



## Physiology

By adaptively modifying their physiology, birds have evolved to live in nearly every habitat on Earth, from the poles to the tropics. Consider a small songbird on a hot summer's day. How does it stay cool at high noon when the air temperature is well above its body temperature? Can the bird get all the hydration it needs from the food it eats or must it drink water? How does it modify its activity (feeding, breeding, territorial fighting, singing and so on) through the day to reduce overheating, yet at the same time manage to reproduce successfully and avoid predators? Answers to such questions fall within the purview of avian physiology, the topic of this chapter. Here, we address how birds regulate their internal environment across vastly different external environments, from the Antarctic ice caps to the hottest deserts, from tropical rainforests to temperate taiga, and across the oceans.

◀ Black grouse (*Lyrurus tetrix*).

# The importance of balance

Birds maintain relatively constant physiological conditions within their body (known as homeostasis) across vastly different external environments, and it is this ability that enables them to be so widespread. They regulate their physiological state for water and salt content, temperature, pH, nutrient and oxygen levels, and waste and carbon dioxide levels. Just as the thermostat in a house detects changes in room temperature relative to a set point and adds either hot or cold air as needed, so a bird's homeostatic system relies on negative-feedback pathways to adjust the animal's physiology when unbalanced.

A useful way to consider how birds regulate their internal environment in the face of vastly different external environments is by constructing 'budgets' for relevant physiological conditions, such as energy, protein, water and salt. For example, a 90 kg ostrich living in the hot African savannah loses about 8 litres of water each day, mainly through urine and faeces production (64 per cent), respiration (29 per cent) and via its skin (7 per cent). To balance these losses, the ostrich must drink about 7.5 litres of water each day – the other 0.5 litres that is required is produced from the metabolism of food. An ostrich that is unable to find this much drinking water cannot maintain water homeostasis and would not survive for long.

## Osmoregulation

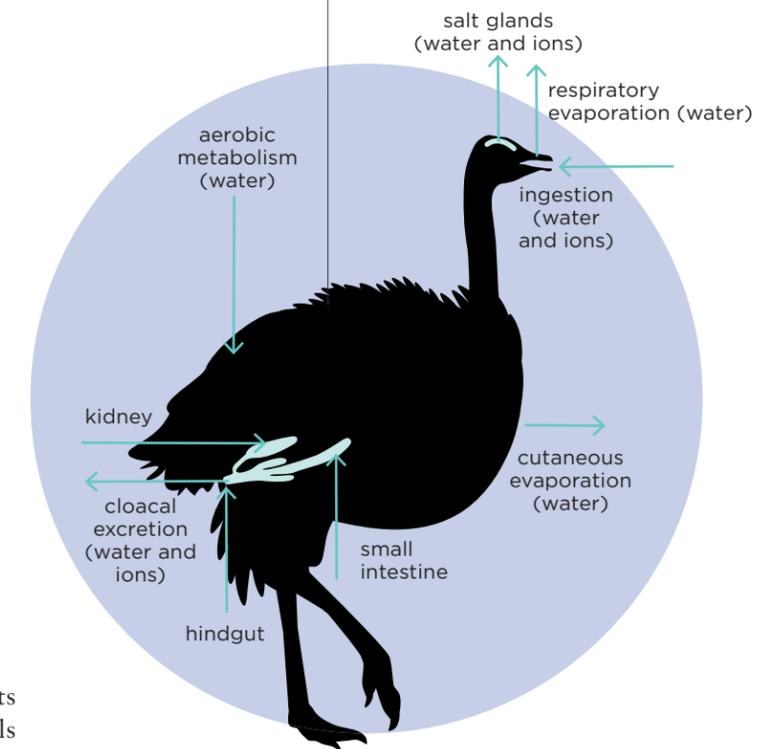
For most birds (and other vertebrates), maintaining an adequate water and salt balance within the body is a major challenge, because dehydration is a constant danger when living in terrestrial or marine systems.

Life on Earth requires water, and the bulk of a bird's body – normally 60–70 per cent – is water. Water is sometimes called the universal solvent and is needed for most chemical reactions and for maintaining many bodily functions. For example, if the water content of blood is inadequate, blood pressure falls and this compromises the delivery of key nutrients to vital organs. Salt balance must be considered along with water balance, because all organisms – including

▼ Budgerigars (*Melopsittacus undulatus*; left) are native to Australia, where hot, dry conditions are common. They must drink to stay appropriately cool, and their distribution is therefore constrained by the location of free water. Other birds, such as this rock dove (*Columba livia*; right), stay cool by ruffling their feathers to increase heat loss from their body and decrease heat gain from solar radiation.



▲► The common ostrich (*Struthio camelus*) inhabits some of the hottest, driest places in Africa and so must find ways to conserve its body water, despite inevitably losing some through respiration, excretion (faecal and urine loss) and perspiration (cutaneous water loss). The birds achieve this by regularly ingesting water, minimising the inevitable losses and using their osmoregulatory system to maintain water and salt balance.



birds – move water across cell membranes passively by the process known as osmosis (hence the term 'osmoregulation' for the entire physiological system that is involved).

Osmosis only occurs though when water, a highly potent solvent, moves across semipermeable membranes (such as the cell membranes within a bird's body) from a less concentrated solution to a more concentrated one. These solutes, or components dissolved in the solution, include important chemicals such as sodium and chloride (the constituents of common table salt), as well as potassium and calcium. Osmosis is clearly demonstrated when limp vegetables such as carrots are placed in water to make them crisp again – water moves into the carrots, because when they are limp they contain a relatively higher concentration of nutrients and salts.

In general, birds maintain their water and salt balance by drinking more and losing less through their skin and during respiration. They primarily achieve water and salt balance with the key organs of the osmoregulatory system: kidneys, intestines and salt glands.

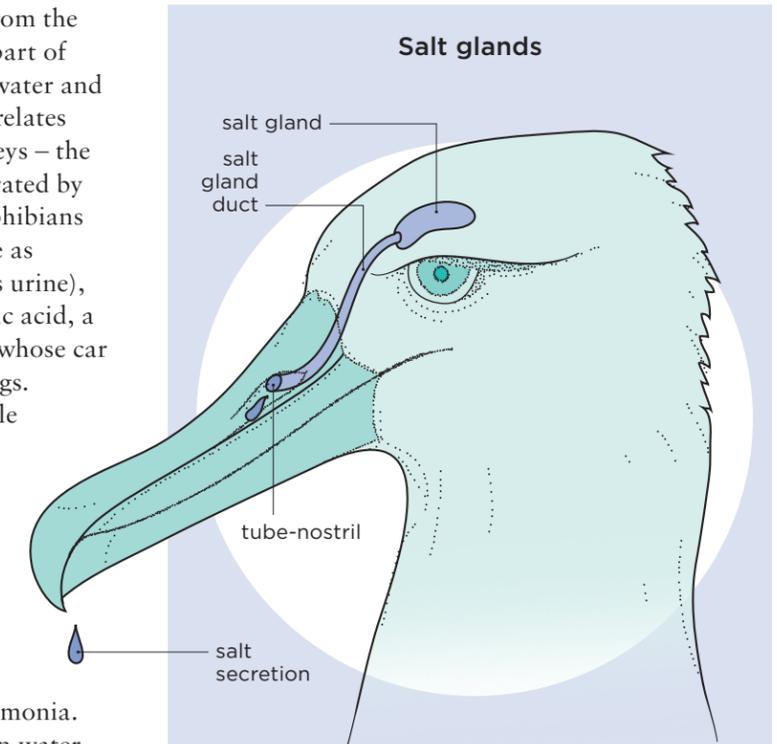
## Kidneys and urine production

Birds and mammals are the only vertebrates that can produce urine that is more concentrated than their body fluids (critical for maintaining water balance) and they achieve this thanks to unique adaptations to their kidneys. In brief, the paired kidneys initially filter the blood to produce a very dilute urine. The urine then flows through a convoluted plumbing system within the kidney that includes tubes (called nephrons) arranged in a series of adjacent loops. As the urine moves through the nephrons, water is reabsorbed and the concentration of salts in the urine increases, so the longer the loops, the more

concentrated the urine. Mammals have much longer, specialised nephron loops than birds and can thus concentrate their urine to a greater extent – up to 25 times that of body fluids, compared to a more modest three times for birds. Birds and mammals can further increase urine concentration by increasing the rate of filtration of the kidneys and, through the action of hormones, modifying the permeability of the nephrons.

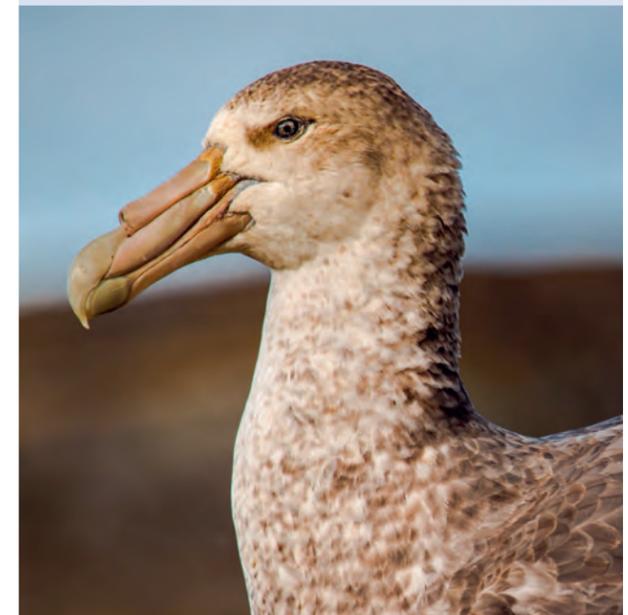
Birds have evolved two other relatively unique ways to reduce their water loss compared to mammals. The first is related to processing the urine after it leaves the kidneys. Unlike mammals, birds

have no urinary bladder and the product from the kidneys is released directly into the lower part of the gut, where important reabsorption of water and some salts occurs. The second adaptation relates to another important function of the kidneys – the excretion of nitrogen waste products generated by protein metabolism. Unlike fish, most amphibians and mammals, which excrete protein waste as ammonia and/or urea (otherwise known as urine), birds and reptiles excrete this mainly as uric acid, a white pasty compound familiar to anyone whose car has been splattered by gull or tern droppings. A benefit of producing uric acid is that little water is required (0.001 litres per gram of nitrogen excreted) compared to the water required for ammonia (0.5 litres) or urea (0.05 litres) excretion. However, the energy cost of producing uric acid (as well as urea) as the nitrogenous waste product (around 18 kJ per gram of protein) is relatively high compared to the negligible energy cost of producing ammonia. For birds, the evolutionary balance between water conservation and energy conservation appears to have fallen towards water conservation.



