to branch and glided from tree to tree. This theory was first proposed by O. C. Marsh in 1880 and was recently revived and refined by Walter Bock.

But there are a few problems with the arboreal theory. One problem is that even though gliding has evolved several times in the history of the vertebrates, it has never served as an intermediate step to powered flight.

Everything you learned about dinosaurs when you were a child is wrong. They weren't scaly, cold-blooded, lumbering reptilian brutes, and they didn't go extinct at the end of the Cretaceous.

Dinosaurs were warm-blooded and agile. Some were covered in feathers, and many of them could fly. And there are billions of dinosaurs alive today in the skies.

Another problem is that climbing trees requires a radically different set of muscles than those required for efficient powered flight. The same thing goes for powered flight versus gliding.

Most modern birds are well adapted to living in the trees, but theropod dinosaurs were not well adapted for an arboreal lifestyle. They were extremely efficient cursorial predators, pursuing their prey by running along the ground. They weren't built to be climbers or gliders.

Nicholas Longrich reexamined several specimens of *Archaeopteryx* in 2006, focusing on the feathers of its hind limbs, and concluded that their aerodynamic structure could have formed a pair of extra winglets.

This brings us to the cursorial theory, originated by Samuel Wendell Williston in 1879 and revived by John Ostrom. A primitive quadruped evolved into a facultative biped, which could run on its hind legs at high speeds. This facultative biped in turn evolved into an obligate cursorial biped, an animal that normally ran on its hind legs.

Elongation of the forelimbs and enlargement of the scales on its arms increased the surface area of the arms to form a larger surface for thrust (forward motion). Flapping these protowings added thrust to increase running speed until eventually the animal achieved flight velocity. Was this how *Archaeopteryx* became airborne?

Its mouth and teeth suggest a diet of small animals, but it wasn't built to chase small animals through the treetops. Besides, there were no real trees in its lagoon environment, and there were no cliffs or other vertical elements to climb and launch into a glide.

If *Archaeopteryx* and other early terrestrial birds were ground foragers, why did they end up in the trees? Andrzej Elżanowski says they did so to escape predators. His escape theory bridges the gap between the arboreal and cursorial theories.

Early theropods were bipedal cursorial ground foragers; they stood on 2 legs and ran along the ground. They probably ran up steep slopes and tall trees to escape predators (cursorial theory) and then glided from tree to tree until finally returning to the ground (arboreal theory). Powered flight arose from steering movements during gliding.

By the end of the Cretaceous, the world was full of birds, coexisting with an incredible diversity of dinosaurs. But most birds disappeared at the end of the Cretaceous, along with the dinosaurs they sprang from.

An explosive divergence of new species about 10 million years ago produced the modern orders of birds. For a brief period, birds ruled the Earth. But their domination was short-lived. Like flightless birds today, they laid their eggs on the ground. Their nests were probably raided by the small mammals who diverged rapidly in the early Cenozoic.

By the Eocene, all modern orders except passerines (the perching birds) are present. Sometime around the early Eocene, the perching birds evolved and rapidly diverged into a very diverse group.

Today, there are about 9000 to 10,000 species of birds, divided into about 30 orders. The order Passeriformes, the perching birds, is the dominant group, containing about 60% of all known species of birds.

SUGGESTED READING

Long, *Feathered Dinosaurs*.

Paul, *Dinosaurs of the Air*.

Pickrell, *Flying Dinosaurs*.

QUESTIONS TO CONSIDER

1. How do we know that *Archaeopteryx* could fly?
2. How are colonial dinosaurs, such as John Horner’s *Maiasaura*, similar to modern colonial wading birds?

BIRDS AND BOEINGS: THE MAGIC OF FLIGHT

LECTURE 2

In this lecture, you will learn how airfoils keep both birds and Boeings airborne. You will discover the ways birds use their wings and feathers to take off and land or glide at low speeds, and you will learn about the many functions of feathers, their basic structure, and how they're maintained.

Bernoulli's principle, which links airspeed with air pressure, is the basic physical principle that helps us understand how birds (and Boeings) become airborne. It is derived from the law of conservation of energy, which states that energy can neither be created nor destroyed. In other words, the total amount of energy in the system comes from air pressure and velocity, and this total has to remain constant.

Treating air as a very thin fluid, increasing the velocity of a fluid results in a corresponding decrease in pressure. Ignoring changes in fluid density—a safe bet at low speeds—pressure is inversely proportional to velocity (increase one and you decrease the other).

How Birds Fly

Birds can fly because their feathers and wings are shaped into an airfoil, which is an asymmetrically curved surface that tapers toward the rear, so the top curve is longer than the bottom curve. A stream of air meets the curved front and is split into 2 streams, one above the wing and one below. The top flow goes up and over the curved front of the airfoil, and as it does so, the streamlines of the flow are pinched closer together as they pass over the top and flow downward over the back of the airfoil.

Like water entering a narrow canyon, this decrease in cross-sectional area in the airstream is balanced by an increase in its velocity. The top airstream speeds up relative to the bottom airstream, and this increased velocity results in decreased pressure above the airfoil relative to the bottom in order to generate lift.

The wing also generates a resultant upward force by deflecting air downward as it hugs the downward curve on the top of the airfoil. This is Isaac Newton's third law at work: For every action, there is an equal and opposite reaction. The downward force generates a reactive upward force that helps lift the airfoil into the air.

Wings are horizontal airfoils, so lift translates to upward motion. Airplane propellers are vertical airfoils, so lift translates to thrust, or forward motion. Helicopter propellers can be held level, go up, or be tilted to translate some of its lift into forward thrust. Every flight feather of a bird is itself an airfoil, as is the entire wing.

The physics and math that lurk behind the fluid dynamics of lift are complicated. (Even Albert Einstein failed to fully grasp the intricacies of lift!) To delve more deeply, consider these Great Courses lectures:

- *The Science of Flight,* "Takeoff: How Wings Produce Lift" (lecture 3)
- *Physics in Your Life,* "Taking Flight" (lecture 10)
- *Physics and Our Universe: How It All Works,* "Fluid Dynamics" (lecture 20)

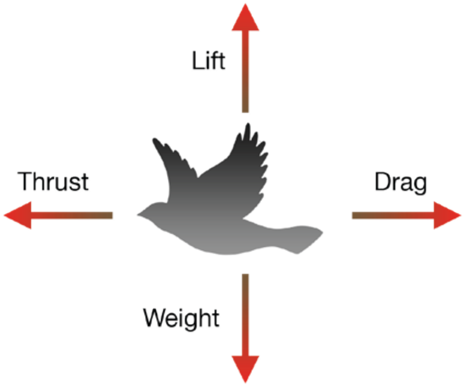
Lift is one of the 4 main forces acting on a bird in level flight.

Lift pulls the bird up.

Weight pulls the bird down.

Thrust moves the bird forward.

Drag, the net forces resisting thrust, slows the bird down.



Birds can't fly unless they can generate enough lift to cancel out their own weight and enough thrust to overcome drag. The inner part of a bird's wing—from the bend of the wing to the base (the secondary flight feathers)—is larger and wider and is mainly responsible for creating lift. The outer, narrower portion of the wing (the primary flight feathers) mainly generates thrust.

Birds exert fantastic control of the air flowing over their feathers. Feathers play a major role in not only keeping birds in the air but also giving them incredibly fine control over speed, altitude, and direction. Birds don't flap their wings straight up and down; instead, their wings trace out a lazy figure 8, moving slightly forward on the way down and slightly back on the way up. As the wing moves down and forward in the power stroke, the feathers are held close together.

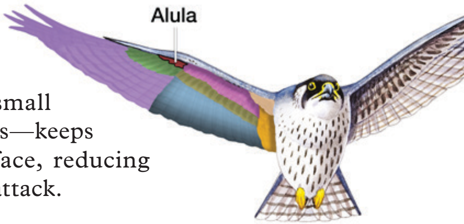
The tips of the wing twist upward. Because of this twisting, the leading stiffened edge of the flight feathers is briefly vertical, and the wing now acts as a propeller. Because lift is always perpendicular to the flow of air over the airfoil, then if the airfoil is vertical, the net force is pushing forward instead of up, generating thrust.

As the wing moves up in the recovery stroke, the feathers are spread apart to reduce air resistance. Birds have a variety of tactics to keep the upstroke from cancelling out the downstroke.

Loss of lift is a real problem, especially at slow speeds. Birds that have to cruise slowly have slots in their wings that are formed by flight feathers spread far apart. Slots increase the amount of lift at low speeds. Air forced through the slot expands on the other side, reducing air pressure and generating lift. Slots also help the thin stream of air stay close to the wing, keeping the airstream from becoming turbulent and preventing a low-speed stall.

Airplanes use their slats and flaps in the same way that birds do to create more lift at low speeds for takeoff and landing.

The alula, the miniature wing that extends from the thumb of birds, gives badly needed extra lift at slow speeds, during takeoff and landing. When the alula extends, it creates a small slot in the wing, which—like feather slots—keeps the airstream close to the wing's surface, reducing the turbulence from the steep angle of attack.



Landing, Gliding, and Soaring

Landings for birds are little more than a controlled crash. They have to quickly shed lift to land, so they tilt their wings and tail to make the angle of attack so high that they stall and drop out of the sky. Takeoffs are equally tricky; birds must leap into the air and flap their wings rapidly to start an airstream flowing over their wings.

Airplanes retract their landing gear in flight to minimize drag.

Birds flap their wings in a horizontal plane to get airborne, unlike the diagonal figure-8 stroke of powered flight. They need to generate thrust to overcome drag, which is the net force of things that slow birds down. The friction of the body's passage through the air is one source of drag, called profile drag. Birds are streamlined to minimize profile drag, which is why they don't have prominent outer ears or noses.

As birds fly, their wings generate little eddies of turbulent air around the wing tips and rear edges of the wing. This turbulent air causes induced drag, reducing the smooth flow of air over the wing and slowing the bird down. Birds that fly in formation reduce the turbulence at their own wing tips by flying near the wing tip of the bird in front, gliding in the slipstream of the leaders.

Gliding, like landing, is a carefully controlled crash. A gliding bird has air passing over its wings, which provides lift. But its only thrust is the forward motion provided by gravity, so drag from friction and turbulence around the edges of the wing slow it down and it gradually drops to the ground.

Pelicans flying in formation use 10% to 15% less energy than those not flying in formation.

Gliding birds ride thermal updrafts (columns of rising warm air) or updrafts on a slope from a wave or a ridge. Updrafts can carry birds high in the air so that they can ride the glide over great distances. Soaring is simply gliding in circles.

Birds have very diverse styles of flight, which are determined by the size and shape of the bird as well as its bill, feet, and wings—traits that are adaptations to the bird's lifestyle.

Purpose and Design of Feathers

Although feathers are our quintessential idea of lightweight, they can make up a significant part of the weight of the bird. A bird's feathers may weigh 2 to 3 times as much as its skeleton and can equal 6% to 7% or more of the total body weight of birds. Although feathers function primarily for flight and insulation, they have an incredible variety of uses.

Songbirds typically have 2000 to 4000 feathers. The tundra swan has about 25,000.

Plumage is a quiet language. It communicates species and individual identity, functions in courtship and territorial displays, signals rank, provides camouflage, and can be used to make and receive sounds. And it allows us to identify birds at a distance. Feathers provide sensory functions and mechanical protection against wind and water. They also function in defense.

Mature feathers are dead tissue, mostly a modified form of keratin, the protein that makes up mammalian hair, claws, and fingernails. The keratin matrix contains lots of little microscopic fibers to bind it together.

Feathers grow from follicles embedded in the skin. New feathers push the older feathers out as they grow. Feathers grow from the base, not the tip. Barbs split off from the basal collar and increase in length as the feather continues to grow.

Feathers start out as living tissue, with their own blood supply. As they age, the cells gradually fill with keratin. At the base of the feather is a tiny hole for the blood vessels to enter, called the inferior umbilicus, a reminder of the feather's living origin.

A typical contour feather, or body feather, is a flat vane mounted on both sides of a long shaft, or rachis, which has a square cross section as it runs through the vane. Each vane, on both sides of the rachis, is composed of lateral branches called barbs. Each barb consists of a horizontal shaft called the ramus and 2 rows of barbules projecting out from the top and bottom of the ramus. The barbules on the lower side are smooth, while those on the upper side have small hooks called barbicels. The hooked barbicels grasp the smooth barbules of the ramus above it, interlocking all the barbs together into a smooth vane.

Birds spend a great deal of time preening, which restores feathers with split vanes. By pulling their feathers through their beak, birds can get the barbicels to reengage. There are many different types of barbicels, including ones that are water repellent and ones that absorb water.

There are also many types of feathers, including vaned feathers, down feathers for insulation, semiplumes for courtship and insulation, bristles and semibristles, filoplumes, and powder down for waterproofing. The vaned feathers include the smaller contour feathers, which cover the body, and the larger flight feathers, which cover the wings and tail.

The flight feathers of the wing are called remiges. Flight feathers are large and stiff, with asymmetric vanes. The outer flight feathers, or primaries, are attached to the hand bones. The inner flight feathers, or secondaries, are attached to the ulna.

There are also several rows of smaller feathers called coverts. They cover the base of the primaries and the gaps between them. The tail feathers are mainly used for steering and balance in flight. The flight feathers of the tail are called rectrices and are attached to the pygostyle, the fused caudal vertebrae that form the birds' stumpy tail.

The longest feathers in the world belong to the male Japanese phoenix fowl, a breed of chicken. Its central tail feathers, used to impress potential mates, grow continuously without molting for up to 6 years, reaching an incredible 6 meters (18 feet)!

Feathers are dead tissue, so they have no way to repair themselves. They eventually wear out and fray and need to be replaced. Birds periodically change their plumage, or molt, at least once or twice a year. If the bird sheds too many flight feathers at the same time, it will be unable to fly and be at the mercy of predators, so the molting of the flight feathers is carefully timed so that not too many flight feathers are lost at once.

Many waterbirds are so heavy that losing even a few of their flight feathers would leave them vulnerable, so they drop all their flight feathers at once during their annual molt to minimize the period of vulnerability. Molting places enormous energetic demands on birds, so in most species it's carefully timed so it doesn't overlap with breeding or migration.

To minimize the wear and tear on their feathers, birds must constantly work to maintain them. They groom and preen themselves as often as once an hour to reduce their load of parasites and keep their plumage in top condition. They frequently bathe to remove dirt or take a dust bath to remove feather parasites. Some birds also lie on the ground and allow hungry ants to clean their plumage, a behavior known as anting.

SUGGESTED READING

Alexander, *On the Wing.*

Shipman, *Taking Wing.*

QUESTIONS TO CONSIDER

1. How is a flying bird like a sailboat?
2. Why do many waterbirds (such as ducks) molt all their flight feathers at once, instead of one or 2 at a time like other birds?

BURNING BRIGHT: AVIAN ADAPTATIONS FOR FLIGHT

LECTURE 3

Everything about a bird—its skeletal anatomy, physiology, metabolism, respiratory system, reproductive system, excretory system, and nervous system—is adapted for one purpose: keeping it aloft. This lecture will explore these various adaptations.

The most important adaptation for flight is feathers. But feathers didn't evolve so that birds could fly.

Warm-blooded animals need insulation, which is why mammals are covered by hair. There's substantial evidence that many dinosaurs, especially the smaller dinosaurs ancestral to birds, were warm-blooded, and these dinosaurs probably evolved feathers for insulation and passed this adaptation on to birds.

Skeletal and Muscular Adaptions

For birds, a skeletal adaptation for flight is hollow bones. Bird bones are not actually hollow the way a straw is hollow, but they have extensive air spaces inside. Bones like this are called pneumatic bones, another innovation birds inherited from dinosaurs.

To keep these fragile bones from breaking, they have internal cross struts, much like the wing of a biplane, and many of them are fused together for extra strength. This gives birds an airframe that is strong, lightweight, and elastic.

The most important muscles attached to this airframe are the flight muscles, which are a mixture of red and white muscle fibers. Red muscle fibers rely on aerobic metabolism (using oxygen) and supply power for endurance; white muscle fibers use anaerobic metabolism, or fermentation (no oxygen). White fibers provide short bursts of energy needed for rapid takeoffs and high-speed predator avoidance.

Chickens and turkeys have many white fibers in their flight muscles (white meat), which let them take off quickly, but they can only fly for short distances. Their legs are mostly red muscle fibers (dark meat), so they have strong legs and can run quickly.

The terms “white meat,” “dark meat,” and “drumstick” come from the Victorian era, when it was considered impolite to use words like “breast,” “thigh,” or “leg” at the dinner table.

Metabolic System

To sustain powered flight, birds—like Boeings—need to burn fuel at an astounding rate. The metabolic furnace of birds burns brightly.

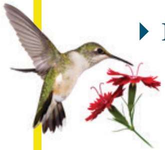
Birds generally seek out high-energy foods, such as insects, fruit, meat and fish, or nectar. Many birds eat seeds or grains, and a few birds can survive on leaves. Some, such as honeyguides, can even digest pure wax.

Chewing their food is a big problem for birds. They have no teeth, though several Mesozoic birds retained the teeth of their reptilian ancestors. To conserve weight for flight, modern birds have replaced teeth—and heavy, bony jaws—with a lightweight bill covered by a horny sheath.

This solves a big weight problem, but the adaptation comes with a price. Without teeth, birds can't chew their food as do mammals and reptiles. They must swallow it whole or use their beaks and claws to tear it into large chunks.

Many birds use their tongues to manipulate food.

- Flamingos pump their tongues back and forth in their highly modified beaks, drawing in water and squeezing it through a filter to extract their tiny prey.



- Hummingbirds have long, coiled tongues for reaching deep into flowers for nectar.
- Woodpeckers have a long tongue, which wraps around the skull, sometimes all the way to the nostrils. Their tongues have tiny barbs coated with a sticky spit to help them snare insects from cracks, tunnels, and holes in the tree.

Food passes through the esophagus into the stomach, through the gizzard, into the intestine, and finally to the cloaca. Many birds have a crop, a portion of the esophagus that is modified as a kind of storage chamber, where food can be stored for a day or more.

Crops may help seedeaters avoid predators. While they're feeding on seeds, they're vulnerable to attack. By cramming seeds into their crops, they can scoop up a maximum number of seeds in a minimum amount of time. Crops also help birds who don't always find regular prey, such as hawks and vultures, who gorge on what they find and store it in their crop.

Birds that eat insects and other wiggly and biting prey have an esophagus and crop lined with an extra-tough layer of epithelial tissue for mechanical protection. Once food passes through the esophagus, it enters the stomach. Bird stomachs are divided into a glandular stomach, called the proventriculus, and a posterior portion, called the gizzard. Gizzards are lined with a tough, ridged layer of keratin, which helps fill in for the lack of grinding teeth.

To help grind tough food, such as seeds, birds swallow grit, particles of sand and stone that lodge in the gizzard. Seedeaters need large gizzards with plenty of grit to help grind their food, but nectar-eaters and meat-eaters have relatively weak, thin-walled gizzards. Gizzards also act as a kind of trap for meat-eating and fish-eating birds. They can roll up all the inedible bits of bone, fur, and feathers and regurgitate them as a pellet.

Turkeys, who are stupid enough to swallow almost anything, can crack walnuts with their gizzards. René-Antoine Ferchault de Réaumur, in 1752, found that a turkey could grind up 24 walnuts in 24 hours.

Birds need to rapidly digest all the food they can get to be able to fly for hours at a time for days on end. Their metabolic furnace burns much brighter than that of humans; their average body temperature is about 104°F, compared to our 98.6°F. And their proteins melt down at an alarming rate.

Outstretched wings make nice heat exchangers, and the air streaming around them plasters the feathers tightly to the body, shedding even more heat.

Birds respond to heat and cold in many ways. They can change the elevation of their feathers to shed or retain heat. Fluffing the feathers traps a layer of warm air on a cold day. Holding feathers very close, or extending them far out to expose bare skin, helps cool the bird down.

