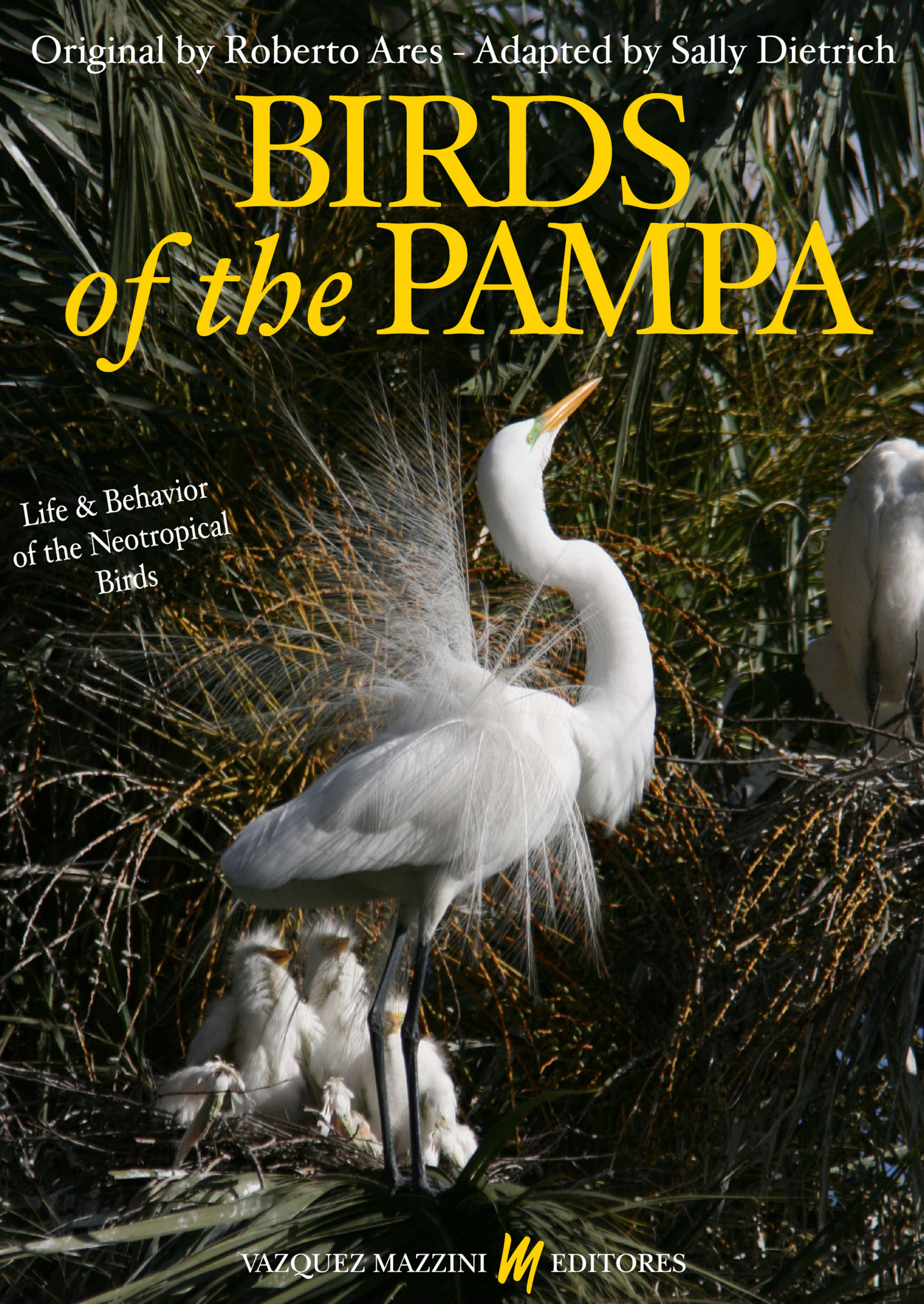
Original by Roberto Ares - Adapted by Sally Dietrich

BIRDS *of the* PAMPA

Life & Behavior of the Neotropical Birds



VAZQUEZ MAZZINI EDITORES

Birds of the Pampa

Life and behavior of the neotropical birds

Original Spanish version by Roberto Ares
Adaptation and translation by Sally Dietrich and Cora Rimoldi

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Contents

It is dawn in the natural reserve of Punta Rasa. As I set up the camera in the half-light I can hear the sleepy cries of the early arrivals, resting on the mud-flats since the day before. As the light grows, the first flocks of Black Skimmers appear, flying in V or W formation from the South. They have been flying all night, passing at times through clouds and rain to reach their destination. From about 1500 feet, they drop almost vertically as they reach the island to join the group. Soon there are thousands of birds, some of which rest on the beach while others attempt to feed, flying low over the water with their long lower mandibles skimming the surface in search of fish.

Introduction

Where have they come from? How have they found their way? What enables them to fly? How have they evolved, and what is their relation to other creatures in the chain of life? These questions have fascinated human beings since the beginning. In this book I have tried to sum up what we know about birds, and sketch the answers that studies of paleontology, anatomy, molecular studies, and field observations can offer.

In the first chapter I deal with the evolution of birds, a theme which persists throughout the book. Evolution is, in fact, the dominant principle around which the understanding of biology must be organized, if it is to make sense at all. Speciation and migration are also treated in this chapter.

In the second chapter I describe the skeleton of the bird, especially the adaptations which enable it to fly.

Plumage is the subject of the third chapter. The feather is a structure unique in nature. Any modern animal which has feathers is a bird, and any animal which does not, is not. Exactly when and how the birds became differentiated from dinosaurs is more ambiguous -it seems that some dinosaur ancestors of birds may have had feathers. The evolution and function of the feather is a fascinating, if somewhat speculative, subject.

Muscles and flight are the theme of Chapter Four. The highly-developed pectoral muscles, anchored on the keel, enable the bird to fly. The aerodynamics of bird-flight is entirely unlike those of planes. he wing of the bird is flexible and mobile, not rigid and stable like that of a plane. The technique of bird-flight is easier to explain than the theory. Here we present a special section of photographs illustrating take-off, flight, and landing.

Chapter Five deals with song and feeding. Respiration (birds have the most highly-developed system of respiration of any animal) and digestion are also examined in this chapter.

The nervous system, sensory systems, intelligence, and circulation are described in Chapter Six. Though their brains are small, birds are remarkably intelligent. The circulatory system is very similar to that of mammals.

Chapter Seven is devoted to reproduction. The reproductive system is relatively simple, but the behavior related to courting, mating, and raising the young is extremely complex and fascinating. An extensive section of photographs on these subjects is included here.

Social behavior is the subject of the eighth chapter. Instinct and learning play a part in the social behavior of birds, as does the function of the endocrine system. Hygiene, pleasure, affection, and intelligence are all treated under this heading. The author feels free to offer his own interpretations concerning them, based on field observations. A section of photographs illustrates some of these concepts.

I began this research in the year 2004, but only in 2006 did I become convinced that I could offer a new perspective on the theme. I have attempted an innovative use of interpretive tools to document the behavior of birds. An extensive library of books and publications dealing with nature, which I have been accumulating for over thirty years, has provided a base from which to work. But I have also ventured to offer personal opinions and interpretations based on my own observations and photographs.

I have used special photographic techniques to illustrate movement, frequently recurring to sequential photography at the rate of three per second. In some cases video might have been useful, but many of these photographs were taken at a great distance, and digital photography offers better resolution.

Three hundred days spent photographing the behavior of birds produced more than 300,000 digital photographs, all taken of birds in the wild. None was photographed in captivity. The original format was at an average of 1.5 MByte per photo, and of the 200,000 taken, I selected about one out of two hundred.

For those who are interested in nature photography, the cameras I used were Canon 350D and 400D, which produced pictures at a resolution of 3500 x 2300 pixels. This is about a double page of this book with a resolution of 300 pixels per inch.

Finding the right lens required various experiments. I finally settled on a fixed 300mm telephoto lens with a multiple of 1,4x, which provided a combination light enough to carry and handle in the field.

When field conditions permitted, I used a monopod for greater stability without affecting mobility as a tripod would have.

Nomenclature used in this book

In this book I have used the scientific names first, followed by the common names in parenthesis. The nearly 300,000 million birds which inhabit the earth have been classified into 30 orders, 193 species, 2,099 genera, and about 9,700 species. This book contains a broad selection of photographs in which 21 orders, 50 families, and almost 150 species are represented.

I have used the AOU (American Ornithologist's Union) system to denominate the orders, families, genera, and species of birds. AOU is the largest and oldest organization dedicated to the study of birds in the New World. They keep the scientific classification and nomenclature of birds up to date. Classification is important because it is thought to indicate the evolution of orders and species through time. The names in Spanish and English are also those provided by the AOU.

Translator's note

This book began as a simple translation of *Aves, Vida y Conducta* by Roberto Ares. However, since the publication of the original book, the author had spent another year photographing birds. He had many new photographs which he wanted to add, which necessitated condensing the text. Condensing the text entailed considerable re-writing to insure continuity. This task fell to the translator. A certain amount of material concerning general biology has been deleted, but everything related to birds of Argentina has been included, and in some cases slightly expanded.

Sally Dietrich. (Translator)

1. Origen and distribution

1. What Is The Origen Of Birds?

1.1. Anatomy and classification

Birds are a class (Aves) within the animal kingdom, as are mammals and reptiles. They are chordates, vertebrates, quadrupeds, and oviparous. That is, they have a spinal cord enclosed within the skeleton, the cranium and vertebral column are developed, they have four limbs and they reproduce by means of eggs which protect the fetus from the surrounding environment.

They are bipedal and their upper limbs consist of wings. They stand on the tips of their toes, that is, they are digitigrades (humans are plantigrades.) The skeleton is strong, with a compact thorax. Modern birds have lost their teeth and have a horny bill as a modification of the jaw. They are homoeothermic, that is, they maintain a constant body temperature, and endothermic, producing heat through metabolism. Their bodies are covered with feathers, a feature unique to birds.

In the first part of this chapter we establish the place of birds in the context of living beings, and show how they evolved to become the birds which we see and study today.

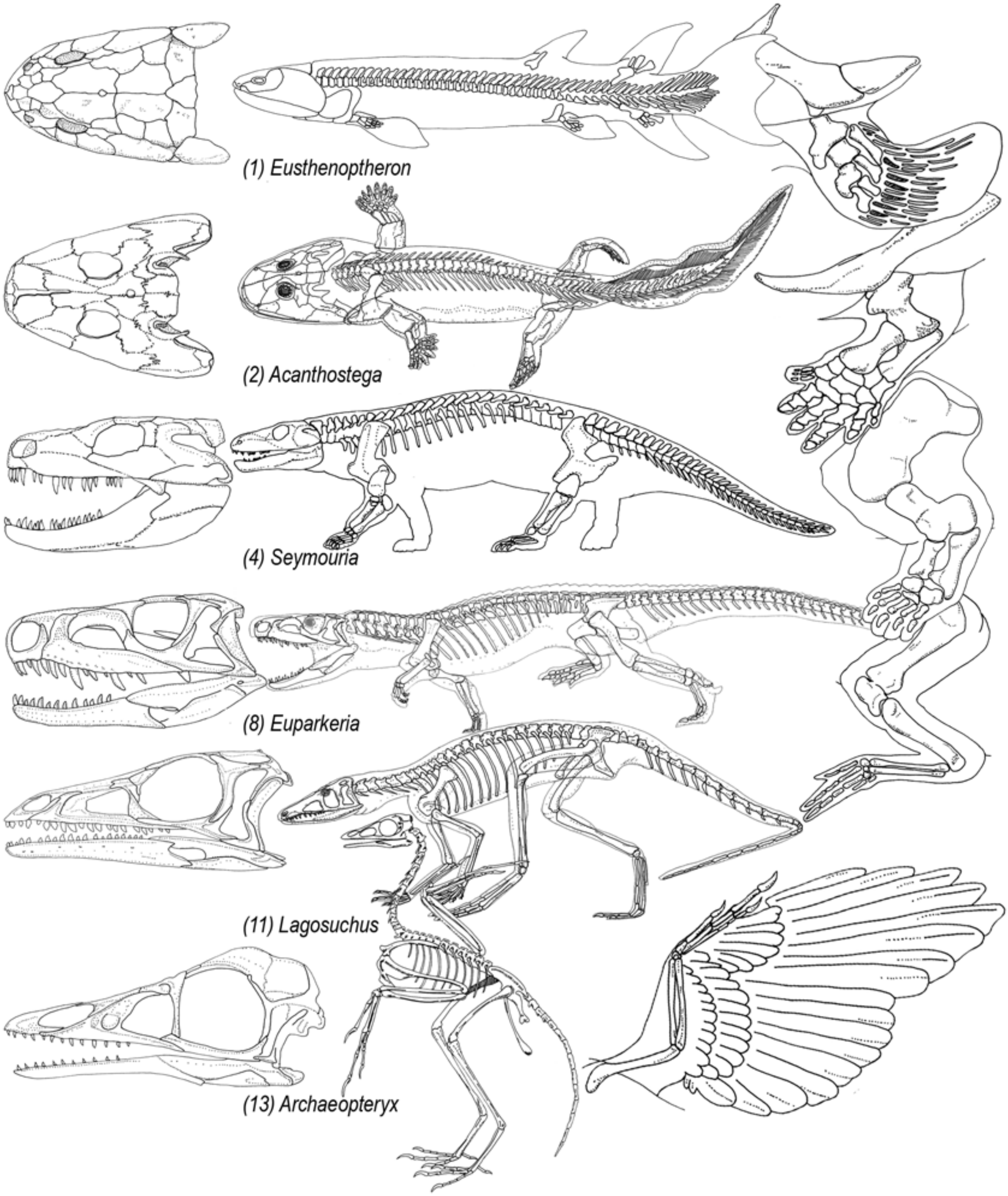
1.2. Reptiles, dinosaurs, and birds

Reptiles and Birds. Similarities and Differences

Birds evolved from reptiles through a line of bipedal dinosaurs which had feathers.

The legs and feet of birds have horny scales and claws similar to those of reptiles. Some groups of reptiles, like all birds, have air sacs. Both birds and reptiles lay eggs. When the young are ready to hatch, they break the shell with an "egg tooth" which they later lose. The eyes have a similar comb or pectin structure and a nictitating membrane. Furthermore there are similarities in the red blood cells and the hemoglobin of the blood.

Among many other differences, reptiles continue to grow throughout their lives, although they grow more slowly as they age. Birds, on the other hand, grow very rapidly while they are young. The bones



The evolution of birds. Tetrapods (four-footed animals) evolved from Devonian fish about 400 million years ago. An early tetrapod, Eusthenopteron (375 million years ago) probably couldn't leave the water but it could survive in very shallow water. Acanthostega, of the same period, had better-developed legs and could probably crawl on land. The more modern Eryops, (295 million years ago) was a fully-developed amphibian, although unlike modern amphibians in many ways. Amniotic reptiles appeared during the Carboniferous era. They could lay their eggs out of water. Seymouria (330 million years ago) is considered to be one of the first reptiles. Reptiles diverged into two lines, the mammal-like reptiles and the archosaurs. The mammal-like reptiles such as Dimetrodon were dominant during the Permian epoch and continued into the Triassic, declined during the age of dinosaurs, and expanded again at the end of the Cretaceous. Toxodon, extinct for

10,000 years is an example. Euparkeria (240 million years ago) is an early representative of the Archosaurian reptiles which came to dominate the Triassic. Chanaresuchus (240 million years ago) is an example of the line which gave rise to crocodiles. Another group evolved into Pterosaurs such as Pterodaustro (125 million years ago.) Lagosuchus was a very agile reptile which formed a link with dinosaurs such as Carnotaurus (90 million years ago.) Certain bipedal dinosaurs developed feathers and the ability to fly, such as Confuciosornis (120 million years ago) and expanded to give rise to birds, both such extinct species as Andalgalornis (5 million years ago) and modern birds.

Pterodaustro guinazui, found in Argentina, is an aberrant pterosaur. The teeth, which form a filter, suggest a diet similar to the flamingo's.

of birds have cartilaginous tips (epiphysis). In the final stage of growth, the cartilage is transformed into bone.

Pterosaurs

These belong to the Class of Reptiles, order Pterosaurs. Although they could fly, they were not the ancestors of birds. Nor were they dinosaurs, although they lived in the same epoch (220-65 million years ago.) They had no feathers and the wings were formed of a thin membrane of skin which joined the single elongated finger.

Most of the pterosaurs have been found in marine sediments, which suggests that they lived near the sea. They had a surprising variety of forms, although only about a hundred fossil species are known.

Brazil and Argentina have been a source of recent pterosaur discoveries. A remarkable example is the *Pterodaustro guinazui* (125 million years old) found in Argentina. It had extraordinarily long mandibles, with 500 long fine spike-like teeth, forming a sort of comb or strainer which it used as a filter in shallow water. It is a unique case in the evolution of teeth. The teeth of the upper jaw were small and were used to comb and clean the lower ones. Its diet must have consisted of tiny aquatic animals like shrimp. Flamingos, which have a similar diet, also have a bill equipped with fine spikes.

Dinosaurs and birds

Early reptiles, like amphibians, had legs which projected sidewards, a position effective for swimming, but ill-adapted for supporting weight on land. Improvements in the pelvic girdle led to the group of reptiles which evolved into dinosaurs, having legs placed vertically under the body, which provided a far more efficient means of locomotion. Later, the front legs were relieved of locomotive function and were free to adapt to other uses, such as manipulating food or climbing. It was an important advance in the evolution of life which permitted a greater capacity for intelligence in the animal.

There is still a certain amount of controversy over the evolution of birds from reptiles. One hypothesis suggests a direct line from the archosaurians (archaic reptiles such as thecodonts) and the other indicates evolution from the theropod dinosaurs. The latter theory is better supported by evidence.

The oldest known ancestor of the birds is *Archaeopteryx lithographica* (150 million years ago.) Its name means "Ancient Wing" and it was found in layers of lithographic slate in Germany. The hardness and fineness of the limestone allowed microscopic details of the feathers to be preserved. The feathers of *Archaeopteryx* are the same as those of modern birds. It was somewhat larger than a large dove and its appearance was like that of a bird today. Nevertheless, it had characteristics which were intermediate between those of a dinosaur and those of a modern bird.

The cranium of *Archaeopteryx* had jaws with teeth, whereas modern birds have a bill. Both have a long neck formed by the cervical vertebrae. *Archaeopteryx* had fine ribs, while modern birds have flattened ribs with extensions which join them together for greater rigidity. *Archaeopteryx* had no keel on the sternum, so its flight muscles must have been rudimentary, and it is probable that it couldn't fly well, although it could glide for considerable distances.

Archaeopteryx had three fingers equipped with claws, which permitted it to cling to branches. Modern birds have reduced fingers and have lost the claws in the wings. Only *Opisthocomus hoatzin*, a bird of northern South America, has vestigial claws on the wings which it uses to climb among the branches. *Archaeopteryx* did not have hollow bones, which makes it doubtful whether it had air sacs in its respiratory system.

Two theories have been advanced to explain the evolution of flight in birds. The first maintains that a group of bipedal dinosaurs developed the habit of flapping their front limbs while running to catch insects. The second theory claims that the ancestral bird was arboreal and used the front limbs to jump from branch to branch. However, this may be a false dichotomy, since their behavior may have included both behaviors.

Archaeopteryx (150 million years ago) is considered the first bird in the evolutionary chain. Archaeopteryx is the oldest known bird fossil but very far from being "first" in the evolutionary chain, since it is highly evolved as a bird.

Evolution in the Cretaceous period (146-65 million years ago)

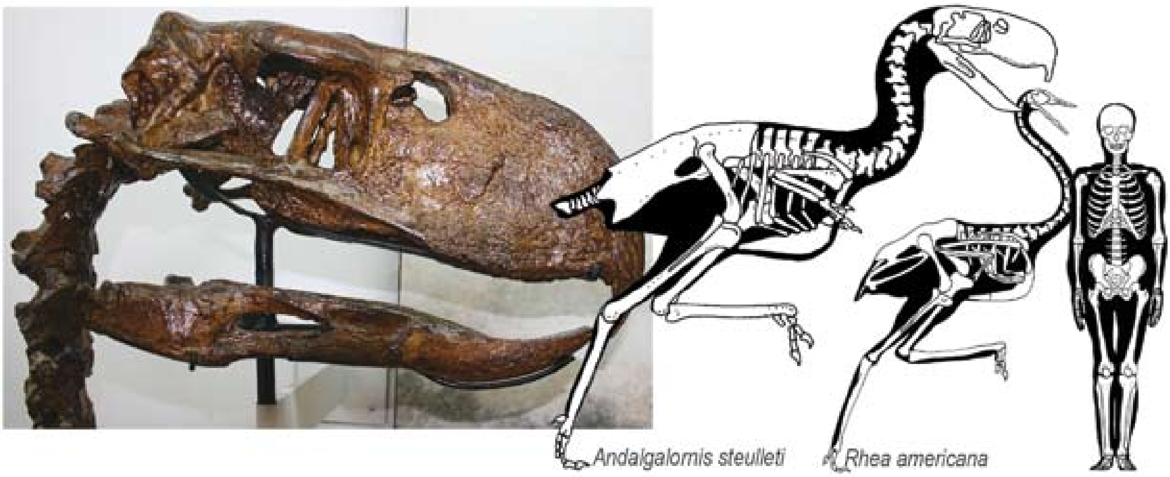
Almost all of the modifications of the modern bird evolved during the Cretaceous period (about 115 million years ago). The most relevant ones include: a short tail of fused vertebrae presaging the pygostyle; a bill without teeth; skeletal fusion; sternum ending in a keel and the appearance of the alula on the wing, making possible greater maneuverability in flight.

Many species of birds were extinguished with the dinosaurs about 65 million years ago, in what is generally believed to have been a planetary catastrophe caused by the impact of a huge meteorite off the coast of Yucatan.

One of the surviving lineages is that of the transitional coast birds. It is the only one or few of which we have definite fossils. But by means of the "molecular clock" we can establish that various lineages were able to survive the 65 million-year barrier. The differences between the orders of modern birds are too great to have evolved from one single lineage in only 65 million years. For example, we have molecular evidence that Struthioniformes began their expansion from South America into the rest of Gondwana about 100 million years ago. DNA studies push the age of modern birds back to 125 years ago. According to one hypothesis, about 20 orders of birds survived the 65-million-year barrier.