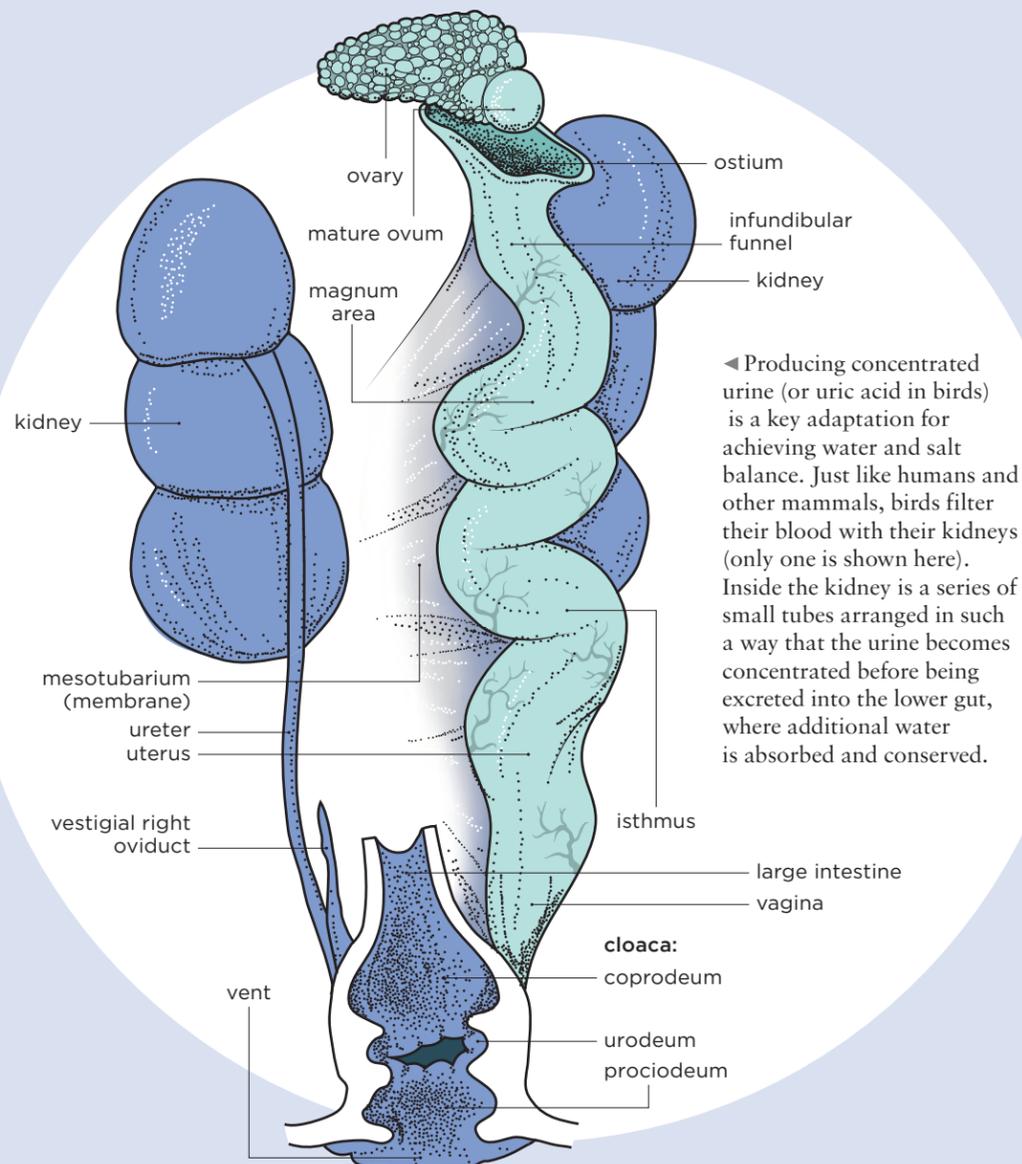
## Salt glands

The final piece to the puzzle of how birds achieve water and salt balance in challenging environments such as deserts and oceans involves a useful pair of glands, the salt glands, usually located just above the orbit of the eye. These enable birds to, for example, drink only seawater because they are able to excrete concentrated salt solutions. The activity of the salt glands depends on a bird's recent exposure to salt, as the glands will grow with use and shrink with disuse. The glands rid the body of excess salts primarily through active transport of sodium chloride across cell membranes. The highly concentrated salt-gland solution exits through the bird's nostrils on top of the beak. If you closely observe marine birds such as penguins, gulls or pelicans, you will often see them shaking their head from side to side – this action jiggles the accumulated salt-gland solution off the tip of the bill, making room for more of the salty secretion.



▲ Salt glands in birds are arranged above the eyes (only one is shown above) and enable them to get rid of excess salts when, for example, they drink only seawater and eat mostly salty prey such as fish or squid. The concentrated salt solution is excreted through the nostrils, which for this southern giant petrel (*Macronectes giganteus*) are within its quite large 'tube nose' at the top of its bill.

## Urinogenital system of a dove



◀ Producing concentrated urine (or uric acid in birds) is a key adaptation for achieving water and salt balance. Just like humans and other mammals, birds filter their blood with their kidneys (only one is shown here). Inside the kidney is a series of small tubes arranged in such a way that the urine becomes concentrated before being excreted into the lower gut, where additional water is absorbed and conserved.

# Respiratory and circulatory systems

The high metabolic rates and extensive daily movement of birds requires an extraordinary capacity to deliver oxygen and energy to their muscles and organs, as well as rapid removal of waste products. The circulatory and respiratory systems of birds accomplish these integrated tasks. The respiratory system transports oxygen from the atmosphere to the circulatory system and moves carbon dioxide in the opposite direction. The circulatory system delivers oxygen from the lungs to the tissues of the body and also delivers digested nutrients from the gut. These systems have several specialisations to meet the high demands of flight.

## Flow-through respiratory system

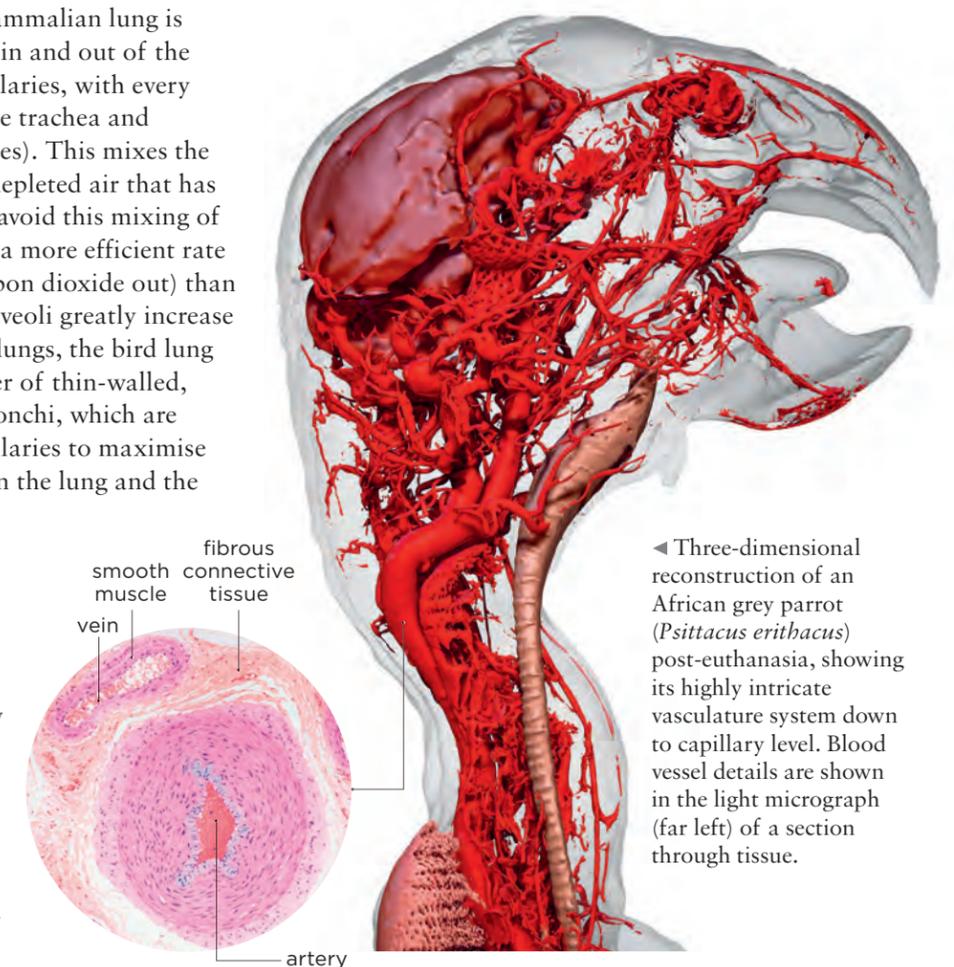
The avian and mammalian respiratory systems are quite different in basic design. Bird lungs are paired to an extensive network of air sacs that extend throughout the chest and abdominal cavity, and even into hollow bones. The air sacs and lungs work together such that air flows in only one direction through the lungs, requiring two complete inhalation/

exhalation cycles to move a volume of air through the respiratory system. This unidirectional routing is important, because it means that the air moving through a bird's lungs, with continuous one-way flow, is constantly refreshed and has a high oxygen content. That is, fresh oxygenated air flows through the lungs both when a bird inhales and when it exhales.

In contrast, airflow in the mammalian lung is bidirectional or tidal (air moves in and out of the blind-ending alveoli, or air capillaries, with every inhalation and exhalation via the trachea and branched bronchi and bronchioles). This mixes the incoming new air with oxygen-depleted air that has already been in the lungs. Birds avoid this mixing of incoming and old air, providing a more efficient rate of gas exchange (oxygen in, carbon dioxide out) than mammals. In addition, just as alveoli greatly increase the surface area of mammalian lungs, the bird lung is subdivided into a large number of thin-walled, tubular structures called parabronchi, which are covered by a rich supply of capillaries to maximise the rate of gas exchange between the lung and the circulatory system.

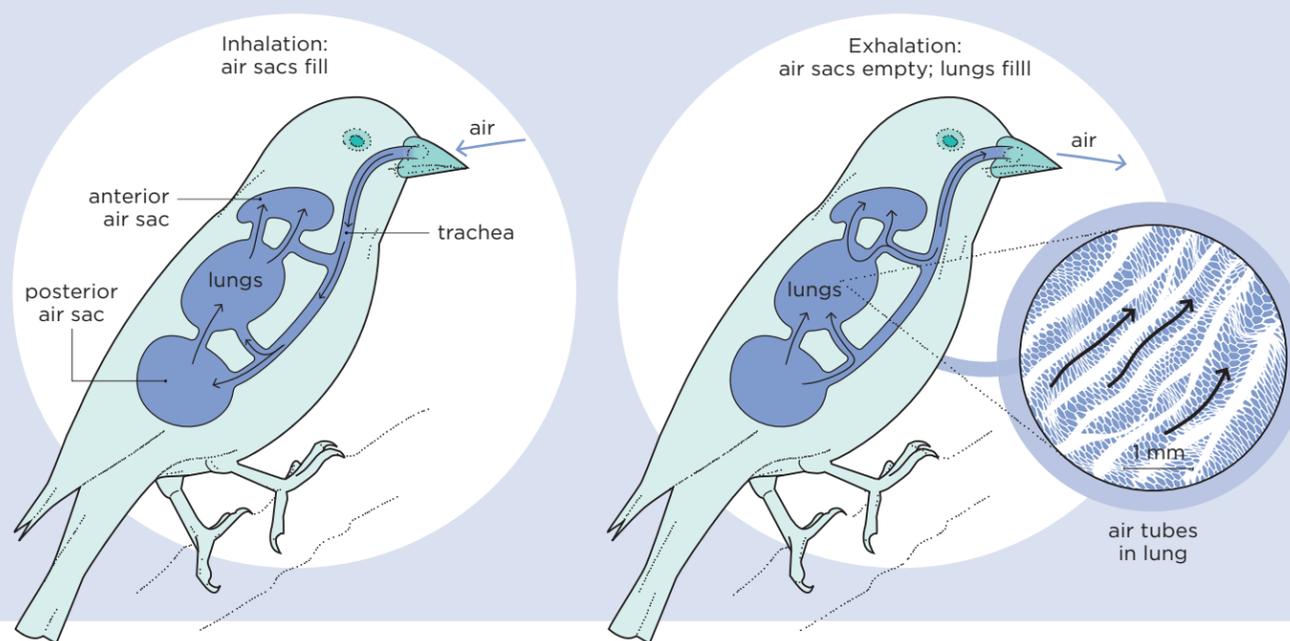
◀ Birds' lungs and air sacs work together to allow fresh oxygenated air to flow through the lungs both when birds breathe in and when they breathe out. This provides a very efficient transfer of oxygen to, and carbon dioxide from, the blood.

▼ High-efficiency respiration helps Asian bar-headed geese (*Anser indicus*) migrate over the Himalayas.



◀ Three-dimensional reconstruction of an African grey parrot (*Psittacus erithacus*) post-euthanasia, showing its highly intricate vasculature system down to capillary level. Blood vessel details are shown in the light micrograph (far left) of a section through tissue.

## Avian respiratory system



## Circulatory system

Much like that of mammals, the avian circulatory system consists of two major circuits. A pulmonary circuit conducts blood at relatively low pressure through the lungs, where gas exchange occurs: red blood cells become oxygenated and carbon dioxide is exhaled. The other circuit, powered by the left half of the heart, circulates blood to the rest of the body. Arteries conduct blood away from the heart, and veins conduct blood towards it. Arteries have thicker, more muscular walls than veins. The large arteries leaving the heart divide and subdivide into smaller and smaller branches, until they become capillaries, the smallest vessels of the circulatory system. It is in the capillaries that blood exchanges gases (e.g. oxygen), nutrients, waste products and chemical messengers like hormones with the surrounding tissues. After passing through the capillaries, blood is collected in venules; these merge into larger and larger veins before returning to the heart.