Birds react to cold by seeking shelter in cavities or dense vegetation and by huddling together to keep warm. They also shiver, the same as humans do, to generate additional heat. Many birds, such as shorebirds and wading birds, sleep on one leg with their heads tucked under their wings to conserve heat.

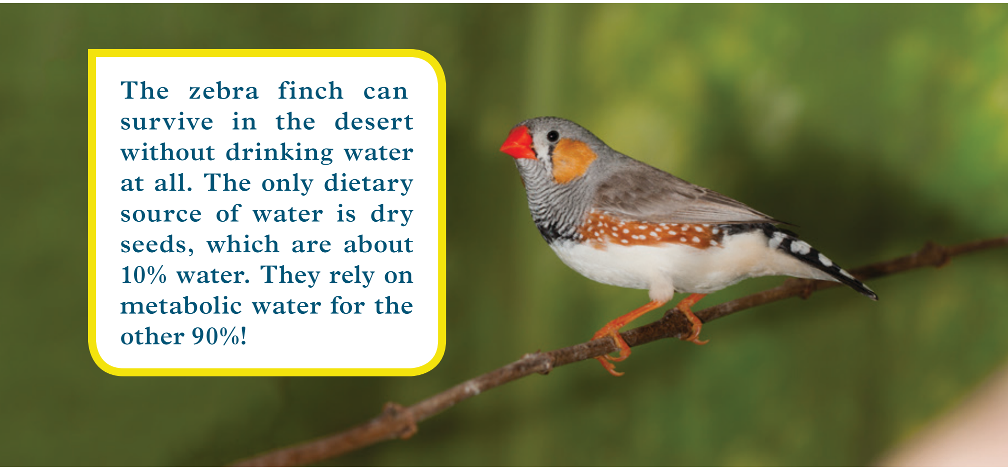
Most birds drop their temperatures a degree or 2 at night, but tiny birds—such as hummingbirds, chickadees, and baby swifts—take it a step further. They have to turn the thermostat way down, leaving only a metabolic pilot light. They enter a state of torpor, a comatose state that uses an absolute minimum amount of energy.

Hot weather can be a big problem for birds because they don’t sweat; water simply evaporates through their skin. Birds seek shade to avoid the heat or cool off in the water, just like humans do. Birds also pant, holding their mouths open to evaporate body moisture. Many seabirds, such as the pelican, can also vibrate their pouch, which increases the evaporation of water from the throat and mouth.

Birds can also shed large amounts of heat through their legs and feet. They can shed heat by increasing the blood flow to their extremities by constricting the blood vessels, and they can conserve heat by directing the return flow of venous blood through a special shunt away from their feet.

Birds have very high basal metabolic rates, or the metabolic level of the bird at rest. But birds are seldom at rest. They’re usually expending enormous amounts of energy at a rapid rate. A bird in flight can maintain a metabolic rate that is 10 to 25 times its resting basal metabolic rate for hours at a time.

One consequence of this turbocharged metabolic rate is that birds produce more metabolic water than other vertebrates. Metabolic water is produced when carbohydrates and other organic compounds that contain hydrogen are oxidized during digestion. This metabolic water can be used to counter excess metabolic heat—by evaporative cooling, such as panting. Birds supplement metabolic water with visits to open water.



The zebra finch can survive in the desert without drinking water at all. The only dietary source of water is dry seeds, which are about 10% water. They rely on metabolic water for the other 90%!

Respiratory, Circulatory, and Excretory Systems

Sustaining very high metabolic levels puts great demands on the bird's transport systems. Their respiratory, circulatory, and excretory systems must rapidly transport food and oxygen to the tissues and quickly carry away waste.

Mammals don't have an especially efficient respiratory system; when we exhale, there is always a residual pool of stale air left in the lungs. Birds, however, completely empty their lungs. Their lungs work in conjunction with air sacs, small sacks of tissue that run throughout the chest cavity. Birds breathe in through their nares, or nostrils, located at the base of the bill.

Air sacs are one of many adaptations that birds inherited from dinosaurs. Air sacs are soft tissue and don't preserve in fossils, but some recently discovered dinosaurs have concave areas in their bones that are just the right size and position for air sacs.

Air sacs don't have a good supply of blood vessels and don't play much of a role in gas exchange. But they do serve other functions, such as cushioning internal organs. Evaporative cooling by air sacs also helps prevent heat stress. Air sacs also provide waterbirds with additional buoyancy. Some birds can control the volume of the air sacs for swimming and diving, analogous to the way bony fishes use their swim bladders.

Supplying the bird's demanding metabolism requires a strong circulatory system. The resting heart rate of most birds is about half that of mammals of the same size, but birds have more powerful heart muscles, so they pump about the same volume of blood as a mammalian heart.

Avian heartbeats average about 220 beats per minute, but hummingbird hearts beat up to 1200 times per minute—that's 20 beats per second!

Avian blood pressure is higher than most mammals. In fact, it can run to twice that of a human suffering from high blood pressure. As a result, birds frequently stroke out; if you catch a wild bird, it sometimes literally dies of fright.

Such powerful metabolic systems create substantial amounts of waste, a serious problem for an animal that needs to travel light. Primitive aquatic organisms use ammonia for liquid waste, which requires a lot of water to dissolve. Terrestrial animals evolved excretory systems relying on urea—which doesn't require as much water to dissolve—for liquid wastes. A full bladder would be a big problem for a bird, so birds use uric acid for liquid waste. It's also not toxic when concentrated, unlike human urea.

This system evolved as an adaptation for egg laying in birds and reptiles. Embryos have no way of getting nitrogen wastes out of the shells. They must store those wastes in the shell in a nontoxic, concentrated form that requires very little water.

Heightened Senses

In addition to skeletal and physiological adaptations, birds rely on heightened senses to survive. Like humans, birds live in a world dominated by sight and sound. Birds can taste and smell about as well as mammals.

Birds have incredible eyesight. Like their reptilian ancestors, the eyes of birds have a third eyelid, which is the one they use when they blink.

The eyes of birds have some distinctive differences from those of other vertebrates. Birds focus images onto their retina, as humans do, but they use both their cornea and their lens to focus the image (humans only use the lens). As a result, birds can accommodate their focus much more quickly than other vertebrates.

Birds can also see colors that humans can't, all the way into the near ultraviolet spectrum. Pigeons can even see polarized light. Avian color vision is also sharper than that of humans.

Many birds have relatively large eyes, and larger eyes give birds larger and sharper images. Birds' eyes are fixed in their sockets because of the large size of the eye relative to the eye socket. They can't hold their heads still and roll their eyes around to see, like humans can. They need to move their heads to change their visual field.

Ostriches have the largest eyes of any land vertebrate at 50 millimeters in diameter.

The eyes of birds are set farther to the side of the head, so birds see best to either side. True binocular vision is uncommon, or restricted to a narrow zone directly in front of the beak. So, despite having excellent resolution of detail, their view of the world is surprisingly flat. Many birds move their heads rhythmically back and forth to gather more depth information and compensate for limited eye movements and limited stereo vision.

The best binocular vision occurs in birds that rely heavily on vision for high-speed aerial maneuvering, such as hummingbirds, eagles, hawks, and swallows.

Birds are very good at integrating visual information. Birds that catch fish from above the water always compensate for the refraction of the image by the water.

Birds also have good hearing, which is not surprising considering the importance of hearing in detecting prey or predators, in courtship, and in territorial defense.

Birds' ears are nearly invisible, below and behind their eyes. Large, floppy ears—like those of most mammals—would add too much profile drag in flight.

The avian ear has only one bone to connect the inner ear to the eardrum (humans have 3). Birds don't hear as well as humans do, but some hear better than others.

Birds that hunt by sound, such as owls, have the best hearing. Owls are more sensitive to high-frequency sounds than humans are and can acquire and process stereo sound information to precisely locate prey in complete darkness.

During World War I, parrots were kept at the Eiffel Tower because they could hear approaching planes that were too far away for humans to see or hear.

Some birds can use echolocation like a bat or dolphin to navigate in dark places. Unlike bats and dolphins, which rely on ultrasound, birds use a lower-frequency range, so they don't have the fine resolution of hunting bats.

SUGGESTED READING

Lederer, *Beaks, Bones, and Bird Songs*.

Proctor and Lynch, *Manual of Ornithology*.

Van Grouw, *The Unfeathered Bird*.

QUESTIONS TO CONSIDER

1 Birds excrete liquid wastes as uric acid rather than urea. How is this advantageous, and why did it originally evolve?

2 Oilbirds, cave swiftlets, bats, and some blind humans can all navigate by echolocation. What do they all have in common that makes this an especially useful skill?

ORIENTATION, NAVIGATION, MIGRATION: BIRD ROAD TRIPS

LECTURE 4

Flying halfway around the world during migration is no simple feat. More astoundingly, birds can end up at the same location year after year. In this lecture, you will discover how birds know where they are (orientation) and where they're going—navigation. You will also explore how birds put their navigation skills to the test in their annual migration.

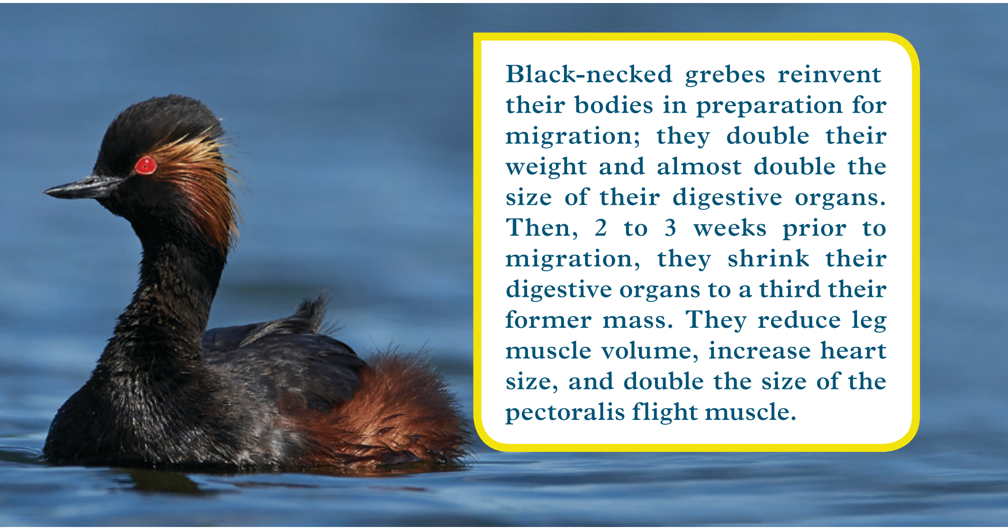
The Art of Navigation and Orientation

Many animals have an innate homing ability—including bees, ants, salmon, lobsters, and even mice—but none can hold a candle to the homing ability of birds.

Homing pigeons are famous for their ability to find their way home from wherever they've been released, but many species of birds are capable of astounding feats of navigation in their efforts to get home. For example, a Manx shearwater that was carried from Wales to Boston was found back in its nest 12.5 days later.

Nothing speaks more to the cost of flying such great distances day after day than the lengths to which birds go to prepare for it. To pump themselves up for such an energy-draining flight, birds build up extensive reserves of fat just before departure.

A typical nonmigratory perching bird has about 3% to 5% of body fat in its overall mass. Shorebirds and other long-range migrants build up 30% to 47% of their body mass as fat before migration. Bobolinks add 50% of their own body weight in stored fat.



Black-necked grebes reinvent their bodies in preparation for migration; they double their weight and almost double the size of their digestive organs. Then, 2 to 3 weeks prior to migration, they shrink their digestive organs to a third their former mass. They reduce leg muscle volume, increase heart size, and double the size of the pectoralis flight muscle.

Once birds are ready for their migratory journey, they need to know where to go. There are many possible ways that birds can orient themselves, including by using magnetic fields, visual landmarks, and the position of the Sun and stars. Like humans, birds rely heavily on visual landmarks. Migrants follow rivers or shorelines, parallel mountain ranges, and funnel through mountain passes.

Although landmarks are important, birds don’t rely on a single navigational clue; they can use several different clues in combination to orient themselves. During the day, for example, birds can use the relative position of the Sun to navigate. The Sun changes its position by about 15° every hour during the day, and birds must compensate for this changing position.

In 1954, Konrad Hoffman found that he could easily confuse starlings by changing light levels in the lab to displace this internal compass. The cleverest experiments on avian orientation were done in the late 1960s on the indigo bunting by Stephen Emlen. He showed that birds, like human sailors, can navigate by using the position of the constellations—a useful skill for birds who migrate at night, like buntings. Indigo buntings have a critical sensitive period shortly after birth during which they need to see the night sky often in order to learn to orient by the stars.

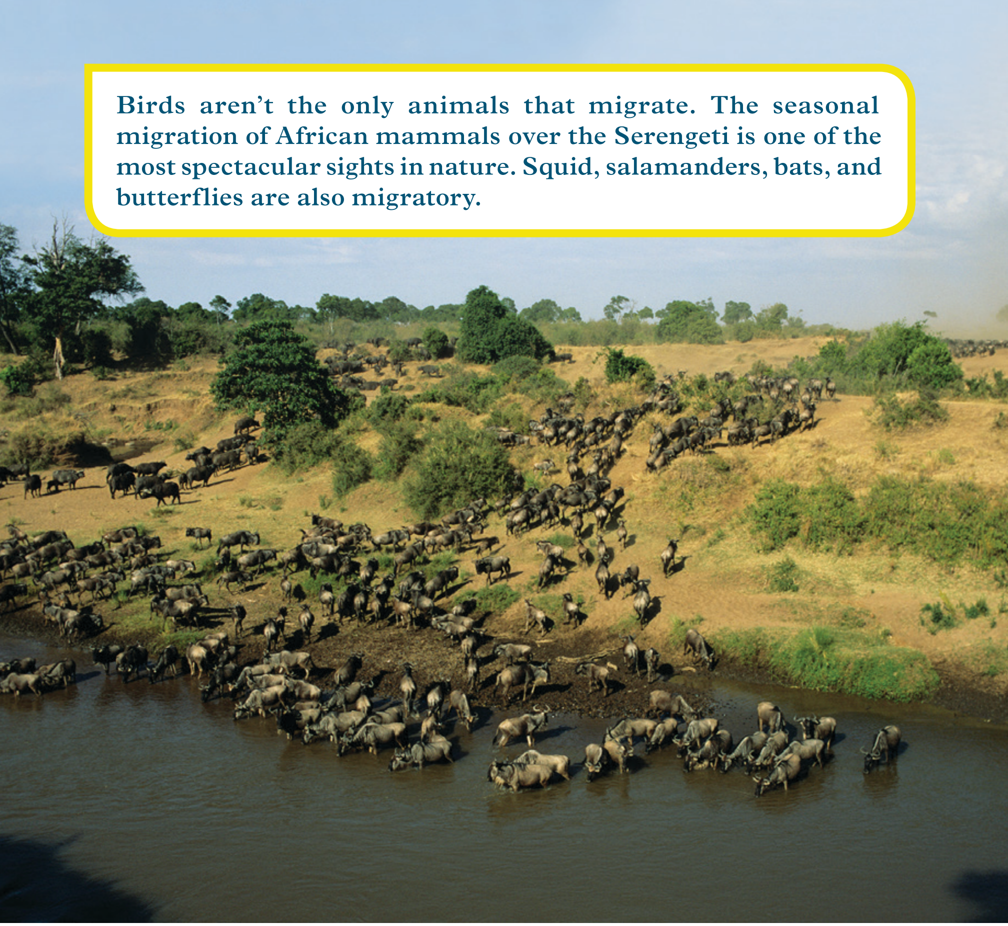
A pigeon received the Croix de Guerre in World War I for delivering critical messages despite severe wounds. In World War II, homing pigeons played a key role in the Normandy invasion, when radio silence was essential. Pigeons in the Confidential Pigeon Service, code name Source Columba, gave resistance fighters a way to send information from occupied Europe.

Many birds can use Earth's magnetic field as a compass. In the early 1970s, William Keeton used tiny bar magnets to show that homing pigeons could orient by magnetic fields. Pigeons need to be exposed to the Sun for at least an hour a day to calibrate their solar compass. Their magnetic compass also needs to be calibrated, probably by comparing it with their solar compass. Once the solar and magnetic compasses are synched together, they can switch between them as needed. Pigeons raised in the absence of sunlight miss the chance to calibrate their magnetic compass and can't navigate on overcast days.

Displacement experiments have shown that orientation has both innate and learned components. Juvenile birds more often rely on innate disposition to migrate in a particular direction. Adult birds will supplement this information with environmental clues.

The Miracle of Migration

Migration is the regular seasonal movement of animals between disjunct areas of their home range. Migration remains one of ornithology's deep mysteries. We can track its course, note species patterns, and worry about our destruction of breeding and wintering habitats, but we still don't understand why some birds do it while others do not, much less all the different patterns within sexes and age groups.



Birds aren't the only animals that migrate. The seasonal migration of African mammals over the Serengeti is one of the most spectacular sights in nature. Squid, salamanders, bats, and butterflies are also migratory.

Many hypotheses have been proposed to explain migration. Migrants may be tracking the seasonal peaks in food supply. Migration to the north in spring lets birds take advantage of the wealth of spring food and longer day length. Tropical food supplies are more uniform throughout the year.

Global climate change poses a new challenge to migratory birds—by changing patterns of seasonal prey abundance. For example, the insects that the European pied flycatcher feeds to its young are responding more rapidly to climate change and peak before the flycatchers can arrive to prey on them. It turns out that flycatchers are delayed by poor conditions in southern Europe, where the advance of spring is slower than in northern Europe.

Migratory birds are already showing signs of responding to climate change. Twenty species now arrive up to 21 days earlier. German cranes and starlings, which normally fly to Spain and Portugal, have stopped migrating altogether, as have many other populations of birds.

One of the benefits of migrating north in the spring is that there are fewer predators in the north temperate zone. The colder northern climate slows the ability of predators to build up very large populations.

None of these hypotheses has been decisively proven, but the most likely explanation is that spring migrants are taking advantage of the superabundant seasonal food supplies in the north. Fall migrants are seeking a more favorable climate.

Whatever the reason, given the high cost and great danger of migration, the payoff must be substantial. More than 200 North American species—about 5 billion birds—leave each year on that ultimate road trip to the southern sunshine. The same number leave Eurasia each year to follow the summer Sun to Africa. Not all birds migrate, and even among migratory species there are nonmigratory local populations.

North American migrants follow north-south migration routes along 4 major paths, or flyways: the Atlantic, Mississippi, Central, and Pacific flyways. Migratory routes like these flyways are an accident of geography. They follow the north-south alignment of major river systems, such as the Mississippi, and major mountain ranges, such as the Appalachians, the Rockies, and the Sierra Nevadas.