Evolution in the Tertiary period

Whether it was one or several lineages which escaped extinction, the radiation of different orders of birds occurred during the Paleocene and Eocene (between 65 and 35 million years ago.) The 30 orders of modern birds emerged during this period.



Andalgalornis steulleti was a non-flying bird and a predator. It is extinct today.

More than half the species of birds (5,700 out of a total of 9,700) belong to the order of Passeriformes. They are characterized by prehensile feet adapted to grasping branches, and by the structure of the uropigial gland. This order is thought to have emerged about 65 million years ago and to have spread to the rest of the planet. They are subdivided into Oscines (with about 4,300 species) and Suboscines, these latter having a less developed syrinx and therefore a simpler song. The Suboscines have diversified very successfully in the neotropical region which harbors about 1,100 of the 1,150 existing species.

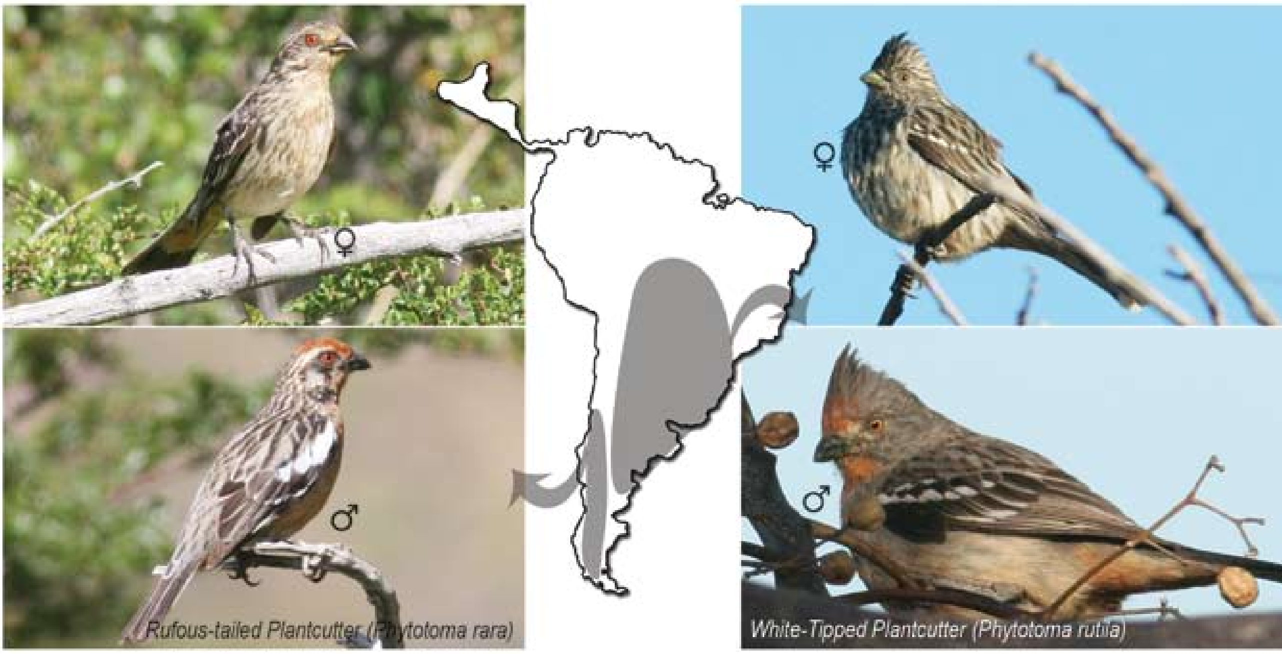
In the northern hemisphere, the order of the Diatrymiformes occupied the niche of the carnivorous mammals (where these were absent.) They were carrion-eaters or large hunters. In the southern hemisphere the equivalent groups were the Fororracoides (presently extinct), and the Ratites (which still exist, but which are no longer hunters.) Since the two continental hemispheres were separated, this was a case of convergent evolution of different groups.

The Fororracoides were large birds (from 50 cm. to two meters high and weighing from 30 to 400 kilograms.) They had little or no capacity of flight. In Argentina about twenty species have been described, many on the base of very fragmentary material. Their disappearance coincided with the arrival of carnivorous mammals from the northern hemisphere.

The Fororracoides were carefully studied in the Museum of La Plata. The museum periodical *Museo* gives an interesting account (June 1998.) It describes two types of cranial structure. The first type is high and narrow, adapted to resist vertical tension and provide the powerful bite typical of the carnivorous hunters. The bones of the feet are well adapted to running and turning swiftly, the behavior of an active carnivore. The smaller ones may have been capable of short flights. The other type of cranium is broader than it is high and biomechanical measurements indicate that its resistance was equal in all directions. This is characteristic of carrion-eaters, which break their prey with powerful lateral blows. They have strong feet not adapted to running. The almost non-existent wings indicate that they couldn't fly.

Our knowledge of these birds is limited because the light and fragile bones do not fossilize easily.

The paleontological evidence registers few species of birds and many rely on fragments which leave much to guess-work. Nevertheless, the class of Aves radiated into every habitat on earth and adapted to extremes of climate or avoided them by means of flight.



Many species diverge due to the differences in the habitat they live in. This is the case of two species of the same genus Phytotoma.

2. Distribution and migration of birds

2.1. Environment and species

Biogeography and speciation of life

To explain the distribution of species, A. Wallace in the 19th Century divided the world into six biogeographical regions roughly corresponding to the continents. A quick glance at this distribution evokes the concept of continental drift, though the distribution is climatic rather than physical. Separation and continental isolation has greatly influenced in the composition of the avifauna of these regions. This is the case of the Neotropical Region where one third of all bird species are endemic due to the fact that South America remained a huge island till the emergence of the Central American land bridge. On the other hand, the Neartic Region holds no avian endemic family but it is distinctive for its blend of Paleartic and New World Groups.

But not only continental isolation or connection has a direct effect upon lineage divergence. Local factors also lead to speciation.

Speciation is the process through which one species divides into two species which thereafter evolve in separate lineages. Speciation begins with some sort of reproductive isolation, which may consist of an inherited characteristic or behavior which prevents mating between populations, causing them to diverge genetically.

Different types of isolation include the following:

- Spatial isolation produced by geographical barriers. A variant is ecological isolation which occurs within different environments in the same space. This is the case with birds which have a very close relationship with a particular kind of tree.
- Temporal isolation occurs when two species have differing reproductive periods.
- Behavioral isolation occurs when differences of behavior—rituals, song, etc.—prevent the formation of couples.
- Mechanical isolation is produced when the genital structures are incompatible for the crossing of species (as in ducks.)
- Gametic isolation is the result of chemical incompatibility of the spermatozoid and the ovum which impedes fertilization. This also includes early

mortality or infertility of the hybrid, which leaves no genetic inheritance.

The theory of Pleistocene refuges asserts that the glaciations of the last 1,8 million years affected the distribution of the biota, which were isolated in regions. Studies of fossil pollen show that during the glacial periods the tropical jungle of the Amazons was reduced to patches surrounded by savannah or prairie-like terrain similar to that of the present pampas. Each jungle "refuge" offered its animals the opportunity to evolve and differentiate. At the end of the glacial period the jungle spread once again and became continuous, but the species had already separated. This process has also occurred in the North American deserts, as demonstrated by the birds (especially sparrows.)

There exists a hypothesis that the number of species is related to the rainfall. More rain means more species. This hypothesis is a variation of what is known as the Ecology of Languages. On studying the number of languages in regions of the world, it has been observed that the greatest density is found in West Africa south of the Sahara, with 700 languages. But the density increases as the equator is approached, that is, as the rainfall increases. An abundance of rain and food keeps the inhabitants in small areas and they have no need to migrate or trade with neighboring regions. In areas where there are periods of rain alternating with drought, it is necessary to maintain contact with other groups of people. Abundance is also an isolating mechanism in the speciation of life.

The study of the ecology of jungles and their edges has enabled us to understand that the edge of the woods is a very important source of speciation. Although the jungles have a higher density of species per unit of surface, the transitional zones between jungle and savannah may be the key to the appearance of new species. Evidence from the Andean jungles of Bolivia, Ecuador, and Peru shows the overwhelming influence of mountain-building and climate in the production and maintenance of species.

Within the Neotropical Region the pampas cover a vast area which includes southern Brasil, Uruguay and the humid pampa of Argentina. The pampa occupies the plains in the east of Argentina, taking up most of the Province of Buenos Aires up to Chaco. It includes marshes, grassland, gallery forest, xeric

Within the Neotropical Region the pampas cover a vast area which includes southern Brasil, Uruguay and the humid pampa of Argentina.

woodland, lagoons and the coast of the Río de la Plata. The diversity of these environments sustains a varied avifauna rich in both resident species and migratory birds. The birds of the humid pampa form the subject of this book.

2.2. The movements of birds

Why do birds migrate?

Some dinosaurs -Hadrosaurs of "Duck-Billed Dinosaurs"- admittedly not in the ancestral lineage of birds - are thought to have migrated over land to their nesting gounds, and sea turtles also migrate to the beaches where they lay their eggs. This suggests that migration evolved before birds. However, the great migrations of birds reach another level of complexity. Whenever migration did begin, it became essential with the change of climate and the advance of the ice caps in the Quaternary Period (beginning 1.8 million years ago) causing great mortality and favoring the migratory impulse.

It was not until the 16th Century, however, that it was understood that the birds which disappeared from France during the winter were the same that appeared in North Africa.

What is migration?

The most simple movement is not periodical and therefore is not considered migration. It may consist of the dispersal of the juveniles as they abandon the nesting area, sudden abandoning of an area because of unfavorable conditions such as cold, rain, or drought, or wandering due to the absence of food (seasonal or cyclical.)

True migratory movements are much more complex. Though other animals also migrate (insects, fish, whales, and bats,) the migrations of birds are spectacular. About 4000 of the 9800 species of birds migrate.

True migrations have the following characteristics:

- They cover considerable distances (hundreds or thousands of kilometers) and last for months.
- They include all or most of the population, not only isolated individuals.
- They are voluntary, not forced by violent atmospheric disturbances.
- They are periodic, repeated every year, and consist of a round trip.
- They permit nesting at one end, and winter resting at the other.

Migration offers advantages:

- It permits access to sporadic food resources for short periods.
- It impedes the development of natural predators, for lack of a year-round food source.
- It takes advantage of better climatic conditions at both extremes and avoids unfavorable climates in animals of high metabolic activity.

The migratory season is clearly established and linked to annual internal physiological rhythms. Birds undergo changes according to the length of the day, variations of climate (rainy seasons) and the reproductive cycle. This causes a hyperactive state (migratory anxiety) when they are uneasy and sleep little. They eat excessively and store fat in the pectoral muscles, the back, and the abdomen, which will be used to fuel their flight.

During migration they do not stop to eat enough, and may lose up to half their body weight.

Tracking birds

To study the movements of birds, the marking methods must be long-lasting without altering the conduct or the chance of survival of the individual.

Banding is the oldest tracking technique, together with coloring of feathers or alares, placed on the wings of chicks. Much of what is known of migrations is due to the banding of almost 100 million birds in Europe during the 20th Century, with a rate of recovery of about 2%. In the United States, a banding campaign in the second half of the last century showed a serious decline in the number of birds migrating to the Southern Hemisphere.

Coloring of feathers is simply to apply though it has the disadvantage of disappearing when the bird molts.

Lately technology has contributed much to bird tracking with transmitters that allow the detection of the bird at different distances depending on the equipment. From a radio tracking device to locate a bird as near as 500 metres on the ground to a GPS receiver that provides the bird location all the time.

A less conventional method of tracking birds consists of analyzing the proportion of isotopes in the feathers. Deuterium is the heavy isotope of hydrogen. The first raindrops to fall are those which contain the greatest proportion of deuterium ("heavy water.") Distance from the sea, altitude, and temperature affect the amount of heavy water in the rainfall. The heavy water enters the food chain (plants, insects, birds) and accumulates in the feathers. Therefore there is a correlation between the place of origin and the amount of deuterium in the feathers. If we have a map of deuterium in the rainfall and we measure the proportion in the feathers, we can establish the origin of the bird.

Types of migrations

Long-distance migrations are latitudinal (north-south) movements made by species which nest in the northern hemisphere. Near the North Pole, the climate undergoes profound seasonal changes. The summers are warm with abundant food, and the winters are cold and snowy.

In the Southern Hemisphere the land masses are far from the poles and the seasonal variations are less, but the available land area is smaller. In South America, many species nest in the south and migrate north in the winter, which is a short-distance latitudinal migration.

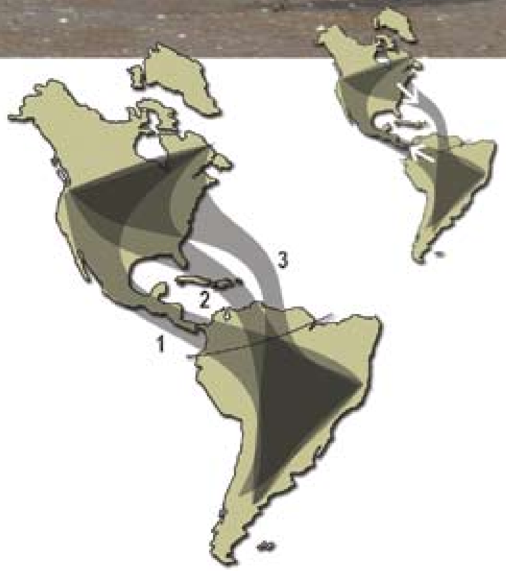
Longitudinal (east-west) migrations occur in the central regions of the northern hemisphere, from the interior of the continent to the coasts. Altitudinal migrations are migrations from high mountains to valleys.

Migration is an instinctive phenomenon, produced by hereditary mechanisms. Study of birds in captivity reveals that they respond to yearly seasonal cycles of molting and the will to fly in a certain direction. Circadian rhythms (daily biological rhythms) are controlled by the pineal gland which produces the hormone melatonin, but they are stimulated by external factors such as the length of daylight. The hypophysis or pituitary gland secretes gonadotropin hormones which act on the fat metabolism and the molting process. This causes excess eating which is assimilated as fat.

A relationship exists between the length of migration and the accumulation of fats. Sedentary birds accumulate from 10% to 20% of their weight, short-distance migratory birds 20-40% and long-distance migrators 50-60% and some even up to 100%. The internal organs of Bar-tailed Godwit (*Limosa Lapponica*), which migrates 11,000 kilometers between Alaska and Oceania, consist of 55% fats before migration. To compensate for the additional weight, the intestines and liver are reduced 25%. These are reconstructed after the bird reaches its destination.

Our understanding of internal circadian rhythms goes back to the work of K. von Frisch in 1911. He discovered that this cycle is not dependant on ambient light but that it is controlled by the pineal gland. It regulates the internal biological clocks, which produce daily cycles of behavioral and physiological events. Today we know that this gland produces melatonin. The control is centered on a group of nervous cells called the supraquiasmatic nucleus, situated just behind the eyes. In the same way circannual rhythms synchronize the annual cycles controlled by a clock with a longer periodicity.

Ambient light contributes to regulate the internal clock, but the clock is self-sufficient.



On the left, the three migration routes between the Americas. The American Golden Plover follows different routes flying from north to south and from south to north. At the right, a banded bird, and a bird marked with paint, for study of the migration routes.

Conditions of migration

The altitude of the flight depends on the terrain, the time of day, and the species. Migrating birds fly higher at night than during the day. Gliding birds depend on the formation of thermal updrafts. Overcast skies, rain, strong winds, or thick fog inhibit migration. Migrating birds also fly on cloudy days and some raptors glide in or over clouds, making them invisible to observers on the ground.

Radar tracking shows that half of all birds migrate at less than 1000 meters, 30% within the 1000-2000 meter range, 15% in the 2000-3000 meter range, and 5% from 3000-4000. The Ansers (*Anser sp.* geese) passing over Everest, reach 9000 meters of altitude and an African vulture collided with a plane at 12,000 meters.

Many species fly in small irregular flocks. Social birds form groups to move, and the larger ones fly in orderly form, each bird at the same altitude, behind, and slightly to one side, forming a "V".

Cruising speed depends on the species and wind direction. It is within the range of 50-60 kilometers per hour. Velocity is not constant. The birds may cover from 50 to 200 kilometers in a day. Night migrators cover greater distances (400-500 kilometers.) To cross the Caribbean they must fly between 2000 to 4000 kilometers without stopping.

Members of the family Charadriidae (plovers) are known to fly 3000 kilometers without a stop at an average rate of 90 kilometers per hour. Some species of the Laridae family (terns) travel from the Arctic to the Antarctic twice a year for twelve years (their average life span.) Some small species are believed to cover 4000 kilometers in six days. The Turnstone (*Arenaria interpres*) can travel 1000 kilometers in a day.

Perhaps for that reason the loss of individuals is large. Dozens of millions are thought to die every year while migrating from North to South America.

2.3. Orientation during Migration

The Blackpoll warbler (*Dendroica striata*) is a passeriform of the Parulidae family. In summer in the Northern Hemisphere it lives in the coniferous forests of Alaska and Canada. In autumn it moves to the Atlantic coast, where it eats and accumulates fat. With the wind from the north and north-east, it heads out to sea for a three-to-five day trip. It flies over the Bermudas, the Antilles, and Puerto Rico. When it reaches Venezuela it may stop or it may continue as far as northern Argentina. This is a 4000 kilometer trip over water for a bird that weighs less than 20 grams. It is an outstanding example of a bird's ability to navigate.

How do birds navigate?

Many hypotheses have been proposed regarding the direction-finding ability of birds. Presently many of the riddles have been answered, but they are not well understood.

Many of the following factors, or combinations of them, influence migration.

Innate genetic influences. The need to migrate becomes urgent at a specific time of year, in a certain direction, and for a certain length of time. An enlightening investigation was that of A. Perdeck of the Dutch Institute of Ecological Studies. He captured 11,000 starlings in Holland in the 1950s during their migration from Scandinavia to western France. They were banded and released to the south, in Switzerland. Three hundred and fifty individuals were subsequently recovered. The birds with previous migration experience reached western France. The inexperienced ones, migrating for the first time, continued to fly in the same direction as if they had not been moved. They ended up in Spain. The experienced birds corrected both time and direction to arrive at the destination of the previous year.

Birds learn by following other birds. The adults begin the trip first. It is also common for the males to begin the pre-nuptial trip before the females, in order to claim the best territories before the females arrive.

They use rivers, mountains, and coastlines as guides. Vision is their basic tool of navigation, except for the first time. Various experiments have demonstrated that birds respond to ultra-violet and polarized light. Perhaps these indicators have something to do with orientation.

They use the sun and the stars as guides, depending on whether they migrate by day or by night. During the trip, they are able to maintain the correct orientation even when the sky is covered by clouds, which shows that they must use other means of orientation, such as terrestrial magnetism. Stellar navigation and magnetism merit separate treatment

One hypothesis suggests that pigeons can detect very low frequency sound waves. These are produced by water currents or wind over mountains. Storms and earthquakes also produce low frequency sound waves, which give the birds early warning.

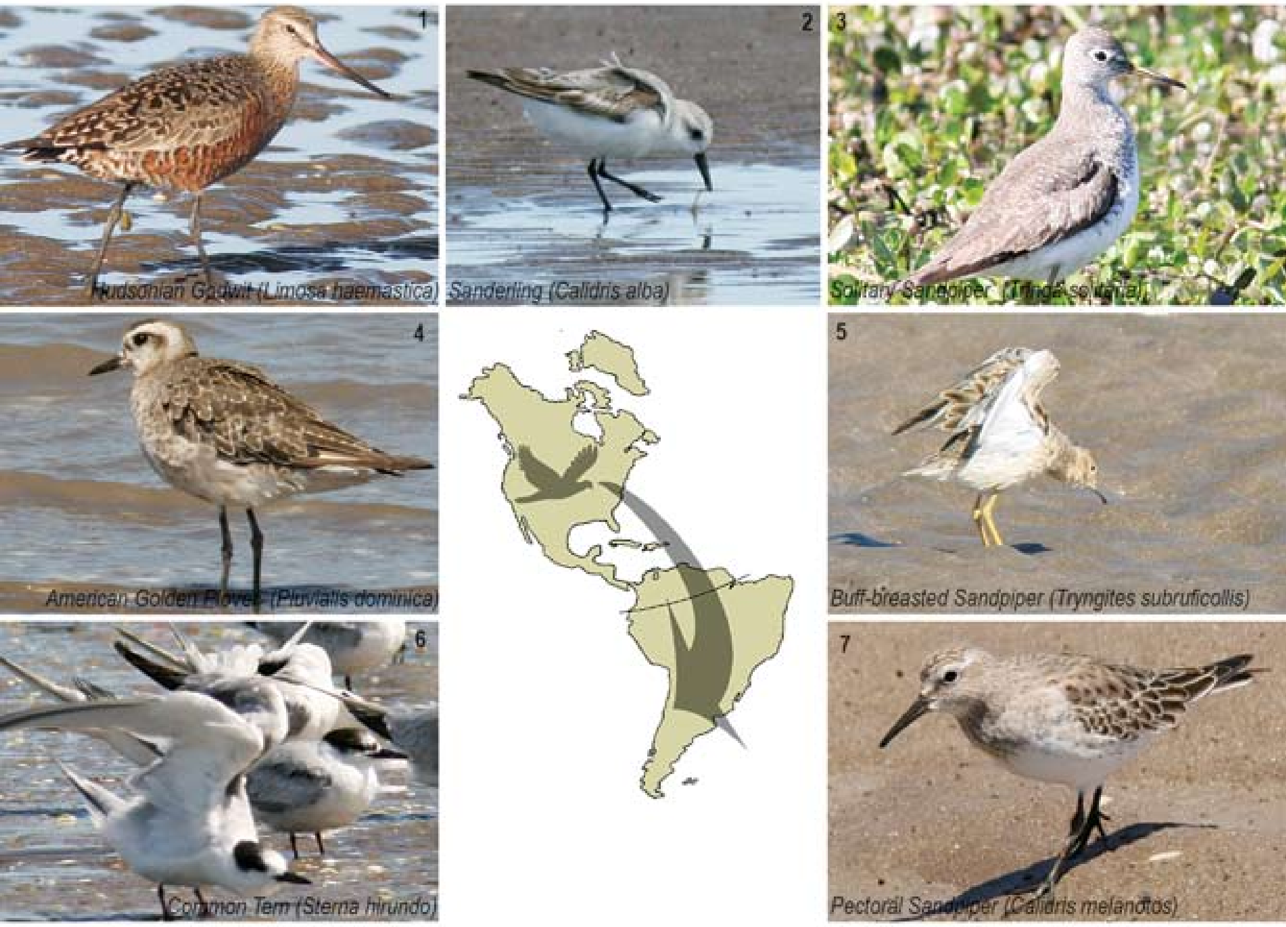
Italian investigations have demonstrated that pigeons have an olfactory map. Although their sense of taste is poorly developed (they have 37 taste buds in contrast to the 9000 which humans have) the sense of smell is better supplied. The olfactory map may be developed in their first weeks of life, if they are raised in a place with a characteristic smell.