## Pumping blood: the four-chambered heart

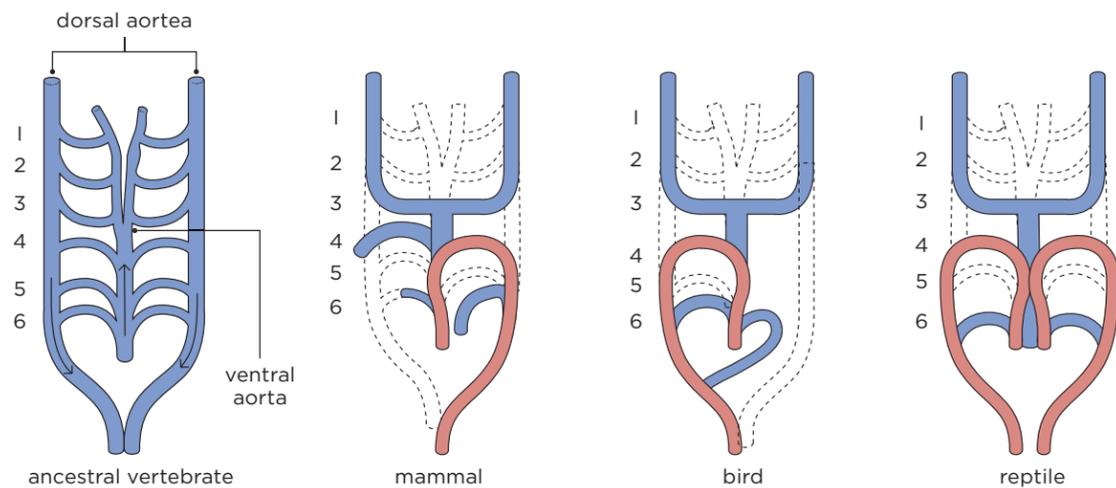
Birds have a four-chambered heart, similar to that of mammals. However, birds and mammals evolved this innovation independently from the more ancestral three-chambered heart still found in amphibians and many reptiles. The heart has two muscular ventricles that act as pumping chambers, connected to two thinner-walled receiving chambers called atria. The two sides of the heart pump blood independently through a lung (pulmonary) circuit and a body (systemic) circuit. In animals with three-chambered hearts, blood from the two circuits can mix in the single ventricle. In birds, the pulmonary circuit can

be maintained at a lower blood pressure than the body circuit to protect the delicate blood vessels in the lungs, because the ventricles can induce different force. Blood enters the heart at the right atrium via the veins of the body, and then flows into the right ventricle. Contractions of the right ventricle pump blood through the lungs, where oxygen and carbon dioxide are exchanged, and then on to the left atrium. From the left atrium, blood flows to the left ventricle, which is larger and more muscular than the right, where it is then pumped out to the blood vessels of the body. One-way valves between the atria and ventricles prevent back-flow in this circuit.

## DIFFERENT PLUMBING

Although birds and mammals both have four-chambered hearts, they evolved these dual circuits independently. Ancestral vertebrates had dual aortic arches carrying blood away from the heart, and these are present in embryonic

stages of mammals and birds. Reptiles retain a double arch into adulthood, but mammals and birds, with their fully separated, dual-circuit, four-chambered hearts, retain only a leftward or rightward arch, respectively.



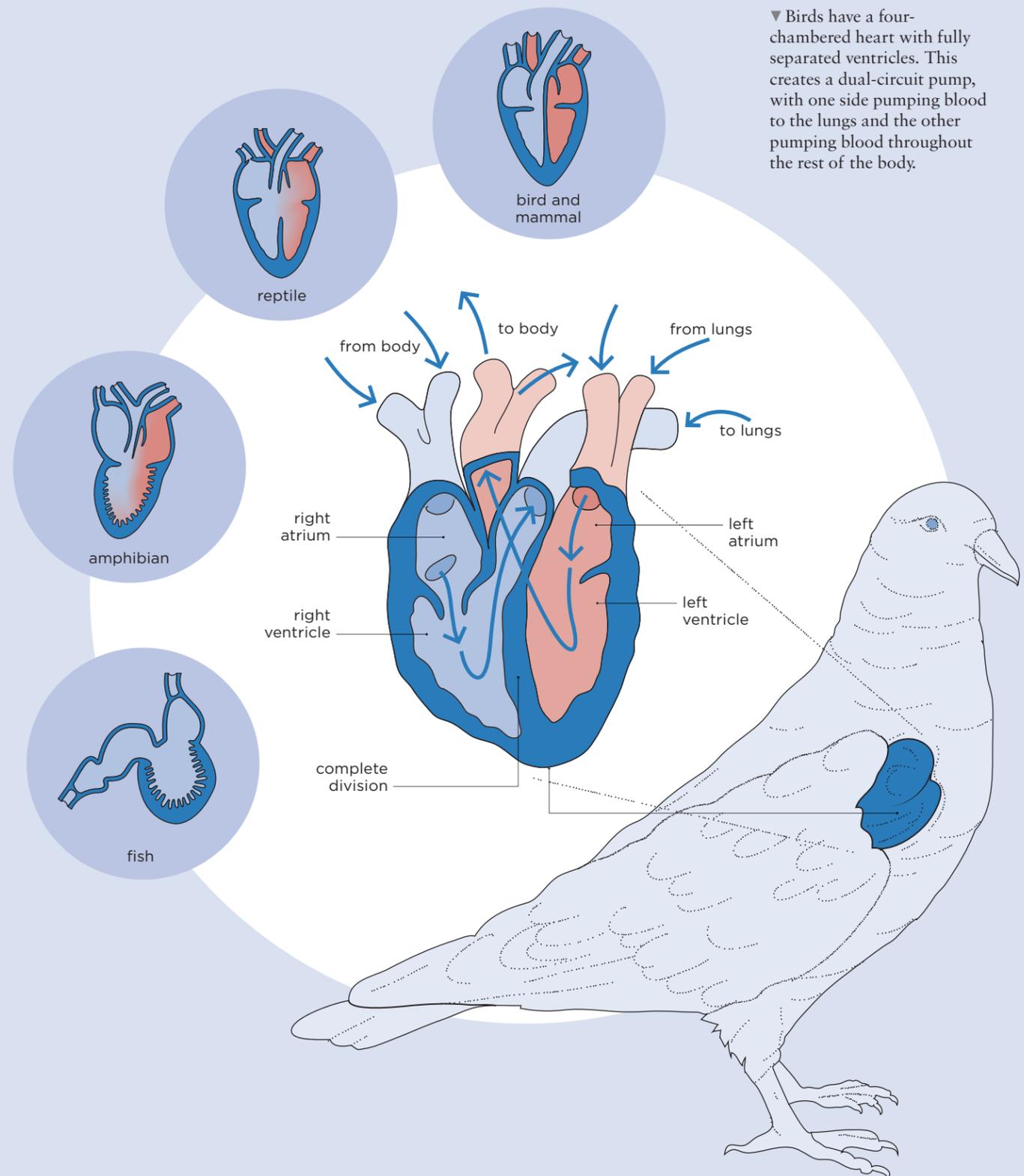
▲ In ancestral vertebrates multiple aortic arches provided blood to the gills. These are seen in early embryology of many modern vertebrates.

▲ In mammals, only three aortic arches develop into blood vessels, and a single systemic aorta develops from the fourth arch on the right side.

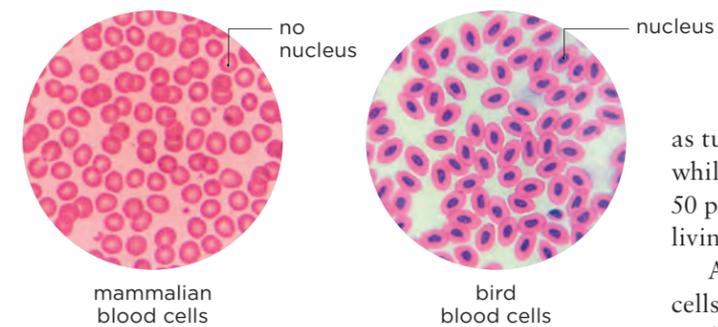
▲ In birds, only three aortic arches develop, but the single systemic aorta develops from the fourth arch on the left side.

▲ Many reptile species also retain three of the aortic arches, but these develop into two systemic aorta.

## Avian heart morphology and comparisons with other groups



▼ Birds have a four-chambered heart with fully separated ventricles. This creates a dual-circuit pump, with one side pumping blood to the lungs and the other pumping blood throughout the rest of the body.



◀ Emperor penguins (*Aptenodytes forsteri*) make extended dives to catch prey, reaching depths of 500 m and lasting up to 20 minutes. During these dives they show bradycardia (slowed heart rate) and reduced blood flow to conserve oxygen.

▲ Mammalian red blood cells are small and dimpled, lacking a cell nucleus. In contrast, birds have retained the large nucleated red blood cells similar to those in reptiles.

as turkeys have a haematocrit of about 40 per cent, while in smaller songbirds the proportion is about 50 per cent – or even 60 per cent in those species living at high altitudes.

Avian blood contains many types of white blood cells, all of which function in immunity to defend against pathogens and parasites. In addition, it contains thrombocytes, which act like platelets in mammalian blood to aid clotting and also have a role in immune function. Following injury or damage to blood vessels, thrombocytes are activated to clot blood and reduce bleeding. This clotting process is slower than in mammals, but as thrombocytes do not form large aggregations in arterial blood like mammalian platelets, it is unlikely that birds suffer from cardiovascular diseases such as strokes.

### Heart size and heart rate

Compared to mammals, birds have larger hearts relative to their body size, and they tend to have lower heart rates. This may seem counterintuitive given the high metabolic demands of flight, but an avian heart still manages to pump more blood per minute than a mammalian heart thanks to very efficient filling of the ventricles and high blood pressure.

In general, heart rates are higher for smaller animals, and this is true in birds. Turkeys can have a resting heart rate of about 90 beats per minute (bpm), while in smaller songbirds the resting heart rate is 600–700 bpm. Of course, heart rates change dramatically depending on the activity of a bird. A hummingbird's heart rate is more than 1,200 bpm during active flight, vultures have a heart rate of about 300 bpm at take-off but only about 100 bpm when soaring, and emperor penguins (*Aptenodytes forsteri*) slow their heart rate from about 73 bpm at rest to about 57 bpm during a dive.

Heart size is also plastic. Prior to prolonged migration, many birds increase their heart size to increase cardiac output. The heart, along with many organs, decreases in size during prolonged migratory flights to meet the bird's protein requirements, and then needs to be rebuilt during stopover periods.

### Bird blood

Blood transports gases, electrolytes, nutrients, hormones, immune factors and other elements throughout the body. It is mostly composed of water, with its liquid component being known as plasma. Within the plasma are a number of cell types, including erythrocytes (red blood cells), leucocytes (white blood cells) and thrombocytes (similar to mammalian platelets).

Avian red blood cells are larger than those of mammals and have a nucleus (unlike mammalian red blood cells). It is thought that the small, dimpled blood cells of mammals arose early in the group's evolution, to increase surface area to volume ratio in response to a period of low atmospheric oxygen during the Triassic period. In contrast, birds retained larger, nucleated red blood cells similar to those of reptiles. Avian red blood cells are relatively short-lived, with a lifespan of about 40 days, and need to be continually replaced. They contain several forms of haemoglobin, the four-part protein or respiratory pigment that transports oxygen.

The structure of haemoglobin varies across species, and in birds that fly at high altitudes (e.g. the central Asian bar-headed goose, *Anser indicus*) or that have extended deep dives (e.g. the emperor penguin), haemoglobin has a higher affinity for oxygen. The proportion of blood that is composed of red blood cells (its haematocrit) varies across species and also with altitude. Large birds such

## KEEPING COOL, KEEPING WARM

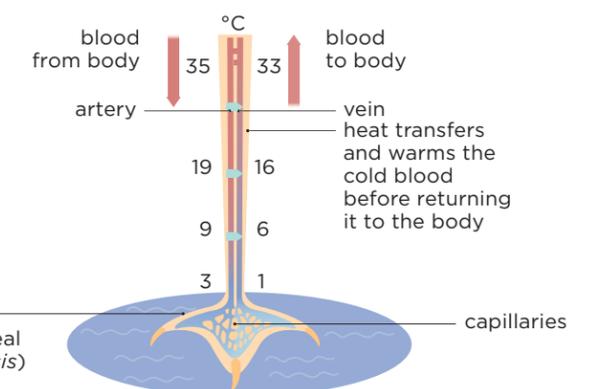
How do waterfowl keep their feet warm in cold water or while standing on ice? The short answer is that they don't. As in other vertebrates, birds use countercurrent heat exchange, so that extremities like the legs and feet are kept at a cooler temperature than the rest of the body. In the legs, veins returning to the body run closely parallel

to the arteries. As warm blood flows through the arteries, heat is transferred and therefore warms the venous blood, which in the process becomes cooler itself. In this way, the feet are kept at a low temperature, decreasing the thermal gradient with the environment and conserving body heat.