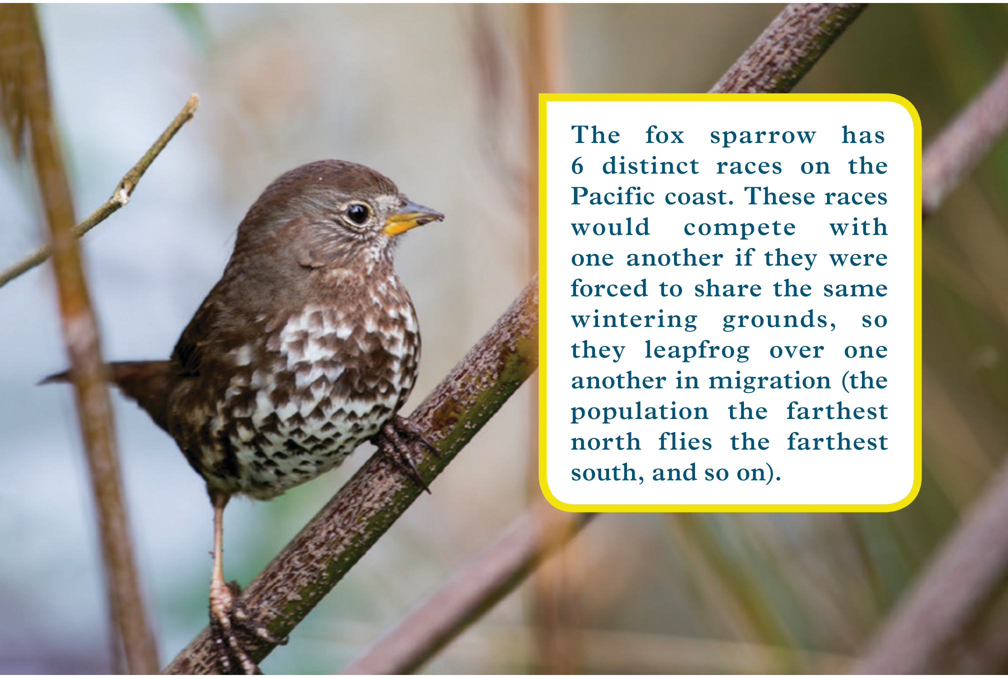
But in Eurasia, major mountains and rivers follow a more east-west axis, such as the Alps and the Mediterranean. As a result, many Eurasian species migrate east to west, although they still end up much farther south than when they started. Their axis of migration is also skewed because Africa is relatively displaced toward the west of Eurasia.

The influence of geography on migration is especially interesting in light of Jared Diamond's *Guns, Germs and Steel: The Fates of Human Societies*, which ties major differences in human cultural development in the New World versus the Old World to the exact same geographic influence.

Studying migration is a big challenge. Traditionally, the best way to study the migratory habits of birds has been to band them with aluminum leg bands and try to recover banded birds. Recovery rates, however, are extremely low—usually less than 1%.

Another time-honored method is moonwatching, which involves watching the face of the full moon for the silhouettes of migrating birds. For species that migrate by day and whose routes are funneled through a narrow area, observers can simply count the passing birds.

Since World War II, radar has been used as a tracking tool for migrating flocks. Avid birders routinely monitor radar reports and weather fronts to anticipate the best times to head out to the field. Once the elements of weather are filtered out, experts can assess the relative numbers of birds on the move. Although we can't usually identify the exact species, experts can often interpret flight speeds and patterns to differentiate between warblers, ducks, or shorebirds.



The fox sparrow has 6 distinct races on the Pacific coast. These races would compete with one another if they were forced to share the same wintering grounds, so they leapfrog over one another in migration (the population the farthest north flies the farthest south, and so on).

For the BirdCast project, birdcall experts joined forces with radar experts to identify the species of nocturnal migrants by matching radar images with the recorded calls of passing birds—which were recorded by microphones on rooftops in migratory flight paths—combined with backyard census data from volunteers.

With the advent of miniature radio transmitters, we can now track tagged birds from the ground or from aircraft.

Migration patterns are complex. They may vary within species, with different races, ages, or even sexes migrating to different areas. In many species, males, females, and juveniles may migrate to different latitudes. Males generally migrate farther north, presumably because their larger body size makes them more tolerant to cold. In species where the female is larger, it's the females who migrate farther north.

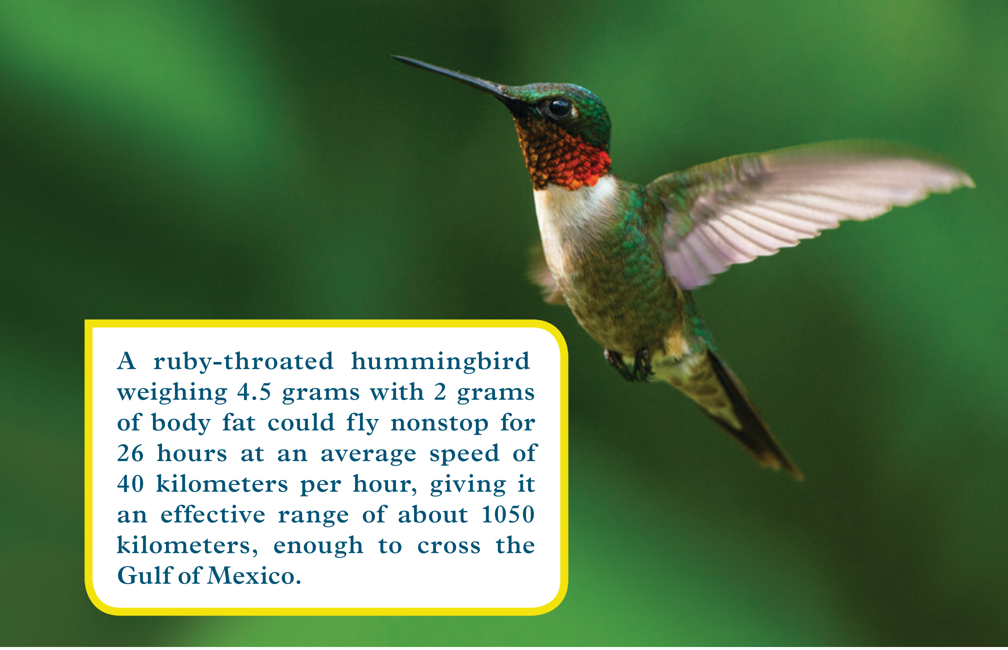
Environmental conditions, such as weather and food supply, seem to act as a proximate cue for migration. But the ultimate cue for migratory readiness comes from photoperiod, or day length.

Birds have an innate sense of which direction they need to go and how long it will take them to get there. Migratory birds show a characteristic premigratory nocturnal restlessness, called *Zugunruhe*. Caged birds will sleep briefly after sunset and then wake up and hop and flutter around with increasing energy until about midnight. The duration and intensity of this restlessness correlates with the distance they will migrate.

Some birds, such as the white-crowned sparrow, also show compass orientation. During *Zugunruhe*, sparrows in circular cages orient toward the south during fall migration and toward the north in spring migration.

Cross-fostering experiments have discovered both learned and innate components to migratory behavior.

M. P. Harris switched 900 young between the nonmigratory herring gull and the migratory lesser black-backed gull. When it came time to migrate, the nonmigratory herring gulls followed their new parents to France and Spain, suggesting learned behavior. The migratory lesser black-backed gulls, on the other hand, showed an innate tendency to migrate and left their foster parents behind.



A ruby-throated hummingbird weighing 4.5 grams with 2 grams of body fat could fly nonstop for 26 hours at an average speed of 40 kilometers per hour, giving it an effective range of about 1050 kilometers, enough to cross the Gulf of Mexico.

Birds typically fly hundreds of miles a day on their epic migratory journeys. The arctic tern, for example, flies from its northern breeding grounds to Antarctica, a round-trip journey of up to 56,000 miles. Like many species of birds, the arctic tern shows philopatry, or site fidelity. Despite their long journey, 98% of migrating terns return to the same breeding grounds every year.

Many migrants fly at night, resting and foraging on land during the day. Birds that feed on the wing, such as swifts and swallows, migrate during the day, when insects are active. Hawks also migrate by day to take advantage of the thermal updrafts.

Of the North American passerines that set out, only half ever return. For ducks and other waterfowl, the death toll reaches 60% or more. For those who survive nature's gauntlet, humans add perils like hunting, reflective glass skyscrapers, power lines, and cell phone towers.

But the biggest problem facing migratory birds today is habitat loss. Our remaining wild places are becoming scattered fragments. The canaries in our global coal mine are the neotropical migrant birds who spend their winters in Central and South America and the rest of the year in North America.

These birds are facing extensive loss and fragmentation of habitat at both ends of their migratory range. They include some of most beautiful and ecologically important species, such as wood warblers, tanagers, buntings, and grosbeaks. The steepest declines are among species that rely on deep forest interiors to feed or breed.

Despite these perils, birds continue to migrate in vast numbers, seeking a warmer climate, more food, and longer days for foraging. Good weather with favorable winds can start birds moving; bad weather can quickly exhaust migrating birds and blow them thousands of miles off course.

Mortality rates during migration are staggering; for many species, most of their annual mortality comes from migration.

From time to time, birds crossing the Gulf of Mexico meet an advancing cold front from the north and a migratory fallout can occur. Tens of thousands of weary migrants settle on the first coastal landfall they see to wait for better conditions to finish their long voyage. For avid birders, migratory fallouts are the Holy Grail.

SUGGESTED READING

Elphick, *The Atlas of Bird Migration*.

Perrin and Mongibeaux, *Winged Migration*.

Weidensaul, *Living on the Wind*.

QUESTIONS TO CONSIDER

1 How are indigo buntings like human sailors?

2 What are some of the navigational clues used by both birds and humans in long-distance journeys?

BIRD BRAINS: TOOL WIELDERS AND SNACK STEALERS

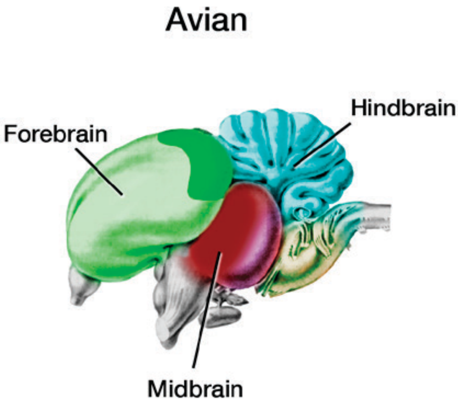
LECTURE 5

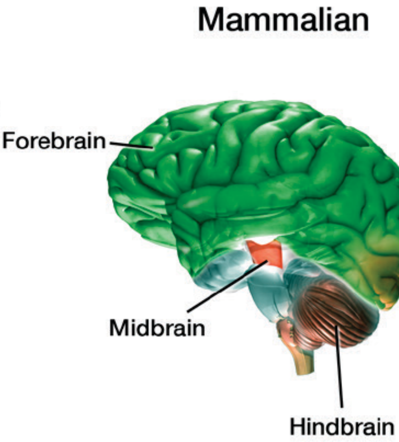
The next time somebody calls you a birdbrain, be sure to thank them for the compliment—because it turns out that birds are much more intelligent than we ever imagined. In this lecture, you'll consider several reasons why we underestimated avian intelligence. You'll examine the structure of the avian brain and the ways in which it's different from our own. You'll consider the importance of instinct in birds and learn about the many ways in which birds use tools. And you'll discover how day length drives the annual cycle of bird behavior.

The Avian Brain

The 3 main areas of the avian and mammalian brain are the forebrain, the midbrain, and the hindbrain .

The midbrain of birds is dominated by large optic lobes and controls vision. This differs from mammals, whose optic nerves are mapped out on an area of the cerebral cortex called the visual cortex.





The hindbrain consists of the cerebellum and the medulla. The cerebellum integrates muscular control and coordination; the medulla interfaces the spinal cord and the brain. The cerebellum fills the same function in both birds and humans, but this function is especially important for birds. Zipping around over the ground and through the trees requires tremendous visual and muscular coordination, and birds have the added task of coordinating extra input on feather position and feather elevation from sensory feathers.

The forebrain governs complex learned behavior and intelligence. The gray matter that covers the surface of the forebrain is called the pallium. In mammals, this layer has evolved into the cerebral cortex, which occupies most of the brain. Birds have a large pallium but lack the enlarged cerebral cortex of mammals.

The top two-thirds of the mammalian forebrain, the neocortex, has flat sheets of cells arranged in 6 layers; the more primitive bottom third consists of cells organized in clusters. The avian forebrain consists almost entirely of clusters.

Given their lack of a cerebral cortex and the more primitive arrangement of the neurons in their forebrain, we assumed that birds could not be very bright, compared to primates. After all, their brain is the size of a walnut.

But it turns out that it's not the size of your brain that's important; what's more important is how large your brain is relative to your body. But there's a fundamental problem with using brain-to-body ratios.

Large brains don't necessarily equate to higher intelligence. Larger animals have a greater skin surface to enervate and more muscle mass to control, which requires more brainpower.

A better way to judge intellect might not be the size of the brain but how many nerve cells it contains and how those nerve cells function. And in that regard, bird brains have taken a different evolutionary path from ours over the past 300 million years.

The mind of the bird is not like our own; it's not centered in the folds and fissures of the cerebral cortex, but in the pallium. The avian pallium, as now defined, makes up 75% of brain volume, as it does in mammals. And recent research shows that the clusters of nerve cells in the avian pallium—once thought to be primitive—function much like the flat sheets of neurons in our cerebral cortex.

Although bird brains may be much smaller than primate brains, their neurons are much more densely packed. Songbirds, parrots, and crows have neuron densities up to 3 to 4 times their density in the primate brain.

Another big difference between bird brains and human brains is that birds have an amazing ability to remember where they put stuff. This spatial memory is centered in a part of the forebrain called the hippocampus. Birds can keep complex spatial maps of places where they have stored food.

Clark's nutcrackers can remember the location of 2000 or more seed caches for up to 8 or 9 months.

Instinctive and Learned Behavior

One of the most important differences between birds and primates is the degree to which our lives are governed by instinct—inborn, stereotyped behavior patterns characteristic of a given species. Because the pallium is known to regulate instinctive behavior in other vertebrates, we've always assumed that bird behavior was primarily instinctive. And, higher intellect to the contrary, birds are surprisingly instinctive creatures.

Birds often play out complex instinctive behavior sequences as a response to some simple external stimuli. Consider the way incubating geese roll their eggs back into their nest. If a goose sees an egg outside the nest, she will touch it with her beak and then roll it back into the nest. But she goes through exactly the same behavior sequence if any object is placed near the nest. She will even finish the behavioral sequence if the egg is removed after she has reached for it.

This is a terrific example of what's called a fixed action pattern, a rigidly stereotyped, predictable behavior pattern in response to a releasing stimulus. Such instinctive behavior turns out to be widespread in birds, more so than in many other vertebrates.

While bird behavior may be partly instinctive, birds also show a great deal of complex learned behavior. Even the lowly pigeon is smarter than we thought; pigeons can remember up to 725 different visual patterns. In laboratory tests, they can even learn to differentiate between artistic styles, such as cubism and impressionism.

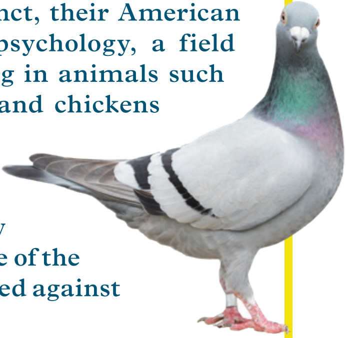
Scrub jays in laboratory studies by Nicola Clayton have shown episodic memory, once thought to be unique to primates. They remember not only where they hid food but also when and, just like humans, prefer to retrieve food first that is most likely to spoil.

But where birds truly shine is their mastery of using tools. The woodpecker finch in the Galapagos Islands uses cactus spines and twigs to probe for insects, and Galapagos finches have learned to roll eggs off the edges of rocks to break them open.

Crows in Japan use cars as nutcrackers. They drop the nuts in the road and then fly up to a safe perch and patiently wait for the traffic light to change. When the cars come to a stop, they swoop in to collect their reward.

Early bird behavior studies were done by a group of scientists called ethologists. This European school was led by the Austrian naturalist Konrad Lorenz, who was fascinated by the degree to which animals were controlled by instincts.

While European ethologists studied instinct, their American counterparts focused on comparative psychology, a field founded on laboratory studies of learning in animals such as rats, pigeons, and chickens. Pigeons and chickens are inexpensive, docile, and readily available experimental animals, but neither species is very bright compared to other birds. Their use in early psychological studies is one of the reasons we became so biased against avian brainpower.



One of the most intriguing and unsettling examples of tool use comes from the Australian outback. Black kites, whistling kites, and brown falcons are often seen near bushfires, feeding on fleeing animals. They have even learned to carry small burning twigs and drop them to start new fires to flush their prey—behavior once thought to be unique to humans.

New Caledonian crows are expert natural tool users, commonly observed probing cracks and crannies with sticks, hunting for insects. To probe for insects, they make complex serrated leaf tools by progressively snipping off strips of leaf to form what looks like a tiny, narrowing saw blade.

Even more extraordinarily, there are many variations in leaf tool design between local populations of crows. These variations are persistent over time, which is an indication that local tool styles are being passed from generation to generation—in human terms, this is cultural transmission! Chimp tools, by comparison, are more opportunistic, with minimal shaping or evolution to more sophisticated forms.

New Caledonian crows also demonstrate a rare instance of technological evolution in animal tool use: using tools on other tools. This behavior was thought to be unique to primates, who quickly learn to use a short stick to retrieve a longer stick to reach food. In a study by Alex Taylor, 6 out of 7 crows solved the same problem on the first try.

Birds have also learned how to take advantage of us to get something good to eat. Green herons have learned to bait fish with insects, seeds, flowers, and even popcorn and bread. House sparrows in New Zealand have figured out how to trigger the sensors that open the doors to a bus station cafeteria so that they can feast on crumbs.

In the early 1920s, blue tits in Great Britain learned to pry or tear the cardboard caps off milk bottles to get the cream. Tool use, incidentally, is often based on day-to-day behavior, and the wild foraging behavior of blue tits includes tearing off bits of tree bark to reach insects.

Flocks of blue tits started following milk trucks around for a free meal. To foil the birds, dairies switched from paper caps to aluminum foil caps. But the birds soon learned to open the foil caps—by patiently tearing them into thin strips. Even more amazingly, other species of birds learned to imitate them; by the end of WWII, 11 other species were doing this.

The most spectacular example of learning by imitation, however, is the New Caledonian crow who learned to make her own tool. Wild crows fashion hooks from natural materials. As far as we know, we are the only other animal that makes hooks to catch food. Birds in the lab were given a hooked wire and a straight wire and quickly figured out how to use the hooked wire to lift a tasty reward from a cylinder. But when a selfish male crow swiped the only available hook, his female cage mate bent the remaining straight wire to create her own hooked tool.

Photoperiod

Bird behavior is timed to follow the seasons, an annual cycle of breeding, molt, and migration. Each new season brings new energetic demands and new patterns of behavior—territoriality, courtship, nesting, molting—all keyed to the annual availability of resources. But how do birds know when it's time to breed, molt, or migrate?

Like most animals, birds have an innate circadian rhythm, a 24-hour internal clock. Captive birds show a regular daily cycle of sleeping and waking, even when kept in cages at a constant low level of illumination. Superimposed on these circadian rhythms are more complex circannual cycles, which are especially important because each main event in a bird's life (breeding, molting, and migrating) requires an enormous amount of energy.

Birds replace 25% to 40% of their lean dry weight when they molt. If this overlapped to a larger degree with migration or breeding, birds would burn themselves out.

The critical element of control that synchronizes internal clocks with the changing seasons is photoperiod, the duration of daily sunlight. Chicken breeders can get hens to nest and lay eggs in winter by keeping their coops lit for several hours every night. Similar experiments on rats, mice, goats, and brook trout have also induced precocious breeding.

This mechanism may be basic to most or all vertebrates, including humans; seasonal variation in photoperiod may explain spring spikes in human fertility and reproduction. The pineal gland and hypothalamus are responsible for tracking day length, using photoreceptors that are sensitive to low levels of light.

To demonstrate the importance of photoperiod, Michael Menaker plucked head feathers from a group of house sparrows to increase light exposure to the brain. He injected India ink under the skin of another group to decrease light exposure. After exposure to artificially long days, only plucked birds developed testes. Their heads were receiving more light.

The longer days of spring and summer induce a series of physiological changes. The gonads begin to develop and swell, and the pituitary gland secretes hormones that trigger breeding behaviors. The shorter days of winter induce a refractory period, which resets the sensitivity of the biological clock. After breeding season is over, the gonads atrophy to the point where they are nearly invisible. Having much smaller gonads most of the year conserves weight for flight. Without this winter refractory period, breeding conditions can continue indefinitely.

Photoreceptors are most sensitive during a critical period each day. More light during this sensitive period cues the bird to the increasing length of the spring days. The Sun's light stimulates the photoreceptive cells in the brain. Neurohormones from the photoreceptors pass to the anterior pituitary gland, where they stimulate the release of hormones that cause the gonads to develop and gametes to form.