Navigating by the stars and by magnetism

Different species of birds use different techniques of navigation. Those that migrate by day steer by the sun, and those that fly at night use the stars. Many can sense the magnetic field of the earth, some use smell, and perhaps other forms of orientation such as polarized light.

Stellar orientation is well demonstrated. When the migratory season approaches, captive birds attempt to fly by night in a specific direction. On cloudy nights their orientation deteriorates. Various decades ago, experiments were made in planetariums, with birds which were shown various constellations in positions advanced or delayed according to the actual time. Nevertheless, the birds were able to maintain their orientation. It was shown that they use various groups of stars at about 35 ^{o} latitude. The fact that they recognize various star patterns enables them to switch from one to the other, if part of the sky is overcast.

But how do they know whether to fly north or south? Scientists used two groups of birds. One, the control group, received normal light conditions and molted twice a year. The other, experimental, group was subjected to accelerated light conditions and molted three times. At the time of migration, the control group flew south, while the experimental group flew north. This demonstrates that there are physi-



Three types of migration in the pampa. The first (1 to 7) consists of the birds which breed in North America and spend the northern winter in Argentina. The other groups migrate shorter distances (next pages).

ological conditions which affect migratory orientation and may be controlled by hormones (prolactin and corticosteron.)

Magnetic orientation is more puzzling. Some investigators have suggested that birds have particles of magnetite (a mineral compound of iron and oxygen) which serve as a compass. Certain bacteria synthesize magnetite, which is found in the heads of pigeons and in the stomachs of bees. But others prefer an explanation based on magnetic sensors in the eye. In this case, pigments in the retina may be capable of translating both light and the magnetic field into electrical impulses, permitting the bird to "see" the lines of the earth's magnetic field.

Experiments are revealing. When the European Robin (*Erithacus rubecula*) was placed in a circular cage with the sky covered, it faced in the right direction in spite of not receiving clues from the sun or stars. When a magnetic field was generated around the cage, the birds changed direction. That is, they used the magnetic field.

Although they do not migrate, pigeons are used for orientation experiments because they can be followed and recovered. In pigeons, particles of magnetite were found in the sensory dendrites of the skin of the upper bill. These dendrites are arranged in a complex three-dimensional pattern with various spatial orientations designed to analyze the three components of the vector of the magnetic field. They react very sensitively and specifically to the external


In this page (8 to 14), we see birds which nest in the pampas in summer and in winter move north to a milder climate.

magnetic field of the earth like a magnetometer with three axes. This could be a universal characteristic of birds. The magnetic sense is located in the nasal region. Crystals of magnetite have been found in the noses of trout and are linked to the capacity of trout to detect magnetic fields. Sea turtles may also have this orientation mechanism.

In one experiment, bobbins were attached to the head and neck which made it possible to change the direction of the magnetic field. Another group of birds was taken to areas where mineral deposits altered the magnetic field of the earth. Both groups of birds were evidently confused. In another experiment, birds were placed in an artificial magnetic field. When they were set free to migrate, they headed in the wrong direction. Nevertheless, they recovered the correct orientation at dawn.

Orientation according to the magnetic field requires vision, since birds deprived of sight were not able to orient themselves. But besides that, they maintained orientation with the pineal gland removed. Evidence demonstrates that detection of magnetism occurs in the eyes and is processed in the part of the brain dedicated to nocturnal vision. The information received from the retina is processed in the hyperpallium of the brain, which also processes the information of stellar navigation and terrestrial magnetism. Evidence indicates that the magnetic field is detected

Collared Plover (Charadrius collaris)

Rufous-chested (Charadrius modestus)

Two-banded Plover (Charadrius falklandicus)

Bar-winged Cinclodes (Cinclodes fuscus)

Black-faced Ibis (Theristicus melanopis)

Snowy Sheathbill (Chionis alba)

In this page (15 to 21) are birds which nest in the far south in summer and move to the pampa in winter.

by specialized molecules in various parts of the retina. The cells of the retinal ganglia show elevated activity during magnetic orientation and a high concentration of cryptochromes, the molecule thought to be related to detection of magnetism. Cryptochromes are also present in plants.

Birds calibrate their magnetic compass based on the pattern of polarized light at sunrise and sundown. Polarized light is light in which the waves move on a single plane with relation to the direction of light source. At sunrise and sundown there is an intense band of polarized light at 90º from the sun which passes directly above the zenith and intersects the horizon 90º to the left and right of the sun. Polarized light seems to be the primary system of reference by which birds calibrate their other systems of guidance.

The ability to orient themselves is not exclusive to birds. While birds migrate several times during a life-time, butterflies do it only once. Some species migrate as much as 5000 kilometers between Canada and Mexico. It has been established that butterflies use ultraviolet light to orient themselves. Using radio-transmitters which weigh three tenths of a gram it has been possible to follow dragonflies on their migrations and show that the rules of migration are very similar to those of birds. This may modify our ideas of migration and show that they originated far earlier than has been thought.

2. The support of the body

1. The skeleton of the trunk

The bones

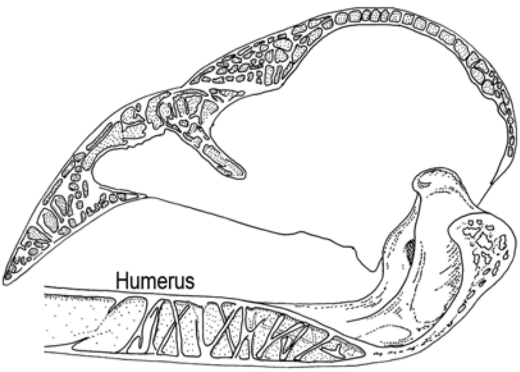
Evolution has produced two basic methods for support of the soft parts of the body, the endoskeleton of the vertebrates and the exoskeleton of the invertebrates. The endoskeleton of vertebrates has the advantage of being able to grow without molting, but offers less protection than the exoskeleton of the invertebrates.

There are two kinds of cells of the connective tissue: cartilage and bone. Cartilage is a gummy mixture of proteins (principally collagen) and polysaccharides. Its elastic texture provides the surface necessary for the joints. It is dominant during the development of the embryo, but it is replaced by bone. In birds the skeleton is totally made of bone.

The bone contains, besides collagen, insoluble crystals of calcium phosphate, which give it rigidity and hardness. It is as hard as iron, but weighs one third as much per unit of volume.

The bones such as ribs protect the organs. They provide support to the soft parts of the body and permit the smooth muscles to be inserted. They make movement possible by interacting with the muscular system. They store minerals (they are a reserve of calcium and phosphorous necessary to maintain equilibrium of fluids in the body.) They are also the center of blood-cell formation, such as the red marrow of the sternum.

Among many birds, the larger bones of the skeleton are pneumatized, that is, they contain air



A cross-section of the skull and the humerus of a bird.

We see this vulture with folded and with open wings. The wing-bones of this rhea are clearly visible from behind.

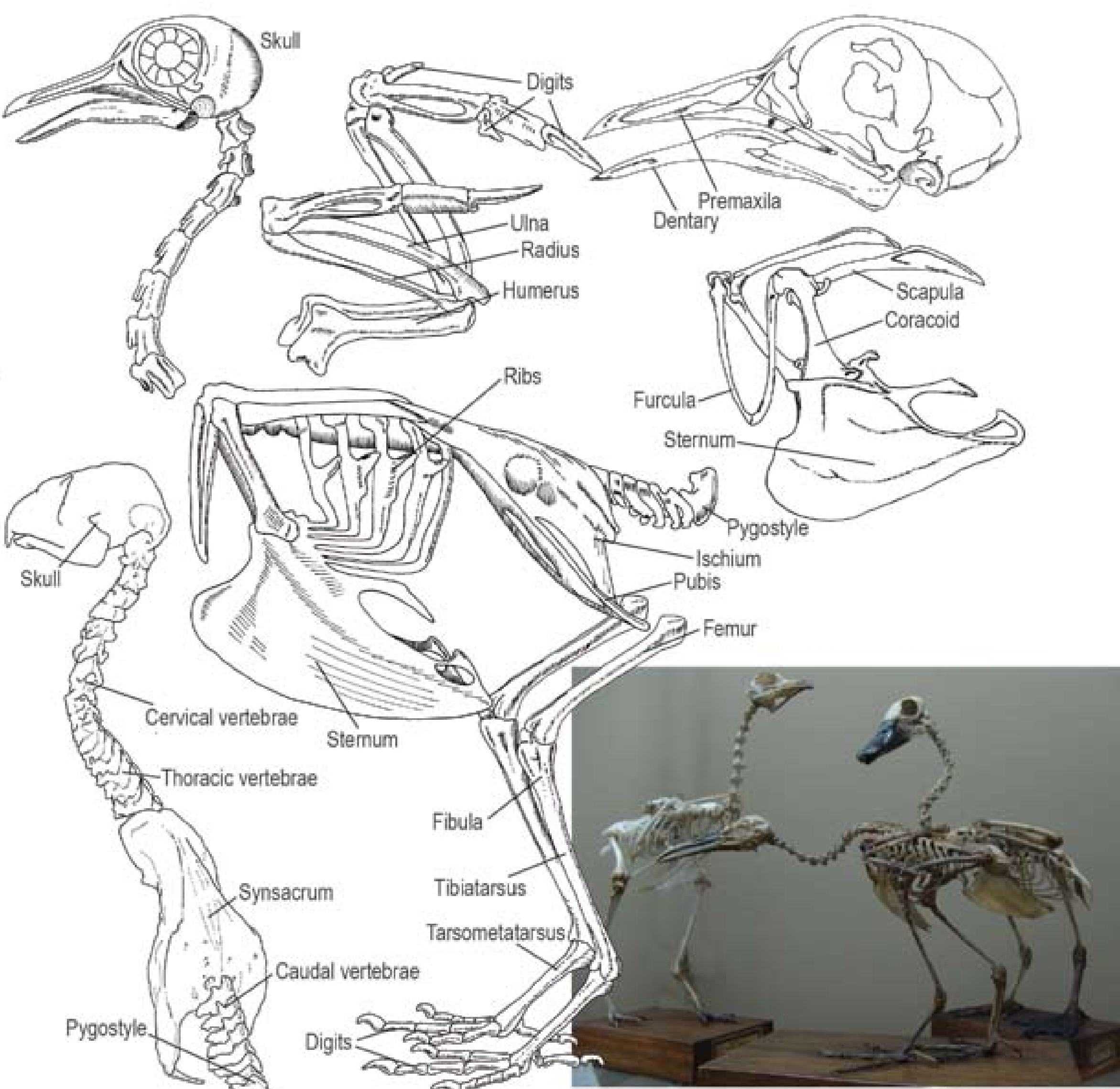
cavities which function as an extension of the air sacs connected to the lungs. To avoid fracture, these bones have interior struts, which are diagonal projections of bone. A tube is stronger than a rod of the same weight and material, so the cavities in the bones are an effective way to reduce weight and improve resistance. However, very small birds do not have pneumatic bones, since they would save very little weight, and diving birds also lack them, because they need greater body weight.

A light-weight skeleton is necessary for flight. The skeleton of the frigate bird (*Fregata minor*) weighs only 110 grams, in a bird with a wingspread of two meters, and even weighs less than the feathers! The skull of a pigeon weighs 0.2% of the total skeleton, and one sixth of the skull of a rat of the same size.

The thorax

The skeleton of the modern bird is totally ossified (it contains no cartilage) and is notable for its adaptations to life on the wing.

The bones of the thorax are extensively fused, especially the pelvis, ribs, and tail. The strength of the wing-beat requires a rigid trunk which will not



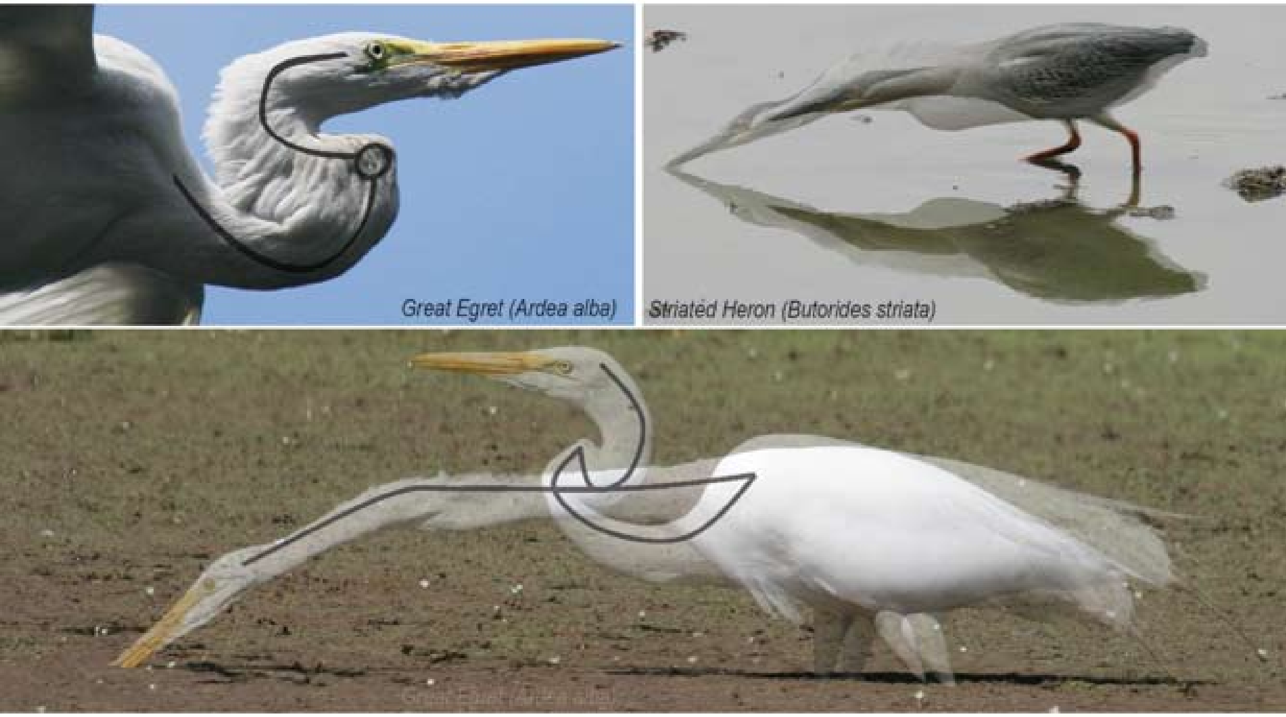
Skeleton of the bird.

transfer tensions to the internal organs, although to some extent these tensions are used to force air from the air sacs into the respiratory system.

The trunk is rigid because the ribs are joined by an uncinate process. This is a bony projection in the center of the rib which extends backward to overlap the next rib. It was present in amphibians and primitive reptiles, but was lost in dinosaurs and re-evolved in modern birds.

The vertebrae are fused to form a rigid structure. The thorax may have from three to ten vertebrae. Some of the vertebrae of the thorax are mobile and articulated with the synsacrum, which is constructed of the lumbar, sacra, and the first caudal vertebrae. The synsacrum is in turn fused with the pelvic girdle to provide more rigidity. The remaining caudal vertebrae are smaller and fused with the pygostyle, which sustains the tail. The tail is reduced to a short structure which allows the center of gravity to remain beneath the wings.

The sternum is greatly enlarged. It has a large



The heron has a special joint which enables it to retract its neck.

keel or bony crest like the keel of a boat, especially in birds which are strong flyers. The pectoral muscles necessary for flight are attached to the keel. The Rhea has no keel and does not fly. It has a flat sternum as in humans. Penguins have a keel and use their wings to "fly" in the water.

2. The skull of the bird

Neck and cranium

Mammals have seven cervical vertebrae in the neck while birds have from eleven (parrots) to twenty-five (swans). They are adapted to provide a light-weight but strong and flexible neck. The neck vertebrae form heterocelic joints with the ends shaped like a saddle. Thus the two vertebrae can rotate around each other in all planes of movement when connecting. Herons have a special joint which enables them to form an "S" shape in the middle of their necks between the 8th and 9th vertebrae. When they hunt, they keep the head drawn back while waiting for the right moment and then suddenly stretch the neck to capture the prey with a lightening blow of the bill.

The head moves freely and is placed so as to maintain equilibrium both in flight and on the ground. The head is joined to the vertebrae by a single joint (the occipital condyle) located below the skull. The head is perpendicular to the neck. Mammals have two condyles. Thus birds can turn their heads much further than mammals, almost 360°.

The skull of birds evolved from the diapsid skull of dinosaurs. Diapsid means that it has two openings behind the eye-sockets. Unlike primitive fish with up to 180 bones in the skull, the skull of modern birds is much modified to reduce weight, with the bones highly fused, a lengthened bill, and a mobile upper mandible. The bones fuse very early in the bird's growth, eliminating sutures which are only visible in very young birds.

The cranial volume is much greater than that of reptiles, and only the pterosaurs have a more or less comparable cranial capacity. The eyes are enlarged and the sense of smell is reduced. The eyes are close together at the front of the cranium, forcing the brain backward. In general the eyes are placed at the sides of the head, and provide limited binocular vision. The

Examples of bills.

nostrils are on the upper part of the bill, usually near its base.

The Bill

The jaw is replaced by a horny bill formed of keratin, without teeth and very light. The upper jaw is mobile, which enables the bird to open its mouth very wide. This occurs when the lower jaw engages the square joint-bone above the arch of the yoke, which pushes the upper jaw upwards. This then moves, because it forms a hinge with the skull. This mobility is necessary since they don't have upper limbs with which to handle and capture food, and teeth with which to cut it. A few birds such as parrots use their feet as "hands" to manipulate food. The lower jaw opens at the base, which permits the throat to expand, in order to swallow food whole.

Among reptiles new teeth appear as soon as the old ones break or wear out. Mammals develop two sets of teeth in sequence - deciduous or "milk" teeth which are shed to make room for the permanent teeth. Among birds, all teeth were lost and the structure of the mouth changed, so that the bill is equivalent to the lips of a mammal.

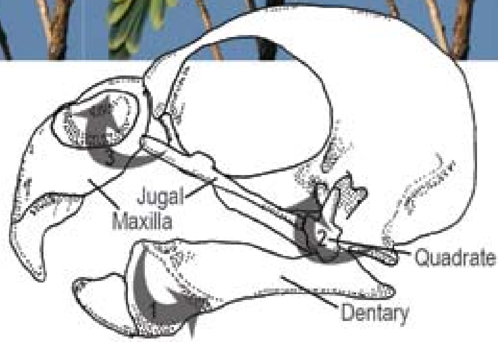
The bill is composed of a protective horny covering, which is located over the bones of the upper and the lower jaw. The horny covering is called the rhamphotheca. The length of the two mandibles is usually the same, but it may be different, as in Parrots, which have a longer upper beak, or in Skimmers, which have a longer lower beak.

The bill, like the claws, scales, and feathers, originates from the skin. The external layers of the epidermis move outward and accumulate keratin (a very resistant fibrous protein.) The dead cell is treated like a scale. It accumulates a horny layer on the bill and the claws. This horny covering grows continually to compensate for wear, which permits some birds to change the color of the bill at different seasons. Keratin is also present in the feathers of birds and in the hair and horns of mammals.

3. The wings

Quadrupeds evolved from Devonian lobe-finned fish. The twenty or so ribs or rays of the fins were reduced, so that about 350 million years ago the tetrapod *Ichthyostega* had seven digits and *Acanthostega* had eight. Reptiles developed a general sequence of five digits which was passed on to mammals and dinosaurs.

Birds have a joint between the upper mandible and the cranium, enabling them to open their bills widely. Parakeets use their feet as hands (they have opposing toes) to manipulate food. But they may also use their bills as hands or feet to grasp branches when climbing (below.)



The line of dinosaurs which evolved into birds had three digits on the forelimbs, the other two being vestigial. The Argentine fossil *Herrerasaurus*, found in La Rioja, is one of the oldest dinosaurs known and already has a reduced number of digits on the forelimbs.

Birds continued to modify this sequence by extending one digit over the other two to form the wing. *Archaeopteryx* has vestigial fingers with claws on the wings. Modern birds reduced these fingers and lost the claws. There has been disagreement over which fingers were retained in birds. By following the evolution of the fetus it has been concluded that they are II, III, and IV. Previously it was thought that they were I; II; and III, as in dinosaurs.

4. Feet and tail

The Feet

Some bones of the upper limbs have been fused (the carpal-metacarpal structure.) The same has happened with the lower limbs. Birds walk "on the tips of their toes." The knee joint is close to the body under the feathers, and the ankle is lengthened, so that it looks as if the knees bend backward as compared with those of humans.

The great majority of birds have little weight to support on land. Some have feet so small that they

The prehensile feet of Passeriformes allow them to grasp twigs and hop acrobatically from one to another. The tendon controlling the toes tightens forcing the toes to grip.

can hardly walk (hummingbirds and cormorants,) or they move by jumping (Passeriformes.) On the other hand, other birds have long slender legs (herons). The fibula is reduced to a small "splinter" joined to the tibia. The tibia and tarsal bones are fused to form the tibiotarsus, and the bones of the metatarsal and tarsal form the tarsometatarsus.

The number of toes varies between two and four (no bird has five) and the orientation is related to the life-style of the bird. The first toe may be directed either forward (Passeriformes) or backward (Piciformes and Psittaciformes.) The African ostrich has only two toes (III and IV), both directed forward, while the South American Rhea has three. In these birds, the feet are adapted to running in open country.