Green-winged teal (*Anas carolinensis*)

### Countercurrent heat exchange



# Immune system

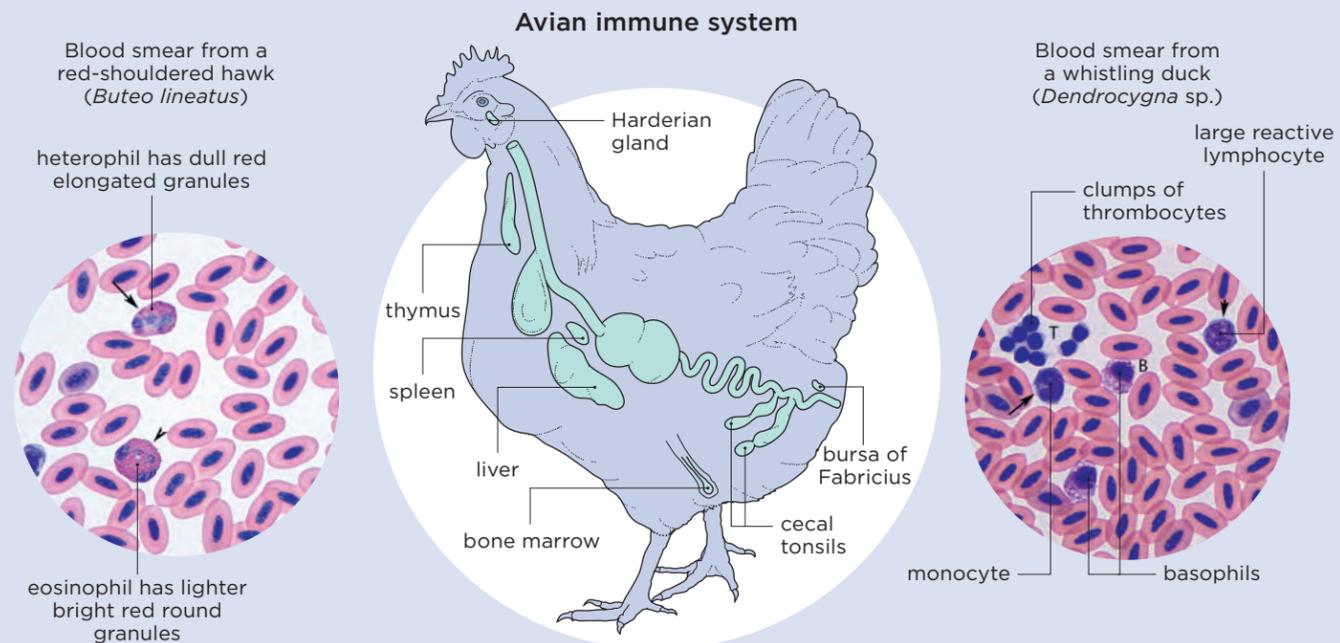
Birds need to defend themselves against infection and disease caused by parasites and pathogens. The immune system is a complex, interacting network of cells and other factors that identify and destroy pathogens that invade the body, and in birds, as in other vertebrates, it has several branches. Innate immunity refers to systems that are general and provide immediate, but non-specific, defences. Acquired, or adaptive, immunity provides defence against specific pathogens that have been previously experienced. Unlike mammals, avian acquired immune responses include both cell-mediated and humoral (antibody-dependent) components.

## Immune system cells

A range of different blood cells contribute to avian immune defences, including various white blood cells: heterophils, lymphocytes, basophils, eosinophils and monocytes. These cells interact with non-cellular, antibody-dependent defences (humoral components of the immune system). Heterophils are the most common white blood cells and play an important role in innate immunity, both through ingesting pathogens such as bacteria (phagocytosis) and contributing to defensive inflammation. Lymphocytes exist in two forms, B and T lymphocytes, which contribute

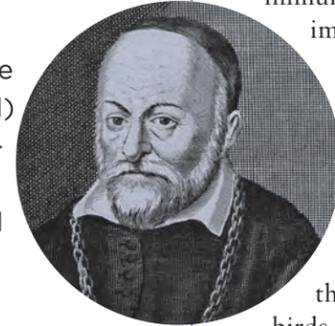
to antibody-driven humoral immunity and cell-mediated immunity, respectively. The functional roles of basophils, eosinophils and monocytes are less understood, and although these are thought to play a role in immunity, mysteries remain as to how they contribute to innate and acquired responses.

Immune cells are primarily produced by the thymus gland, located in the neck, and the bursa, located near the cloaca. Other glands such as the spleen, the Harderian gland (behind the eye), tonsil-like glands in the intestine, and other lymphoid tissue are also involved in the immune system.



## MAKING HISTORY

The two major arms of the acquired immune system are T-dependent (cell-mediated) and B-dependent (humoral-mediated) immunity. These two systems were identified in birds prior to their discovery in any other vertebrate animal. The bursa of Fabricius, a small pouch on the lower gut in birds, was first described in the seventeenth century by the Italian anatomist Hieronymus Fabricius. In the 1950s, following a series of experiments on birds in which the bursa was removed, scientists confirmed that cell- and humoral-mediated immune responses are carried out by distinct cell populations. These studies demonstrated that cells from the bursa, subsequently named B-cells, control antibody production. Others showed that cell-mediated immunity depended on the thymus, and these cells became known as T-cells. Later work demonstrated that mammalian B-cells are produced in bone marrow, but the B-cell designation, acknowledging their discovery in the bursa, has remained.



Hieronymus Fabricius

## Ecoimmunology

The growing field of ecoimmunology takes an evolutionary approach to understanding how various immune responses interact with other traits to improve survival and reproductive success. Studies of birds have been at the forefront of this field and have focused on some long-standing questions. For example, do birds use attractive signals like plumage or courtship to advertise their ability to cope with pathogens? Do they select mates based on genetic compatibility for genes that encode antibodies? How do migratory birds cope with exposure to a greater variety of pathogens when they travel? Do the energetic costs of migratory flight put them at a greater risk of infection? The evidence to answer these questions is mixed, in part due to the fact that the immune system itself is so complex and multifaceted.

▼ Some ornamental features, such as the fleshy red wattles and comb of the red junglefowl (*Gallus gallus*) rooster, are thought to indicate how strong a male's immune system is and whether he has had a recent infection.



◀ The immune system comprises several organs throughout the body, which produce multiple kinds of immune cells as well as non-cellular immune factors such as antibodies. Various types of white blood cells can be distinguished visually with a microscope.

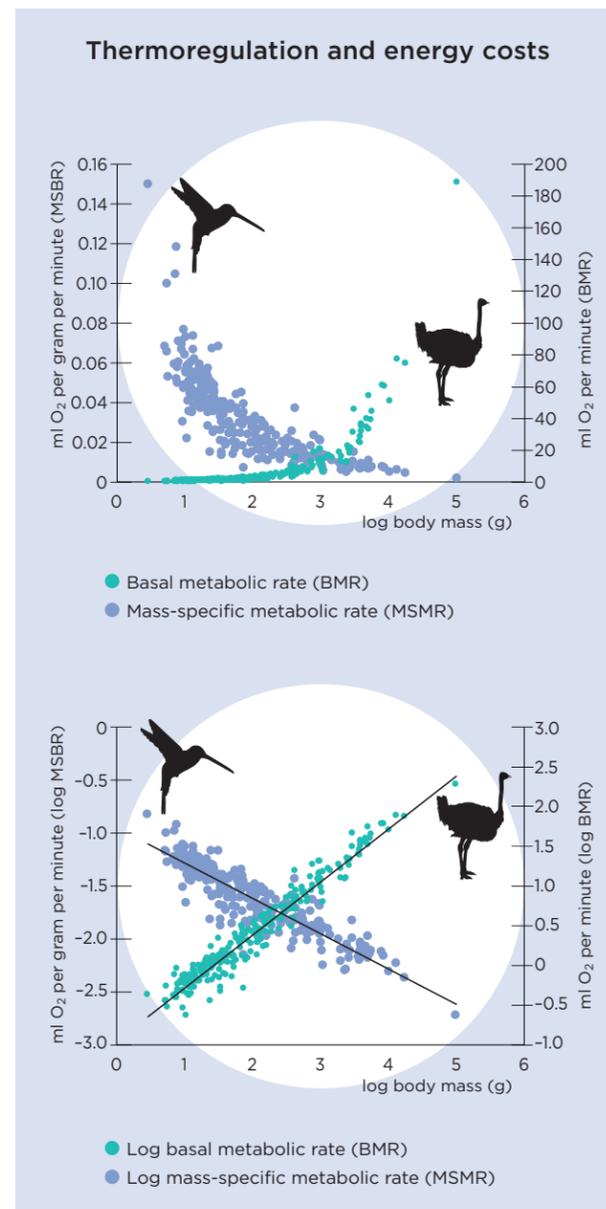
# Thermoregulation and energy costs

The daily energy requirements of a bird and the energy value of its food largely determine how much it must eat each day. A bird's metabolism continues even when it is at rest and not digesting, and ambient temperatures are relatively benign. Energy use during such periods of inactivity is known as the basal metabolic rate, and for birds (and all other animals) this increases with body mass in a very predictable way. The total energy requirements of a bird include the additional energy it needs for production (e.g. growth, reproduction), thermoregulation and activity.

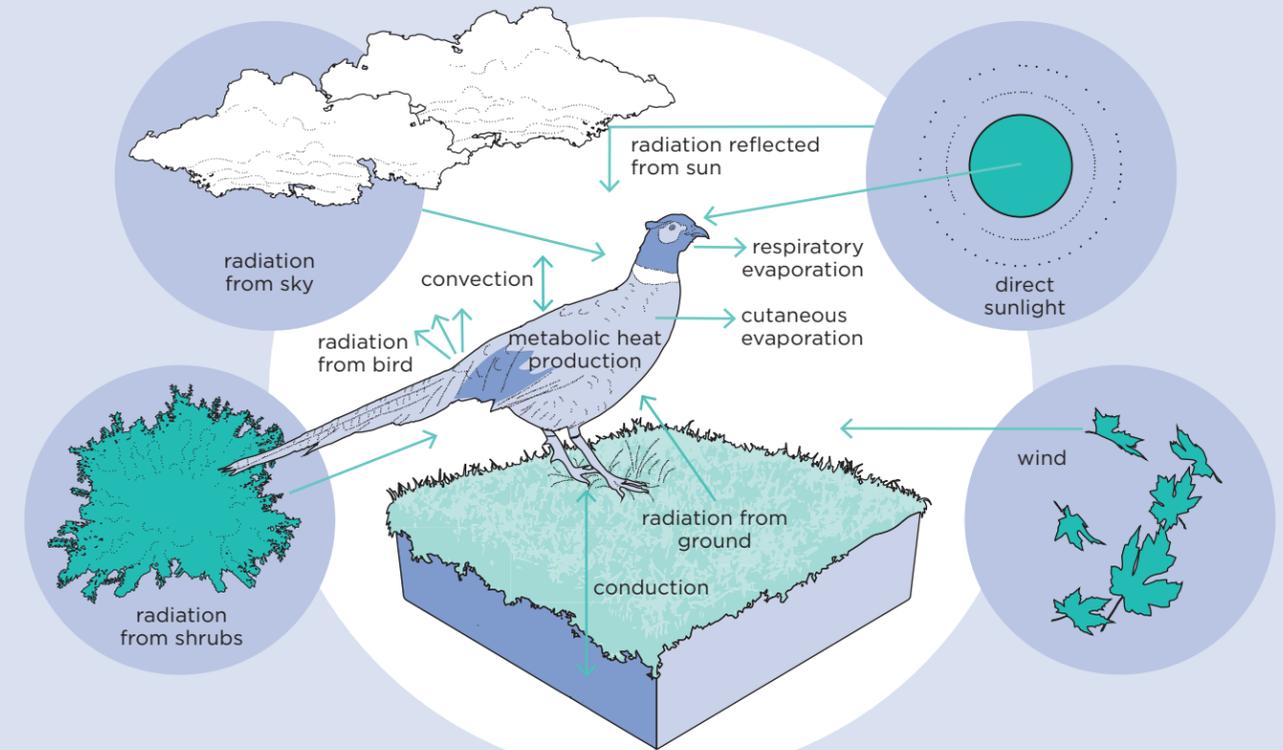
## Pros and cons of endothermy

Birds and mammals are the only groups of animals that are endothermic, producing heat to keep their internal environment at a high and fairly constant temperature. Bird body temperatures (39–43°C) tend to be slightly higher than those of mammals, and also quite high relative to average air temperatures over most of the globe. But why did birds evolve a strategy of spending such a large amount of energy to maintain high body temperatures? The reason seems to be that by having a constant high body temperature birds become relatively independent of ambient temperatures, and hence could fill new niches and habitats. Cold reptiles (ectotherms), for example, are usually quite inactive, whereas birds living in the same chilly ambient temperatures can continue to forage, fly and defend territories. The trade-off is that birds expend orders of magnitude more energy maintaining their high body temperature than reptiles. Also, regulating a body temperature that is on the high side means that only occasionally will air temperatures be higher than body temperature. This is important, because when birds must cool down in the face of hot ambient temperatures, the only way they can do so is through evaporative cooling, which expends precious body water.

► The cost of living in birds is closely related to their body mass. Thus, ostriches expend more energy per unit time (basal metabolic rate, or BMR) than hummingbirds. However, hummers expend much more energy per gram of body mass, which helps to explain why they are such busybodies. Log-transformation (bottom figure) makes both relationships linear.