SUGGESTED READING

Ackerman, *The Genius of Birds*.

Emery, *Bird Brain*.

Savage, *Crows*.

QUESTIONS TO CONSIDER

1 How did we misjudge the intellectual capacity of birds?

2 How do birds know when it's time to fly south for the winter?

BIRDS OF A FEATHER: FLOCKING AND FORAGING

LECTURE 6

In this lecture, you'll learn how birds behave when they come together to form flocks or colonies and how sometimes the best way to cooperate is to be selfish. You'll also consider feeding and foraging behavior, the advantages and disadvantages of feeding in flocks, and how birds work to optimize their foraging success.

Social Foraging

Although birds prefer to eat certain kinds of food, they are very opportunistic diners. They may prefer to eat caterpillars, for example, but, like us, they are open to suggestions. For example, snowy egrets prefer small fish, especially during breeding season. Their reproductive success directly correlates with the availability of small fish. But they will capture crawfish if they are available.

Foraging strategies are essential if birds want to get a maximum of energy from a minimum of effort. Foraging strategies are shaped by the amount of energy required to catch and eat an item of prey relative to the amount of energy the bird can potentially get from that prey item. Different prey sizes and shapes, for example, may require different handling times, the time needed to manipulate the food in order to eat it.

Optimal foraging theory has emerged as a broad-scale attempt to model animal foraging in general. The model tries to determine the best way to maximize profitability in foraging. Profitability includes search time, which is the effort required to find the prey, and handling time, which is the effort required to eat the prey.

A simple equation can be derived to measure profitability:

$$P = E/(h + s).$$

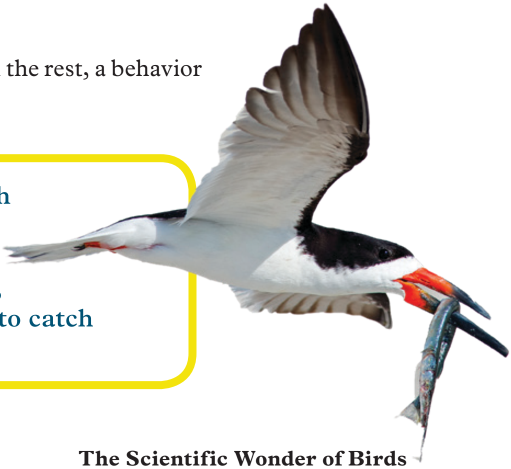
This equation says that profitability equals the energy from prey divided by the sum of handling time and search time.

Birds get a much better deal when they feed together in flocks, which often catch more food than solitary birds. Birds can spend less time looking up and more time feeding. The movement of the flock also flushes out more prey as the flock forages through the trees and meadows.

Groups of species often divide up food resources among themselves in a way that minimizes competition. For example, different species may form foraging guilds, which eat the same types of food. Despite the extra competition, they can forage side by side with little or no competition because each species exploits the resource in a slightly different way.

Some birds steal their food from all the rest, a behavior called kleptoparasitism.

Pelicans plunge-dive to catch fish below the surface, whereas the black skimmer flies over the top of the water, using its long beak as a scoop to catch fish at the surface.



Birds have evolved a way to turn selfish behavior into communal cooperation, something humans have tried to do for centuries. This behavior is called resource partitioning, referring to the way the flock divides up, or partitions, the prey.

Mixed-species foraging flocks of small warblers, for example, can all feed in the same tree at the same time by feeding in different zones. Some warblers specialize in gleaning small insects from the surface of leaves. Other birds, such as chickadees, may look on the undersides of the leaves. Nuthatches, downy woodpeckers, and brown creepers will examine cracks in the bark for insects. Each favors a slightly different feeding zone in the same tree. These temperate forest flocks average 10 to 15 birds of 6 to 7 species.

At first glance, the presence of so many different species feeding in the same tree at the same time would seem to be counterproductive. But by feeding in different ways and in different parts of the tree, birds minimize the potential competition, so their selfish individual behavior becomes a cooperative communal effort.

Mixed-species foraging flocks actually have higher rates of food capture than solitary birds. Temperate foraging flocks are twice as successful as birds foraging alone.

There is also a subtle pattern to this behavior that is not immediately apparent. The species composition of these flocks remains roughly the same, but individual birds change places as the flock moves through the forest.

Birds (like humans) defend a territory, an area where only they can hunt or mate. Individual birds drop out as the foraging flock leaves their territory. Their presence in the flock is replaced by new individuals of the same species, who join in when the flock enters their territory.

These mixed-species foraging flocks are much more common in tropical forests. Tropical flocks typically contain about 60 birds of 30 different species. Several different species of wading birds are often seen feeding peacefully together. Long-legged species, such as great egrets and great blue herons, feed in deeper water than the shorter-legged snowy egrets and ibises. In the shallower water, egrets hunt by sight and prefer fish, while ibises forage by touch and prefer crawfish.

But social foraging is not always mutually advantageous. When does it pay to scrounge the food that other birds find rather than try to find your own?

Luc-Alain Giraldeau and Guy Beauchamp proposed a model of producers and scroungers, in which producers locate new patches of food while scroungers move in to exploit it. Using elements of game theory, they showed that producers would move to a new patch as competition from scroungers increased. The payoff from leaving exceeds the payoff for staying.

The relationship between resource distribution and territorial behavior shapes the likelihood of birds flocking together or going it alone. If resources are patchy and easy to monopolize territoriality makes sense. If resources only occur in patches, one male can easily defend them. But if resources are homogenous or superabundant, then flocking makes more sense, because no one individual can monopolize resources.

Sanderlings will defend a feeding territory on the beach, but they are only territorial at intermediate prey densities. When food is scarce or extremely abundant, they feed together in flocks.

Sometimes, as with humans, it all comes down to raging hormones. Birds that are fiercely territorial during breeding season may form large, peaceful flocks when breeding season is over and their gonads begin to atrophy.

A major advantage of flocking is increased vigilance; more eyes and ears are attuned for predators. Larger flocks also reduce the risk of predation by offering predators more potential targets. The more birds in the flock, the lower the probability becomes for each individual bird that it will be captured.

W. D. Hamilton proposed a general mathematical model for herding and flocking behavior.

Predators will usually attack the nearest prey. Standing near another individual cuts off half the possible avenues of approach. Standing in a group of 4 individuals cuts the risk by a quarter, and so on. The safest position mathematically is in the center of the flock.

Birds keep their social dominance in flocks by establishing a pecking order, a series of dominant and subdominant males—alpha male, beta male, and so on. Dominant birds in a flock will select the center spots when they roost or nest. Dominant adult blackbirds seem to favor central spots in their evening roost. Wading birds who nest in the center of colonies significantly reduce the risk of nest predation.

Flocks help birds conserve heat when the weather turns chilly. In fact, more than 60 European wrens were found packed into a nest box measuring only 140 cubic inches.

Birds often flock together to form evening roosts containing large numbers of birds from several species. Double-crested cormorants in Mississippi form roosts near catfish farm ponds of up to 50,000 birds. Winter roosts of blackbirds in the Mississippi Valley can contain more than 15 million birds.

A massive invasion of bramblings in 1951, driven by extreme cold farther north, formed a winter roost of about 72 million birds in a 17-acre forest.

One of the most extraordinary things that birds do in flocks is stay out of one another's way. A computer model called Boids has finally succeeded in imitating the synchronized wheeling and swooping of large flocks of flying birds. Craig Reynolds modeled this aerial ballet with uncanny accuracy. The rules he assigned for his computer-generated flocks were to avoid collisions, match your nearest neighbor's speed and direction, and move toward the center of gravity of nearby birds (their average position).

Site Fidelity and Coloniality

Birds often show site fidelity, or philopatry, returning to the same territory year after year to breed or feed. In a study by J. J. Hickey, 74% of the robins he banded were found within 16 kilometers of their capture point the following year.

Many species of birds, such as colonial waterbirds, show strong site fidelity in the location of their colonial breeding grounds. Previous nesting success, which is directly related to local food abundance, seems to be the ultimate cue for site fidelity in birds.

There is good evidence that at least some of their dinosaurian ancestors were also colonial breeders. These dinosaurs showed strong site fidelity in their choice of a communal breeding ground. In John Horner's brilliant work in the badlands of northern Montana, he discovered dinosaurs that behaved very much like modern colonial waterbirds. His study site was a communal nesting ground for large herds of a new species of the herbivorous duck-billed dinosaurs that he called *Maiasaura*.

These dinosaurs, who lived 80 million years ago, nested very much like gulls, terns, herons, egrets, and ibises today. For one thing, they returned to the same location year after year to nest; they were philopatric. The dinosaur's choice of a breeding ground also echoed the choices made by colonial waterbirds today. The spacing of the individual dinosaur nests was very regular, much like that of modern waterbirds. These similarities between *Maiasaura* colonies and colonies of modern colonial wading birds suggest that coloniality is an effective evolutionary strategy.

Many species of birds that flock together to feed and roost are also colonial breeders. Joanna Burger, one of the leading experts in this area, defines a colony as a group of birds nesting in close proximity, regularly interacting with one another, and feeding outside the breeding territory.

The great ornithologist David Lack estimated that only 13% of all birds were colonial, and most of these colonial species are waterbirds. In fact, 98% of marine bird species are colonial. The reason for this stems from the patchy distribution of their food supply and the sharply limited number of sheltered nest sites, such as seamounts and seaside cliffs. About 26% of the bird species that feed in flocks also nest in colonies; only 1% of species feeding alone are colonial nesters.

Coloniality is not a golden ticket. There are several disadvantages:

Colonies attract more predators.

There's more competition for nest sites and materials.

There's more competition for mates.

Birds spend more time guarding their mates from other would-be suitors.

There's more competition for food.

The evolution of coloniality must represent a trade-off between these advantages and disadvantages.

Some of the advantages of flocking also apply to colonies, such as increased predator vigilance and the potential role of the colony as an information center. Colonies also provide more potential mates.

Colonies also decrease the risk of predation by predator swamping. By synchronizing reproduction, most of the young are hatched at the same time. Synchronized breeding can result from what's called social facilitation. The sights and sounds of nearby birds performing courtship displays or constructing nests seems to have a stimulating effect that brings other birds into breeding readiness.

There appear to be several stages in the evolution of coloniality. Birds start as solitary nesters, foraging in their breeding areas. They move to habitats that terrestrial predators can't reach. True colonies form when resources become variable and unpredictable.

Unpredictable resources are the most likely cause for the evolution of coloniality. Coloniality is an adaptation for exploiting resources that are temporally and spatially unpredictable; in other words, resources are ephemeral or scattered in patches.

SUGGESTED READING

Horner and Gorman, *Digging Dinosaurs*.

Stephens, *Foraging Behavior and Ecology*.

QUESTIONS TO CONSIDER

1 Why do birds forage more effectively in medium-sized flocks rather than large or small flocks?

2 If you carefully track a mixed-species foraging flock, you would find that the species mixture remains roughly the same, although each species might be represented by different individuals at different times as the flock moves through the forest. Why is this the case?

AVIAN TURF WARS: DEFENDING A TERRITORY

LECTURE 7

Humans are fiercely territorial animals, and most birds are territorial as well. In this lecture, you'll be introduced to display behavior, a critical part of territory defense, and you'll learn how stereotyped behaviors can avert a bloodbath. You'll explore the nature of competition and the many different types of territories that birds defend, such as feeding and nesting territories and group territories. You'll also discover that territory size is driven by individual needs and population density.

Display Behavior

Birds rely on sound and vision to communicate, just like humans. And like all aspects of avian behavior, verbal communication in birds is an odd and interesting mix of hardwired behavior and learning.

The same thing applies to visual communication, such as the colors and patterns of plumage. Birds have striking color patterns and readily identifiable field marks. Plumage is a quiet language, serving many functions. Birds can easily identify members of their own species and particular individuals in their local population.

Visual identity is especially important for baby birds. During a critical period in their early development, they learn to recognize their parents. This process of recognition is called imprinting. For better or worse, whatever bird or other creature they see during imprinting is identified as their parent, sometimes with amusing results—such as when a line of baby ducks follows a person they have imprinted on rather than their mother.

Visual displays have many other functions in addition to species and individual recognition, including territorial displays to defend resources or attract a mate, courtship displays, and distraction displays to lure predators away from their helpless young.

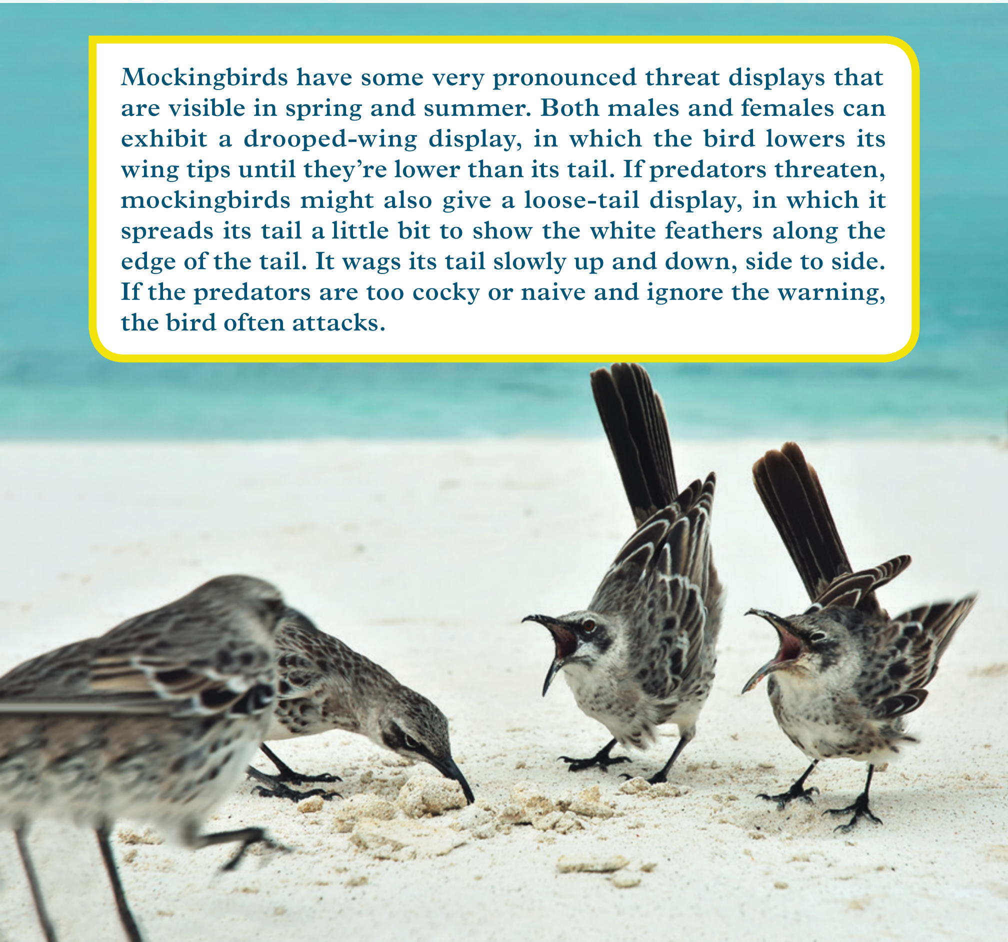
Displays are movements or postures that convey information to another bird. Display behavior in general is very stereotyped. Sequences of ordinary behaviors are strung together into a ritualized routine that is very exaggerated and very predictable. Typically, displays are enhanced by multiple signals being displayed at the same time, such as helpless fluttering or feeble chirping. Julian Huxley called this process ritualization and thought it was the primary pathway by which display behavior evolved.

Courtship displays include highly stereotyped vocalizations and plumage displays.

Antagonistic displays are very common, especially in the spring. Such displays include threatening other birds over mates or territory or acting submissively toward birds making such threats. Threat behavior usually involves a display of the wings or beak, or both. It reminds the victim that the aggressor has some effective weaponry at its disposal. If these signals are ignored, the attack can suddenly become very real. One of the birds will usually give way with a gesture of submission, such as turning its head away from its rival.

Display behaviors are adaptive, and like any adaptive trait, behavior can evolve. Complex vocal and visual signals that birds initially use to communicate are carefully shaped by natural selection into stereotyped sequences of behavior that can fill many other functions.

Mockingbirds have some very pronounced threat displays that are visible in spring and summer. Both males and females can exhibit a drooped-wing display, in which the bird lowers its wing tips until they're lower than its tail. If predators threaten, mockingbirds might also give a loose-tail display, in which it spreads its tail a little bit to show the white feathers along the edge of the tail. It wags its tail slowly up and down, side to side. If the predators are too cocky or naive and ignore the warning, the bird often attacks.



Territoriality

One of the most important functions of vocal and visual displays is to establish and defend territories. Many animals are territorial. A territory is any area that an animal defends against other animals, usually members of its own species. But this is not always the case. For example, acorn woodpeckers keep jays and squirrels away from trees where they store their food.

Territoriality is one of many ways that animals can compete with one another. Competition can take many forms. For example, resources can be exploited by consuming them so they are no longer available to use. This preempting of resources is called exploitative or scramble competition, in which competitors scramble to gobble up as much of the resource as they can get. Everyone gets at least some of the available resources.

Another way to compete is simply to fight for the limited resource in a classic face-to-face showdown. This type of winner-takes-all competition is called interference or contest competition and is typical of animals that defend a territory. Most vertebrates, and many invertebrates, are territorial. This contest is a high-stakes game. In most species, only animals with territories will succeed in attracting a mate.

But defending a territory only makes sense if resources can be monopolized. Sometimes the nature of the resources means that they can't or shouldn't be defended. Food might be abundant and evenly dispersed, such as grass seeds for wild parakeets, or it might occur in dense patches, such as flowers used by hummingbirds and sunbirds.

Territorial competition between males also gives females a basis for choosing mates. If you defend a desirable territory—a place with ample resources for you and a mate to raise your young—you are more likely to get a mate.

Sunbirds will defend a patch of flowers from other sunbirds because they can monopolize the nectar. But when hunting for flying insects, which can't be monopolized, they'll tolerate one another at close range.

Like humans, many birds rely on badges to show their territorial dominance. We use badges as a token of rank, and birds use them in much the same way. A badge is an arbitrary visual cue, such as a bright, contrasting patch of plumage.

The brilliant red epaulettes on the wings of the red-winged blackbird are a familiar avian badge. During breeding season, these bright red feathers, with their rich gold trim, are puffed up and conspicuously flashed at rival males. The red feathers can be kept covered, with only the golden border visible, or prominently flashed, often reinforced by the male's territorial call. Badges play a critical role. Douglas Smith found that 64% of the males whose epaulettes had been dyed black lost their territories, compared with 8% in undyed birds.

Species that are not territorial must find other ways to establish social dominance and compete for mates. One solution is to fight to establish a dominance hierarchy, sometimes called a pecking order, which is a linear sequence of dominant and subdominant animals in a social group (alpha male, beta male, etc.). Females acquire the ranks of their mates. Males generally dominate females, and older males usually dominate younger males.

In addition to breeding and feeding territories, birds may also defend territories used for courtship displays (called leks), nesting, and roosting.

Territories may also only be defended at certain times of the year, such as breeding season. Northern mockingbirds defend breeding territories in the spring and feeding territories in the fall. Sun bitterns, on the other hand, only defend a feeding territory.

Territories can even be portable. Sometimes resources that can be monopolized are constantly changing their location. Sanderlings on the beach will follow the much larger willets who have captured a crab, knowing that the willet will usually drop a few choice bits that the sanderling can seize. Sanderlings will defend the area around the feeding willet from other sanderlings.

Territories may enhance survival in many ways. They give individuals an assured supply of food and nesting sites as well as allow them to monopolize a mate. In the case of the orange-rumped honeyguide, territories provide a more direct access to potential mates. They trade access to food for sex. Males defend areas around hives of the giant honeybee, and females can only approach the hive if they copulate with the male.