The back toe may be at the same level as the front ones, (incumbent hallux) or higher (elevated hallux). The incumbent hallux is a characteristic of Passeriformes.

Certain basic types of feet can be distinguished according to the disposition of the toes. The most common is the anisodactyl with three toes pointing forward and one back. It may have a well-developed hallux when it is useful for grasping a branch or capturing prey. In the case of the jacana, the toes are greatly lengthened to permit this species to walk on floating vegetation. Among walking birds, the hallux is usually reduced, so as not to impede the gait. It may be elevated or totally absent. Other birds have zygodactyl feet, with toes II-III pointing forward and I-IV back, or heterodactyl with toes III-IV forward and I-II backward. Feet which have four toes pointing forward are called pamprodactyl. The swifts can move the thumb forward and hang from the claw of it when resting. Other birds are syndactyl and have the outer toe joined to the middle one.

Some birds which walk long distances have long legs and short toes and tail, to reduce the area of contact with the soil. Birds which live in trees, whose feet are adapted for climbing, tend to move about with short jumps from branch to branch (wood creepers.) Occasionally they use this means of movement on the ground (sparrows and woodpeckers.)

The perching foot of arboreal birds (Passeriformes) is evolved to grasp and stand on the branch without consuming energy. The arrangement of the tendons allows the weight of the bird to force the foot closed. The tendons of the toes keep the bird secure on the branch, because on stretching they catch among themselves, so that birds have been known to remain clinging to a branch even after death.

Atrophied wing of the penguin.

Some birds use their feet like hands to capture prey or manipulate food. Birds of prey have very long claws to capture prey. The Osprey has a series of spines in the soles of its feet to hold slippery fish. Some magpies hold acorns in their feet while breaking them with powerful blows of their beaks.

Aquatic birds and those which walk on soft surfaces (snow or mud) need special structures for walking. Ducks, seagulls, and flamingos have a web uniting the three front toes (interdigital membrane.) This enables them to use their feet as oars (palmate ducks.) The Pelicaniformes have a membrane uniting all four toes. Some birds which walk on silt or aquatic vegetation have a membrane which only extends part way up the toes (semi-palmate feet of herons, ibis, and plover).

But the interdigital membrane is not the only adaptation of birds to dive or swim. Phalaropes and coots have palate-shaped horny projections at the side of each toe (lobate feet). The lobes play an important role in swimming. Some birds which live in snow in the Northern Hemisphere have developed elon-

Wing spurs of the Southern Screamer.

gated scales at the sides of their toes, which serve as snow-shoes enabling them to walk on snow.

The tail

Bipedal dinosaurs had a long heavy reptilian tail which did not drag on the ground but projected behind them as a counter-weight to the head and neck, enabling them to balance on two legs. In birds the center of gravity is more forward, under the wings. Therefore, the tail is much shorter, leaving only a vestige. Lacking the vertebral tail, the birds evolved a tail of feathers, lighter-weight and maneuverable. The principal use of the tail is in flight control, but it also may be used for climbing (woodcreepers and woodpeckers), noise-making (South American Snipe), or to distinguish the sexes (Fork-tailed Flycatcher).and the species (coots)

Different types of tails are designated according to their general shapes, which depends on the relative length of the feathers. The tail may be rounded (Passeriformes), square (Falconiformes), or rectangular (Guira Cuckoo), or it may be forked, having the external feathers longer than the internal ones, or pointed, or it may have a rough surface used as a support (woodpeckers).

Other appendages

The claws (horny projections which cover the tip of the toe) also play an important role in locomotion and in obtaining food. They are long and curved in birds of prey and in those which climb and perch on branches. They are short and dull in those which walk on the ground and flat in the divers. In some groups (herons and owls) the middle claw has a comb-like structure (pectinate claw) which is used to clean and maintain the feathers.

Other accessory tools of the birds are the spurs. They are rigid thorn-like structures which are used for fighting. Among cocks and pheasants they are on the feet, while Lapwings, Jacanas, and Southern Screamers have them on the wings.

The tail can be used for balance.

3. Protection and Color

1. Construction and type of feathers

1.1. Skin and feathers

The skin of the bird

Birds have a loose thin skin which is easily torn. It has few nerves and blood vessels compared with mammals. For this reason birds bleed little and show little distress at manipulation of the skin. The skin is usually yellow but may have areas of less or different pigmentation. Crests, wattles, and lobes are ornamental thickenings of the soft skin.

The skin consists of epidermis (the superficial layer) and endodermis (the internal layer.) The ornamental structures have a thicker and more vascularized endodermis, but the epidermis is thin and therefore subject to injury. The fleshy crest of the Condor is formed by a fold of bare skin which protrudes from the head. A similar structure is the caruncle, a fleshy appendage found on the head, over the bill (Black-Necked Swan *Cygnus melancoryphus*). In parrots and doves it surrounds the nostril.

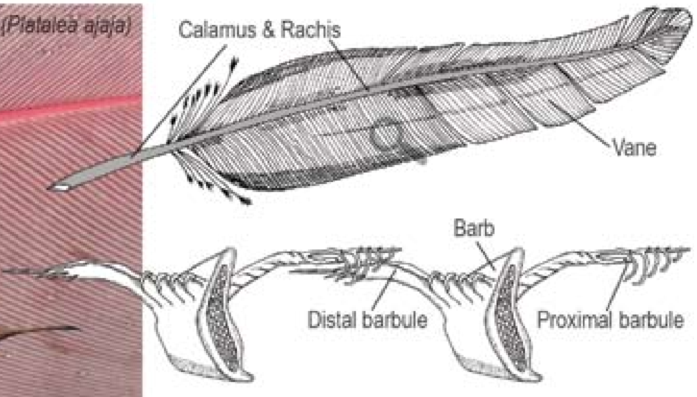
Some species have a frontal shield over the bill which may be brightly colored (coots and jacanas). The gular fold or wattle is a bare area between the sides of the mandible, throat, or front of the neck (Condor).

Some birds have other areas of bare skin, sometimes brightly colored. They may also have other peculiar structures around the eye (periocular ring), on the head, or on the neck.

The endodermis is the base of the scales, feathers, claws, and some glands. Wear on the claws and scales is replaced by continuous growth from the base. On the other hand, the feathers grow rapidly to reach their final size, and then remain stable for months.

Birds have no glands in the skin. The only gland is the uropygial (preen) gland, on the upper part of the tail. It produces wax and oil which are spread over the feathers with the bill or the neck. It is highly developed in aquatic birds to water-proof the plumage, but some species do not have it.

Under the skin the smooth muscles control the movement of the feathers, erecting them in fights, fluffing them in hot weather to enable air to cir-



Detailed view of a feather.

culate, and to let the sun penetrate to the skin in cold weather. The body of the bird is not completely covered with feathers. The legs are almost always bare and covered with scales. The head and neck of carrion-eaters is bare, without feathers or scales, for the sake of hygiene.

The usefulness of feathers

Our understanding of the evolution of feathers remains incomplete due to the absence of intermediate fossils. The oldest known feathers are similar to modern ones. Recently, fossils have been found of bipedal dinosaurs with feathers, which affects our belief that only birds have feathers, and changes our vision of the metabolism and general biology of certain species of dinosaur.

Different hypothesis have been proposed to explain the evolution of such a complex structure. The most plausible reason is for temperature control. Perhaps they began as down without barbs which later evolved for sexual exhibition and species definition by means of different forms and colors. Those who do not accept this theory ask, “How could such a complex structure have developed for such a simple purpose?” This leaves us with the question, “What are feathers good for?”

Their uses are many and their mechanical structure is marvelous. This flexible and resistant structure is composed of the same material as the scales. Feathers serve the following purposes:

According to the position they assume, feathers may conserve heat or allow ventilation of the skin. The relation between surface and volume of birds is great because birds are small. That is to say, they have a large amount of surface to dissipate the heat of their internal metabolism. At the same time, the body temperature must be kept high. They have the highest metabolic rate of any animal. The feathers function as a layer of thermal insulation by providing a layer of stagnant air between the skin and the surface. They are more efficient than the fur of mammals.

The shape of the feathers provides the lift of the wing. The ability to fly depends on the economy of weight, force, and the strength of the structure. Feathers form a light, flexible, and resistant surface.

They keep the body dry. Clean healthy feathers form an insulating layer which is water-repellant. Drops slide off the plumage without penetrating it. Feathers allow birds to float on the surface of the water, since they increase the volume of the body without increasing its weight. For example, the specific gravity of a duck is 0.6 with feathers and 0.9 without them (they weigh less per unit of volume), when among other animals it is 1.0. A swan floats with almost its whole body above the surface of the water, while a human can barely keep his head out.

The colors of the plumage serve as sexual signals in courting, and as camouflage in the surroundings. The feathers are changed by molting once or twice a year. Some birds have special plumage during mating season, for example the long decorative feathers on the egrets. The Great Egret (*Ardea alba*) was hunted for years for the sake of these feathers, which were used in ladies’ hats of the period.

In some cases, the feathers of the wings or the tail are used to produce sounds during courting. Owls, on the other hand, have fringes on the borders of the feathers of the backs of their wings, which silence their flight when they attack.

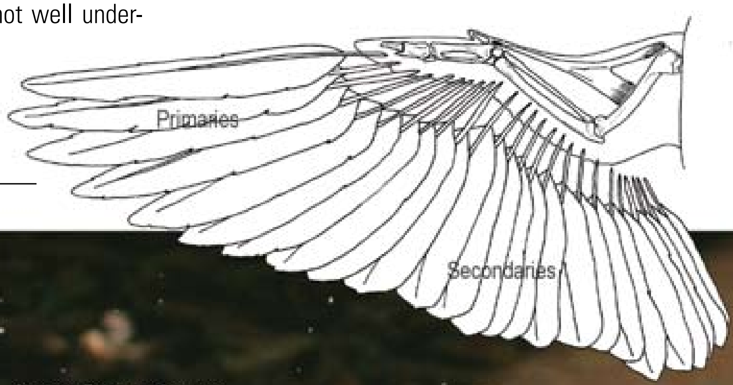
Certain stiff whisker-like feathers near the bill, called vibrissa or rictal bristles, have tactile sensitivity. They are used to detect and capture insects.

1.2. Technology of the feathers

To use the word technology in relation to animals is not new. Karl Marx used it to describe the way the work of Charles Darwin helped us understand the way "the technology of nature" functions in evolution. Though the origin of the feathers is not well understood, we do know how they function.

The feather originates from a papule which develops in a thickening of the skin. It lengthens and inclines during growth. This occurs in the same way the scale of the reptile grows, and is thought to be derived from them. Both structures are composed of the same protein, keratin (from the Greek Keros, horn). It is a protein-like substance rich in sulfur, formed of chains which twist around themselves, to give strength and rigidity to the structure (like the thick ropes used on boats.)

The thickening of the skin in which the feather originates forms a follicle. The internal cells diversify and force the growth of the feather toward the surface. At a certain point, growth stops and the nucleus



Names of feathers according to function.

This male Cream-backed Woodpecker shows a peculiar pattern of wear on the secondary feathers.

of the follicle separates. The structure becomes dead and hollow. Nevertheless, there are some birds with very long feathers which may grow for years to reach their final state. The "powder feather" is another example of indefinite growth.

The follicle in which the feather originates produces a protein called BMP. This protein inhibits the skin from forming another feather follicle nearby. If an overdose of BMP is applied locally, a bare spot results, while if a BMP inhibitor is applied, the quantity of feathers increases. This explains why the feathers are distributed so evenly over the skin.

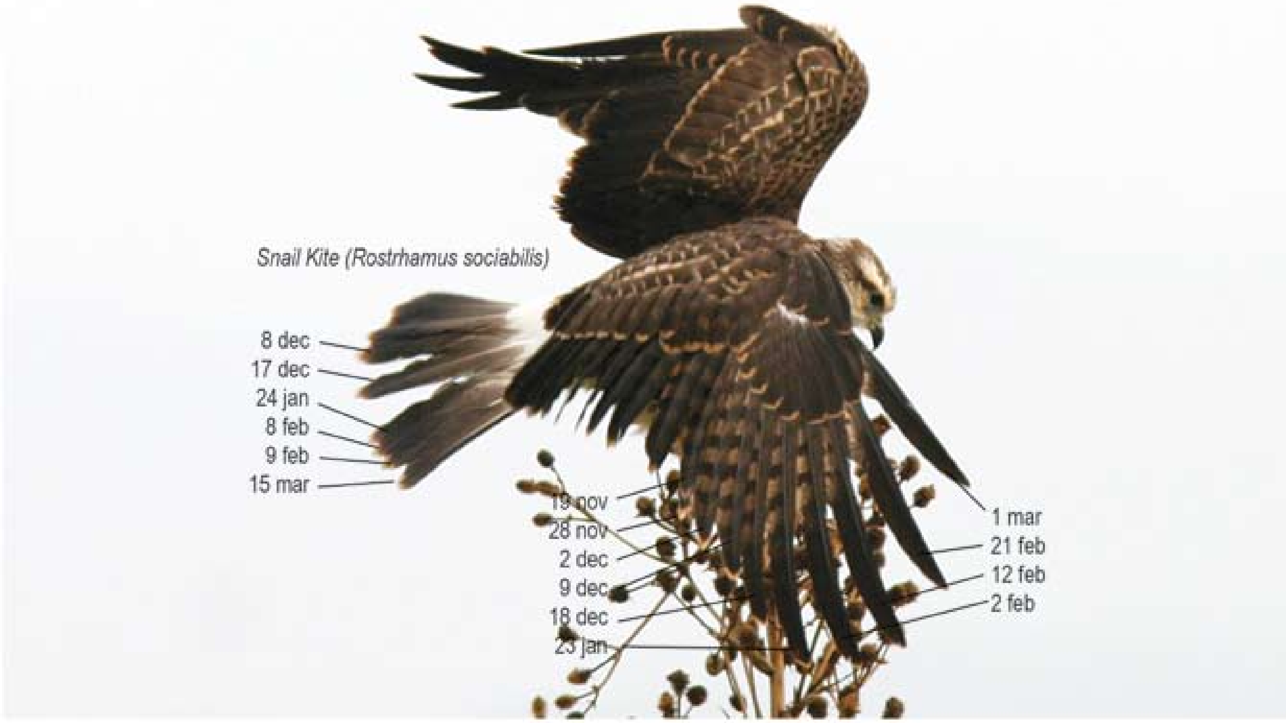
The feather has a central shaft and a vane. The central axis nearest the skin is called the quill or calamus. It doesn't have barbs and is inserted in the follicle of the skin. The rest of the axis is the shaft or rachis, which supports the vane. The quill is round and the rachis is flat or channeled along its inner surface. The vane consists of parallel barbs which extend from the shaft. Each barb in turn has parallel barbules on either side. The barbules are different on each side. One side has tiny hooks and the other has rounded borders. The hooks of one barbule catch on the rounded borders of the next one, so that they cross at right angles forming a mesh. It is a sort of natural Velcro® which can be pulled apart and re-united. The bird can easily re-adjust the barbules which have been pulled apart by combing them with its bill or its feet. There may be up to a million barbules on a feather.

1.3. Types of feathers
Feathers according to structure

According to their use and position on the body, feathers may be classified as:

The pennates (feathers with barbs). The flight feathers of the wing (remiges) are asymmetrical, that is, the barbs of either side of the rachis are of differ-

The plumage is waterproof. Water slides off a bird body so that it can float. Birds which frequently dive, like cormorants, have semi-waterproof plumage.



The molt. Most birds molt their feathers sequentially from the body outwards. In the photograph we show an estimated date of molt for the Snail Kite (Rostrhamus sociabilis). It is a gradual process and the bird always has enough feathers to fly without difficulty. The new feather grows under the old one, forcing it out. Some birds, such as ducks, molt all at once and temporarily lose the ability to fly.

ent sizes. On the other hand, the feathers of the tail (rectrices) and those on the body are symmetrical. The rest of the body may have down, pin-feathers, or may be naked. Feathers are grouped in linear patterns called pterylae, which may differ among species. They do not grow uniformly over the body except in penguins. Penguins have feathers completely covering their bodies, since they need considerable insulation against the cold.

The down has a shorter structure and is more hidden under the pennates. It has no rachis and the barbs lack hooks, so it doesn't maintain a regular shape. The down looks like a feather duster. It forms the first feathers of the newly hatched bird, and acts as thermal insulation in the adult. The semi-feathers are intermediate between the feathers with barbs and the down. They are found on the sides and breast of the bird.

The hair-feathers are like hairs which form circles around the base of the feathers with barbs. The vibrissae ("whiskers") surrounding the mouth of some birds are also like long stiff hairs. They function as sensory organs in the capture of insects.

The "powder feathers" are found in birds lacking a preen (uropygial) gland. They are never shed and grow continuously from the base. The tips disintegrate to form a powder similar to talcum, which water-proofs the feathers and gives them a metallic sheen. They grow in patches on the breast and the back, and look like a wisp of dusty, untidy feathers. Herons, some parrots, and falcons have them. They use their bills and their neck to distribute the powder over the body.

The crest on the head or the neck is another appendage formed by the feathers. It may be erected in aggression, or appear with the nuptial plumage. The "ears," on the other hand, are groups of feathers which protrude on either side of the head but have nothing to do with hearing. The facial disk is also formed of feathers of the face radiating from the eyes. The "ears" and facial disks are common in owls. The ruff is a collar of feathers which surrounds the base of the neck of the Condor. Egrets are long fine feathers which grow on the breast and the back of egrets and other herons during mating season.

The flight feathers

The most important flight feathers are the primaries. They are at the outer joint of the wing and are inserted in the metacarpal or "hand" bones. They are long, strong, and rigid. In general, flying birds have nine to twelve primaries. The *Rhea* has more, but they are only ornamental. The shape of these feathers determines (or is determined by) the type of flight of the bird. Very good flyers have highly asymmetrical flight feathers.

The secondary feathers are found close to the body, behind the primaries. They are inserted into the bone of the forearm. Their function is to hold the air during flight, providing lift and support. They form a continuous surface from the primaries to the body, where they overlap the scapulars, which extend from the humerus. The number of feathers varies, and depends on the length of the forearm. The hummingbird has only six secondaries, but the average in all birds is ten, and the great gliding sea-birds may have as many as thirty-two.

The alula (thumb-wing) is composed of feathers inserted in the reduced thumb. They are few and rigid. Their function is to reduce turbulence during low-velocity flight with the wing inclined at an angle. They form a slot half-way up the wing.

The steering feathers form the tail and help determine the direction of the flight, like the tail of a plane, during turning and landing. Some birds use them for support while climbing vertical tree-trunks (wood-

The color of the plumage may be produced by pigments or by the microscopic structure of feathers (structural color). Pigments can be seen even after destroying the physical structure that houses them. Structural colors disappear if the structure of the feather is destroyed.


White-faced Ibis (Plegadis chihi)


Shiny Cowbird (Molothrus bonariensis)


Southern Lapwing (Vanellus chilensis)

Plumage color may be eye-catching for courtship or cryptic (to remain concealed in the environment).

peckers and woodcreepers). The number and length varies according to necessity. Some birds, such as the hummingbird, do not use their tail to steer. They have only four to six feathers in their tails. Most birds have twelve and pheasants have thirty-two. The length and strength varies according to the type of flight and whether they are used in courtship.

The remiges (primaries and secondaries) and the tail-feathers are called "flight feathers." At the base of each of them, both above and below, they are covered with a layer of contour feathers called "coverts". These contribute to flight by forming a smooth aerodynamic surface. They are classified by various names according to their size and location.

The elasticity of the flight feathers is a fundamental characteristic which differentiates the wings of birds from the wings of other flying animals and the airplanes of humans. This elasticity is provided by the asymmetry of the barbs with respect to the rachis, the curvature of the rachis, and the flexibility of the materials. It seems that asymmetry is also used by lobed feet of grebes to achieve flexibility. For example *Podiceps sp*. has asymmetrical lobes on its feet which it uses to paddle in the water. The function of the asymmetrical structure is to stabilize the feather (or the toes) in the power-stroke of flight (or swimming).

2. Covering of the bird

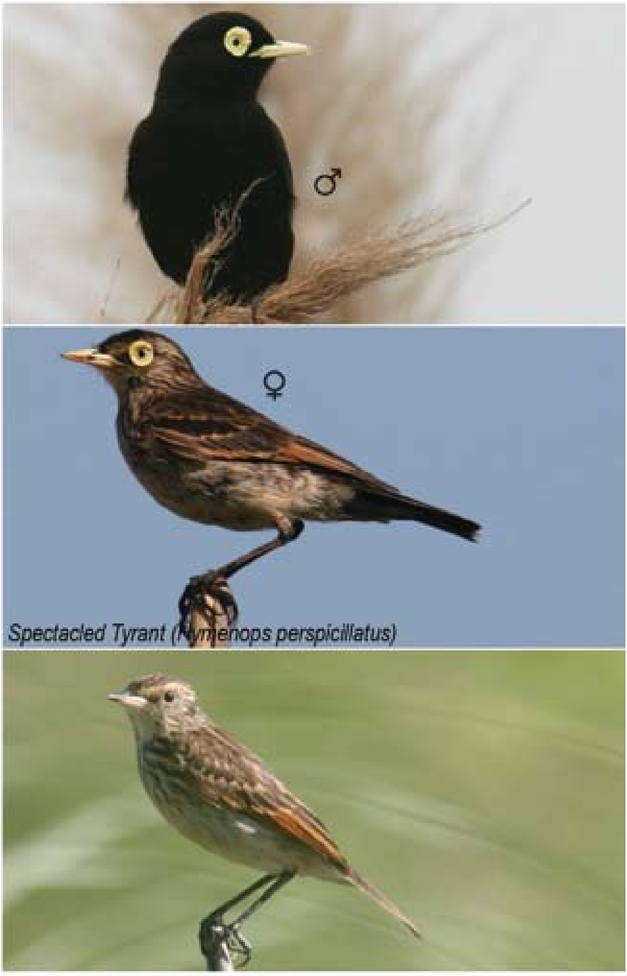
Types of plumage

Plumage is not continuous over the whole surface of the bird, but it does cover it almost entirely. A swan has 25,000 feathers, 80% of them on the head and neck. Small birds, such as the Passeriformes, have between 2000 and 4000 feathers, with 30 to 40% on the head and neck. The feathers may comprise 20% of the total weight of the bird, weighing more than the skeleton.