## Heat gains and losses for birds living in cold places



▲ Birds gain heat through direct and reflected radiation from the sun, and lose heat through radiation and breathing. The wind and ground can provide or dissipate heat depending on their temperature.

▼ Hummingbirds are energy powerhouses even when at rest. They expend more energy per gram of body mass than the majority of other (larger) birds and live a very fast lifestyle.

## Staying warm in cold places

For a bird's body temperature to remain constant, heat loss must equal heat gain. Birds that live in cold places do not undergo major seasonal adjustments in insulation that are common in mammals, which often add both hair and fat as winter approaches. And nor do birds truly hibernate like mammals, which involves significant lowering of the body temperature to very low levels close to freezing point. Birds do add some fat insulation during winter, they puff up their feathers to stay warm and they try to find warmer places out of the wind, and some more social birds such as penguins huddle together to retain heat. However, only a few types of birds (e.g. hummingbirds, some poorwills and nightjars, mousebirds and some swifts) can lower their body temperature for extended periods of time (more than 24 hours) to conserve energy, a physiological state known as torpor. The primary way birds stay warm in cold places is by increasing their metabolism to increase heat production. However, they then have to recoup the substantial energy costs of this strategy by eating lots.



## Staying cool in hot places

How do birds live, breed and stay relatively cool in the world's hottest, driest, low-productivity deserts, such as those found in the Arabian Peninsula? Not only are birds present in these extremely challenging environments, but they are often active at the hottest times of the day – unlike most desert rodents, which retire to cooler underground burrows. It was previously thought that birds were pre-adapted to desert life because of their high body temperatures. However, such temperatures are actually dangerously close to the thresholds at which molecules like proteins start to change their structure and lose their function, leading to death. Thus, staying cool in such hot places is essential.

The only physiological way that heat can be lost when ambient temperatures are greater than body temperature is through evaporative cooling, from water loss across the skin or respiratory surfaces. Birds can increase the efficiency of respiratory evaporative water loss by panting or through gular flutter (vibrating the throat with the mouth open). Even though birds do not have sweat glands, they

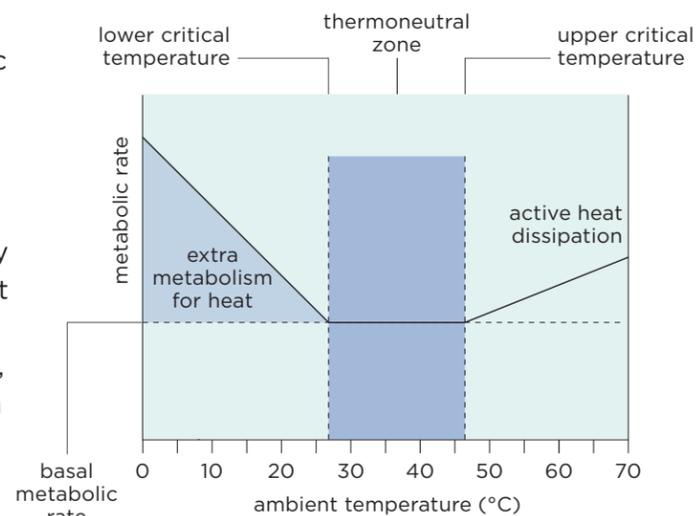
still lose significant water across their skin, which can contribute to evaporative cooling. Cutaneous evaporation often accounts for half or more of total evaporative heat loss when birds are not active and surrounded by warm, dry air. Birds that live in hot places have evolved adaptations to reduce the cost of thermoregulation, including decreasing their metabolic rate to limit heat production, having efficient kidneys or salt glands to limit unnecessary water loss (see page 129), and decreasing water loss across the skin and respiratory surfaces whenever possible.

Given that birds lose heat by increasing evaporative cooling across their skin and lungs, staying cool in hot places increases their water requirements. Andrew McKechnie and Blair Wolf have predicted that the expected increases in global temperatures associated with climate change will substantially increase the water requirements of birds, to the point where their survival rates will significantly decline by 2080 and the frequency of catastrophic mortality events will increase.

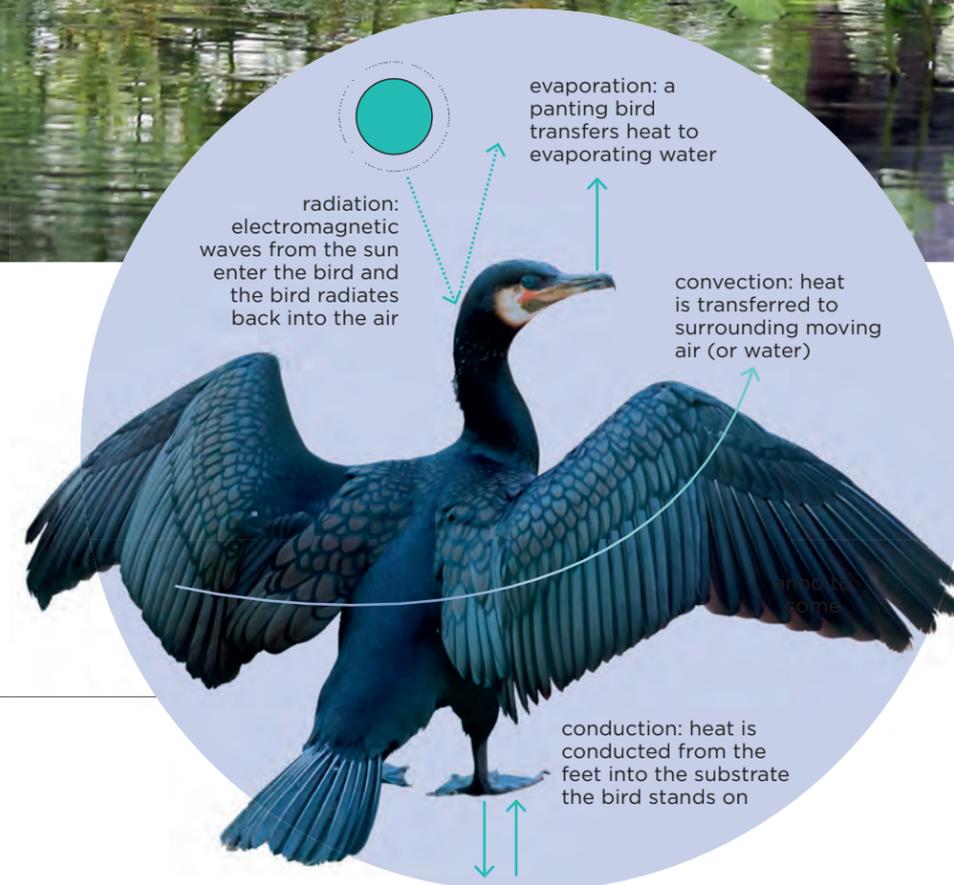


## THE THERMONEUTRAL ZONE

The range of ambient temperatures over which a bird's rate of metabolic heat production does not change is known as the thermoneutral zone. Metabolism remains constant because the bird relies on behavioural, insulatory or circulatory mechanisms to minimise heat loss at essentially no energy cost. On the cold side of the thermoneutral zone, a bird can face into the sun to warm up, tuck its beak under a wing or fluff up its feathers. Conversely, on the warmer side of the thermoneutral zone it can increase heat loss by increasing the blood supply to its skin.



▲ Birds use no additional energy for thermoregulation and are in the 'thermoneutral zone' when outside temperatures are benign. Otherwise, birds must use more and more energy to stay warm when cold, or cool when hot.



▲ As in all birds, great blue herons (*Ardea herodias*) open their bills and flutter their throat (called 'gular fluttering') to increase heat loss on very hot days.

◀ Birds like this cormorant stay cool on hot days by posturing, panting, increasing the surface area of their body exposed to the wind and standing on cooler surfaces.

▼▼ When temperatures drop, birds can huddle together to stay warm, as seen in these European bee-eaters (*Merops apiaster*).



# Digestive and excretory system

The digestive system of birds is relatively simple and similar to that of mammals. Food passes from the mouth to the oesophagus (where some birds have a crop for storing food) and the stomach, and then through the small intestine and large intestine before exiting via the cloaca. A remarkable feature of this system, especially in birds that migrate long distances, is the ability to rapidly and reversibly change the size of key organs – including the flight muscle, liver, intestine and heart – in response to changes in demand.

## Chemical and mechanical digestion

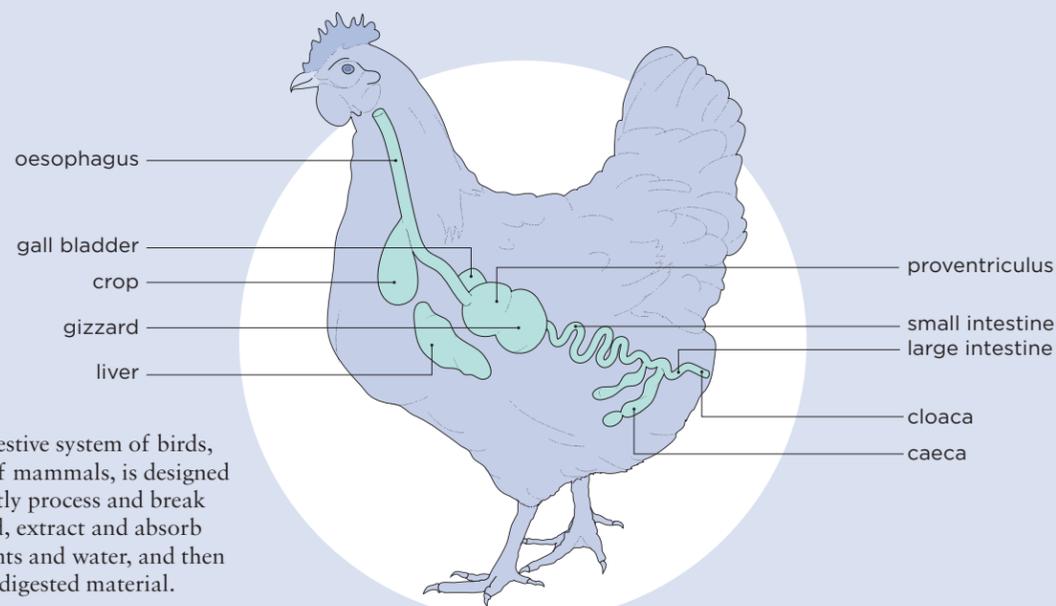
The breakdown of proteins, fats and carbohydrates in food takes place primarily in the stomach and small intestine using both mechanical and chemical processes. In most birds the stomach is divided into a proventriculus, where chemical digestion is initiated, and a gizzard, where ingested food is mechanically mixed and ground (this therefore replaces the function of teeth). Many birds (e.g. geese, songbirds, penguins, pigeons) regularly swallow small, hard objects such as grit or pebbles to aid in the grinding of food in the gizzard.

Digestive enzymes are proteins produced by cells of the stomach, intestine and pancreas to regulate the rate of chemical breakdown of food compounds. Like

all enzymes, digestive enzymes are, to some degree, specific to a certain substrate or reactant molecule, and their activity is sensitive to temperature and pH in particular.

The absorption of the end products of digestion in the foregut primarily occurs in the bird's small intestine. Digestive enzymes secreted from the liver and pancreas are delivered into the first portion of the small intestine, and in the latter portion digestion is completed and absorption takes precedence. The products of digestion (amino acids, fatty acids, glucose and fructose) are absorbed across the intestinal wall and then move via blood circulation to the bird's tissues and cells.