Territory holders also gain familiarity with their territory. They know where to find the best food resources and where to hide from predators when chased. Territory holders also appear to have a distinct psychological advantage over trespassers when they are on their own territory. Birds that are submissive when passing through other territories become belligerent and aggressive when defending their own territory.

There are also ecological benefits to territoriality. Territorial behavior helps disperse birds throughout the landscape, preventing local depletion of resources. Territoriality helps regulate population density by limiting reproduction to birds holding a limited number of territories.

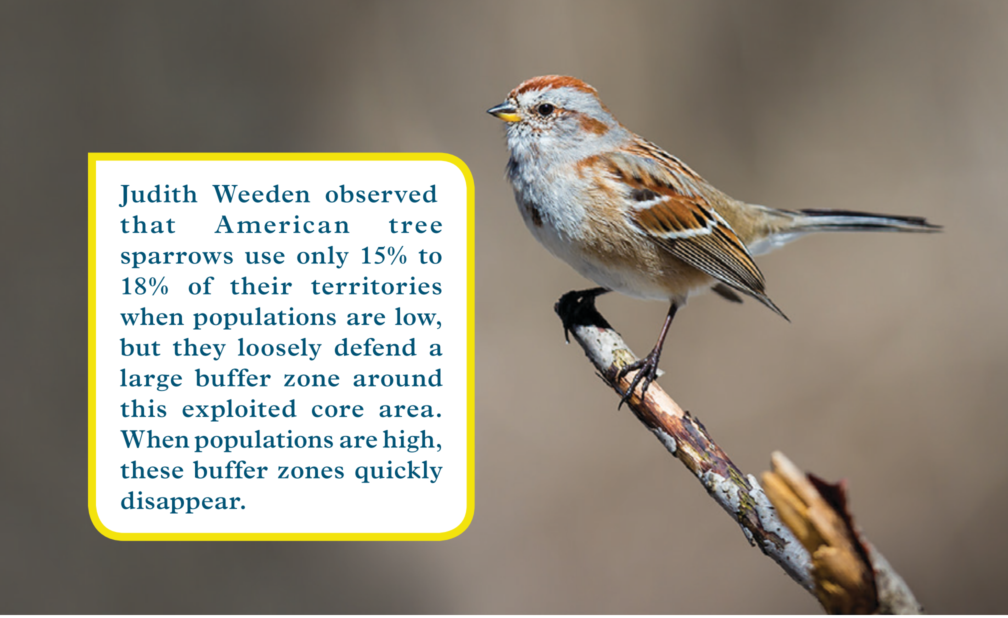
As in human society, there's always a population of floaters—bachelor males who don't hold a territory. Males usually acquire territory by arriving early in the spring and holding a desirable territory until migrating females arrive and select their mates. Male and female Carolina wrens mutually defend their shared territory throughout the year, but only males can establish the territory. If the male dies, a floater will probably take over, and the female will be driven off, perhaps to her death.

Nesting territories are often fiercely defended, even by birds that feed and flock together during the rest of the year. These tiny territories extend only as far beyond the edge of the nest as the parents can reach with their bill without leaving the young unprotected. As a result of their aggressive defense of nesting territories, the nests of colonial waterbirds, such as gulls and terns, are very regularly spaced.

Snowy owls get by with territories of about a half of a square mile when lemmings are abundant, but their territories expand to about 20 square miles when lemmings are scarce.

Nesting territories remind us that territoriality only makes sense if resources, such as good nesting sites, are in limited supply and resources can be monopolized.

Sometimes individuals mutually defend a group territory, a shared resource that may be indefensible by any one bird. The acorn woodpecker defends a group territory. It drills hundreds of holes into the bark of a big tree and stuffs the holes with acorns; each tree can have 11,000 holes or more, and each hole takes 30 to 60 minutes to drill. Given the amount of effort involved, even a tree with empty holes is defended as a valuable resource.



Judith Weeden observed that American tree sparrows use only 15% to 18% of their territories when populations are low, but they loosely defend a large buffer zone around this exploited core area. When populations are high, these buffer zones quickly disappear.

Territory defense consists mostly of highly ritualized behavior. Injuries and deaths are relatively rare. Animals advertise their ability to defend a territory with a set of recognized signals—body postures, plumage displays, pursuit, and vocalizations. But actual combat may occur if these threats are ignored.

Herring gulls are typical of most territorial birds. They work their way up to actual combat in a series of steps, a repertoire of stereotyped behavior patterns aimed at a nonviolent resolution. Trespassers are greeted with a swaggering approach. If neither bird backs away, the 2 birds square off and begin pulling up clumps of grass with their beaks. This rapidly escalates to trying to pull the grass out of one another's beak. Then, they try to grab one another's wings or beaks.

Territories can be acquired in many ways, such as by territorial contests, by the death or departure of neighboring birds, by getting there first in migration, or by inheriting territory as part of a family group.

Territory size is determined by the balance between population density and resource abundance. When resources are scarce, territories need to be large. Territory size is also affected by population density. Territories also vary greatly in shape and often follow natural boundaries, such as forest edges, streams, and rivers.

Geometry keeps territories small. Doubling the radius of a circular territory would quadruple the area to defend. But territories can only be compressed so far before they no longer contain sufficient resources to outweigh the cost of defending them.

Territorial defense can be very costly. When you advertise yourself to females by singing loudly, you also draw the attention of predators.

SUGGESTED READING

Dhondt, *Interspecific Competition in Birds*.

Stokes and Stokes, *A Guide to Bird Behavior.*

QUESTIONS TO CONSIDER

1. What are some of the similarities between the ways in which birds and humans acquire and defend their territories?
2. Birds defend their territories with a variety of vocal and visual threat displays. Why is this behavior advantageous to their survival?

BIRD SONGS AND CALLS: MUSIC WITH A MESSAGE

LECTURE 8

In this lecture, you'll learn how birds sing, including the mechanics of vocalization, the acquisition and practice of songs, and the different types of songs and calls. You'll also discover that birds have local dialects, like humans do. You'll find out that songs are both innate and learned and that a bird's repertoire can increase mating success.

Differences between Songs and Calls

Bird songs fill a multitude of functions in their world, as speech and song do in ours. Songs are a series of notes that form a recognizable pattern over time. Calls are simpler and shorter vocalizations, rarely more than 4 or 5 notes.

The distinction between them is fuzzy. Calls are generally less complex and usually fill a specific function, such as alarm calls, mating calls, and contact calls (which hold flocks together). Songs vary in complexity; both amplitude and frequency can be modulated, or changed over time, like AM and FM radio.

Some birds, such as chickadees, have songs or calls in which the fundamental frequencies have overtones, or harmonics, which are usually multiples of the fundamental frequency. It's the acoustical difference between the simple sound of a whistle and the complex sound of a piano, with its many harmonics.

Different types of sounds are adaptive in different habitats. Low-frequency sounds carry over greater distances. Birds in dense forests often use lower-frequency sounds and simpler calls. Low-frequency sounds are less likely to reflect off trees and other obstacles and become distorted.

Birds such as meadowlarks use more complex songs with higher frequencies. These songs are physically more suited for open habitats; they carry well for short distances, with minimal reflection and distortion.

Recent studies have shown that city birds don't sing like their country cousins. Cities are noisy places, with a lot of low-frequency ambient sounds, such as the rumble of traffic and trains. Birds in urban environments sing louder and at a higher pitch to compensate.

In addition to songs, birds also make many nonvocal sounds that carry information, such as the mating call of the ruffed grouse, as it drums its wings against its puffed-out chest. Many birds, such as the common snipe, have specialized feathers that can be used to make sounds used in their courtship displays. Nonvocal sounds can also be made with the beak. For example, the male white stork clacks his bill to impress a potential mate.

An alert birder can easily tell the downy woodpecker, the hairy woodpecker, and the yellow-bellied sapsucker apart by listening to the rate and pattern of their hammering.

The downy woodpecker hammers at a constant rate of 15 strikes per second.

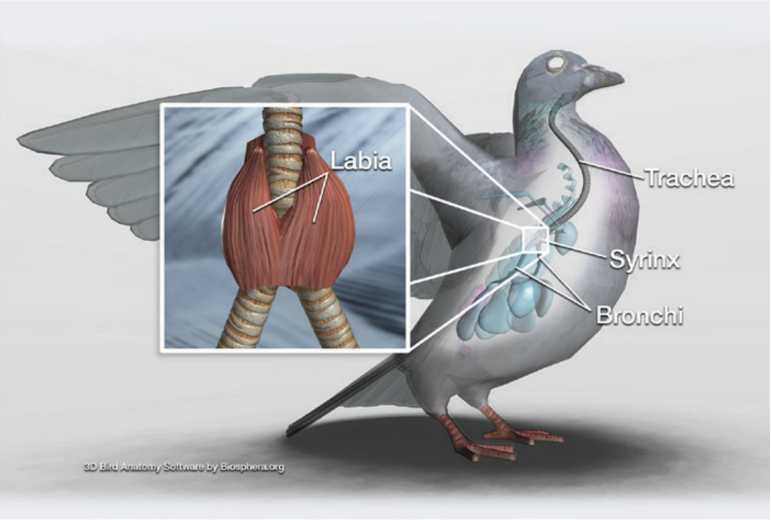
The hairy woodpecker strikes at a much faster constant rate, around 25 times per second.

The sapsucker has a different pattern than the hairy or downy, with rapid strikes that gradually taper off.

How Birds Sing

Some birds are such good singers that they can actually sing 2 songs at once, such as the nightingale or the wood thrush. Their ability to do this is due to fundamental differences in the structure of the syrinx, the vocal organ of birds. The syrinx is unique to birds; it's well placed, right where the trachea forks into the 2 primary bronchi.

Songbirds have 6 sets of muscles that control small pads of tissue called labia, which can be independently pushed out into the air passage, causing them to vibrate when the exhaled air passes over them. The labia, trachea, and beak are used to shape the final sound. Because the labia on either side of the syrinx are under independent neural control, many birds can sing 2 songs at the same time.



Birds are able to make an astounding variety of sounds by pumping out air from their lungs and anterior air sacs while varying the tension on the labia and the extent to which they stick out into the bronchial passage.

The syrinx is incredibly efficient, using virtually 100% of the exhaled air passing by to make sounds. Compare this to the human larynx, which barely manages an efficiency of 2%.

The neural pathways controlling sound production and recognition are fairly complex, involving structures in the forebrain, midbrain, and hindbrain.

Passerines are divided into songbirds, which are called oscine birds, and nonsongbirds, which are called suboscine birds. Suboscine birds lack the neural nuclei that mediate song in oscine birds.

To some extent, song production is under hormonal control. Castrating male chaffinches removes their ability to sing, but testosterone injections restore it.

The word "oscine" comes from the Latin word *oscen*, meaning songbird. The word *oscen* derives from *ob canere*, to sing. It translates roughly to singing for augury, or a bird that gives omens by its cry.

Innate and Learned Components

There are both innate and learned components to song. This was discovered by 18th-century naturalists using cross-fostered birds who found that species song was innate, but there was a learned component as well. Birds reared by other species acquired the song of their foster parents.

There is a wide range of innate versus learned songs among different groups of birds. Brood parasites, for example, whose eggs are laid in the nests of other species, never get to hear their parents. They are born knowing their species song. Song also appears to be innate in birds like chickens and doves.

But in swifts and parrots—and at least 31 families of songbirds—at least part of the song is acquired by learning. Most songbirds need to learn and practice their songs to perfect them.

William H. Thorpe performed a series of experiments on the European chaffinch designed to test the effects of isolation on song development. He raised the birds in sonic isolation in lead-lined boxes, and they developed a much simpler song than the songs of birds who were exposed to recordings of wild chaffinches. Chaffinches that were raised together, however, but in total isolation from wild birds learned a more complex song. This learned song was very different from that of wild birds but very similar to that of their cage mates; it was the best they could do by just comparing notes with one another.

Chaffinches could only learn adult songs if they heard them within 13 months of hatching. Thorpe concluded that the birds were born with a species-specific template of their song—an idea of what a chaffinch is supposed to sound like. This predisposes them to select adult chaffinches as models to perfect their songs.

Thorpe found that there was an early critical learning period during which birds learn the basic song. This initial learning period was followed by a silent period of several months before they began to practice the songs. Following the silent phase is subsong, in which juvenile birds begin to babble, like young humans. In the subsong phase, they are practicing and rehearsing the elements of their song. The elements of the song come together in the final phase, called song crystallization. Feedback is critically important at this stage. If the bird is deafened before song crystallization, it never learns to sing properly.

The Purpose of Songs

Songs fill an amazing variety of individual, social, and reproductive functions. Most birds have from 5 to 14 different calls or songs. Songs can be used for species recognition and to identify individuals of one's own species.

Songs establish species identity. And like human speech, birds have many local variations, or dialects, in different geographic areas. Dialect is a geographical variant of the basic species' song pattern. For example, fish crows in South Florida sound different from fish crows in Louisiana; one has a distinctly nasal sound that the other one lacks.

One of the important functions of bird calls is to hold flocks together during foraging and migration. Contact calls keep individuals in touch. Above all else, songs and calls convey information. Songs can be used to intimidate predators or sound the alarm when predators are around.

Many birds have alarm calls that are context-specific—usually with one call for aerial predators, such as hawks, and a second call for ground predators, such as snakes or people. Chris Templeton studied how black-capped chickadees in Montana communicate information about potential predators and found that they can change the number of trailing "dees" in the chickadee-dee call, adding up to 20 or more "dees" to indicate the threat level—the type of predator and the degree of threat posed.

Songs can proclaim the sex of an individual and indicate the individual's fitness or social dominance. Songs can also be used to establish and defend a territory, to attract a mate or stimulate that mate's sexual behavior, and to strengthen the pair bond between mates or between parent and chick.

Many birds (like some humans) can draw on an enormous repertoire of notes and songs. Even the lowly blue jay has a wide array of songs and calls. Several species of wrens are also accomplished vocalists; sedge wrens and marsh wrens can draw on more than 100 songs.

Like humans, birds can even invent new songs or imitate the songs of others. The lowly European starling is a master mimic; it can mimic 15 to 20 other birds as well as manmade sounds, such as telephones and car alarms.

European starlings may have even mastered syntax. Neurophysiologist Timothy Gentner invented new rules of starling language using the modular elements from which starlings assemble their song. Assigning the letters A and B to 2 different starling phrases, rattles, and warbles, he found that starlings could be taught to recognize different combinations of sounds. The birds could identify the simple ABAB combination with relative ease, but with intensive training, they also learned to identify the more complex AABB pattern—something even tamarin monkeys had failed to do in earlier studies.

Was it just a reflection of their innate vocal and memory skills, or are they practicing a simple grammar? The paper is controversial, but if future studies bear this out, it would be a major feather in the avian cap. Up until now, the use of syntax has been considered unique to humans.

The superb lyrebird of Australia not only imitates other birds but also manmade sounds, such as car alarms, chain saws, camera shutters, and construction noise.

Starlings may be accomplished vocalists and excellent mimics, but the grandmasters of mimicry are the mimic thrushes in the family Mimidae. A typical northern mockingbird can have more than 150 songs at its disposal, and mockingbirds can imitate both natural and manmade sounds.

Mockingbird songs seem to function more in attracting a mate than in challenging other males. In some species, such as the great tit, mating success is directly related to the size of the male's repertoire. Why do females prefer to breed with males that have larger repertoires? The male's ability is an indication of the bird's relative age and experience.

The brown thrasher has one of the largest repertoires, able to retain up to 1000 or more songs or variations. In fact, *Ripley's Believe It or Not!* lists a brown thrasher with a repertoire of 2400 distinctly different songs!

Many birds, such as mockingbirds and marsh wrens, will even engage males of their own species in vocal duels. This countersinging is very different from the male-female duets that many birds use during pair bonding and contact calls.

SUGGESTED READING

Kroodsma, *Backyard Birdsong Guide (Western North America)*.

———, *The Singing Life of Birds*.

Kroodsma, McQueen, and Janosik, *Backyard Birdsong Guide (Eastern and Central North America)*.

Lang and Read, *Common Birds and Their Songs*.

QUESTIONS TO CONSIDER

1 How are bird songs different from bird calls?

2 The size of a male mockingbird's repertoire correlates directly with its reproductive success. What message does repertoire size send to potential mates?

AVIAN MATING: LADY'S CHOICE

LECTURE 9

For birds, the traits that make for a desirable male are the same ones humans look for: good genes, as expressed by his health and general appearance; males who can provide the best food, territory, and protection; males free of disease and parasites; and males who can provide the best parental care. There are several possible explanations for why females make the choices they do, but there are 2 models that best explain what is seen in nature: the good genes model and Amotz Zahavi's handicap model. There are also 4 basic mating systems used by birds, and having made one choice, females are free to change their minds and make another choice—the avian version of divorce and adultery.

In 1871, Charles Darwin published his most controversial book: *The Descent of Man, and Selection in Relation to Sex*, in which he claimed that males competed with other males for mates and that females then chose between them.

The fact that Darwin's theory of sexual selection—which focused on female choice—was so controversial is a tribute to the extent of male dominance in science at the time. It took nearly 100 years for this theory to gain widespread acceptance.

Models of Female Choice

The good gene model says that the male's appearance, and his ability to survive, suggests that he has good genes. He would add these positive traits to your offspring.

For example, according to the sexy son hypothesis, females prefer mates who are physically very attractive, knowing that their offspring will also be attractive and will most likely be successful themselves in attracting mates.

There are many studies that support the good genes model. For example, Monica Mather and Raleigh Robertson showed that male bobolinks in good physical condition have longer flight displays, and the number of mates they attract correlates with the length of their flight display. They clipped the wings of certain males and observed that these altered males got fewer mates.

Amotz Zahavi's handicap model is a variation on the good genes model. The giant antlers of the extinct Irish elk and the long tail of the peacock can make these animals sitting ducks for predators. But if a male elk can carry such heavy antlers—or the male peacock can carry its enormous tail—and still avoid predators and feed and groom himself, he must have his act together.

Or maybe, as Darwin believed, females were simply making an aesthetic choice; they choose what appeals to them. In other words, birds appreciate beauty in its own right, just like humans. Why else might a female prefer a bright-yellow plume on a male bird's head or the staring-eye pattern of the male peacock's plumes?

Whatever the basis for the female's choice, once it is made, it is self-reinforcing. Birds with a prominent yellow feather on their heads, if that yellow feather appealed to females, would mate more often than those that lacked one. The trait would be reinforced generation after generation. It might become so exaggerated that it could become a dangerous burden, what R. A. Fisher called runaway selection. This might explain the gigantic antlers of the Irish elk.

Two ways that males can provide females with a basis for choice are courtship displays and holding a quality territory. Sometimes females just love a male who is up to the challenge, and females have many ways to put males to the test—the harder the better is the general rule.

Female swamp sparrows are attracted to males who can sing trills extremely fast. Brown skuas are even fussier. The females prefer mates who can not only make the most calls per second, but also do this over a very wide range of frequencies.

Female black wheatears base the number of eggs they will lay with a particular male on how many rocks he can carry back to the nest—as well as how heavy the rocks are!

In shrikes, as in human courtship, the males often provide the female with a choice treat to eat—the avian equivalent of a box of chocolates. This behavior is called courtship feeding or tidbitting. For both shrikes and humans, the bigger the gift, the greater the chances of copulation. By offering a potential mate a juicy morsel, such as a ripe berry or juicy grub, you not only show her you are interested but that you know how to find food in the wild. In fact, Ian Nisbet observed that the intensity of courtship feeding by male common terns correlated strongly with their ability to feed their young.

Male birds present nest materials to females during courtship, showing her that he can find the things she will need to build her nest. In the same manner, human males traditionally give expensive rings to brides-to-be, suggesting that if he can afford that prize, he can also provide the rent and groceries.