The plumage of many species of birds differs in shape and color according to the age, sex, and season. When a bird first hatches, it is covered with fine down. Then the juvenile plumage emerges, and depending on the species of bird, it may take months or years for the adult plumage to develop. Males and females often have different plumage. When this occurs, the dominant sex has the more striking colors, which it uses in courting. Some birds molt just before the mating season. Instead of being different from the female all year, they change twice a year, wearing their nuptial plumage only during the mating season.

The first, natal plumage, is called down. Some birds have a more highly developed first plumage. These are "precocial" birds such as ducks and seagulls. Others are naked at first and until they grow their down they are called "altricial." The natal plumage is inconspicuous and does not have striking colors, though newly-hatched partridges, ducklings, etc. may have camouflage colors. Penguins and certain birds of prey have dense natal down to protect them from cold during the long period of parental care they require. The natal plumage is soon replaced by juvenile plumage. The forms of the feathers are similar to those of the adult, but the flight feathers are shorter, softer in texture, and the color pattern is often different. In many cases the juveniles look like the females.

The adult plumage has the final color pattern, although the feathers are molted periodically. The basic or winter plumage is typical of the season when the bird is not reproducing. It may appear at the end of mating season or before migration. The other is the



Example of different plumage within a species. Male, female and juvenile Spectacled Tyrant (below). The latter is very similar to the female but lacks the periocular ring.

Some animals lack the ability to produce melanin. This defect may affect only the plumage or patches of it (partial albinism or leucism), or the plumage and the unfeathered areas, eyes, legs and feet (albinism).

reproductive or nuptial plumage, with more striking colors and sometimes with feathers of unusual length or shape.

Some male ducks have an "eclipse" plumage shortly after nesting, which is similar to that of the females.

Birds that live in rocky areas often show broad bands of contrasting colors, called "disruptive patterns." In some cases spots of bright color (white or yellow) are located on the wings, tail, or rump, which are only visible when they fly, as in the Ringed Teal (*Callonetta leucophrys*). They are thought to function as a warning to other birds to take flight. They are called "warning signals."

Color of the plumage

Color may be produced either by pigments contained in the cells of the barbs (pigmentary color), or by refraction of light due to the physical structure of the barbs (structural color.) Pigmentary colors are produced by three types of molecules: Melanin, which produces dark colors, carotenoids, which produces reds and oranges, and porphyrins, which produce reds, browns, and greens. Melanin also strengthens the feathers, which is why long-distance flyers such as albatross have dark borders on the wings. Excess melanin produces dark, "melanistic" individuals, and lack of it produces pale, "leucistic" ones. Animals totally lacking melanin are albinos.

Structural colors are produced by the disposition of microscopic elements within the feather. Feather barbules are responsible for iridescent colors. Iridescence results from light interference created by a complex structure of layers. The more layers involved, the brighter the color. Noniridescence results from the scattering of incoming light. Tiny vacuoles of air within the cells of the barbs are responsible for this effect. There may be a thin, semi-transparent layer containing carotene. Beneath that is the area containing tiny air bubbles which refract light like a prism. At the center, there is a core of melanin which absorbs reds, so the refracted color is usually green or blue, depending on the amount of carotene in the outer layer.

Some birds are known to have ultraviolet coloration produced by structural color. Because these colors are beyond the range of human perception, they have been little studied.

4. Propulsion and Flight

1. The Strength to Fly

1.1. The Muscular System

Types of Muscles

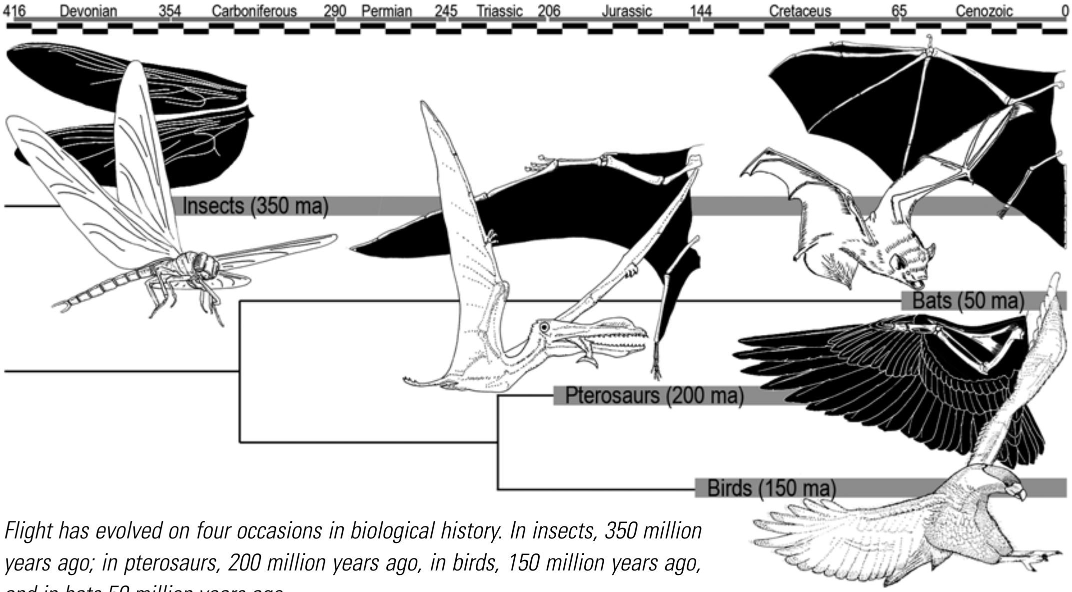
The internal skeleton of vertebrates is a scaffolding which requires a system of muscles for support and movement. Classified by function, the types of muscles are smooth, striated or striped, and cardiac, and white or red, determined by the blood supply which provides the oxygen necessary for activity.

The smooth muscles provide the tension of the body. The bones require tension to maintain them in position, even in repose. The internal organs also need support to keep them in place. Smooth muscle is activated by the autonomous nervous system, and is not subject to voluntary control. Among other functions, it transports food within the digestive system, and pumps blood in the vascular system. This muscle is composed of the simpler cells.

Unlike the smooth muscle, the striated muscles move voluntarily. The smooth muscles do not exhibit the striped structure of the striated muscles. The striations are due to the regular geometric structure of the filaments of actin and myosin. They are highly elastic, which is necessary for locomotion.

This elasticity is due to the filaments of actin, which form a cylinder, and the myosin, which is curled inside of it like the spring of an automobile. The stretching depends on a supply of energy from without. In resting condition, the actin-myosin combination is firm and the muscle is contracted. To release the union and permit stretching, energy from the molecule ATP (adenosine tri-phosphate) is necessary. The global distribution of ATP suggests that it is a very ancient molecule. When an animal dies, the energy supply is interrupted and the muscles contract and harden (*Rigor mortis.)*

To reconstruct the ATP, energy is provided to the ADP which comes at first from glycogen accumulated in the muscle. When the glycogen runs out, fats are consumed instead. Prolonged muscular activity consumes much oxygen and if it is very prolonged, it produces an "oxygen deficit". This deficit is partly covered by the supply of myoglobin in the red muscle, which gives us the following classification of the muscles.



Flight has evolved on four occasions in biological history. In insects, 350 million years ago; in pterosaurs, 200 million years ago, in birds, 150 million years ago, and in bats 50 million years ago.

Red muscle is rich in myoglobin Mb (the muscular hemoglobin which stores oxygen), oxidizing enzymes, and fats. In birds, this muscle serves for long-distance flights. White muscle, on the other hand, is poor in Mb and rich in glycogen, and is best for swift brusque movements, but tires easily. The proportion of each kind of muscle (red or white) depends on the kind of flight which the bird practices. For example, migratory birds have only red muscle, and much fat is accumulated before migration.

Brief violent exercise intensifies the production of actin-myosine filaments, making the muscles large and strong. Endurance exercises cause the cells to develop more mitochondria and accumulate more myoglobin, which supports prolonged activity. These are two types of flight which require different adaptations and each species has its specific proportion of each muscle.

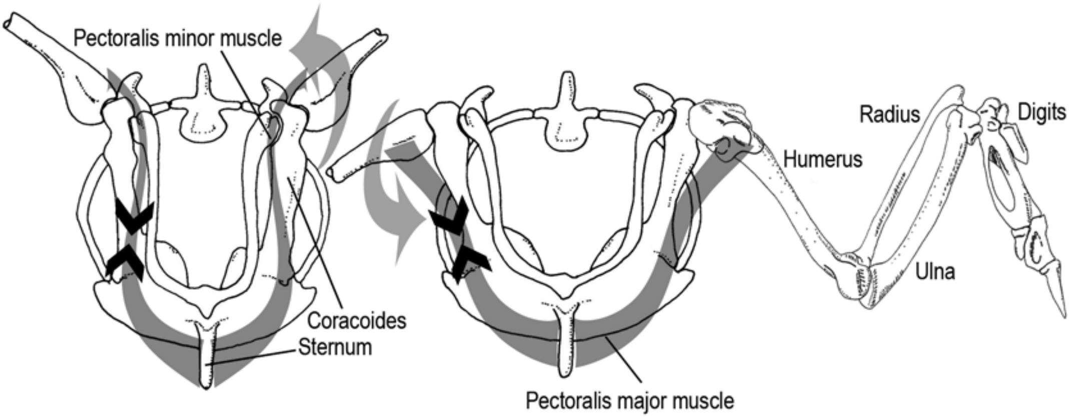
The flight muscles

A muscle produces force only when it contracts, so the muscles are paired, flexors with extensors. The bones are held together at the joints by ligaments (flexible bands of connective tissue). The muscles are inserted into the bones by tendons.

Since nearly all the thoracic and lumbar vertebrae of birds are fused, they have little need of dorsal muscles and these are small. On the other hand, flight requires well-developed pectoral muscles (located in the breast.) Birds which don't fly (such as turkeys and chickens) still have breast muscles, but these are weak. Since they are little-used, they do not require an abundant blood supply, nor do they store myoglobin. Therefore the breast of domestic fowl is white.

The muscles used in flight are the great pectoral, which operates the downward wing-stroke, and the lesser pectoral, which elevates it. The lesser pectoral is called the supracoracoid because it is located over the coracoid bone. Both muscles are located in the breast and connect the keel or sternum with the humerus of the wing. The wing is elevated by a combination of the lesser pectoral muscle and a tendon. They act together as a rope (the muscle) and pulley (the tendon), enabling the wing to be pulled up from below.

To join these muscles to the trunk, birds have evolved a keel. It is a projection like that on the base of a boat, located on the sternum (at the front of the breast.) Bats (which are mammals) and pterosaurs (extinct flying reptiles) also evolved keels, an example of convergent evolution. This structure places the mass of the muscle below the level of the wings, thus maintaining aerodynamic stability of the animal in flight.



The wing muscles work in coordinated pairs, one to raise and the other to lower the wing. The supracoracoid raises the wing and the pectoral muscle lowers it.

1.2. Flight. Birds compared with other flying animals

Flight has evolved at various epochs and in various classes of animal. Insects were the earliest. They are the only invertebrates capable of flight. The oldest known insects date from the Devonian Epoch (410 million years ago) but the first flying insects appeared in the Carboniferous (359-299 million years ago.) Some were as much as 40 cm. long with a wing-spread of up to 70 cm. The wing structure of the insects is very different from that of vertebrates. While in vertebrates the wings evolved from the forelimbs, in insects they are appendages of the thorax specifically evolved for flight.

Among vertebrates, flight evolved much later. The first to fly were the reptiles known as pterosaurs which appeared about 200 million years ago and persisted until the extinction of the dinosaurs about 65 million years ago. Certain dinosaurs evolved into birds about 150 million years ago. Mammals only conquered the skies much later with the appearance of bats, about 50 million years ago.

The true flying vertebrates have similar wing structures, but while the wings of bats and pterosaurs are formed of skin which unites the bones of the hands, legs, and body, the aerodynamic surface of the birds' wing is composed of feathers.

Among the pterosaurs, the fourth finger was lengthened and a fold of skin joined it to the body and legs. Three pairs of muscles moved the wings. The pectoral muscle joined the humerus to the sternum, which was not highly developed. This muscle lowered the wing when it was contracted. The lesser pectoral muscle (supracoracoid) and the deltoid which joined the scapular in the back with the humerus of the wing served to raise it.

Twenty-five percent of the species of mammals belong to the order of Chiropterans (bats, "hand-wings"). Their wings are formed by a prolongation of the second, third, fourth, and fifth fingers. There is a thin layer of skin (the patagium) between the fingers. Some species also have a fold of skin between the hind limbs and the tail.

When the bat flies, it moves both its fore-limbs and its hind limbs, as if it were swimming in the air. (So does the cormorant when it takes off.) Bats sleep during the day hanging by their feet and wrapped in the membrane of their wings, so that they take off simply by letting go and falling. They are principally nocturnal and detect their prey by means of ultrasonic waves which they emit from their mouths. To receive these sounds, their ears are very large. Their body temperature drops sharply during the winter (as does that of hummingbirds), and may even fall below freezing, that is they hibernate. Many species also migrate to avoid the cold.

Flight of Insects

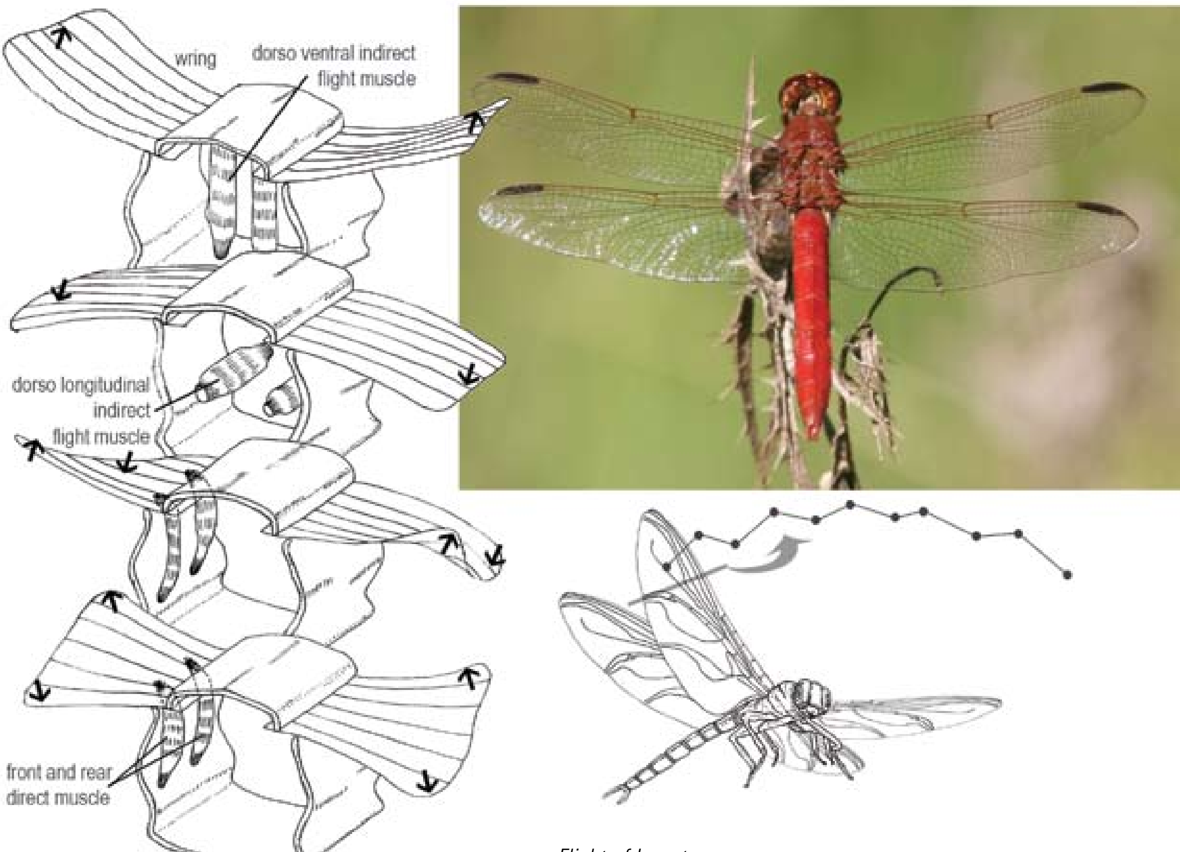
No intermediate fossil forms of flying insects are known, so the evolution of wings is purely speculative. Unlike the wings of birds and bats, the wings of insects are not modified limbs. The wings of an insect resemble the wings of a bird in function but they don't share the same ancestry. This is known as analogy. Perhaps the ancestors of flying insects were designed to be dispersed by the wind, like winged seeds, and later developed the capacity of active flight. In spite of the great variety of forms, all insects have a similar pattern of wing development, which suggests they were all derived from a single evolutionary line.

The wing is made of the same cuticle which covers the body of the insect. It is dead tissue and if damaged cannot be renewed. The chitin molecules are organized in microfibers which are laminated in different directions like plywood to increase their strength. The protein called resilin provides the necessary elasticity in the joint.

The wings are attached to the thorax, and to move them, the whole thorax moves or pulsates. Three sets of muscles are involved. The first, the indirect transversal muscle, joins the upper part of the thorax to the lower. When it contracts, it changes the shape of the thorax, pulling the tergum down and the wings up. When it relaxes, the tergum and wings return to their original positions.

Another muscle, the indirect longitudinal muscle, runs from the front to the back of the segment of the thorax. It closes the lateral walls when it contracts and expands the tergum upwards, so that the wings

The Black Skimmer (Rynchops niger) uses the oncoming wind to provide lift from the surface of the water as hang-gliders do. (Pilots always prefer to take off into the wind.)



Flight of Insects

lower. Whether up or down, the wings are moved by the changing shape of the thorax.

Some species also have two pairs of direct muscles at each side of the thorax which change the angle of attack of the wings. They connect the lateral wall of the thorax with the outer part of the wing. They work in coordination, and when one contracts the other relaxes. While one modifies the angle of attack of the front of the wing, the other acts on the back part. The front of the wing rises while the back lowers, or vice versa.

The nervous control of the wing-beat is achieved in one of two ways. Synchronous control consists in a sequence of one impulse to one wing-beat. This occurs in insects with slow wing-beat, such as butterflies which beat their wings at a rate of 2-4 times per second. Asynchronous control occurs when one nerve impulse generates several wing-beats. This allows flies to beat their wings 100 times per second and reaches 1000 beats per second in certain mosquitoes, avoiding the time-lapse of the synapses of the nervous system.

Insects may reach maximum speeds of 50 kilometers per hour, but they face the difficulty of having to beat two pairs of wings. The front wings generate turbulence which affects the rear wings. Among some insects, either the front or the rear wings are very tiny. For example, the grasshopper has small front wings and flies have lost the rear wings. In the order of the Diptera, (flies and mosquitoes) the second pair of wings has been transformed into balancers, called halteres, which work like a gyroscope to maintain equilibrium during flight.

The dragon-flies beat their wings in opposite directions. While one pair moves up, the other moves down, eliminating interference. Other insects use the two wings as if they were one, creating in effect one large wing. They achieve this by means of hooks which hold the wings together, rather like the barbules on feathers. Butterflies have no hooks to hold their wings together, and therefore fly slowly.

Insects are exothermic (cold-blooded) but they need a high internal temperature (more than 40º C.) to beat their wings at flight speed. They achieve this by pre-heating before taking off (as does the hummingbird.) Dragonflies conserve energy thanks to their large wings, which enable them to flap and glide intermittently. (Many birds do the same.)

2. On how to fly

2.1. Theory of flight

A flying body needs force to support it, which is produced by the wing. The feathers give the wing an aerodynamic profile which enables it to generate air-lift. As the profile of the wing moves forward in the air, the air slides above and below it. The air passing above the wing travels farther and therefore must move at greater speed to reach the rear at the same time. More than two centuries ago, D. Bernoulli discovered that the air above the wing produces less pressure than the slower-moving air below it. This difference in pressure is known as "lift".

The shape of a bird's wing, the type of flight, and the bird's life-style are all intimately related. Short, broad, slotted, elliptical wings increase maneuverability at the cost of lift and speed. These are typical of birds such as owls and most Passeriformes which live in forests, woodland, or shrubby areas and need to maneuver in dense vegetation. High-speed wings are tapered, pointed, and unslotted. To generate sufficient lift the bird must flap constantly. This type of flight is energetically expensive. These wings are typical of birds such as swallows and terns which feed on the wing or migrate long distances. They provide high speed and control. Slotted high-lift wings are broad with a deep camber or curve and very prominent slotting. A broad wing helps to catch rising air. Slotting produces additional lift when soaring. These wings are typical of birds such as eagles, storks and vultures which use rising air masses to obtain lift while using little energy. They then glide to move cross country,

Feathers provide an aerodynamic surface, which becomes distorted (when landing) at low speed due to turbulence.

Flight training of Ardea Alba. Only a few weeks old, these herons exercise their wing-muscles before learning to fly from the tops of the trees where they were born. Flight is innate but practice is required to manage the body in the air.

cover a territory or in search for food. They fly slowly. Long, narrow and unslotted wings generate lift by the great elongation of the wing. But length reduces ease of take off and maneuverability. These wings are typical of birds such as gulls that spend most of their lives soaring over the ocean and usually land on water or in open areas.

Factors which provide lift are:

Speed of the wing in relation to the air. Birds, like the pilots of planes, prefer to take off into the wind.

Surface of the wing. A larger surface provides greater lift, so to descend, birds fold their wings, whereas they expand them totally while gliding.

Curvature of the wing. A curved surface produces more lift than a flat one.

Inclination of the wing with respect to the horizontal ("angle of attack"). A sharper angle produces more lift, up to the point at which it loses sustaining force and the angle must be corrected.

In airplanes, lift is achieved by the force of the motors which push the plane forward, forcing air to move beneath it. Birds may use wing-beats or glide. Lift is increased by slanting the wings upward or by increasing the surface. Planes recur to the same principal using movable ailerons which take advantage of both possibilities. They function during take-off and landing. Birds, on the other hand, can move their wings and their primary feathers at will, creating slots which in this way generate a larger or smaller surface and modify the angle of attack.