Avian digestive system



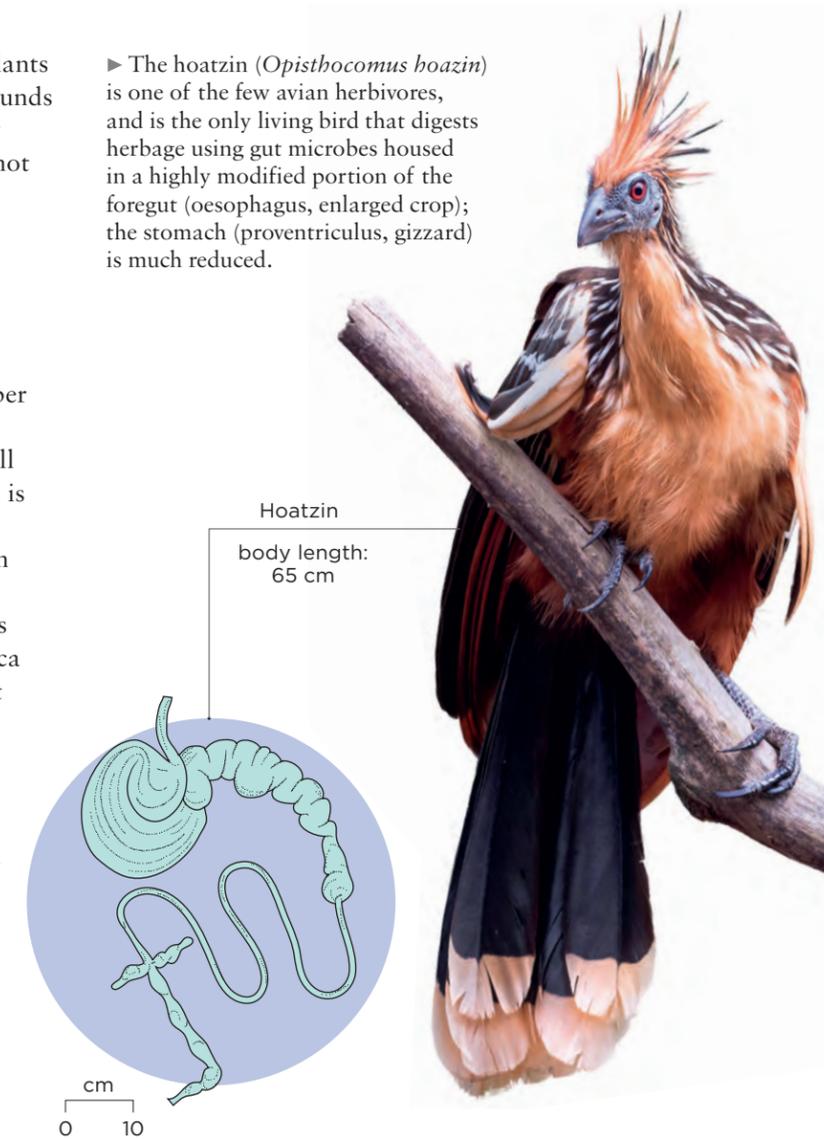
► The digestive system of birds, like that of mammals, is designed to efficiently process and break down food, extract and absorb the nutrients and water, and then excrete undigested material.

## Avian herbivores

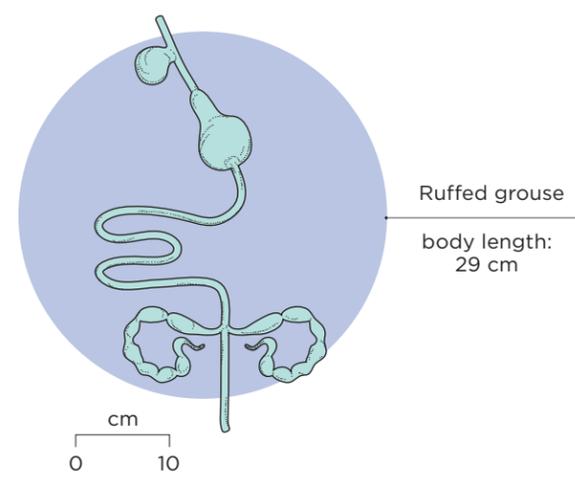
Cellulose is the primary structural material in plants and one of the most abundant biological compounds on Earth. But birds and other vertebrates do not produce cellulose-digesting enzymes and so cannot break cellulose down unaided. The evolution of enlarged portions of the foregut and/or hindgut to house symbiotic microbes (primarily bacteria and some protozoa) was crucial in the radiation of herbivorous mammals, because it provided the appropriate conditions for the microbial fermentation of cellulose. However, less than 3 per cent of living bird species have evolved a similar feature, perhaps because birds are relatively small and have high metabolic rates, and fermentation is a relatively slow process.

With the exception of the Amazonian hoatzin (*Opisthocomus hoazin*), the only living example of a foregut-fermenting bird, all avian herbivores harbour microbes in the hindgut (intestines, caeca or colon), where plant material is digested albeit much less effectively and efficiently than in mammalian herbivores. In general, the rarity of avian herbivores suggests that the nutritional challenges associated with eating leaves and other high-cellulose material are formidable and not often compatible with a bird's high-energy lifestyle involving a lot of flying.

► The hoatzin (*Opisthocomus hoazin*) is one of the few avian herbivores, and is the only living bird that digests herbage using gut microbes housed in a highly modified portion of the foregut (oesophagus, enlarged crop); the stomach (proventriculus, gizzard) is much reduced.



▼ The ruffed grouse (*Bonasa umbellus*) is an avian herbivore that uses gut microbes housed in its very enlarged paired caeca to digest plant material.



▲ It has been estimated that more than 25 per cent of the energy needs of ruffed grouse are provided by microbial fermentation in the hindgut.



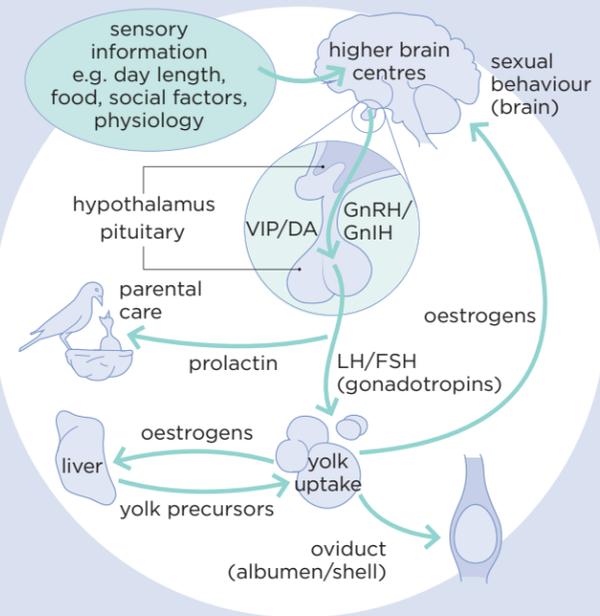
# The endocrine system

The endocrine system comprises a network of specialised endocrine glands (e.g. the pituitary and adrenal glands) and diffuse cells in the gut and fat that release potent organic chemical signals called hormones. Hormones are transported in the circulatory system to distant target cells in the animal's body, changing their function. While the nervous system mainly regulates short-term processes such as movement, the endocrine system regulates longer-term processes such as growth and development, energy balance and reproduction.

## Endocrine networks

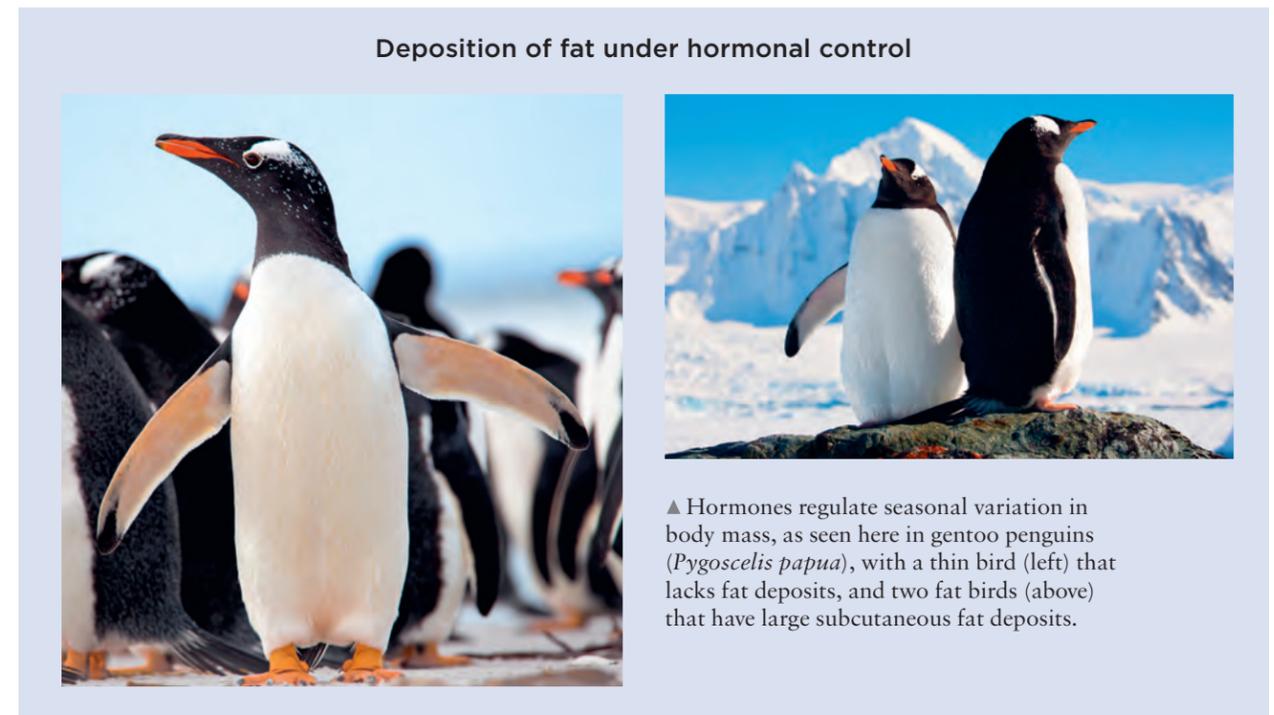
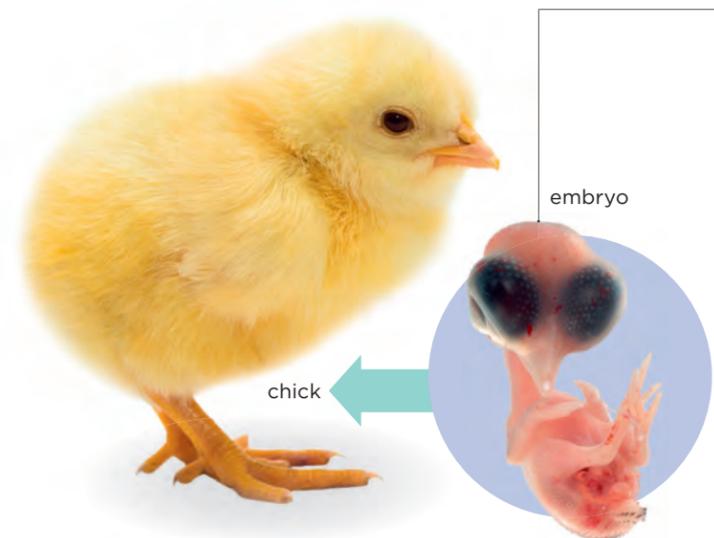
The brain and central nervous system are constantly receiving information from the body's sensory systems, including environmental information (e.g. light, temperature, social signals) and internal information from the physiological system (e.g. body temperature, blood nutrient levels). All of this information is integrated by the animal's neural circuitry and converges on the hypothalamus at the base of the brain. The hypothalamus transduces or changes neural signals into chemical, hormonal signals via neurosecretory cells. These cells receive neural input but synthesise and secrete 'releasing hormones' or 'release-inhibiting hormones' that target the pituitary gland – a small, lobed endocrine organ hanging just below the hypothalamus. This stimulates the pituitary

### Hypothalamic–pituitary–gonadal–liver axis regulating reproduction in a female bird



- VIP gonadotropin-inhibiting hormone
- DA dopamine
- GnRH gonadotropin-releasing hormone
- GnIH gonadotropin-inhibiting hormone
- LH luteinizing hormone
- FSH follicle-stimulating hormone

◀ Growth and early development from an embryo to a hatched chick are regulated by the hypothalamic–pituitary–thyroid axis, and by growth hormones and many other hormones.



Deposition of fat under hormonal control

▲ Hormones regulate seasonal variation in body mass, as seen here in gentoo penguins (*Pygoscelis papua*), with a thin bird (left) that lacks fat deposits, and two fat birds (above) that have large subcutaneous fat deposits.

to produce a wide range of specific hormones that are released into the circulatory system. Neurosecretory cells in the hypothalamus therefore sit at the top of a cascade, or neuroendocrine axis, that regulates the function of peripheral cells, tissues and organs via the pituitary. Peripheral endocrine glands (e.g. the thyroid, gonads) synthesise and secrete their own hormones, which can feed back to the hypothalamus and pituitary, or change the function of other non-endocrine target cells – for example, promoting muscle growth, altering metabolic rate, or initiating gonad development.

The three main neuroendocrine networks, or axes, in birds are each defined by a suite of key organ(s) that communicate with specific regions of the brain, and that regulate different aspects of physiology. The hypothalamic–pituitary–thyroid axis regulates growth and metabolism, the hypothalamic–pituitary–adrenal axis regulates metabolism and stress, and the hypothalamic–pituitary–gonadal axis regulates reproduction. The digestive system is also a major endocrine organ, releasing 'brain–gut' hormones that regulate the digestive process locally in the gut, but that also integrate with the hypothalamus to regulate feeding behaviour, food intake and energy expenditure.