Mating Systems

Once a female bird has chosen her mate, the birds come together to form a pair bond. Stephen Emlen and Lewis Oring, in a seminal paper in 1977, define mating systems as behavioral strategies used to obtain mates, which include the number of mates acquired, the way in which mates are acquired, the formation and characteristics of the pair bond, and patterns of parental care.

There are 4 basic mating systems: monogamy, polygyny, polyandry, and promiscuity.

> In monogamy, one male mates with one female, forming a pair bond that can endure for a single season or for a lifetime. More than 90% of birds are monogamous.

Only about 14% of monogamous birds are faithful partners.

> In polygyny, one male mates with several females, while each female only mates with one male. Only about 2% of birds are polygynous.
>
> In polyandry, one female mates with more than one male, while each male only mates with one female. Less than 1% of birds are polyandrous.

In promiscuity, males mate indiscriminately with any female and no pair bond is formed. About 6% of birds are promiscuous.

Mating systems are shaped by the way in which resources and mates are distributed and exploited.

Most birds are monogamous, a mating system that is relatively rare in mammals. The prevalence of monogamy in birds, compared to mammals, relates to their different energetic needs and the roles of the sexes in raising young.

The traditional viewpoint is that monogamy is widespread in birds because baby birds have extremely high energetic needs. A female bird, unlike a female mammal, cannot hope to supply those needs by herself. She needs the full-time help of her mate to provide for their young.

Birds spend several weeks or months building nests and raising young, unlike fish or turtles or frogs, who just dump their eggs and leave. Raising baby birds requires a high parental investment, so monogamy is essential to survival.

But there are several different ways to be monogamous. Some birds—such as swans, geese, eagles, albatross, petrels, and some owls and parrots—actually mate for life. Most birds, like many humans, practice serial monogamy; they are faithful to one mate at a time, over and over again. Some birds, such as robins, tree swallows, and mourning doves, keep the same mate for several seasons before choosing another mate, or the pair bond only lasts for a single breeding season, as is the case with most passerines.

In some species, such as the laysan albatross, monogamy is not restricted to the usual male-female pair bonds. Some female birds set up shop as a same-sex couple; in fact, one pair stayed together for 19 breeding seasons. They copulate with males from the colony but prefer the company of other females when it comes to nesting and parental care.

Maintaining a pair bond significantly enhances reproductive success. John Coulson conducted an intensive 12-year study on monogamy in kittiwakes and found that females who kept their mates from prior breeding seasons bred earlier, laid more eggs, and were more successful in fledging their young. Jim Mills found the same to be true for red-billed gulls; changing mates resulted in lower hatching and fledging success.

Female birds are assumed to make the larger parental investment. Making large eggs is energetically costlier than producing sperm. The relative investment of the male varies greatly in monogamous species. Females usually take on the primary nesting duties, while the male guards the territory to preserve the resources she will need.

Most males also share in provisioning, or bringing food to the nest for the incubating female and the young. In herons, egrets, and a few species of woodpeckers, males also share incubation duties. In ground-nesting birds, such as ducks and geese, males often risk their lives by defending the nest against predators.

A genetic analysis of offspring has revealed some interesting facts about supposedly monogamous birds. Many of the young they are raising together are of mixed parentage, representing infidelity on the part of one of the partners. Extra-pair copulations (EPCs) are relatively common. In more than 90% of bird species that we know of, EPCs are a regular occurrence.

This may be why so many species practice mate guarding, in which the male stays physically close to the female to keep her from straying from the marital path. There's a big payoff for keeping a wary eye on your mate. For example, when bluethroat males were caged for only a single morning, the next clutch of eggs laid by their mates had twice as many eggs from EPCs.

Australian fairywrens get the award for greatest infidelity: More than 80% of their young come from extra-pair copulations.

Although both partners cooperate to raise the young, there are both selfish and altruistic aspects to monogamy. Being selfish, each partner seeks to maximize its individual reproductive success by mating with other partners. Being altruistic, the pair cooperates to rear all the young in their nest, regardless of parentage.

Monogamy is now viewed as less of a sentimental bond between lovers and more of a temporary truce between selfish individuals coming together for a common goal. Males are unable to monopolize females and therefore must cooperate with a mate to ensure their own reproductive success.

Selecting a mate for a long commitment requires the same sort of critical judgment about mate quality that humans use to select lifelong partners. And, like birds, humans sometimes make bad choices and have to start all over. Divorce is a fact of life among monogamous birds, as it is for humans.

Not all birds are monogamous. Many species are polygamous, choosing more than one mate. Of the 2 forms of polygamy, polygyny is relatively common and polyandry is relatively rare. Both polygyny and polyandry are expected to occur when either sex is able to monopolize mates or critical resources that mates need.

European pied flycatchers sometimes act like the perennial stereotype of the traveling salesman. After settling down with their mate, males will fly several miles from their territory to start a new territory and attract a second mate. Both mates will be unaware of his bigamous behavior, and because he usually abandons the second mate to devote his attention to his primary mate, the reproductive success of the second mate takes a big hit.

The evolution of polyandry is an interesting unsolved problem. Polyandry is found in less than 1% of bird species, mainly in some button quails, roatelos, and a few rails as well as in jacanas, painted snipes, some plovers, and phalaropes.

In some polyandrous species, role reversal is nearly complete: Females are larger with bright plumage, compete for males, and are the aggressors in courtship, while males are smaller and cryptically colored, incubate the eggs, and drive females away from the nest.

In North America, red phalaropes, red-necked phalaropes, and spotted sandpipers show the usual pattern, called sequential polyandry, in which females leave a given male after the eggs are laid to pursue a new male.

SUGGESTED READING

Darwin, *The Descent of Man and Selection in Relation to Sex*.

Parry, *The Mating Lives of Birds*.

Stutchbury, *The Private Lives of Birds*.

QUESTIONS TO CONSIDER

1 Why was it so difficult for Charles Darwin to get people to accept the idea of female choice in mate selection?

2 Why are most bird species monogamous while most mammals are not?

AVIAN MATING: SINGLES BARS AND BACHELOR PADS

LECTURE 10

Polygyny—which occurs when one male mates with several females but each female only mates with one male—is more common in birds than polyandry, although it's limited to about 2% of all species. Polygynous males form a temporary pair bond and make at least some contribution, if only defending the territory for the female. But in many polygynous birds, even this fragile pair bond is nonexistent; the male contributes only his sperm and the energetic cost of his display. Such birds are considered promiscuous. This lecture focuses on polygyny and the arenas in which males sing and dance to impress potential mates.

Types of Polygynous Mating Systems

Within the traditional model of polygyny, several subtypes of polygynous mating systems can be differentiated, including harem-defense polygyny, resource-defense polygyny, and male-dominance polygyny. These subtypes also apply to polyandrous mating systems.

Polygyny makes good sense if little effort is needed to raise the young. Birds like chickens, whose young can fend for themselves at birth, are often polygynous.

In harem-defense polygyny, males control access to females directly by taking advantage of social gatherings of females. This type of polygyny is common in mammals but very rare in birds, limited to the rhea and a few tinamous and pheasants.

Polygyny can evolve as resource-defense polygyny, in which males control access to females by defending some critical resources that females need. Resource-defense polygyny is common in birds who live in habitats where resources are patchy, with big differences in the quality of male territories. An example of this type of polygyny is the orange-rumped honeyguide, who exchanges access to beehives for sex.

Savannah sparrows are monogamous in the Arctic tundra, where the breeding season is too short for one parent to find enough food. But they are polygynous in temperate habitats, where breeding seasons are longer and there is a longer window of food abundance.

One of the most important ways that males can maximize their reproductive success is to monopolize the best resources by establishing a territory. But all territories are not created equal. The best territories will be claimed by the dominant males, while other males will have to settle for an inferior territory.

Eleven of the 14 North American polygynous species of birds live in marshes or meadows, where high-quality territories are relatively scarce. This poses a problem for female birds, who must make a very substantial energetic investment in eggs and are limited in how many eggs they can produce over their lifetime.

It's imperative that females select the best male, usually a male with a high-quality territory. But if the best males are already taken, then females are faced with a tough decision: Should they select an inferior male and hope for the best or share a superior male with someone else?

The classic model of polygyny was formulated by Gordon Orians, who proposed that there is a polygyny threshold—a point past which it is in the female's best interests to share a male. The polygyny threshold represents the minimum difference between the quality of male territories. If the difference in territory quality is great enough, she will be better off sharing a male in a better territory than pairing with an unmated male on an inferior territory.

Jared Verner found that female marsh wrens frequently chose to share a male, even though there were many bachelor males available. The number of females held by each male correlated with the amount of emergent vegetation on the male's territory, which in turn correlates with the abundance of insects. Dickcissels, red-winged blackbirds, and lark buntings show similar relationships between territory quality and mating success.

Male-dominance polygyny is the most intriguing mating system. In it, males cannot easily monopolize either mates or resources; instead, they establish their dominance by strutting their stuff. They aggregate during breeding to engage in dominance contests, such as courtship displays, and females are free to choose from among the dominant males. These communal displays usually occur in arenas called leks.

Birds have especially elaborate courtship displays, with bright plumage and beautiful songs. Courtship displays give females a chance to determine which males are superior mates—males who are socially dominant, experienced, and energetic. Such displays are especially important in polygynous birds, where dominant males will attract the most females.

Evolution of Leks and Bowers

A lek is an arena in which females gather to watch males perform. Paul Sherman, in his interesting study of the evolution of leks, calls them "nature's version of a singles bar." Males compete for mates at leks by courtship displays—dances, songs, and other elaborate behavior.

About 30 species of birds practice lek behavior, including grouse, prairie chickens, some cranes, parrots, hummingbirds, some birds of paradise, and several species of bowerbirds.

Within the 42 species of birds of paradise that live in Australia, New Guinea, and the Moluccan Islands, some are monogamous and others are polygynous. Each system is shaped by the distribution of resources needed by each species.

Sherman proposes 3 models for the evolution of leks: the hotspot, in which males gather in spots where they have the best chance to cross paths with roaming females; the hotshot, in which males gather around dominant males in the hopes of being noticed by females; and female preference, in which females prefer large clusters of males over solitary males.

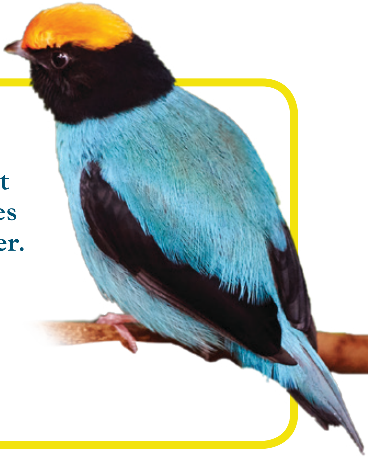
The Raggiana bird-of-paradise and magnificent bird-of-paradise provide an example of the hotspot model. Males can hang out near the fruit trees that roaming bands of females are searching for.

The sage grouse and the turkey are good examples of the hotshot model. Like many humans, turkeys rely on a wingman in their quest for mates. A group of wild turkeys will typically court a female, and the wingmen help to attract the female, but only the dominant male will get to mate with her.

At first glance, there seems to be no benefit for being a wingman. But it turns out that these birds are close kin to the dominant male, often brothers. They may benefit through kin selection—the theory that by helping close kin, animals ensure that at least some of their shared genes are passed on to the next generation.

In the sage grouse, 54% to 62% of all matings come from one or 2 dominant males. These hotshots are socially dominant alpha males. They occupy central positions in the lek and are more active and energetic in their courtship displays. The teammates of hotshots may have to wait a long time—perhaps until the dominant male dies—to be noticed.

The blue manakin assembles a team of acrobats that lines up along a branch with their dominant male. They then do a dizzying series of sideways leapfrogs over one another. When the female agrees to mate, a sharp call by the dominant male dismisses his team and he alone gets to copulate with the starstruck female.



The most curious and interesting courtship displays of all are the miniature leks used by a group of Australian species called bowerbirds. Fourteen of the 18 species of bowerbirds build bowers—tiny structures whose only purpose is to attract a mate. Bowers are the avian equivalent of a swinging bachelor pad.

There are 4 different types of bowers: a simple cleared area with decorations; a cleared area with a mat of lichens and decorations; avenue bowers, with 2 upright rows of sticks and one or more decorated courtyards; and maypole bowers, with a central pole or tentlike enclosure and numerous decorations.

Construction can be very elaborate, with lots of decorations, a central roofed hut big enough to climb into, and a courtyard surrounded by "picket fences." Some birds even paint the walls with berry juice, chewed grass, or charcoal.

Such complex architecture requires a lot of brainpower, and bowerbirds that build bowers have bigger brains than those that do not. In fact, those species who build the more complex maypole bowers have larger brains than those that build the simpler avenue bowers.

Males perch near the bower and call frequently. When a female appears, the male hops down to the bower and starts his display. His courtship display includes a prancing dance together with synchronized calls. He also displays choice decorations in his beak.

If a female approves, she enters the bower to show her willingness to mate. When mating is over, the female leaves immediately—to build her nest far away from the bower. This is because the male bowerbird's display will not only attract females, but it might also attract predators, so the safest course for the female is to build her nest some distance away from the bower.

The male will not see the female again until next year. The only contribution he makes is his sperm and the energetic cost of his display. As a result, some ornithologists classify the bowerbird mating system as promiscuous rather than polygynous—but bowers represent a huge energetic investment.

Bowers are scattered throughout the forest, but their locations are fairly permanent from year to year, so females know where to go to check out the competition.

Males aren't born knowing how to build a bower; there's a very large component of learned behavior in bower construction. Females, for their part, have to learn how to recognize a well-built bower and a good potential mate. Juvenile females learn by hanging out with the older females as they travel through the forest to visit the males.

Juvenile males build practice bowers. It takes 5 to 7 years before juvenile males can build a bower good enough to attract a mate. Adult males will lend a hand, sharing interior design tips with the novice juveniles.

But as soon as mating season starts in earnest, the first thing that adult males do is trash all the practice bowers. Males will also try to trash the bowers of their rivals and steal their best decorations. This can be a risky business. While one bird is out raiding the bowers of his rivals, the rival might be returning the favor by damaging or destroying the undefended bower.

Certain ornaments are highly prized, and preferences are species specific. Satin bowerbirds prefer blue feathers, but the females are not impressed if the bowerbird uses its own blue plumage. The right shade of blue feathers is relatively rare and usually comes from one of the 2 local species of parrots.

Decorations can include mosses, orchids, fresh flowers, beetle wing covers, and butterfly wings. Some bowerbirds collect leaves with different-colored sides and flip them all over for a uniform carpet. Flowers and leaves that wilt are regularly replaced.

Bower decorations also include many manmade objects, such as bits of glass, pieces of ribbon, chalk, discarded candy wrappers, and matchbooks. The scarcer the object, the more likely it is to impress the female.

Gerald Borgia determined that the number of blue feathers and scarce snail shells on the bowers of the satin bowerbird was highly correlated with a male's mating success. He also found that females preferred birds with well-constructed and highly decorated bowers. There is a high payoff for collecting the most feathers; the number of blue feathers correlates highly with the number of copulations.

Females know what to look for in a good-quality bower. Male success in avenue bower builders correlated with the symmetry of the bower, the size and density of the sticks, and overall bower quality.

Ernest Thomas Gilliard observed that the brightness of a male bowerbird's plumage was inversely correlated with the size and complexity of his bower. Brightly plumed males built primitive bowers while species with elaborate bowers had relatively drab plumage. Gilliard called this the transfer effect, concluding that the function of secondary sexual characteristics like bright plumage in attracting a mate were replaced, or transferred, during evolution to an external trait—the construction of a high-quality bower.

There are additional benefits of the transfer effect. Males become less conspicuous to predators, and it shifts male competition toward feather stealing, bower destruction, and similar behaviors rather than actual combat.

Bowers are perhaps best explained by the good genes model. Females prefer males with well-constructed and highly decorated bowers as well as males with glossy, healthy plumage and vigorous display behaviors. These qualities indicate an older, more experienced, and healthy male—a male with good genes for her offspring.

Good bowers indicate an aggressive and competitive male. Males with these traits will mate more often, enhancing survival traits in the next generation.

SUGGESTED READING

Frith and Frith, *Bowerbirds*.

Rowland, *Bowerbirds*.

QUESTIONS TO CONSIDER

1 Why do brightly plumed bowerbirds build unimpressive bowers while bowerbirds with drab plumage build elaborate and highly decorated bowers?

2 Human females are impressed by diamond engagement rings for the same reasons that female satin bowerbirds are impressed by blue feathers. What do these prized objects have in common?

NESTS AND EGGS: A HOME IN THE STICKS

LECTURE 11

In this lecture, you'll learn how avian eggs are structured, how they develop, and how they are laid. You'll also explore the construction of nests, the materials birds use to build them, and the many functions of nests.

All about Avian Eggs

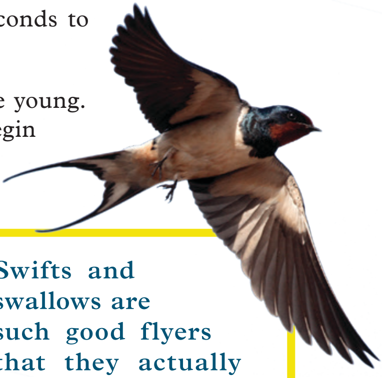
The egg freed vertebrates from relying on water to reproduce. Reptiles evolved eggs and, by so doing, became the first fully terrestrial vertebrates. Eggs are a marvelous evolutionary invention; each egg is a miniature survival pod, complete with its own food and water.

It all starts with hormones. As the days begin to lengthen, photoperiod induces the hypothalamus to secrete hormones that slowly bring the bird into sexual readiness. Testes swell from minute sacs to prominent structures 400 to 500 times larger than their nonbreeding size. Testosterone and estrogen influence the development of secondary sexual characteristics, such as bright plumage. Other hormones regulate the development of the gonads and the eggs. Like reptiles, but unlike mammals, female birds bear the sex chromosome.

Heat is deadly for sperm. Human testes are housed in external sacs, or scrota, which helps reduce sperm temperatures. Birds, however, can't afford the added profile drag that would result from external genitalia, so their testes are inside their bodies. But birds have a much higher body temperature than mammals, so spermatogenesis in male birds takes place mostly at night, when body temperature is at its lowest ebb.

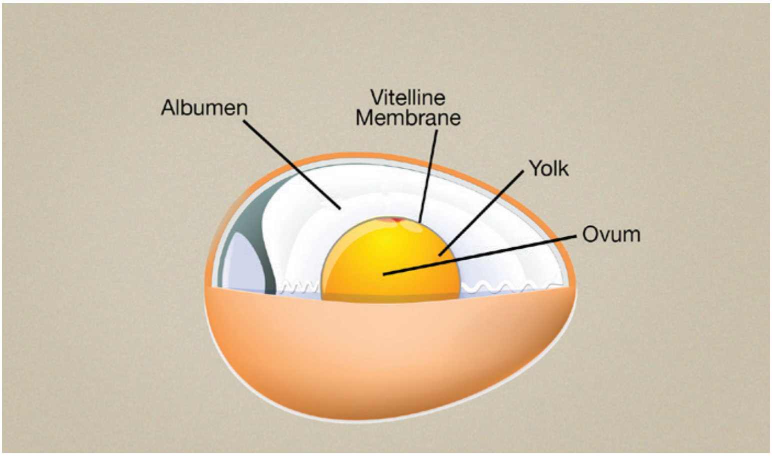
Because birds have no external genitalia, they must briefly bring their cloaca into contact for sperm transfer to take place. The cloaca is the common opening used to expel solid waste and uric acid—and to lay eggs. It only takes a few seconds to transfer sperm.

Unlike mammals, birds never give birth to live young. Birds lay eggs, and the embryos within usually begin to develop as soon as the egg is laid. Eggs are minute at first but increase in size more than a thousandfold by the time they are laid.



The mature egg consists of an ovum attached to a supply of yolk that is encased in a vitelline membrane. The yolk is surrounded by a thick layer of albumen, or egg white. The entire structure is then protected by a thick, hard shell made mostly of calcium.