A transversal section of the birds' wing reveals a thin, curved plane. The front edge is formed of feathers and skin, very resistant and elastic (the propatagium). Flight produces turbulence at the edge of the upper surface. Three techniques are used to reduce it. The alula is a little wing of three or four feathers located in the front center of the wing. It is controlled by the thumb. Its function is to generate an air channel which delays the loss of lift at low speeds (during landing). Other tools which reduce turbulence are the opening of the primary feathers (like fingers) and the freedom of movement of the coverts (flaps).

In large birds air-flow is smooth, but in small birds and insects it becomes turbulent and chaotic. The air tends to behave as a liquid and becomes "sticky". The smaller the bird, the faster it must beat its wings. The dynamics of flight in small animals is not well understood.

2.2. The flight of birds

Flight may be divided into three phases: Take-off, flight, and landing. The greatest danger occurs during take-off and landing. The relative velocity of the air is low and so is the lift. Different techniques are used during take-off. Large light-weight birds, such as herons, may use their long legs to jump into the air. But

The Energetics of Flight

To measure the energy cost of flight, birds have been tested in wind-tunnels, in order to measure the rate of metabolism as compared to speed, direction, and duration of flight. One of the most interesting of these studies was presented by V. Tucker.

The flight of parrots weighing 30-40 grams was compared with that of sea-gulls weighing 300-400 grams. Because of the different style of flight, the parrot required 152 calories per gram for an hour of flight, while a sea-gull only needed 50. The energy consumption for the parrot during flight is between 13-20 times the metabolic rate in repose, and 11-14 times for the seagull.

The parrot consumes 1.1% of its body weight per hour in fuel, and the seagull half as much. It is difficult to estimate the autonomy, since not all the fat is available for fuel and the energy requirement decreases as weight is consumed. But it is sufficient to confirm the fact that many birds can travel long distances without eating. For example the Golden Plover (*Pluvialis dominica*) flies more than 3000 kilometers from Alaska to Hawaii without feeding.

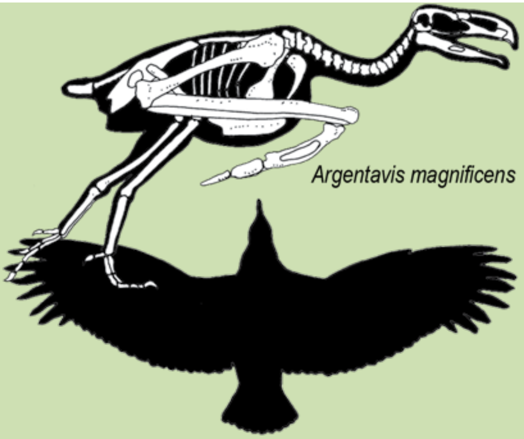
In some ways, flight is more efficient than travel on land. Even small birds may fly for hours at speeds greater than 30 km. per hour, and large birds, such as ducks, may travel at speeds of 70-80 km. per hour. Another point of comparison is the energetic cost of transport measured in calories per gram per kilometer. A mammal uses 10 to 25 times more energy than a bird of the same size. In some cases the bird may be more efficient than a jet.


White-cheeked Pintail (*Anas bahamensis*)

Argentavis magnificens

In 1981 researchers from the Museo de La Plata found fossil remains of a giant condor, *Argentavis magnificens*. The modern Condor, *Vultur Gryphus*, weighs about 15 kilograms and it has often been remarked that this seems to be the upper weight for flying birds. Nevertheless, *Argentavis* is estimated to have had a wing-spread of seven meters and to have weighed as much as 60 kilograms. The remains are about six million years old, and have been found in the provinces of La Pampa and Catamarca, Argentina.

With such a weight and wing-spread, take-off is difficult. Probably it would only have been able to fly by taking advantage of the strong winds from the Cordillera of the Andes. Calculations suggest that it could only have taken off at an air-speed of 40 kilometers per hour. It wouldn't have been able to run, due to its size and weight, so it wouldn't have been able to take off without a strong wind. Once in the air, *Argentavis* must have used thermal updrafts to ascend, but the strong winds from the Andes push these currents east, so that the bird would have been forced to return gliding. If it had been a hunting bird, it would have needed a territory of more than 500 square kilometers. Therefore it is thought to have been a carrion-eater. Gliding at a high altitude, it would have watched the movements of smaller carrion-eating birds to detect dead animals far below. Its metabolism probably required between 5 and 10 kilograms of meat a day.



Argentavis, an extinct vulture, is the largest flying bird ever known.

Remains of mammals found in the same deposit with *Argentavis* indicate that the region was a savannah with a sub-tropical climate and a dry season. The surroundings would have been propitious in summer for a bird which depends on thermal updrafts, but not during the rest of the year. Probably the bird had to make short migrations to nest in the mountains, where winds are strong all year round. This is the habitat of modern condors. Extrapolating from the behavior of modern condors, it is thought to have laid one egg weighing one kilogram every two years.

the flamingo prefers to run a few steps to gain velocity. Other large birds such as swans need to "run" on the water. The smallest birds spend their time in trees and bushes. They take off either with rapid wingbeats or simply by letting themselves fall.

Large birds save fuel by flying in V formation. By measuring cardiac rhythms in pelicans, it has been calculated that the pelican saves between 11% and 14% energy by flying in formation. It can be seen that the birds following a V formation glide more and flap less than the leader. Therefore, the leader of the group changes. Other large birds fly in lines, each bird flying close behind the tail of the bird in front of it, taking advantage of the suction created by the leading bird. It is like the coordinated movement of a team of cyclists relieving the leader.

The largest birds need to glide. This is because the mass of the body increases with the cube of the length (volume,) while the production of energy increases with the square (the area of the transverse section of the muscles.) Large birds have a low relation of mass/energy but they can rise and glide at great altitudes for hours. To do it they take advantage of thermal updrafts created when the sun heats the surface of the ground.

There is evidence that birds know very well where to find these currents, for example, where the terrain shows dark spots due to vegetation (which absorbs more sunlight) or over rocks. They must wait until mid-morning before finding updrafts. In them, they glide in a rising bubble of warm air.

Some birds take advantage of the "obstruction current" produced when the wind meets an obstacle such as a hill, mountain, or even a wood. The air rises to pass over the obstacle and lifts the bird with it.

Sea-birds use the steady winds over the ocean. Since thermal updrafts are not produced at sea, birds ascend against the wind, and descend with it. Sea-winds flow in layers at different speeds. The speed of the bird increases as it swoops downwards, and it uses this increased speed to gain altitude against the wind. Satellite photography has shown albatrosses flying at 80 km. per hour, and covering 900 km. per day for various weeks before returning to land. These birds fly not only all day, but also all night if there is moonlight.

The maximum speed of the bird depends on the design of the wing. Swans beat their wings less than once a second, while a small bird beats its wings 4 times per second. A hummingbird beats its wings 10 times per second and reaches a velocity of 100 km. per hour. The fastest bird is the Peregrine Falcon (*Falco Peregrinus*). Its wing design enables it to fly at 150 km. per hour in level flight, and by diving with folded wings may reach 300 km. per hour.

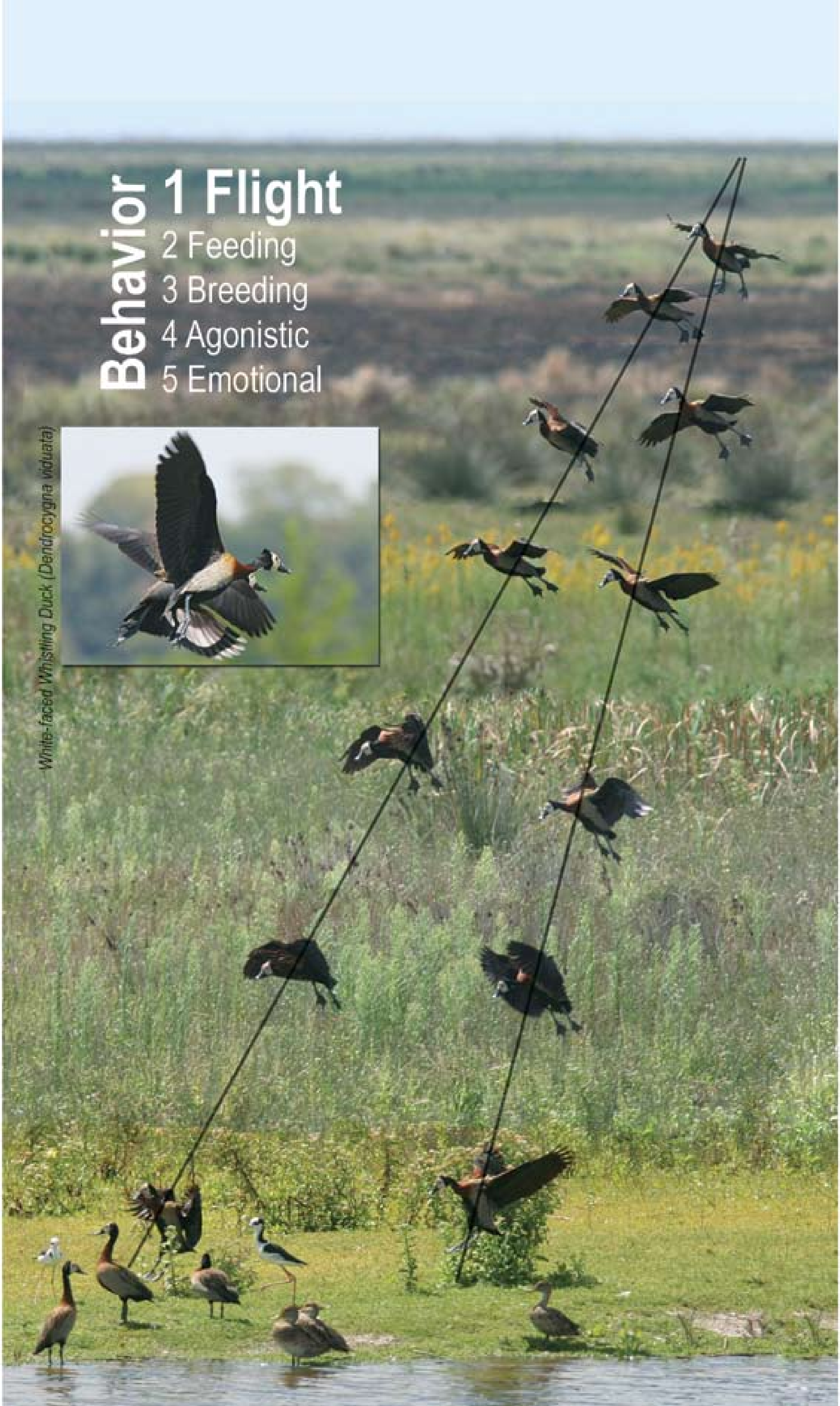
Landing is riskier than take-off, since it must be done slowly. The birds which land on water have the advantage of a soft, flat surface without obstacles to land on. Ducks and swans slide in on their feet and bodies. Herons and flamingos land on foot running.

Landing on branches is more difficult. First the bird reduces its wing-beat and lets itself fall. Then it twists its wings to increase the surface area, which produces lift and reduces velocity. The tail is opened like a fan and lowered to act as a brake. If the bird is approaching very fast, it may "reverse propellers" by flapping in reverse with the wings in a vertical position. The moment of impact is risky because a gust of wind may move the branch or destabilize the bird. The legs are extended forward and grasp the branch, while the muscles of the legs absorb the impact. (When space permits, birds land on branches by letting themselves drop below the level of the branch and then rising to reduce velocity before gripping it.)

Whether or not a bird can turn at high speed is partly determined by the design of the tail, which serves as a rudder. The feathers are broad and rigid and can open and close like a fan. They move up and down or twist to control the turn. Other ways of turning are to hold one wing higher, or to beat one win more strongly, than the other.

Great Egret (Ardea alba)


Great Egret (Ardea alba)



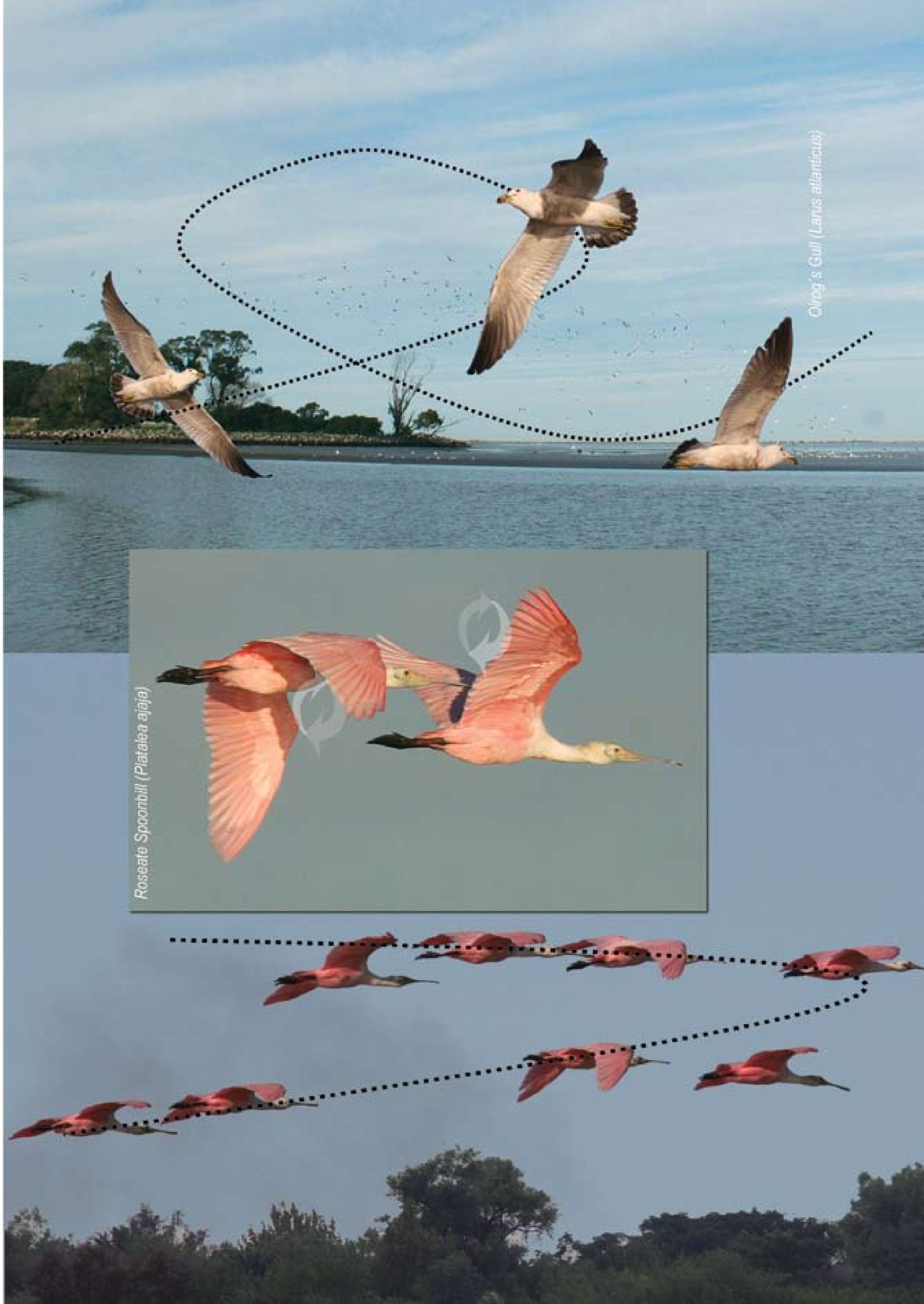
White-faced Whistling Duck (Dendrocygna viduata)

Shown here are three ways of saving energy during flight. The first two cases refer to non-powered flight. The bird does not provide thrust.

The first one, static soaring, takes advantage of an up-draft produced when the sun heats the ground enough to make the air rise. Up-drafts are produced over dark areas (vegetation which absorbs sun-light, plowed land, or rock). A bird must wait until mid-morning for them to form. It then can gain altitude with little input of energy within an air-bubble ascending at a rate of four meters per second. As it rises, the up-draft cools and when it cannot rise more, the bird may circle within it with little or no flapping, or glide away from it, until it finds another to ride up on. This is used by birds with slotted high-lift wings.

Thermal up-drafts are not produced over the sea, so among marine birds gliding requires a different strategy (dynamic soaring). The steady winds provide lift. The sea-winds are usually steady, and the bird rises against the wind as a kite does. Then it turns and swoops down-wind, gaining momentum which enables it to turn back against the wind and rise again. This is used by birds with high-aspect ratio wings.

Flocks which fly in "V" formation also use an energy-saving strategy involving powered flight. When a bird flies, each wing-beat generates a vortex which may be used by the bird behind it. The vortex is a spiral of air which revolves from the outside toward the inside of the wing, so that the ascending part of the vortex can be used to lift the following bird. A "V" formation saves energy for the bird following behind at the same altitude, and to one side of the bird ahead. Therefore the leadership of the flock changes, so that each has a chance to take advantage of the saving. Other large birds fly in straight lines, with the following bird flying very close to the one ahead, to use the suction produced by the preceding bird, as race-cars do. This type of flight is most often used by birds with elliptical o high-speed wings.

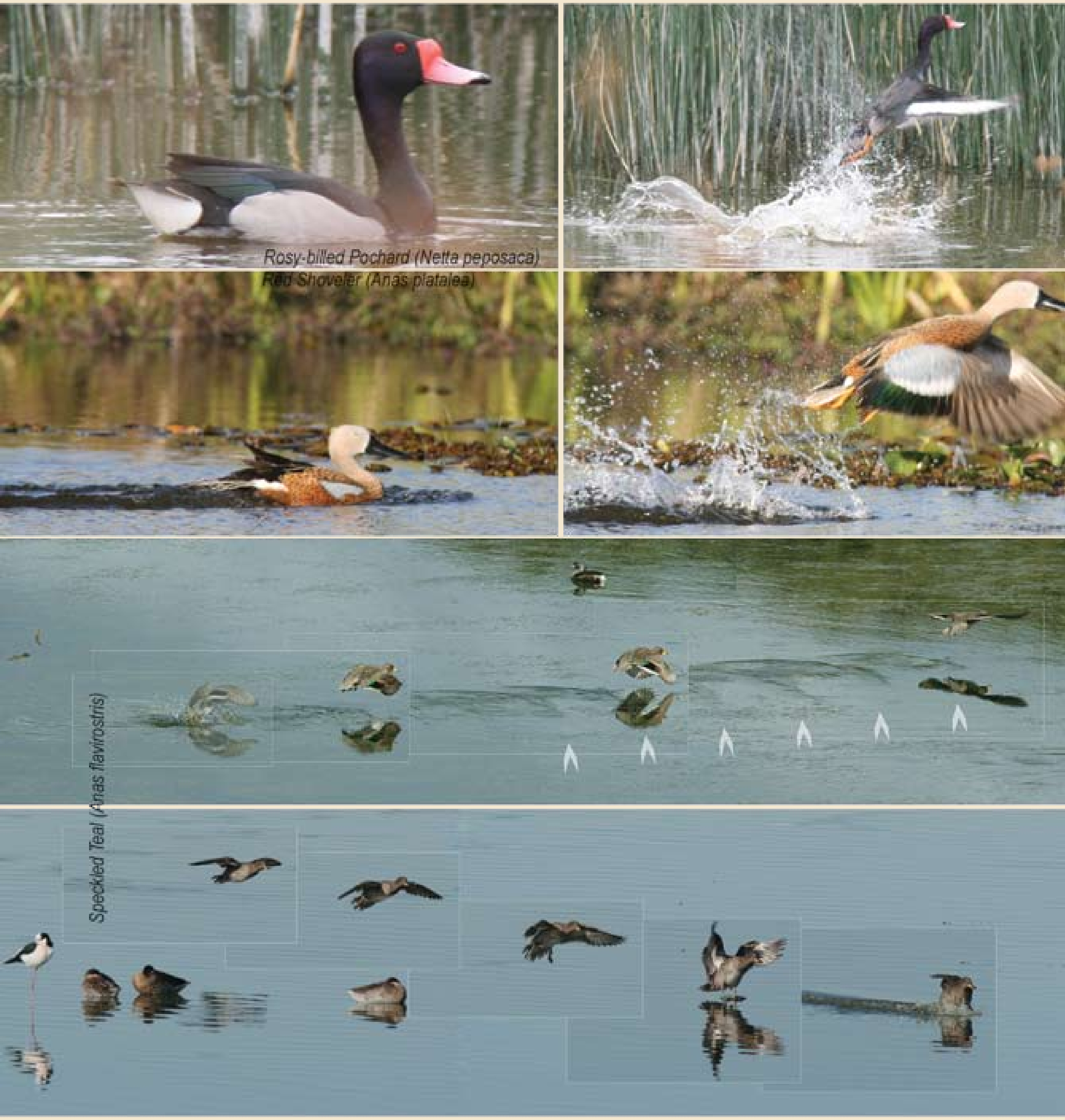

Olrog´s Gull (Larus atlanticus)
Roseate Spoonbill (Platalea ajaja)

A short run to facilitate take-off. The lobed foot of the coot barely penetrates the surface of the water and the wing-beat is synchronized with the steps.

Red-gartered Coot (*Fulica armillata*)

Flamingos (Phoenicopterus chilensis) taking off. They gain impetus running with long strides while flapping their wings. These are running in shallow water parallel to the coast line. In photo 1, bird A remains passive and is the last to start, while C is already in the air. In photo 2, bird B has not yet taken off, but all are either running or flying. In photo 3, bird C and several others are air-born, while A and B are still running. They form a compact group and fly together to their destination. Flamingos are gregarious birds and imitate each other.

The Neotropic Cormorant (Phalacrocorax brasilianus) has such short legs it can't walk. It takes off with both legs working together in short jumps, wings out-stretched to the maximum. The webbed feet continue to beat together against the air as it gains altitude. In the upper right photograph, its feet are also seen beating reflexively against the air as it takes off by dropping from a post.



Ducks taking off and landing. The vortex of each powerful wing-beat of the Speckled Teal disturbs the surface of the tranquil water, leaving a clear pattern.

Falconiformes, (this page) and Passeriformes (next page) prefer to take off and land from a high perch such as a branch or post. Passeriformes and many Falconiformes have short broad wings which give them maneuverability in thick vegetation. But they also have short legs, and cannot take off with a run as wading-birds do. Birds are able to fold their wings to reduce the surface area, bend them, or twist them, and use inertia to improve maneuverability.