## Stress and growth hormones

Corticosterone is the main glucocorticoid hormone in birds, and is released from the adrenal gland. It is often referred to as a stress hormone, because plasma levels of corticosterone increase rapidly within three to five minutes of a stress-related event, such as a predator attack or a researcher catching the bird (although many other hormones also change in response to stress). Increases in plasma corticosterone concentrations redirect behaviour and physiology towards immediate survival – for example, increasing locomotor activity, inhibiting reproduction and enhancing immune function. At baseline levels corticosterone plays a fundamental role as a metabolic regulator of energy homeostasis during 'predictable' life-history events such as growth, migration and reproduction.

Growth hormones, thyroid hormones and growth factors regulate growth and development in birds, although these pathways are much less well understood than in mammals. Similarly, many of the 'brain–gut' hormones (e.g. ghrelin, leptin, insulin) known to regulate hunger, rate of food intake and meal size in mammals have been identified in birds and likely play similar roles. However, little work has been conducted on these potential regulatory mechanisms in birds beyond work in poultry.

# The reproductive system

Like most vertebrates, birds do not maintain their reproductive system and gonads (the egg-producing ovary and sperm-producing testes) in a fully developed state year-round. Instead, the gonads are fully regressed during much of the year (the non-breeding phase), and grow and become functionally mature during the breeding phase. In birds breeding at mid- to high latitudes, this is triggered by environmental cues such as increasing day length and temperature. At the end of the breeding season, the gonads regress through a process called photorefractoriness. In males, the hypothalamic-pituitary-gonadal axis regulates testis function, and in females the hypothalamic-pituitary-gonadal-liver axis regulates ovary and oviduct function.

## Seasonal reproductive cycles

Most birds have seasonal breeding cycles, with courtship, mating, egg-laying and rearing of young restricted to a particular time of year (often spring and early summer) when environmental conditions (e.g. food, temperature) are optimal for successful reproduction. These breeding cycles reflect underlying cycles of reproductive physiology, with the gonads of both sexes maturing and regressing annually. However, the timing of gonadal development – and the environmental cues critical for seasonal gonadal development – differ between the sexes.

## Male reproductive system

Male birds have internal paired testes suspended from the upper wall of the body cavity just above the kidneys. Testis size varies seasonally, representing as little as 0.005 per cent of body mass in non-breeding males, but increasing 500- to 1,000-fold during breeding. In male European common starlings (*Sturnus vulgaris*), testis volume increases from less than 10 mm<sup>3</sup> in midwinter to 500 mm<sup>3</sup> during breeding in early April.

Each mature testis has thousands of coiled seminiferous tubules, containing germ cells (responsible for sperm production, or

▶ A male green-winged teal (*Anas carolinensis*) with his large corkscrew-shaped penis extended.

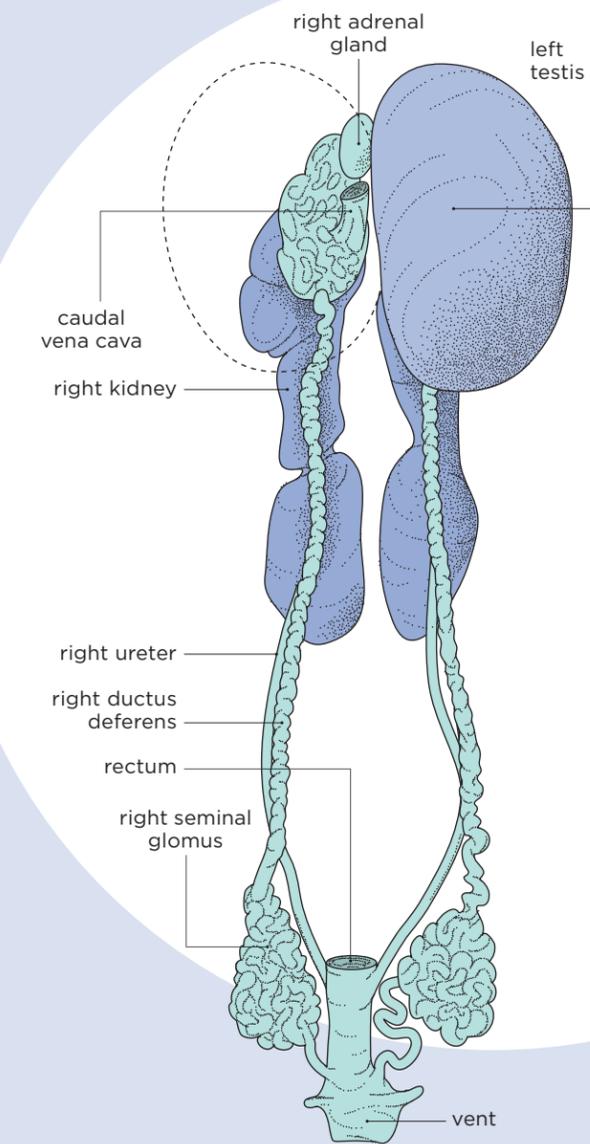
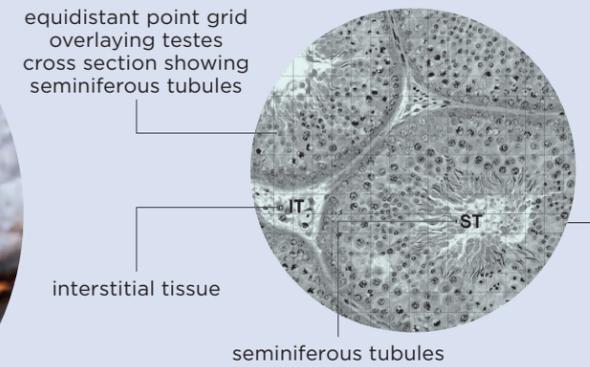


spermatogenesis) and Sertoli cells (which assist in sperm maturation). Sperm are generally short and relatively simple in non-passerines and longer and spiral-shaped in passerines, but our understanding of the adaptive significance of this diversity remains limited. Interstitial or Leydig cells lying between the tubules secrete steroid hormones (e.g. testosterone), which control sexual behaviour (e.g. song, copulation) and the development of some, but not all, secondary sexual characteristics (e.g. plumage, bill colour). The seminiferous tubules connect to form a long epididymis and deferent duct, which carries mature sperm in seminal fluid to the cloaca, the common external opening for sperm transfer and excretion of urine and faeces.

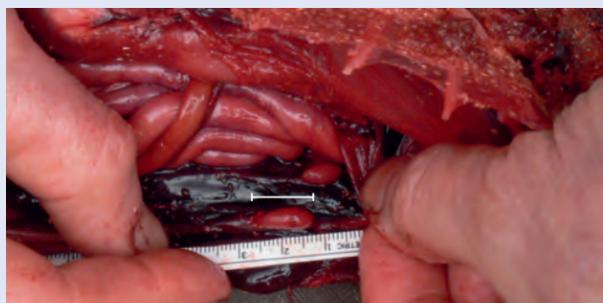
Male birds lack a true intromittent organ, or penis. During courtship the male's cloaca swells, forming a cloacal protuberance, and in most species copulation and sperm transfer involves simple cloacal contact, with the male everting his cloaca into the opening of the female's oviduct. Some ratites (e.g. ostriches), ducks and geese have a more developed and erectile phallus, or pseudopenis, which is used in mating, but this lacks the internal urethra for passage of urine that occurs in mammals.

▶ The male reproductive and urogenital system, with enlarged testes during breeding, and (inset) the ultrastructure of the testes, showing the seminiferous tubules (ST), where sperm formation occurs, and steroid-hormone-producing interstitial tissue (IT) comprising Leydig cells.

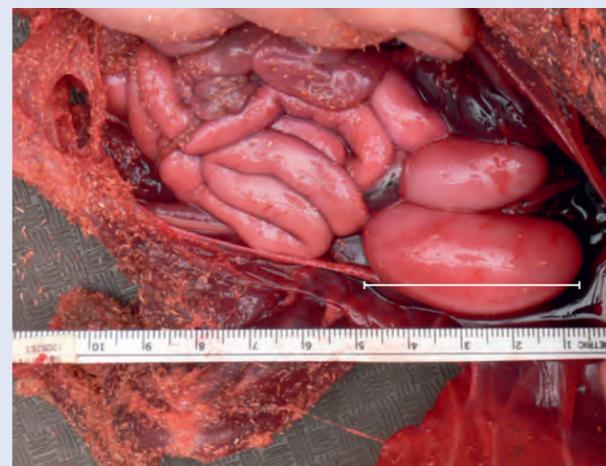
## Male reproductive system



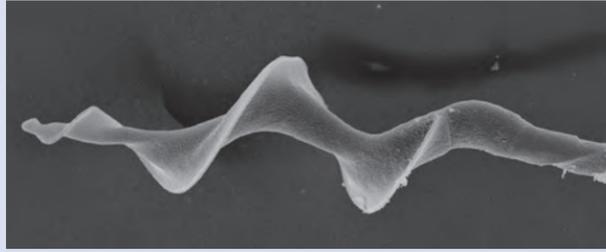
## Seasonal variation in testes size in male common murre or guillemot (*Uria aalge*)



▶▶ A male non-breeding common murre (*Uria aalge*) with fully regressed testes (left), and during the breeding season with fully developed testes (right). (Testis shown by white bar.)



### Variation in sperm morphology



▲ Helical sperm of the bluethroat (*Luscinia svecica*).



▲ Straighter sperm of the goldcrest (*Regulus regulus*).

### Physiological control of testis function

In male birds, light levels appear to be a sufficient environmental cue for full gonadal maturation – long artificial photoperiods alone stimulate testis maturation and spermatogenesis in males of most wild birds when they are held in captivity and isolated from natural cues. So, testis maturation occurs gradually over several weeks or months, from midwinter to just before breeding, in response to increasing day length – in other words, it is mainly photoperiod-dependent. In birds, detection of light controlling seasonality involves extra-retinal photoreceptors in the brain not the eyes (unlike mammals)

As the days get longer following the winter solstice (21 December in the northern hemisphere), neurosecretory cells in the male's hypothalamus produce gonadotropin-releasing hormone (GnRH),

with a concomitant decrease in gonadotropin-inhibiting hormone (GnIH). This stimulates endocrine cells in the pituitary gland to release two gonadotropin hormones, luteinising hormone (LH) and follicle-stimulating hormone (FSH), into the circulation. In turn, LH and FSH regulate steroid hormone production and spermatogenesis by the testes.

### Female reproductive system

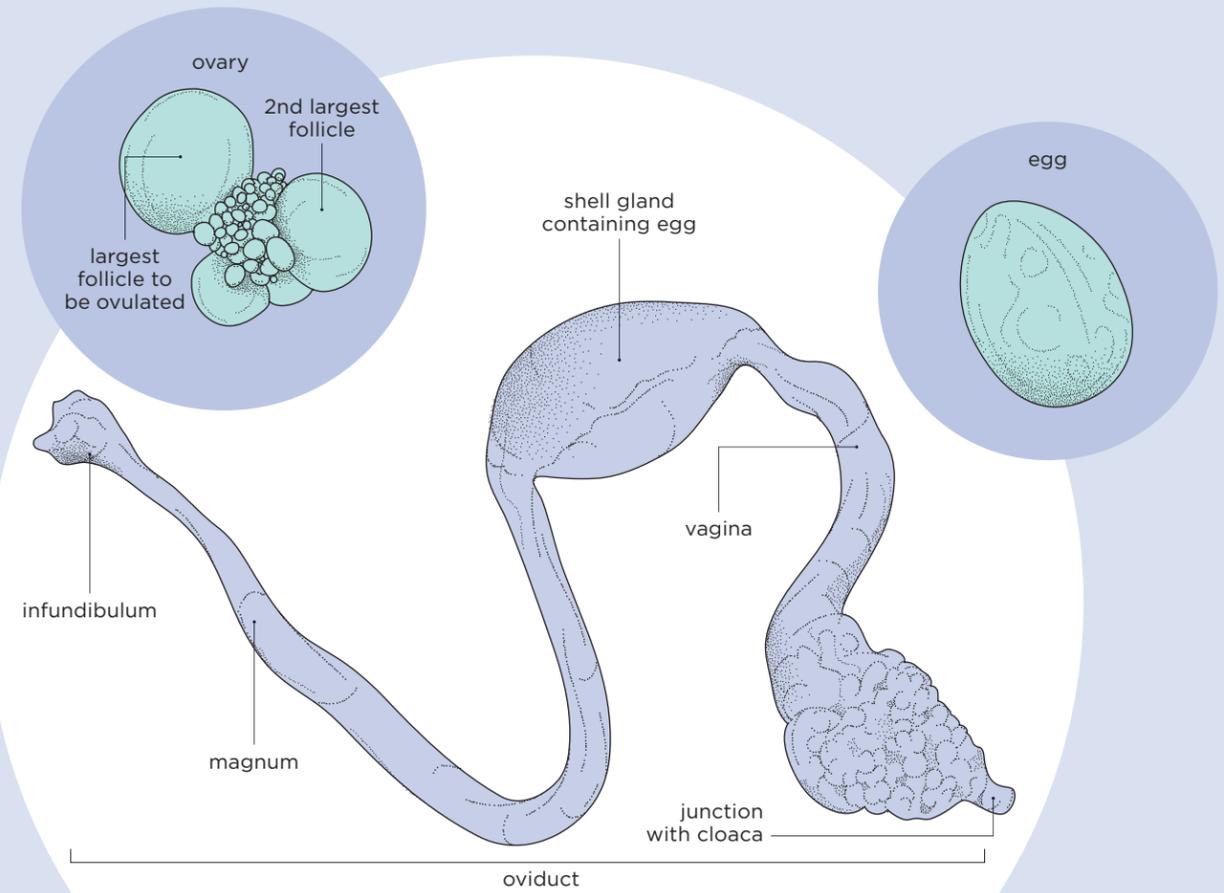
In many ways, the female reproductive system in birds is much more complex than that of males. Not only do the ovary and oviduct have to function together to form a complete egg, with yolk, albumen and shell, but the female's liver synthesises yolk lipids and proteins (hence, females have a true hypothalamic–pituitary–gonad–liver axis).