Swifts and swallows are such good flyers that they actually copulate in flight!



The yolk is the food supply. Yolk consists of 16% to 22% protein and 21% to 36% lipids, with water making up the rest. Albumen provides water, protects the yolk from mechanical shocks, and buffers the egg against sudden temperature changes. Albumen is 10% protein and 90% water.

Reptilian eggs use protein as their energy source. Because bird eggs use a fattier yolk, the embryo's metabolism generates a larger amount of metabolic water. Birds can therefore lay their eggs in much drier places than reptiles.

Eggs are usually fertilized within 2 to 3 days of copulation and take about 24 hours to develop. It only takes a few hours for the egg to move down the oviduct—with each new layer added as it passes along the coiled tube—but shell formation in the uterus, the final stage, takes about 20 hours. The outer shell isn't deposited until the egg is ready to be laid, reducing the weight for the flying female. Eggs are usually laid early in the morning, one egg per day.

Eggshells are remarkable structures, retaining fluids but porous enough to allow gas exchange by diffusion for the respiring embryo and to allow excess water vapor to escape. Nitrogenous wastes are excreted as uric acid. This allows waste material generated by the developing embryo to be stored inside the shell in nontoxic crystalline form.

Eggs vary in size, shape, and color. Larger birds lay larger eggs, although the eggs of smaller birds are actually larger in relation to their body size. Precocial birds, who are born ready to fend for themselves, have larger eggs than altricial birds, who are born naked and helpless. Birds that lay more eggs per nest lay smaller individual eggs.

Eggs can be round, oval, elongated, or pyriform (pear-shaped). Elongated and pyriform eggs have the extra advantage that they can be compactly grouped. They also roll around in a circle, not away from the nest.

Birds that nest in cavities lay snow-white eggs; there's no need to camouflage the eggs against predators. White eggs are also more visible to parents in the dark nest cavity. Birds nesting in the open lay eggs that are camouflaged with specks and blotches.

Eggs are an enormous energetic drain on female birds, adding 13% to 16% additional daily energy needs for altricial birds and 51% to 70% for precocial birds.

Sitting on eggs is called incubating; sitting on chicks is called brooding.

There are 2 basic strategies for incubation. If eggs are incubated as soon as they are laid, they will develop asynchronously and hatch hours or days apart. If incubation is delayed until all the eggs are laid, the brood will hatch synchronously. This opens up a strategy for raptors and other birds to adjust the size of their brood to fit the resources available to feed them.

Some birds are determinate layers and always lay a fixed number of eggs per clutch; clutch size is the number of eggs laid per nest by a given species. Indeterminate layers can continue to add eggs to replace those lost or stolen, until they regain their normal clutch size. Clutch size ranges from 2 in penguins to an average of 3 to 4 for most passerines and to 20 or more for bobwhite.

Fortunately for humans, hens are indeterminate layers. They will lay an egg a day all year round, as long as we keep taking the old eggs away and keep the coop lit at night.

The record for indeterminate layers may be held by a northern flicker that laid 71 eggs in 73 days!

Nests Are Best

Like many of their reptilian ancestors, birds build nests to hold their eggs. Primitive nests were probably simple depressions scraped in the earth, like most reptilian nests. Scraped depressions evolved to depressions lined with vegetation to shallow woven cups and then to more elaborate roofed cavities. The construction of an adequate nest is an important part of avian reproductive success.

Nests serve many functions. They protect eggs and young from bad weather and from predators, supply a supporting platform for eggs and young, and satisfy deep instinctual urges in birds. Nest construction strengthens the pair bond and prepares mates for laying and incubation. Nests also provide a suitable microclimate for incubation.

Birds use an amazing array of nest materials, both natural and manmade. Nests are most often made of sticks and twigs. Nests can also be made of mud. Nests can include leaves, grasses, fungi, lichens, snake skins, seashells, saliva, bits of cow dung, ribbons, and string. Nests are lined with soft materials, such as tissue paper, caterpillar silk, silk from moth cocoons, spiderwebs, hair, and feathers.

Many of the leaves and grasses added to nests are carefully selected for insecticidal properties. Birds take advantage of the chemicals that plants store to deter herbivores in order to reduce the load of bacteria and other parasites in the nest.

Predators are a major cause of nest failure. Nest predators include snakes, rodents, raccoons, and other birds, especially crows. The best response to predators is to locate the nest in an inaccessible place, such as the top of a cliff or deep in the swamp. Birds that nest in plain sight try to camouflage their nests. Ground-nesting birds are especially vulnerable to predators.

The Galapagos mockingbird often levies a tourism tax by plucking hairs from the heads of tourists.

Some birds nest near raptors or stinging insects, such as wasps and bees, and 49 species of birds scoop their nests out of termite mounds. The African water dikkop, a species of plover, builds its nest amid nesting crocodiles. Nesting near predators can be effective but may come with a price when the babies are hatched.

Many birds build a dummy nest, with a concealed opening beneath the obvious cup. Birds can also be very sneaky about returning to their nest. Meadowlarks land in the grass some distance away from the nest and slink to the nest through the tall grass. If all else fails, birds can lure predators away from the nest with a distraction display. Nest predators are also subject to mobbing, in which small birds gang up to drive off larger birds.

A few species of birds build communal nests, of which the African social weaver is the most famous. More than 100 nest chambers may share a common roof in their enormous nests. The entire community works together to weave the huge roof.

More than half of all avian orders nest in cavities. Cavity nesters have a 66% fledging success rate, compared to about 46% for other species. Such nests are usually less subject to predation. Unfortunately, introduced birds, such as house sparrows and European starlings, often evict native species from cavities. The spread of killer bees, which like to make their hives in cavities, also poses a threat to southern cavity nesters.

The usual practice of modern foresters has been to remove most of the old or dead trees, which has also hurt cavity nesters. More enlightened forest managers now realize the value of these old trees to cavity nesters and as a food source for woodpeckers and other animals.

Some birds lay their eggs in a large mound covered by vegetation. The decaying vegetation generates a great deal of heat. These mound builders, or megapodes, can add or remove vegetation to change the temperature, controlling it to within 2° to 3°. The young birds have to dig their way out when they hatch. Megapode nests seem primitive, like alligator nests, but they evolved from species that build normal nests.

The thermal properties of nests are critically important. The thicker the nest, the better it retains heat and the less time and energy is needed for incubation. Eggs must be kept at a constant temperature of 98° to 100°. If they slip below 95° or rise above 104°, the embryo may die. Nest placement also makes a big difference in nest temperature.

Egg temperatures slowly rise during the first 2 weeks of incubation. The time the adult needs to sit on the nest, called attentiveness, also increases during this period. Incubation is very costly, consuming up to 25% of a bird's daily energy requirements. But the stable thermal environment of the nest actually reduces the energetic needs of the incubating parents.

Birds must take great care not to overheat their eggs. They frequently turn the eggs and switch them from the warmer interior to the cooler edges of the nest. Birds that nest in deserts or hot beach sand often sprinkle water on their eggs or shade them with their bodies.

Most birds never reuse their old nests because they can build up a significant load of parasites and bacteria that might threaten a new brood.

Some birds use the same nest year after year. One eagle's nest in Florida, in use for 35 years, reached 9.5 feet across and 20 feet deep and weighed more than 2 tons when it finally collapsed.

Incubation times vary from species to species. Precocial birds have longer incubation times than altricial birds, because they are more fully developed when they hatch.

Eggs lose about 15% of their water content during incubation. Birds in drier climates therefore have shorter incubation times. Up to a point, water loss from the egg is adaptive. The air pocket left behind in the shell will supply the chick with its first breath as it struggles to hatch out. If water loss exceeds 20%, however, the embryo may die.

Birds have a special bare spot on their chest or abdomen called a brood patch that is free of feathers and functions to convey body heat directly to the eggs. The skin of the brood patch is tough enough to resist blistering or chafing from endless hours of incubation. The brood patch is usually found in females, but sometimes also in males; it depends on which sex does the incubation.

Males and females share incubation duties in 54% of all species. Females are the sole incubators in 25% of species, and males alone incubate in 6% of species. The other 15% of species are too weird to classify!

As hatching approaches, males begin to supplement the female's diet, practicing for the great demands about to be imposed by hungry chicks. In a few species, such as hornbills, males supply all the female's needs during incubation.

One of the most unusual problems faced by avian parents is having to raise chicks of other species. Many species of birds are brood parasites; rather than build their own nests, they simply lay their eggs in the nests of others.

Precocial chicks start to talk to one another through the shell. Younger chicks click rapidly, letting older chicks know they need to slow down. Older chicks click slowly, letting younger chicks know it's time to get going. The final stimulus is the jostling of the adjacent eggs as the lead chick begins to hatch.

Parents sometimes intervene to help shatter the shell, especially in species like the ostrich, whose massive eggs may require several days of effort to escape. But for the most part, it's a lonely struggle in the dark.

SUGGESTED READING

Dunning, *Secrets of the Nest*.

Hansell, *Bird Nests and Construction Behaviour*.

QUESTIONS TO CONSIDER

1 What is the most interesting fact you learned about birds' nests from this lecture? What about birds' eggs?

2 Why do brood parasites, such as cuckoos, usually prey on much smaller species?

PARENTAL CARE: BIRD FAMILY AND FRIENDS

LECTURE 12

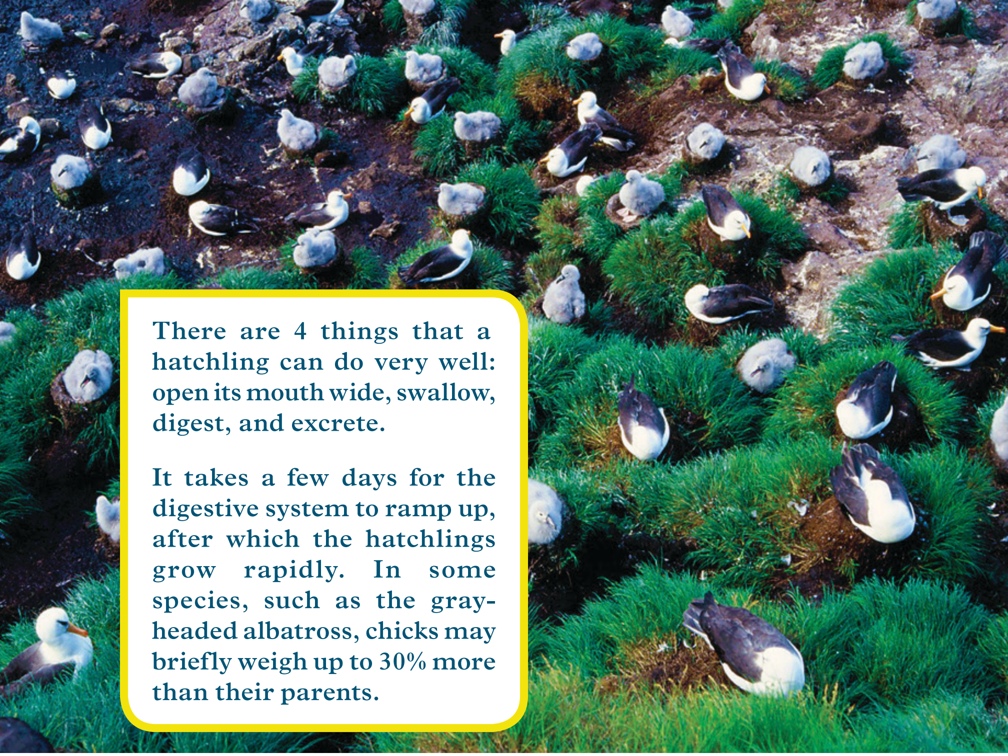
To end this survey of these wonderful and intriguing animals, this lecture will examine how birds care for their young. You'll learn the sad fate of many birds, who are ruthlessly killed by their own nest mates, and you'll discover the benefits for birds of helping their family and neighbors.

Altricial versus Precocial Development

Altricial birds, such as baby robins and mockingbirds, are born naked and helpless. Precocial birds, such as ducks and shorebirds, are born ready to leave the nest and follow their parents.

Altricial chicks can't regulate their body temperatures very effectively at birth. They're so small that they have a high surface area relative to their volume, so they lose a lot of heat.

Precocial birds develop full control of thermoregulation—maintaining a constant body temperature—much faster than altricial birds. Their covering of downy feathers is a big help in the early stages of thermoregulation. It takes about a week for the ability of thermoregulation to develop. During this time, parents must continue to keep the chicks warm by brooding them.



There are 4 things that a hatchling can do very well: open its mouth wide, swallow, digest, and excrete.

It takes a few days for the digestive system to ramp up, after which the hatchlings grow rapidly. In some species, such as the gray-headed albatross, chicks may briefly weigh up to 30% more than their parents.

At the same time that parents need to brood, they must also spend a large part of each day gathering food for their hungry nestlings. Parents must budget their time on and off the nest, either brooding or foraging. As the chicks age, brooding time decreases and feeding visits increase.

The type of food that birds bring back to the nest may be different from the bird's normal diet. Baby birds need protein, and only insects can supply that protein in sufficiently concentrated form. Most birds try to time their broods to coincide with the seasonal peak in insect abundance. Even birds that eat mainly grains and fruits switch to an insect diet to feed their young.

Precocial birds have longer incubation times, larger egg size, and higher yolk content. These costs are balanced by a reduced maintenance cost after hatching. Altricial birds have shorter incubation times, and their eggs are energetically less costly; they are smaller and have a lower yolk content. These energetic savings are balanced by much higher maintenance cost after hatching.

There are many variations on the altricial and precocial strategies.

- Herons and hawks are semialtricial. They stay in the nest for a long time, although they are physically capable of leaving in a day or 2.
- Gulls and terns are semiprecocial. They can thermoregulate and move about but prefer to stay in the nest and be fed.
- Megapodes, or mound builders, are superprecocial, needing no parental care whatsoever. They must struggle through 24 to 48 hours of digging to emerge from their underground nest, and by then they are so fully developed that within another 24 hours they can fly away.

Ultimately, these 2 strategies may be driven by food supply. Altricial chicks grow up to eat insects and other prey that has to be hunted and captured. This involves a great deal of learning about what's good to eat, where to find it, and how to catch it. Precocial chicks, on the other hand, tend to feed on seeds and small invertebrates, which are easily found and eaten.

Baby birds grow very rapidly, which dramatically increases the rate at which they must be fed. Altricial birds, such as starlings, develop 3 to 4 times faster than precocial birds, such as quail.

Species-specific growth rates are affected by many environmental factors. The abundance and distribution of food as well as the local temperature and rainfall can have a big impact on early development.

The number of chicks in the nest also affects growth rates. The more mouths there are to feed, the less food each one will get. Sadly, smaller chicks often starve. Many species practice brood reduction to bring brood size into line with food availability.

Provisioning rates vary greatly from species to species. Baby eagles may be fed only 4 to 5 times a day; baby robins must be fed 35 to 40 times a day. Feeding habits also vary widely from species to species. Chicks of pelicans, penguins, and anhingas stuff their entire heads into their parent's mouth. Seabirds usually regurgitate food and water into the nest, or even directly into the nestling's mouth. Passerines crane their necks upward with gaping mouths.

Great tits must feed their young 990 times each day; house wrens make 491 feeding trips per day.

A single European pied flycatcher, which carries insects to the nest in its beak one at a time, was observed making 6200 feeding trips to fledge its young.

The common swift, which catches insects in flight, has to fly a staggering 620 miles every day to feed its brood.

A typical parent must double or triple its daily energetic needs to feed itself and its young. Of course, this constant feeding means a great deal of excrement.

Young passerine birds conveniently excrete in a small package surrounded by a membrane called a fecal sac. Most birds carefully remove eggshell fragments and fecal material from the nest and usually drop them some distance away to keep predators from finding the nest. The ability to make fecal sacs fades away as the nestling grows and is gone by the time it leaves the nest.

Nonpasserine birds simply defecate over the side of the nest. In large colonies of waterbirds, the excrement rapidly coats the surrounding vegetation and, in some cases, kills it.

Baby birds develop rapidly, especially altricial birds. Hatchlings grow into nestlings, which grow into fledglings. The difference in growth rates between altricial and precocial birds results mainly from the continued feeding of altricial young by their parents. Precocial birds must forage by themselves.

Within a few days, altricial birds can open their eyes and move about. Within a week, they are relatively coordinated, and their first primary feathers are starting to appear. Within about 2 weeks, they begin to flutter about, ready to leave the nest. At this stage, the nestling is about to mature into a fledgling.

Parents have a variety of tactics to get young out of the nest. Some parents reduce the amount of food they provide, and some stop feeding their young altogether. Others, such as bald eagles and coots, hold food outside the nest. Some parents, such as tree-nesting ducks, call to their young to entice them outside. Others, such as Japanese paradise flycatchers, continue to feed only those young that have left the nest, ignoring the begging calls of the remaining chicks until they also vacate the nest.

As birds grow from hatchlings to fledglings, the moment draws near for their traumatic and dangerous journey from the shelter and comfort of the nest into the real world.

Altricial birds are unable to fly for the first few days after leaving the nest, but they're very good at freezing and staying well hidden when they sense a predator or hear their parents' alarm call. Their vulnerability on the ground is actually less than their ever-increasing vulnerability in the nest.

If you find a baby bird hiding on the ground, don't undo the parents' hard work by trying to return it to the nest.

For precocial birds, that first step can be a scary one. Birds that nest on the sides of cliffs, such as murres, face a formidable plunge of several hundred feet to the wave-tossed rocks below. They usually just bounce off the rocks and swim safely away.

Parental care doesn't stop when fledglings leave the nest. Now the burden on the parent shifts to provisioning, predator detection, and teaching. Young birds still have a great deal of learning to do after they fledge. Even innate behaviors—such as singing, preening, and nest building—must be refined by observation and practice.

It's a long period of development—from eggs to hatchlings, to nestlings, and finally to fledglings. Parents must maintain a delicate balance between supplying their own needs and attending to the needs of their offspring throughout this period. The need to forage during incubation and brooding is balanced by the increased vulnerability of the unattended eggs or young to heat loss and predation. As a result, the needs of the parents and the chicks are often in direct conflict with one another.

Threats versus Helpers

Baby birds face many perils. Half of all nests are lost to predation. But for many birds, the biggest threat may come from their siblings. Siblicide is any sibling behavior that contributes directly to the death of a sibling. Many large predatory birds, such as raptors, pelicans, herons, and egrets, commonly practice siblicide. Their formidable weapons—sharp beaks and talons—are very effective in the close confines of the nest.

The key to understanding siblicide is asynchronous hatching, which results when eggs are incubated soon after they're laid, allowing some nestlings to gain a significant weight and height advantage.

How can such seemingly barbaric behavior as siblicide be adaptive? There is evidence to support all of the following ideas, but no clear winner has emerged.

> Maybe it's all about food supply. More chicks means more mouths to feed. If food supplies are reduced or uncertain, the youngest and weakest chick pays the price.
>
> Maybe it's all about predators. By speeding up the fledging process for at least some young, the impact of predation might be minimized.
>
> Maybe parents are just hedging their bets. The second or later offspring are an insurance policy against the possible loss of the firstborn.
>
> Maybe parents are just trying to lighten the load, spreading out offspring so that their individual peak demands for food will not coincide as they grow.

Killing all of your siblings is a dangerous game. Parents usually desert a sole survivor, perhaps because they could hedge their bets by renesting and raising an entire brood.

Some birds go to the opposite extreme and spend their lives helping their parents raise the next generation. About 250 to 300 species are cooperative or communal breeders, where several individuals contribute to the upbringing of the brood.

From one to 6 young birds, usually from last year's brood, remain with their parents to help out at the nest. About half the territories are held by a bonded pair; most of the rest are held by a pair with one or 2 helpers. But how could it be adaptive to remain unmated, devoting all your time and energy to raising brothers and sisters?