Hooded Siskin (Carduelis magellanica)

White-crested Tyrannulet (Serpophaga subcristata)

Blue-and-Yellow Tanager (Thraupis bonariensis)

Tropical Kingbird (Tyrannus melancholicus)

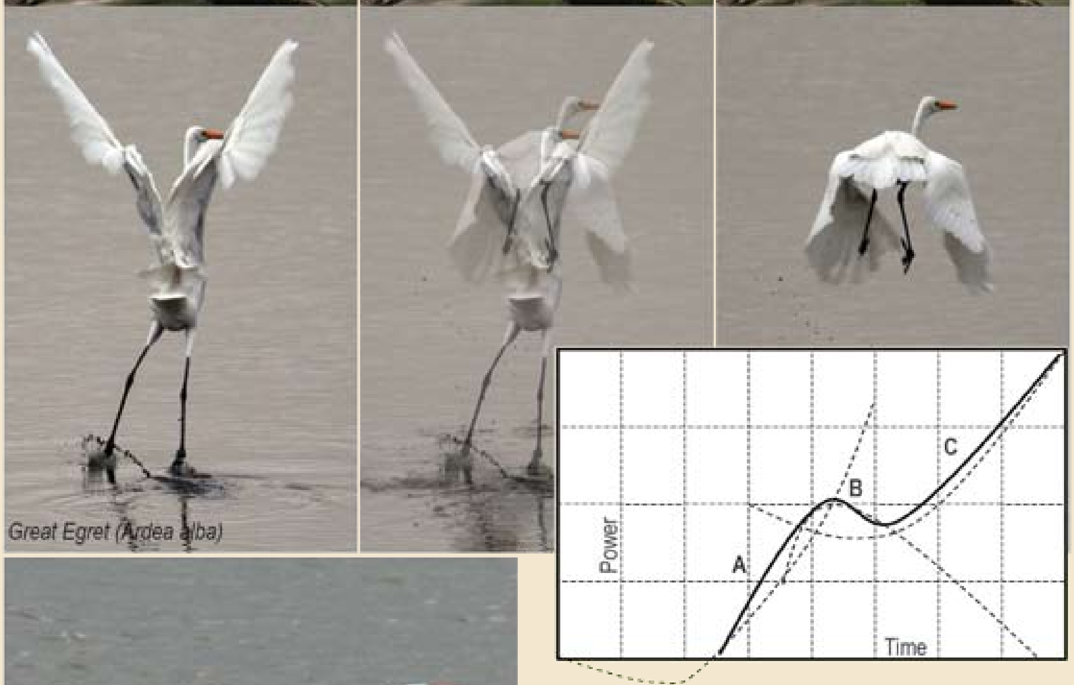
Vermilion Flycatcher (Pyrocephalus rubinus)

Double-collared Seedeater (Sporophila caerulescens)

Rufous-bellied Thrush (Turdus rufiventris)

Passeriformes usually let themselves fall from a branch to take off. They only spread their wings for take-off when they have a head-wind to provide lift.

Bran-colored Flycatcher (Myiophobus fasciatus)



Take-off with two successive thrusts. The first thrust (A) is with the legs, which provides the greater part of the take-off speed. The second is with the first wing-beat (C) which overlaps the first thrust. Many birds do not have feet strong enough to obtain initial thrust and must either take off into the wind, or by dropping from a branch.

Snowy Egret (Egretta thula)

Snowy Egret (Egretta thula)

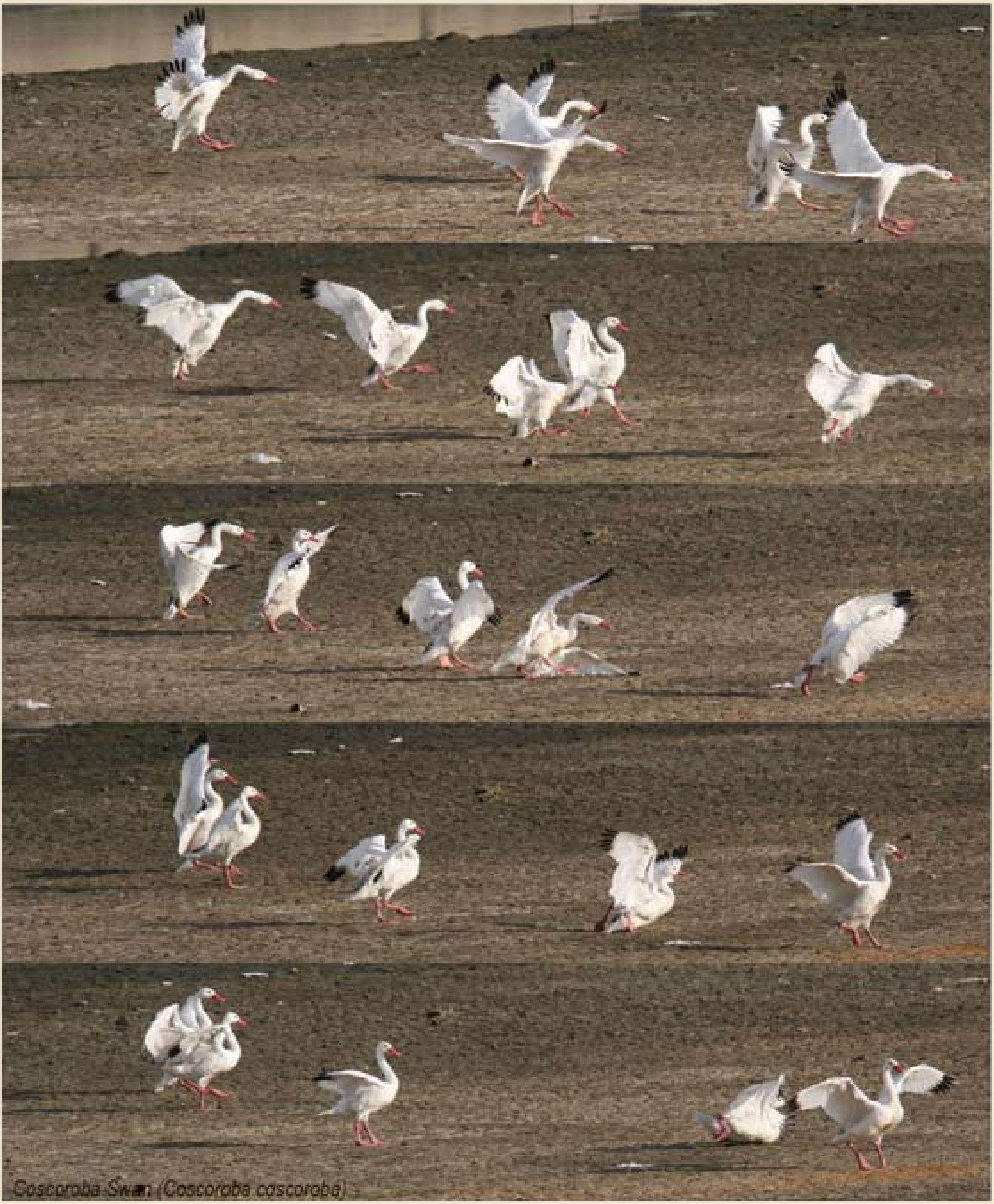
Great Egret (*Ardea alba*)

Great Egret (*Ardea alba*)

Great Egret (Ardea alba)

White-necked Heron (Ardea cocoi)

White-necked Heron (Ardea cocoi)



Coscoroba Swan (Coscoroba coscoroba)

A Coscoroba Swan (Coscoroba coscoroba) takes off by means of a short run with its webbed feet on the water. It also uses its feet as brakes, and slides on the water when landing. These birds are not adapted to descend on land, which is difficult for them and may cause them to fall. For landing they require a long glide, and have very little maneuverability.

Chilean Flamingo (*Phoenicopterus chilensis*)

South American Stilt (*Himantopus melanurus*)

Limpkin (*Aramus guarauna*)

Southern Screamer (Chauna torquata)

Black-crowned Night-Heron (Nycticorax nycticorax)

Roseate Spoonbill (Platalea ajaja)

Even when the difference in size is considerable (for example between Flamingos and Stilts) the landing technique is similar. In both cases the legs are disproportionately long. In flying they trail behind the body, but on landing they are flexed forward. Finally, as they touch down, they run a few steps to stop. Many other birds land the same way.


Anhinga (Anhinga anhinga)


Southern Caracara (Caracara plancus)

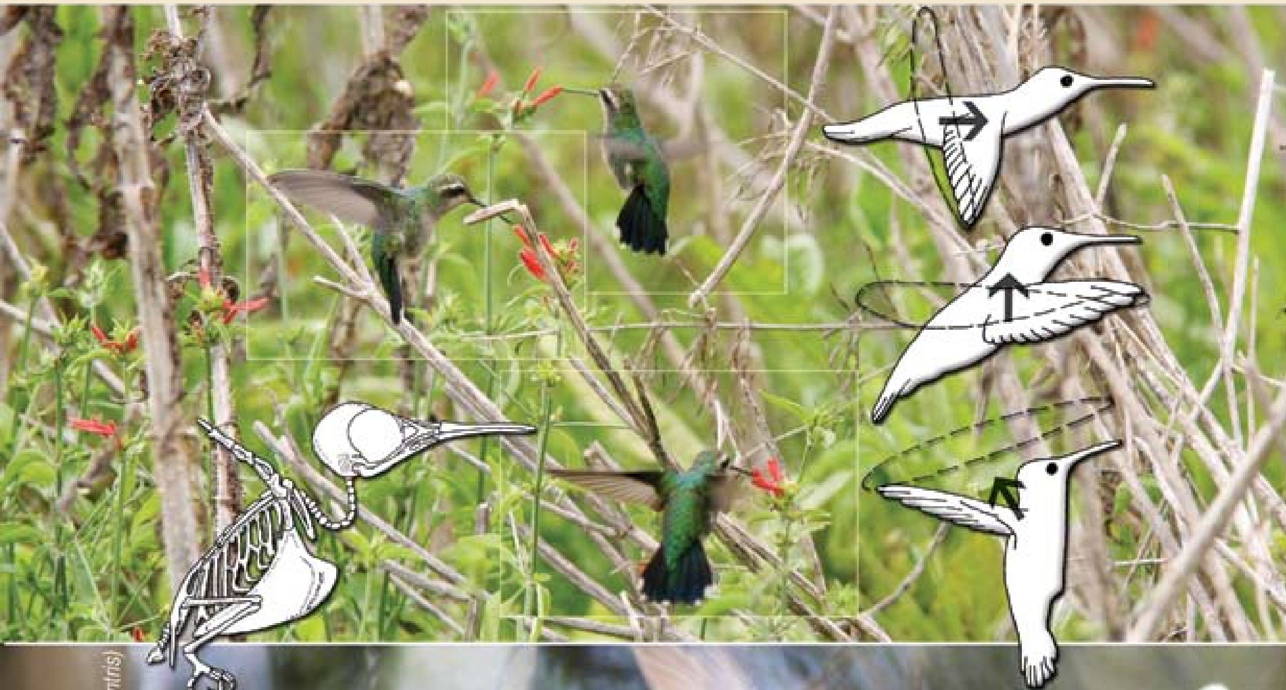
For large birds, landing on a branch can be risky. However, they are well equipped for these maneuvers. Only very young birds, or birds landing in a strong wind which moves the branch, may be seen to miss. In such cases they prefer to land in thick foliage which makes it safer.

Whistling Heron (Syrigma sibilatrix)

White-tailed Kite (Elanus leucurus)

Two forms of hovering. The White-tailed Kite (Elanus Leucurus) is hovering in place watching for prey. They often take advantage of the wind to hold a position without wasting energy in flapping.

For a hummingbird (Glittering-bellied Emerald - Chlorostibon aureoventris) hovering is very different. A hummingbird can fly backwards, holding its body vertically. The wings then move back and forth (instead of up and down). This forces the air down, instead of backwards. The strength of the wing-beat is the same on the up-beat as the down-beat, because the structure of the pectoral muscles is symmetrical, the muscles which lift the wings having the same strength as those which lower it. Thirty percent of the body weight is devoted to these muscles. The joint cavity of the



Glittering-bellied Emerald (Chlorostilbon aureoventris)

shoulder is very wide, and the keel is highly developed. Measurements show that 75% of the force is obtained on the down-beat and 25% on the up-beat. Among insects the power is equally distributed, and the rest of the birds obtain the 100% of the lift on the down-beat. This is one of the most complicated forms of flight, but the one with the greatest capacity of maneuverability. The painting of the hummingbird is a pre-Columbian tapestry in the Fine Arts Museum of Buenos Aires.


American Wood Stork (Mycteria americana)

5. Song and feeding

1. Respiration and song

1.1. The respiratory System

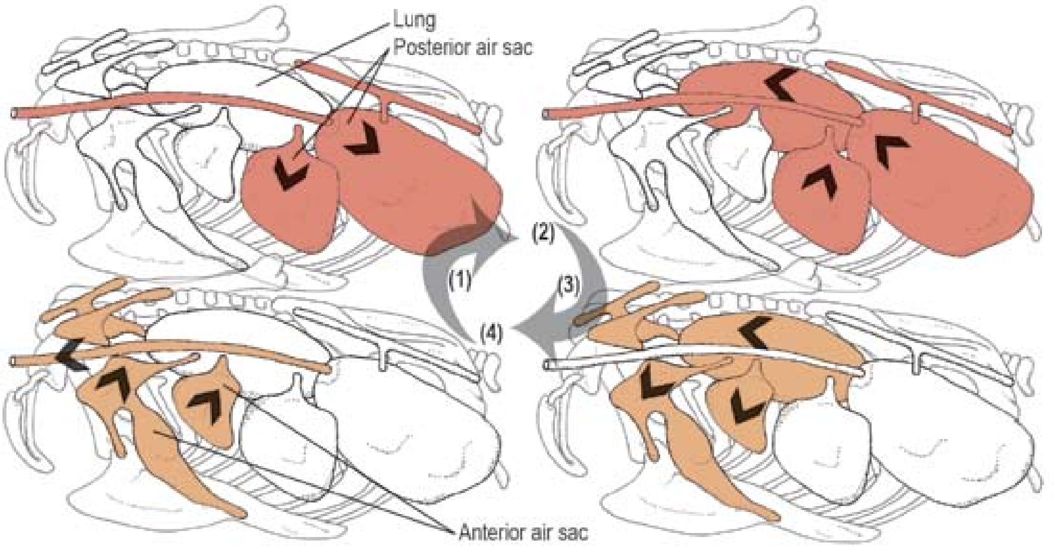
Birds compared with mammals

The respiratory system of most vertebrates is composed of closed sacs (the lungs) with an exterior connection (the trachea). This system does not permit the total emptying of the interior air during exhalation. The fresh air entering the lungs mixes with used air which cannot be completely exhaled. Among birds, the process of breathing occurs in a four-phase cycle of two inspirations and two exhalations. The air moves in a one-way airflow system through the lungs and the air sacs before being exhaled. Two batches of oxygen-rich air reach the lungs and the air sacs.

The bird achieves a nearly continuous flow of air passing through the gas exchange sites with the extraction of oxygen both during the inspiration and the exhalation. As a result of this there is little oxygen-poor air in the lungs of birds after the completion of the cycle in contrast to that of mammals. Mammals inhale and exhale in a two-phase cycle, in which the gasses exchange takes place in the alveoli only during inspiration. In the exhalation phase carbon dioxide is released.

The respiratory system of birds occupies more volume than that of mammals. Among humans, the lungs occupy 5% of the volume of the body, while in ducks the respiratory system occupies 20%, 2% for the lungs and 18% for the air sacs. The lungs of birds are almost rigid but the air sacs are flexible. Among mammals, the lungs are flexible, but harden with aging. In 1758 it was observed that a bird could breathe even with the trachea blocked, if it had a connection between the bones and the exterior. Some bones of birds contain air instead of marrow (as mammals have) and they are connected with the respiratory system.

A century before this discovery, it was already known that birds have membranous sacs full of air, which occupy more volume than the lungs, but have less available surface for the interchange of gasses. The bird does not breathe with these sacs, nor do they aid in flight -inflating them does not make flight easier.



The respiratory system of birds includes air sacs as well as lungs. The air circulates through the lungs in one direction from the posterior sacs to the anterior ones in four steps.

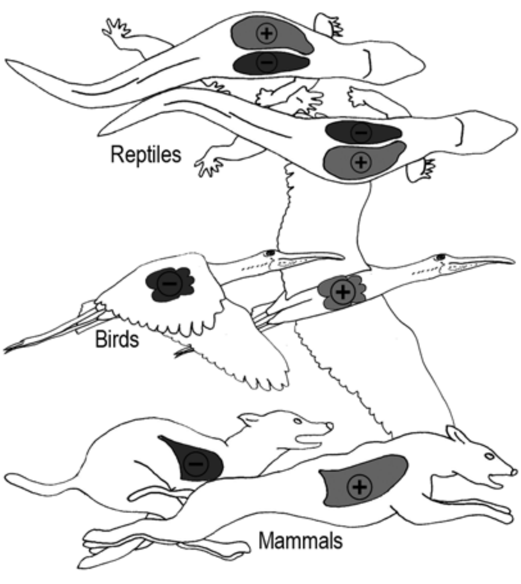
However, they may provide buoyancy for water-birds. Birds have between six and twelve air-sacs, most often nine, associated with the lungs and distributed within the body. Some of the bones are hollow (pneumatic) and form part of this system of air-storage.

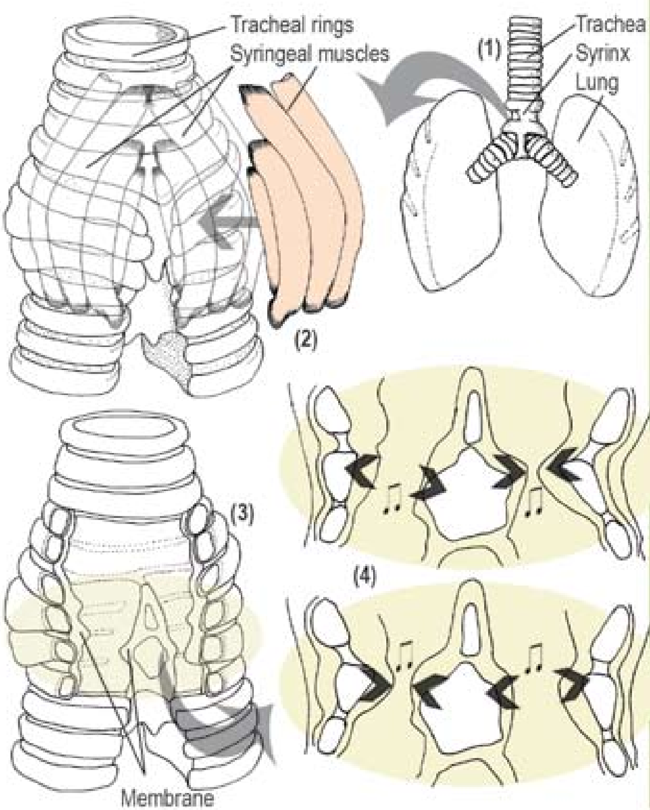
Another difference between birds and mammals is that mammals have a diaphragm between the lungs and the liver, which acts to fill and empty the lungs. Birds do not have this diaphragm since its structure would be incompatible with the network of air-sacs branching throughout the body. A mass of smooth muscle surrounds the soft organs and acts on the air sacs making them function like bellows. When the smooth muscles contract, they put pressure on the respiratory organs, moving the air.

The trachea divides into two bronchi before reaching the lungs (in mammals it divides inside the lungs.) The bronchi have branches which supply air to the air sacs. The bronchi are subdivided to form small parabronchi with walls perforated by air capillaries. They are like an air-filled sponge. These capillaries are the site of the interchange of gasses with the blood, which flows in the opposite direction. It is speculated that the dinosaurs ancestral to birds already had air sacs and pneumatic bones, which could have helped supply the necessary energy to allow them to walk and run on two legs.

The low concentration of oxygen believed to have existed in the atmosphere during the period 275-175

Birds synchronize their breathing with flight to force the air into the lungs. Reptiles cannot do this because their lungs expand and contract alternately, that is, one lung expands while the other contracts, but some mammals do synchronize their breathing when running.





The syrinx (1) is the instrument of song of the birds. The muscles which surround it (2) permit movement (3) of the internal membranes which modulate the passage of air.

million years ago may have stimulated the development of an efficient respiratory system in animals of high metabolism. During that period the concentration of oxygen in the air was about half that of the present (11% as against 21%), which would be the equivalent of living at an altitude of 5000 meters. A respiratory system like that of birds would have offered an important evolutionary advantage to dinosaurs, as against mammals which fell behind in evolution.

Advantages of this type of respiration

Since the air passes through the birds' lungs in only one direction, the maximum interchange of gasses is assured, without mixing fresh with used air. The air flows against the direction of the blood, that is, air and blood flow in opposite directions.

On entering, the air has the maximum quantity of oxygen and interacts with blood which has already passed through the lungs. When it goes out, the air contains less oxygen and comes in contact with blood which has just entered, and is starved of oxygen. In this way, a steady pressure of oxygen is maintained during the whole course and the interchange of gasses is constant.

Flight requires about fifteen times as much oxygen as repose. Bats can fly, but their mammalian lungs do no permit them to breathe well at high altitudes as birds do. The efficiency of the birds' respiratory system permits high-altitude flight.

The air sacs are not a reserve of air. The consumption is much greater than the reserve they can supply. Their utility is linked with the four-phase cycle and it is speculated that the air sacs act as bellows to move the air. This system helps maintain the volume of air in the body almost constant, which contributes to stability during flight. The volume of the air sacs in the chicken (*Gallus domesticus*) is about 500 cc. and each normal breath replaces about 10% of this volume.

The Gruiformes, and some other groups of birds, have a long trachea coiled in the sternum, which enables them to produce loud cries which carry great distances.

The movements involved in flight help the bird to breathe. The respiration of ducks and swans is audible when they fly low, and the rhythm is synchronized with the wing-beat. This synchronization is facilitated by the structure of the thorax, that is, by the movement of the sternum which is transferred to the ribs by the furculum which functions as a flexible arch and transfers the movement of the wings to the ribs. This has been verified by X-rays of starlings, which breathe 15 times per second.