Avian embryos have two bilateral ovaries attached to the internal body wall at the top of the kidneys. Most adult female birds retain only a single functional ovary, with the loss of the second one having occurred far back in avian evolution – the egg-laying dinosaurs (maniraptorans), which lived more than 125 million years ago, had only one ovary. For unknown reasons, small raptors (Falconiformes) and the kiwi retain two functional ovaries. An ovary consists of many oocytes, cells that will give rise to ova or eggs, embedded in a matrix of connective tissue. Production of oocytes (oogenesis)

◀ Zebra finches are a valuable model species since they breed readily in captivity; females of many wild species do not become reproductively mature, or lay eggs, when held in standard, small cages typically used by researchers.



### Female reproductive system



▲ The female reproductive system during breeding, showing the ovary, with a hierarchy of developing yolk follicles, and the oviduct, containing an ovulated follicle undergoing albumen and shell formation in the uterus.

is completed at hatching, with the ovary containing around 450,000 primary oocytes, although in most species as few as one to 20 of these will mature and be laid as eggs.

At the start of each breeding attempt, a small number of follicles are 'recruited', destined to become yolks. These start to develop into mature ova and contain the germinal disc region of cells that ultimately forms the embryo. Follicle development involves a variable phase of rapid yolk development, lasting 3–25 days depending on the species, in which lipid- and protein-rich yolk precursors are taken

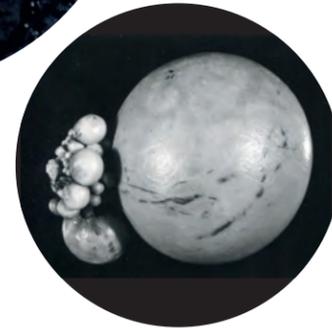
up from the circulatory system to form the yolk. Specialised cells (called granulosa and thecal cells) proliferate and surround the follicle during oocyte maturation, synthesising and secreting hormones (e.g. progesterone, oestrogens, growth factors) required for yolk development, oviduct function and control of female sexual behaviour. Yolk precursors are produced by the liver in response to stimulation from ovarian oestrogens; this represents a major shift in the lipid metabolism of egg-laying females.

Mature follicles are released into the oviduct (equivalent to the mammalian fallopian tube) typically every 24 hours in smaller birds, with the number of ovulations matching the bird's clutch size. Oviduct size varies seasonally and through the laying cycle. For example, in the Australian zebra finch (*Taeniopygia guttata*) the mass of the oviduct increases more than tenfold over five days at the onset of egg production. At ovulation, the yolk follicle is captured by the infundibulum, the first part of the oviduct, and fertilisation occurs here within 30 minutes of ovulation, before albumen deposition prevents sperm reaching the egg. Females can store sperm – often from multiple males – in special tubules in the oviduct. Sperm can remain viable for days to weeks and are released at the time of ovulation for fertilisation, so females do not need to mate at a specific time around ovulation. Females might even be able to control the sperm they use, effectively controlling paternity of their offspring!

Each yolk follicle then takes about 24 hours to move down the oviduct, where albumen, shell membranes, the shell and a cuticle are added, completing egg formation. Birds' eggs can be highly



▲ Females laying multi-egg clutches have a hierarchy of developing yolk ovarian follicles, these ovulating at 24-hour intervals, starting with F1, then F2, etc.

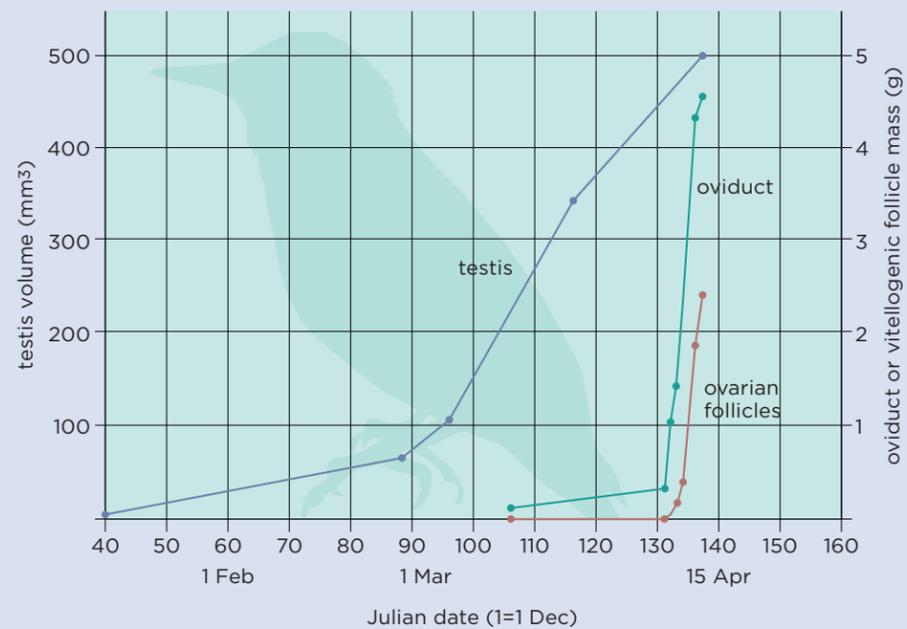


▶ Albatrosses lay a single-egg clutch and develop a single large yolk follicle in the ovary.



▲ Shorebirds, like this red-wattled lapwing (*Vanellus indicus*), develop a limited number of yolk follicles and lay a fixed clutch size of three or four eggs.

Timing of gonadal development in spring contrasting male and female common starlings



◀ Sex differences in the timing of gonadal maturation in spring in male and female common starlings (*Sturnus vulgaris*), comparing testis development with ovary and ovarian development.

and variably coloured by red/brown (porphyrins) and blue/green (biliverdin) pigments, but the sometimes intricate mechanisms that produce these patterns are still not well known. Oviposition, or egg-laying, occurs most commonly once a day (although birds can skip days), and at a similar time of day, with the fully formed egg being expelled by muscle contraction via the female's cloaca.

### Physiological control of ovary function

It has been known for more than 60 years that, in contrast to males, females of most free-living avian species held in captivity will not undergo complete ovarian development: yolk formation and egg production is very unusual in captivity (except when females are kept in large aviaries at low density). This suggests that the environmental cues regulating female reproduction may differ from those influencing males, and recent studies are confirming this. Increasing day length in spring clearly stimulates the female's hypothalamus, leading to GnRH release, and this leads to LH and FSH release from

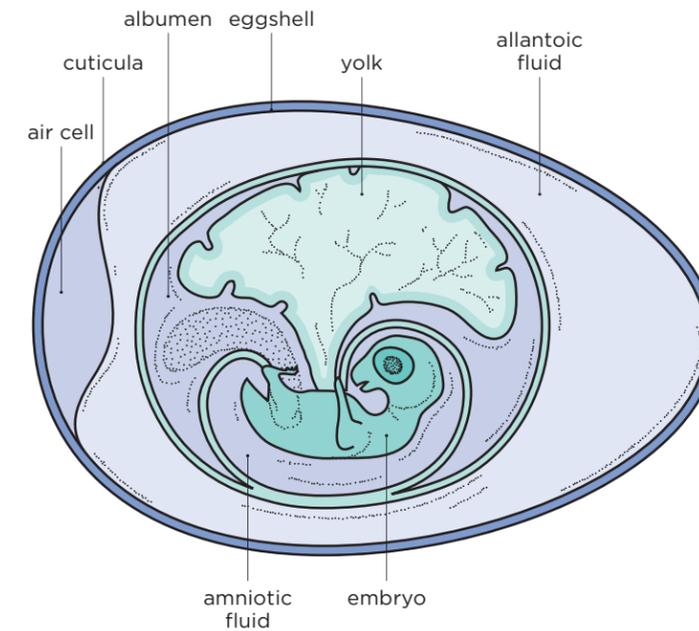
the female's pituitary. However, the ovary does not respond immediately to higher circulating levels of LH (unlike the testis), and there appears to be some level of 'peripheral' control in females at the level of the ovary and/or liver. Consequently, ovarian development and yolk formation do not occur gradually over weeks or months (as with testes development), but over just five to 20 days immediately before the first egg is laid. Final maturation of the female reproductive system before egg-laying is thought to be influenced by additional environmental cues (called supplementary factors), including temperature, food availability, and social information such as the presence of a male partner and a nest.



## THE STRUCTURE OF A BIRD'S EGG

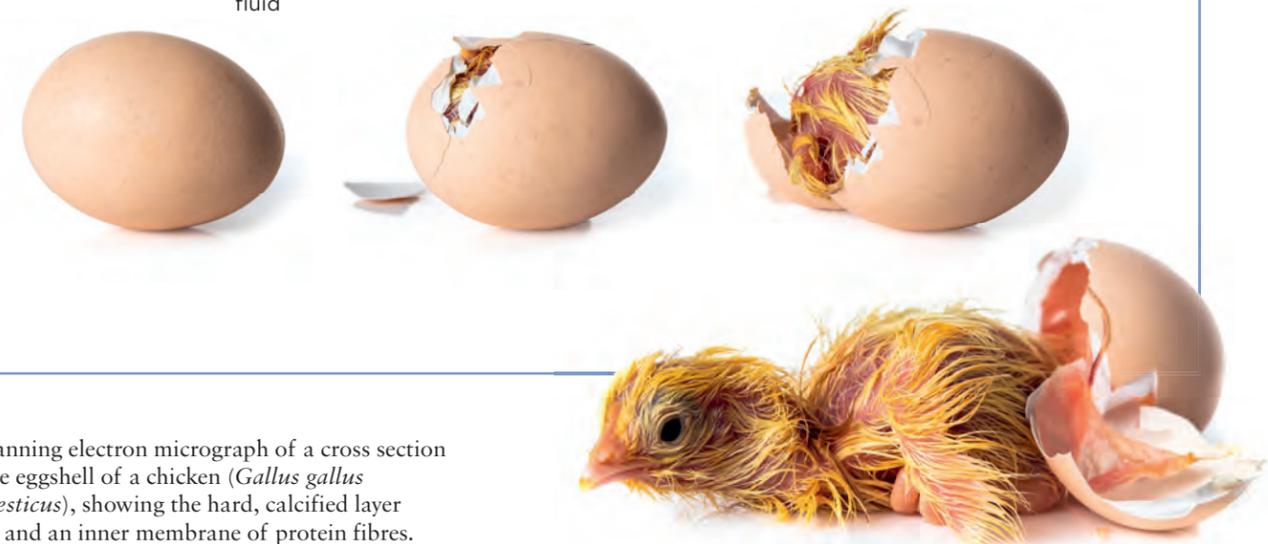
Eggs are sealed capsules that contain all the nutrients and energy used during embryonic development. The yolk supplies protein and energy-rich lipids for growth, as well as antioxidants for protection against oxidative stress, and the albumen provides additional protein and water, as well as having antibacterial properties. The shell provides physical protection, and is important in regulating

water and gas exchange via large numbers of intricate channels or pores that connect the embryo with the external environment. Eggshell is an amazing substance: strong enough to avoid cracking during incubation and protecting the developing embryo, but weak enough to allow the chick to break out of the egg at hatching.



◀ A cross section through a bird's egg, showing a well-developed embryo.

▼ To hatch, chicks must crack the eggshell; they often do this using a specialised 'egg tooth' on the beak.



◀ Scanning electron micrograph of a cross section of the eggshell of a chicken (*Gallus gallus domesticus*), showing the hard, calcified layer (left) and an inner membrane of protein fibres.