For some cooperative breeders, the answer is clear. For example, some species of anis share a communal nest, in which several females lay their eggs and the entire group of males and females cares for the nest. In Sandra Vehrencamp's study of greater anis, she found that up to 4 monogamous pairs—and sometimes an unmated helper—shared a common territory and that females of this species fledge more young than single pairs living in the same type of habitat. In this case, helpers have a direct interest in protecting their shared offspring because the brood includes at least some of their own young.

The advantage becomes less obvious when helpers are unmated relatives. What could they possibly gain by helping their parents raise younger siblings generation after generation? Explanations for the evolution of helpers usually invoke kin selection; natural selection will favor helping close relations because in doing so you ensure the success of a certain percentage of your own genes.

Green wood hoopoes show how a scarcity of territories can require a bit of help from the family. They turn the siblings they help raise into minions, close allies in their struggle for limited territories.

Helpers are also poised to take advantage of the deaths of territory holders or increased available territory during productive years. And they benefit from the skills and experience they have acquired and can now apply to their own parenting. So, there's a significant payoff from this seemingly altruistic behavior.

Communal breeding is ultimately driven by competition for scarce or unpredictable mates, resources, or territories. This so-called ecological constraints hypothesis is supported by the fact that communal breeding is most common in Africa and Australia, where there are vast stretches of arid and semiarid terrain, so a pair of birds all by themselves can't find enough food for chicks.

Sometimes, like in the best human neighborhoods, it comes down to a simple case of neighbors helping neighbors. Reciprocity makes good sense if helping a neighbor to drive off a predator makes your own family safer.

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Clutton-Brock, *The Evolution of Parental Care*.

Koenig and Dickinson, *Ecology and Evolution of Cooperative Breeding in Birds*.

Royle, Smiseth, and Kölliker, *The Evolution of Parental Care*.

Skutch, *Parent Birds and Their Young*.

QUESTIONS TO CONSIDER

1. If you find a baby bird on the ground, should you try to return it to its nest? Should you call social services?
2. What are the trade-offs between the altricial and precocial strategies of avian development?

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Dyke, G., R. De Kat, R. C. Palmer, J. Van Der Kindere, D. Darren Naish, and G. Bharathram. "Aerodynamic Performance of the Feathered Dinosaur *Microraptor* and the Evolution of Feathered Flight." *Nature Communications* 4 (2013): 2489. Could *Microraptor* fly? Its 4 feathered limbs seem designed for gliding. The authors make a strong case to support this hypothesis, combining a detailed technical analysis with wind tunnel tests.

Ehrlich, P. R., S. Dobkin, and D. Wheye. *The Birder's Handbook: A Field Guide to the Natural History of North American birds—Including All Species That Regularly Breed North of Mexico*. New York: Simon & Schuster, 1988. A real gem that deserves a space on every birder's shelf, despite its unusual format. Two species are summarized on each left-hand page, with facing pages devoted to a discussion of various aspects of bird behavior and biology. A great book for browsing that is tied together by a subject and species index.

Elphick, J. *The Atlas of Bird Migration: Tracing the Great Journeys of the World's Birds*. Buffalo, NY: Firefly Books, 2007. A beautifully illustrated introduction to avian migration that is suitable for the whole family.

Emery, N. *Bird Brain: An Exploration of Avian Intelligence*. Princeton, NJ: Princeton University Press, 2016. This beautifully illustrated survey of avian neuroanatomy and intelligence from a leading authority provides a thorough review of current research. The author's former career as a primatologist makes him particularly adept at comparing the intelligence of birds and primates.

———. "Cognitive Ornithology: The Evolution of Avian Intelligence." *Philosophical Transactions of the Royal Society B* 361 (2005): 23–43. Emery discusses the proper theoretical approach to analyzing the evolution of avian intelligence, focusing on episodic memory and the theory of the mind, and concludes that the intelligence of parrots and crows equals or exceeds the intelligence of primates.

Emlen, S. T. "Migratory Orientation in the Indigo Bunting, *Passerina cyanea*: Part I—Evidence for Use of Celestial Cues." *The Auk* 84, no. 3 (1967): 309-342. The first of 2 articles describing the celestial navigation of the indigo bunting. Emlen tested the birds in a planetarium to conclusively demonstrate that the birds could navigate by the stars. Each bird had a preferred constellation close to Polaris and one or more backup constellations to allow for cloudy skies. He was able to get the buntings to orient correctly with changing seasonal skies and even taught them to navigate using a different "north star."

———. "Migratory Orientation in the Indigo Bunting, *Passerina cyanea*: Part II—Mechanism of Celestial Orientation." *The Auk* 84, no. 4 (1967): 463–489. The second of 2 articles describing the celestial navigation of the indigo bunting. [See previous Emlen entry.]

Emlen, S. T., and L. W. Oring. "Ecology, Sexual Selection, and the Evolution of Mating Systems." *Science* 197, no. 4300 (1977): 215–223. A classic paper defining the primary types and subtypes of mating systems in birds and mammals. The authors were influential in getting scientists to accept Darwin's theory of sexual selection.

Frith, Clifford B., and D. Frith. *Bowerbirds: Nature, Art & History*. Malanda, AU: Frith & Frith, 2008. Two of the world's experts present the results of more than 30 years of research on the natural history of bowerbirds. Well written and lavishly illustrated, the book covers every aspect of bowerbird biology and behavior, bower construction, and bower decoration.

Gill, F. B. *Ornithology*. 2nd ed. New York: W. H. Freeman, 1995. The best current textbook of ornithology. It is well written and profusely illustrated.

Giraldeau, L. A., C. Soos, and G. Beauchamp. "A Test of the Producer-Scrounger Foraging Game in Captive Flocks of Spice Finches, *Loncbura punctulata*." *Behavioral Ecology and Sociobiology* 34, no. 4 (1994): 251–256. Develops and tests a foraging model for the trade-offs of being a producer or scrounging off the producers, concluding that spice finches can adjust their strategies depending on the cost of production to achieve a balanced payoff.

Hamilton, W. D. "Geometry of the Selfish Herd." *Journal of Theoretical Biology* 31, no. 2 (1964): 295–311. A classic paper that has become required reading for all graduate students in ecology. Hamilton discusses the theoretical implications of an individual's position in a herd or flock, especially with regard to the threat of predation, like the proverbial riverboat gambler who sits with his back to the wall.

Hansell, M. *Bird Nests and Construction Behaviour.* Cambridge: Cambridge University Press, 2000. An authoritative guide to everything you ever wanted to know about nests, including materials, construction, types, cost, site selection, and the evolution of nesting behavior. Includes a chapter on bowers.

Hansen, A. J., and R. S. Rohwer. "Coverable Badges and Resource Defence in Birds." *Animal Behaviour* 34, no. 1 (1986): 69–76. An important paper that studies the role of the red and gold epaulettes (wing patches) of red-winged blackbirds. Birds can flash the patches to defend their territory or partially hide them to avoid confrontation. The authors used mounts (stuffed birds) to artificially create birds with various sizes of epaulettes.

Horner, J. R, and J. Gorman. *Digging Dinosaurs: The Search That Unraveled the Mystery of Baby Dinosaurs*. New York: Workman, 1988. This excellent book follows Horner's incredible detective work in uncovering the breeding grounds of *Maiasaura*, a new species of duck-billed dinosaur he discovered. His analysis reveals many similarities in breeding behavior between colonial dinosaurs and modern colonial waterbirds, such as herons and egrets, including site fidelity, defense of nesting territories, and the altricial versus precocial strategies of development. Worth tracking down and highly recommended.

Jarvis, E. D. “Bird Brain: Evolution.” In *Encyclopedia of Neuroscience*, edited by L. R. Squire, 209–215. Amsterdam: Elsevier, 2009. Jarvis spearheads the modern movement to reconsider our outdated ideas about the structure and function of the avian brain, especially with regard to the role of the pallium in avian intelligence.

Kelley, L. A., and J. A. Endler. “Illusions Promote Mating Success in Great Bowerbirds.” *Science* 335, no. 6066 (2012): 335. Avenue bower architecture creates a narrow aisle with the female in a fixed position, allowing the male to display his decorations in a manner that creates an illusion based on forced perspective. Such use of illusions may be more common among other animals than expected.

Ketterson, E. D., and V. Nolan. “Male Parental Behavior in Birds.” *Annual Review of Ecology and Systematics* 25 (1994): 601–628. The *Annual Review* series solicits review articles from the foremost authorities on important research topics in a variety of disciplines. Every article includes an extensive bibliography of the best and most current literature on that topic. Articles from this series are often used by graduate students as a starting point for dissertation research.

Koenig, W. D., and J. L. Dickinson. *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge: Cambridge University Press, 2004. A collection of 12 papers focused on the ecological basis and evolution of helping behavior in birds, including sexual selection, sexual conflict, physiology, and endocrinology of helpers.

Kroodsma, D. E. *Backyard Birdsong Guide (Western North America): A Guide to Listening*. Apex, NC: Cornell Lab Publishing Group, 2016. An audiovisual introduction to the songs of common birds of western North America.

———. *The Singing Life of Birds: The Art and Science of Listening to Birdsong*. Boston: Houghton Mifflin, 2005. The most important book available about the role of song in the life of birds, covering the anatomy and development of birdsong, the many functions of various calls and songs, avian dialects, and mimicry. Engaging, comprehensive, and a pleasure to read, the book is accompanied by a CD containing the songs and calls highlighted with pictorial sonograms in the text. Highly recommended.

Kroodsma, D. E., L. B. McQueen, and J. Janosik. *Backyard Birdsong Guide (Eastern and Central North America): A Guide to Listening*. Apex, NC: Cornell Lab Publishing Group, 2016. An audiovisual introduction to the songs of common birds of eastern and central North America.

Lang, E., and M. Read. *Common Birds and Their Songs: With Photos and Sound Recordings by the Authors and Others*. Boston: Houghton Mifflin, 1998. A great introduction to the songs of common garden birds, suitable for birders of all ages. Each species is covered in a single page, with facing pages devoted to colored illustrations of that species. The accompanying 65-minute audio CD contains all the songs for the species covered in the text.

Lederer, R. J. *Beaks, Bones, and Bird Songs: How the Struggle for Survival Has Shaped Birds and Their Behavior*. Portland, OR: Timber Press, 2016. An engaging and well-written guide to the many amazing things birds do to stay alive, providing a good survey of the physiological and behavioral adaptations that contribute to their survival.

Lindsay, W. R., J. T. Houck, C. E. Giuliano, and B. D. Lainy. "Acrobatic Courtship Display Coevolves with Brain Size in Manakins (*Pipridae*)." *Brain, Behavior and Evolution* 85, no. 1 (2015): 29–36. A comparison of brain size and acrobatic displays in manikins reveals that increasing complexity in their acrobatic displays correlates directly with their relative brain size, suggesting that brain size in this taxon evolved in response to sexual selection.

Long, J. A. *Feathered Dinosaurs: The Origin of Birds*. Edited by P. Schouten. New York: Oxford University Press, 2008. Focuses on the many recent and spectacular fossil discoveries from China, with 80 full-page illustrations depicting feathered dinosaurs. An attractive and accessible book for bird and dinosaur lovers of all ages.

Lovette, I., and J. W. Fitzpatrick, eds. *The Cornell Lab of Ornithology Handbook of Bird Biology*. 3rd ed. Chichester, West Sussex: Wiley & Sons Ltd., 2016. The standard reference for ornithology, this encyclopedic work covers every aspect of avian biology and behavior, with copious illustrations and extensive references. Belongs on the shelf of every serious birder.

Meier, P. T. “Polyterritorial Polygyny in the Pied Flycatcher: Male Deception or Female Choice?” *The American Naturalist* 121, no. 1 (1983): 145–147. One of 3 papers selected to introduce readers to the different ways the same hypotheses can be analyzed by different scientists. [See also Alatalo and Lundberg (1984) and Sherry (1991).]

Mumme, R. L. “Do Helpers Increase Reproductive Success? An Experimental Analysis in the Florida Scrub Jay.” *Behavioral Ecology and Sociobiology* 31, no. 5 (1992): 319–328. Removing helpers from scrub jay families resulted in lower reproductive success. Helping behavior is a valuable trait in natural selection.

Olkowicz, S., M. Kocourek, K. Radek, M. Portes, W. T. Fitch, S. Herculano-Houzel, and P. Nemec. “Birds Have Primate-like Numbers of Neurons in the Forebrain.” *Neuroscience* 113, no. 26 (2016): 7255. The size of the avian brain is misleading with regard to the intelligence of birds. The authors show that even though birds have relatively small brains, the density of their neurons actually equals or exceeds that of primates.

Padian, K., ed. *The Origin of Birds and the Evolution of Flight*. San Francisco: California Academy of Sciences, 1986. Memoirs of a landmark conference that set the stage for the current theoretical discussions of how and when birds learned to fly.

Parry, J. *The Mating Lives of Birds*. Cambridge, MA: MIT Press, 2012. A beautifully illustrated introduction to avian mating systems that is suitable for all ages, covering the evolution of monogamy, polygyny, and polyandry; territorial behavior; courtship behavior; nests; eggs; and young.

Paul, G. *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds*. Baltimore: Johns Hopkins University Press, 2002. An extensive, profusely illustrated, and authoritative survey of the origins of flight written by the leading authority in the field, who surveys the origins and evolution of birds and dinosaurs and raises the controversial hypothesis that some dinosaurs were capable of flight.

Perrin, J., and J. F. Mongibeaux. *Winged Migration*. San Francisco: Chronicle Books, 2003. This absorbing and well-illustrated book is the companion piece to the best film ever made on the subject of bird migration. The movie took several years to film and includes some of the most spectacular footage ever recorded on the migratory habits of birds. Both the book and the film are highly recommended.

Pickrell, J. *Flying Dinosaurs: How Fearsome Reptiles Became Birds*. New York: Columbia University Press, 2014. A great introduction to the evolution of birds from dinosaurs, starting with *Archaeopteryx* and proceeding through the recent explosion of discoveries from China. The author's personal familiarity with the growth of the field gives him a unique perspective and makes the science come alive. Highly recommended.

Proctor, N. S., and P. J. Lynch. *Manual of Ornithology: Avian Structure & Function*. New Haven, CT: Yale University Press, 1993. An authoritative guide to avian anatomy and physiology, covering feathers, skeletal structure, musculature, and the digestive, circulatory, respiratory, excretory, and nervous systems.

Remes, V., R. P. Freckleton, J. Tokolyi, L. Liker, and T. Szekely. "The Evolution of Parental Cooperation in Birds." *Proceedings of the National Academy of Sciences 112, no. 44* (2015): *13603–13608*. This theoretical analysis of the evolution of parental care uses a large data set of 659 species to compare 3 hypotheses—sexual selection, social environment, and environmental harshness—concluding that the first 2 hypotheses offer the best explanation.

Rowland, P. *Bowerbirds*. Clayton, AU: CSIRO Publishing, 2008. A good introduction for the general reader, written by a former staff member of the Australian Museum. Includes in-depth accounts of all the Australian species and basic information on the New Guinea species.

Royle, N. J., P. T. Smiseth, and M. Kölliker. *The Evolution of Parental Care*. Oxford: Oxford University Press, 2012. A collection of essays from top authorities that examines how the evolution of parental care in birds has contributed to avian biodiversity. It includes articles on parental care in other vertebrates and invertebrates, parent-offspring conflict, and sibling competition.

Savage, C. S. *Crows: Encounters with the Wise Guys of the Avian World*. New York: Greystone, 2015. One of the best books available on avian intelligence. Crows are the rocket scientists of the avian world. Highly recommended.

Sherry, T. W. "Polyterritorial Polygyny in the American Redstart." *The Wilson Bulletin* 103, no. 2 (1991): 190–203. One of 3 papers selected to introduce readers to the different ways that the same ecological problem—the ecology of avian bigamy—can be analyzed by different people. [See also Alatalo and Lundberg (1984) and Meier (1983).]

Shipman, P. *Taking Wing:* Archaeopteryx *and the Evolution of Bird Flight*. New York: Simon & Schuster, 1998. An excellent account of the origin of flight, with extensive coverage of the cursorial and arboreal theories. The author has a rare talent for making science come alive.

Sibley, D. *The Sibley Guide to Bird Life & Behavior.* New York: Alfred A. Knopf, 2009. A superb introduction to every aspect of bird behavior, including short essays on general ornithology, followed by 80 short chapters devoted to major avian families. A good companion volume to the author's field guide *The Sibley Guide to Birds* (one of the top 3 field guides, the other 2 being *Peterson's Field Guide* and the *National Geographic Field Guide to the Birds of North America)*.

Siegfried, W. R., and L. G. Underhill. "Flocking as an Anti-Predator Strategy in Doves." *Animal Behaviour* 23, no. 3 (1975): 504–508. A classic paper exploring the optimal size of foraging flocks in the face of predation and intraspecific competition. If flocks are too small, birds are too wary of predators to forage effectively, but if flocks are too large, birds spend too much time fighting rather than foraging.

Skutch, A. F. *Parent Birds and Their Young.* Austin: University of Texas Press, 1976. A classic text covering every aspect of parental care, from hatching to fledging. Well written and highly recommended.

Stephens, D. W. *Foraging Behavior and Ecology.* Chicago: University of Chicago Press, 2007. A general survey of territorial behavior in vertebrates, with a lot of material devoted to birds. The 14 collected essays address such topics as individual and social foraging, predation, community ecology, and parental behavior.

Stokes, D. W., and L. Q. Stokes. *A Guide to Bird Behavior.* Boston: Little, Brown, 1983. Published in 4 small volumes, this series is an invaluable reference for anyone interested in understanding the behavior of common birds. The extensive illustrations and clear descriptions are first-rate.

Stutchbury, B. *The Private Lives of Birds: A Scientist Reveals the Intricacies of Avian Social Life.* New York: Walker & Company, 2011. A wide-ranging discussion of the intimate details of the lives of birds, including sexual selection, monogamy and divorce, territoriality, parental care, and migration. The author makes the point that conserving threatened or endangered birds requires a deeper understanding of their nature. Originally published as *The Bird Detective.*

Van Grouw, K. *The Unfeathered Bird*. Princeton, NJ: Princeton University Press, 2013. A thorough and up-to-date survey of every aspect of avian anatomy and physiology.

Wehr, T. A. "Photoperiodism in Humans and Other Primates: Evidence and Implications." *Journal of Biological Rhythms* 16, no. 4 (2001): 348–364. Birds aren't the only vertebrates whose lives are governed by photoperiod; humans are also affected, although to a much lesser degree. There is evidence that seasonal reproduction in humans may be tied to photoperiod, but artificial changes in our environment since the Industrial Revolution have dampened the influence of exposure to changing day length.

Weidensaul, S. *Living on the Wind: Across the Hemisphere with Migratory Birds*. New York; Basingstoke: Farrar Strauss Giroux; Palgrave Macmillan, 2002. An absorbing and accessible account of orientation and migration, with an emphasis on the rapid declines in migratory populations due to habitat destruction and fragmentation. Highly recommended.

Wesoowski, T. "The Origin of Parental Care in Birds: A Reassessment." *Behavioral Ecology* 15, no. 3 (2004): 520–523. Examines the early evolution of parental care, especially with regard to avian monogamy, a topic generally overlooked until recently. The appearance of parental care in ancient reptiles was a significant step toward the evolution of birds.

Xu, X., Z. Zhou, R. Dudley, S. Mackem, C. Chuong, G. M. Erickson, and D. J. Varricchio. "An Integrative Approach to Understanding Bird Origins." *Science* 346, no. 6215 (2014): 1253293. Outlines the current status of the evolution and classification of birds, with suggestions for future directions for research.

Young, J. *What the Robin Knows: How Birds Reveal the Secrets of the Natural World*. Boston: Houghton Mifflin Harcourt, 2012. An interesting and unique approach to what we can learn by observing birds, uniting Native American wisdom with a modern knowledge of natural history. Tuning in to the avian world brings a deeper understanding of the natural world.

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