1.2. Behavior related to song

The sound-producing mechanism

The difference between the song of birds and the sounds produced by mammals is due to differences in the sound-producing apparatus. The song of birds is produced not by the larynx as in mammals but by the syrinx (from the Greek "pan pipes"), a widening of the trachea after it branches, just as it reaches the lungs. Since each branch of the trachea has his widened box, the bird can produce two notes at once.

After many years of research, C. Greenwalt was able to explain many of the secrets of birds' song. The form and size of the syrinx, and the presence of vibratory membranes, and the muscles which control them, varies in different species.

The syrinx is a highly-developed and complex organ. Some birds, such as storks and rheas, have no syrinx, and therefore do not sing. The Passeriformes have the most highly developed syrinx, and within this order the birds of the family of Oscines possess the best musical instruments.

The syrinx is formed of tracheal and bronchial rings, which are widened to form a resonating box. External muscles dilate or contract the aperture of the tube to regulate the passage of air. It has one or two vibrating membranes, the tympaniform membranes. According to the tension of the membranes and the wideness of the aperture, different types of sounds are produced. An increase in the tension of the tympaniform membranes increases the frequency of vibration and raises the pitch of the sound. An increase in the diameter of the aperture increases the sound's volume (loudness).

The complexity of the song depends on the number of muscles and tracheal rings which come into play. The syrinx of the Passeriformes is very complex, and therefore their voices are highly varied.

Ducks and sea-gulls have only one pair of muscles to operate the syrinx. The hummingbird has two, and some Passeriformes may have up to nine.

The two sides of the syrinx are independently controlled. Some notes are produced by the right side and others by the left. So the bird can sing "duets" with itself, the two sources of sound producing sound-waves of independent frequencies which are not related harmonically. Sometimes only one pair of membranes functions when a bird sings, but in a complex syrinx all four function independently.

The lungs and air sacs contain an air column which passes through the tympaniform membranes, which are contracted by the muscles of the syrinx. The trachea is the resonating box and its length and volume is related to the tone and frequency of the song. The voices of large birds are deeper and hoarser, while small birds produce shriller notes.

The frequency of the note is a function of the length of the trachea. A bird may modify the frequency of the note by lifting its head, which changes the length of the trachea without producing resonance. Flapping the wings while sitting on a branch and singing, also modulates the song.

Some birds, such as storks and herons, have long tracheas, which could be a disadvantage with regard to respiration. This column of used air, which will be re-inhaled, can be converted into an advantage in large birds. For aerodynamic reasons, large birds beat their wings slowly and can synchronize their wing-beats with their respiration so that the flight muscles press rhythmically on the thorax and air sacs. This slow respiration may diminish the level of carbon dioxide (CO_2) in the respiratory system. This affects the balance of gasses which therefore requires a certain amount of used air in the system to maintain the correct balance.

In other birds, the trachea is lengthened within the sternum. For example, the Gruiformes (cranes) have deep loud cries which can be heard at a great distance. This is due to the trachea which is curled within the sternum, making it longer than the neck.

In mating season some birds combine song with wing-flapping exhibitions, which modulates the passage of air through the syrinx and gives the song greater variety.

On the uses of song

The song is one of the tools of communication of birds. They also emit various other sounds which have significance. It is not possible to define a limit between "songs" and "calls." "Song" is related to territory and sex, while "call" signals fear and warning. The calls consist of short and simple notes, while song is complex and rhythmic.

Birds also communicate in other ways. Woodpeckers signal each other with blows of the bill on wood, when they peck at a trunk. Storks communicate through posture and body movements. Sounds are also produced by the feathers or by beating the wings. In certain cases, the external feathers of the tail are thin and rigid, so that brusque movements produce whistling sounds.

Song may indicate sex and individual identity, may stimulate sexual desire, attract a mate, or frighten away a rival, or indicate curiosity, alarm, or fear. Since song is different in each species, as a sexual signal it functions as a mechanism to isolate each species reproductively.

The individual singer can be distinguished by variations of tone, rhythm, and repertory. Vocabulary also differs between different populations, forming dialects. Individual differences in birds' songs enable them to recognize their mates within a colony. Such variations are related to modulations of volume or frequency of the song. An extreme case of recognition by call occurs among the Emperor Penguin (*Aptenodytes forsteri*). The total population of these birds may be 300,000 couples and they nest in twenty-three colonies on the Antarctic continent during the winter. They don't build nests, so to find their mates or their young they depend on calls. Among thousands of individuals, the noise has been measured at 70 decibels, so it requires skill to pick out the cry of a single baby penguin.

Territorial song, like the exhibition of plumage, is a battle of nerves. Sometimes it is accompanied by wing-beats, which may have an effect on the modulation of the song, as in the Oven-bird and the Wren. It is a way of discharging tension and a manifestation of contradictory impulses of fight and flight.

The technique consists in singing and waiting to listen for a possible rival to answer, to recognize and locate him, and to estimate his aggressivity. Song must be repeated persistently.

While song is a long-distance warning, plumage has a limited radius of action. There is an equilibrium between song and striking plumage. The best singers are usually birds without striking plumage, such as the Chalk-browed Mockingbird (*Mimus saturninus*), a bird with a varied and melodious song but drab plumage. Birds which live in densely wooded areas sing louder than those which live in open areas where sound carries better. (Recently it has been demonstrated that birds which live in the city and sing in competition with the noises of traffic, sing louder than those of the same species living in quiet country habitats.) Some birds, such as the Guira Cuckoo (*Guira guira*), always sing while flying, but most prefer to sing while perching in visible places.

Song has annual cycles related to the reproductive cycle, and daily cycles which depend on the length of day. Song is loudest and most continuous at dawn and sunset. During midday, when the temperature is high, birds rest. They sing the most in spring when hormones are active and they are claiming their territories.

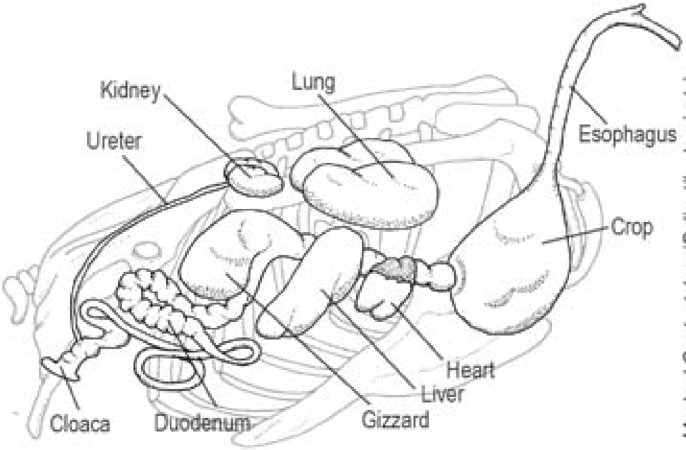
The development of the syrinx is the same in females as in males, but in many cases, only the males sing. When the male hormone testosterone was injected into female birds during the spring, the regions of the brain which control song developed, and they sang just as the adult males do. It seems that females have the same capacity, but lack the hormonal stimulation for singing.

Learning the tune

The basic structure of the song is innate, species specific, and transmitted genetically. This has been demonstrated in studies of the White-crowned Sparrow (*Zonotrichia leucophrys*) which uses different dialects. When young birds were raised in soundproof rooms, at maturity they all sang a simplified version of the basic song of their species.

Baby birds hear their parents and assimilate the song by imprinting. The imprinting stage occurs during the first three months of life, before the young birds


Grassland Yellow Finch (Sicalis luteola)



The digestive system of birds.

Masked Gnatcatcher (Polioptila dumicola)

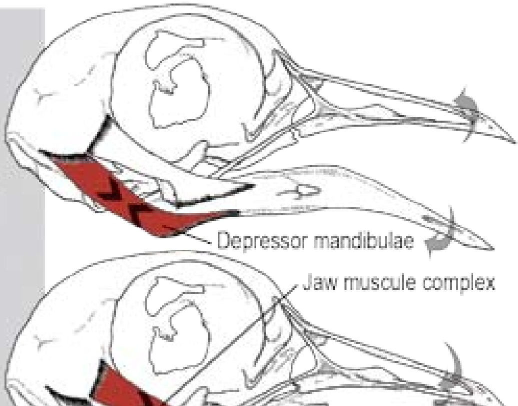
begin to sing. When the bird reaches adulthood and its hormones stimulate it to sing, it will remember the parental song pattern it learned as a baby.

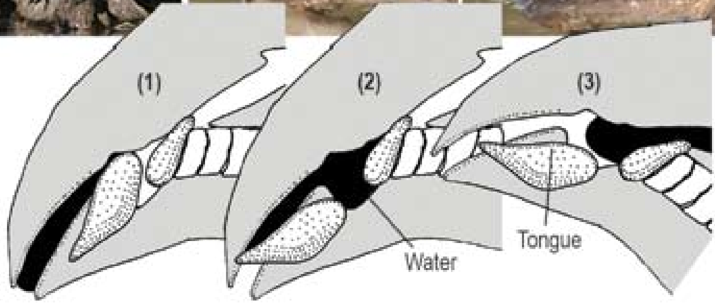
Birds which were born deaf sing a truncated, disconnected song, proving that imprinting is necessary. On the other hand, birds which lost their hearing after the period of imprinting sang in the dialect learned from their tribe. But this dialect underwent gradual changes over a period of time, showing that feedback is necessary to maintain the dialect. If a bird only hears the song of another species, it does not learn.

Song may be modified in some species more than in others. Some never change their song, while others may do so throughout their lives. Some birds can learn to mimic and repeat sounds. Parrots and crows are good mimics, but some birds incorporate songs of other species or sounds produced by inanimate objects. Some birds are known to imitate sounds such as the ring of a telephone, automobile sounds, even an electric saw. But they are not always mere imitations. Investigations into the intelligence of birds have shown that they can understand human language much more than has been thought.

The muscles which open the bill.

Great Pampa Finch (Embernagra platensis)





When birds drink, water enters the bill (1) as a result of adherence and the action of surface tension (as in a capillary tube.) Then the head is lifted, the tongue moves and the throat opens simultaneously as the water is swallowed.

2. Digestive system and feeding behavior

2.1. Digestive system

Flight requires swift and complete digestion. A thrush eating fruit will excrete the seeds within 45 minutes. A bird must eat constantly, but undigested food is a weight which cannot be transported.

Birds have no teeth and must depend on the bill to cut their food. If they can't cut it, they must swallow it whole or abandon it. Their scarcely developed salivary glands function only enough to moisten the tongue.

Birds which eat dry food have mucous glands which lubricate the food. In some cases, such as that of the swallows, the salivary glands are adapted to produce a glue-like substance which holds together the nest. Aquatic birds have no glands in the mouth. In general, they have very few taste buds.

The tongue may vary in shape according to the kind of food the bird eats, but usually it is thin and triangular. The tongue and the muscles that provide for tongue movement are supported by the hyoid apparatus. The tongue cannot be extended beyond the bill, except in a few specialized birds such as the woodpeckers and hummingbirds. In these birds the horns of the hyoid apparatus are so long that they enable the tongue to project extensively.

The size and structure of the tongue is adapted to different feeding habits. A long and barb-tipped tongue secures food, a hair-like structure strains food, a feathery one absorbs juices, a short and flat one manipulates food, a long and forked tongue laps up nectar, etc.

A muscular tube called the esophagus extends from the mouth to the stomach. It contains some mucus glands and a widening called the crop in which food is temporarily stored. This permits rapid eating, without waiting for digestion. Birds without a crop

The kidneys release a whitish material (due to uric acid) which is semisolid (because the water is reabsorbed.) Since birds have no bladder, they release wastes frequently.

may store food in the esophagus. Neither the crop nor the esophagus digests food. Some birds, such as pigeons and flamingos, produce a highly nutritive liquid called “crop milk” with which to nourish their young. This “milk”, produced by superficial cells of the lining of the crop, contains no sugar but is rich in protein and fats.

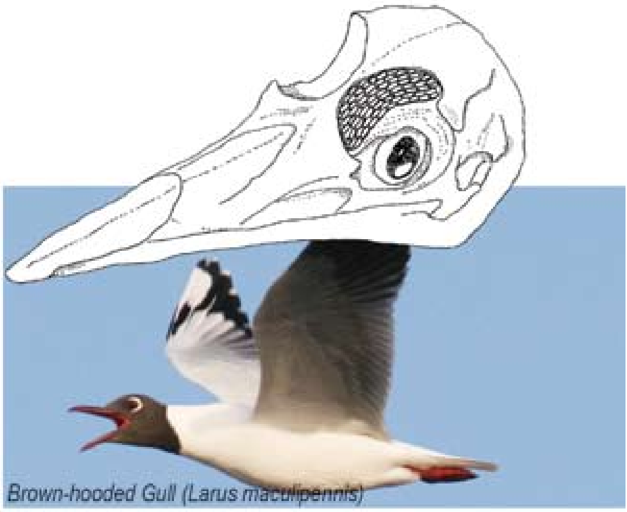
The esophagus leads to the stomach, which is divided into two parts. The upper one is soft and has glands which secrete digestive enzymes, particularly pepsin. The lower part is called the gizzard. The gizzard is better developed in grain-eating birds than in meat-eating birds. The digestion of seeds requires much more mechanical grinding than the digestion of proteins. The walls of the gizzard produce a keratinous substance, like that which composes the scales, which forms plaques or ridges. These ridges contract with alternating movements and with the help of ingested grit can grind up food. Grain-eating birds swallow small stones or gravel which is accumulated in the gizzard for this purpose.

Some carnivorous birds, such as owls, swallow their food whole. In these cases the gizzard does not grind, but stores the waste material (hair, bones, and feathers) forming pellets which are regurgitated and expelled from the mouth. These almost intact waste products allow us to identify what the bird has eaten.

2.2. Excretory system

The excretory system is located in the large intestine which is composed of the colon and blind pockets or appendices. Bacteria in the pockets digest cellulose. The cloaca is a unique organ which serves the digestive, urinary, and reproductive systems. It leads to the exterior by the external cloacal orifice. The large intestine connects the digestive system to the cloaca, the ureters connect the excretory system to the cloaca, and the deferent duct, the left oviduct and semen storage receptacle connect the reproductive system to the cloaca. The outlets are at different levels of the cloacal tube.

The functional unit of the kidneys is the nephron, as in other vertebrates. It filters various waste products from the blood and produces urine. Urine is produced through three physiological processes: by filtration due to greater blood pressure on each side of the nephron, by re-absorption, and by secretion.



The salt gland of marine birds.

The metabolic consumption of proteins and nucleic acids produces nitrogen-bearing wastes (NH). Fish excrete this waste in the form of ammoniac through their gills directly into the water. Mammals concentrate the ammoniac into urea, and birds and reptiles concentrate it still more into uric acid. In all vertebrates the kidneys convert this waste into more efficiently excreted forms. Mammals excrete urea.

Coprophagy enables birds to ingest vitamins from partly-digested food. Kleptoparasitism is the attempt to steal food from others.

Birds excrete uric acid. For land dwelling animals, the accumulation of ammoniac is dangerous and can be lethal at concentrations above 5 mg. per 100 ml. of blood. Urea contains two molecules of ammoniac and requires abundant water. Uric acid, in turn, unites two molecules of urea.

Uric acid is slightly soluble in water and is excreted in a semi-solid state. It forms the white material in the excretion of birds and is the base of guano accumulated by marine birds on the islands of Peru. Guano was an important source of raw material for making explosives (dynamite and gun powder) until the Second World War.

The excretion of uric acid evolved together with the egg-shell, which may explain why mammals never developed this more efficient way of eliminating wastes. Uric acid contains twice as much nitrogen as urea, and requires only half as much water in the urine. Furthermore, at high concentrations, it precipitates out as a solid, liberating water which can be re-absorbed. Therefore, mammals require more water, while birds can survive on a very reduced water-ration. In birds, the process of concentration of uric acid and the re-absorption of water takes place in the cloaca.

In egg-laying animals, the waste and the embryo are in the same solution, and the urea may reach levels which are toxic for the fetus. So the crystallization of uric acid, deposited on the outside of the egg, is an advantage. It is interesting to remark that the embryo of a chicken, in its first four days of development, eliminates waste in the form of ammoniac, as do fish. Then it increases the elimination of urea, reaching a maximum on the seventh day. Finally, by the tenth day, 95% of the waste product is in the form of uric acid. This is an example of biochemical recapitulation, that is to say, an embryo passing through a phase during which it resembles an earlier evolutionary ancestor.

Uric acid is carried to the ureters and from there to the cloaca. The re-absorption of water is very efficient and energy-saving. Only a small amount of water is needed to cause the uric acid to precipitate as a low-volume mass. The remaining nitrogenous-free water is reabsorbed easily. In contrast, mammals require a great deal of cellular energy to expel urea.

The waste is so compact that requires no blad-

The Eared Dove (Zenaida auriculata) produces a "milk" in its crop by sloughing off cells, which it uses to feed its young.

A Kelp Gull (Larus dominicanus) with a fish much larger than it can carry in its bill, and a Neotropic Cormorant (Phalacrocorax brasilianus) with its prey dangerously cross-wise in the throat.

der to store the urine. It is not surprising to find that only a few species (South American rheas) have a urinary bladder. Birds are frequently seen excreting a semi-solid white mass before taking off, to reduce weight. However, the hummingbird also eliminates some urea, because together with nectar it swallows a large quantity of water.

The intestine, unlike that of mammals, is not divided into large and small parts. But it has a pair of blind pockets which help re-absorb water. The fecal content is darker and is not eliminated together with the intestinal wastes. Fecal excretion occurs one time out of ten.

2.3. The salt gland

The kidneys are poor concentrators of soluble substances such as the ions of sodium, potassium, and chlorine. If a man drinks sea water, which contains sodium chloride, his thirst is only intensified. In order for the kidneys to excrete salt, more water is needed, which is obtained by "borrowing" liquids from the tissues. To make matters worse, sea water contains magnesium sulfate, which produces diarrhea.

Man must maintain the salt concentration in the blood at less than 1% by weight. This is one-third of the concentration of salt in sea-water. Few organisms can tolerate more than 6%, because the membranes become permeable or break down.

To control salinity, sea-birds have evolved a gland located in a cranial depression above the eye, called the "salt gland". This is typical of the Laridae (seagulls) but in other groups (Falconiformes and other desert birds) it may be located in the palate or within the eye socket. The skulls of some fossil birds (Hesperornis and Ichthyornis) have similar cranial depressions, which indicates their habitat. This gland consists of lobes. Blood circulates on the outside, while in the interior a central canal drains the secretions. It is an active process of pumping sodium chloride in the cells which form the dividing wall. The sodium and chlorine ions are transported by the blood to the lobe, which carries the saline solution to the nasal cavity. The solution is secreted through the nostrils and then flows to the tips of the bill in droplets.

Most birds shake them off with the exception of petrels, which eject them with force like a sneeze. The solution contains 5% salt, saltier than tears and almost twice as salty as sea-water.

Though it works like a kidney, the gland is much simpler because it only eliminates salt and functions intermittently. When the salt-level in the blood increases, it is detected by the heart, the information is relayed to the brain, and from there to the gland where acetylcholine is released. This initiates the pumping.

Birds of prey, with some exceptions, also have this adaptation, but it is not known whether its function is the same as in sea-birds. Many birds which possess salt glands use them when the diet is rich in proteins. Among ostriches, the gland is activated when the temperature is high.

2.4. Feeding behavior

Most birds have varied feeding habits and supplement their principal food with others. All of them depend on seasonal abundance.

Feeding behavior may be individual or collective. Feeding in groups has advantages. In large flocks, some individuals may feed or rest tranquilly while relying on others to look out for danger. Birds which feed individually usually do so because their food source is scattered, irregular, or difficult to find.

Though birds usually eat early, it has been shown that dominant individuals prefer to eat later and generally eat less than their subordinates. The possibility of being able to feed at any time allows the dominant bird to eat at the most propitious moment and need not accumulate fat. This makes him more agile, which reduces risks. The subordinate bird must eat when the dominant is not present, stay away from less frequented places of low yield, and store fats against times of scarcity.

The following text follows the food chain from the top (birds which feed on animals) to the bottom (those which feed on plants.)

Hunters and carrion-eaters

Birds which eat fresh meat are called predators and those which eat decomposing animals are carrion-eaters. Some adaptations are found in the bill and the feet, in the sharpness of the senses (sight, hearing, smell) and in the specialized techniques of locating food. Here we describe birds which hunt mammals, reptiles, and birds, but not fish and insects, since the latter two require special techniques and adaptations, whether physical or of behavior.

Fresh meat is the most nourishing food. It is at the top of the food chain. It is difficult to obtain and requires a high expenditure of energy. On the other hand, the supply of carrion is apt to be irregular and difficult to foresee, and requires highly-developed techniques to locate it.

Being at the top of the food-chain has its disadvantages. The Falconiformes are at risk from pesticides. DDT (Dichloro-diphenyl-trichloroetane) degrades into DDE which affects the egg-shell and persists for two

to fifteen years. Both are soluble and accumulate in fat, passing from prey to predator and increasing their concentration at each level.

Most birds of prey belong to the order Falconiformes (day-light hunters such as eagles, kites, and hawks) and Strigiformes (night hunters such as owls.) Both have evolved powerful bills and claws to trap prey. The bill is strong and hooked, sometimes with a tooth, formed to kill the victim. Usually, they can break the skin and muscular tissue. The carrion-eaters have a weaker bill because their food is decomposing and softer. Their claws are not as strong, since they do not catch their prey. Some of them have no feathers on their heads, to reduce the risk of infection when they stick their heads into the decaying body.

Among the Falconiformes, some have long strong wings adapted to gliding in thermal updrafts while they hunt. They may perch in tall trees watching for prey. Smaller hawks have narrower wings and their flight is rapid and agile, adapted to hunting smaller game such as rodents, reptiles, smaller birds, and large insects. Sight, smell, and hearing may function in different ways. For example, the Turkey Vulture (*Cathartes aura*) is one of the birds with the best sense of smell for detecting carrion, while the Black Vulture (*Coragyps atratus*) depends more on its eyesight to detect dead animals.

The Strigiformes (owls) are nocturnal and depend on their hearing. They have large eyes directed forward, and the openings of the ears are asymmetrical (one is higher than the other) which enables them to locate sounds with great precision. The borders of their wing-feathers have fine soft fringes to reduce friction and minimize turbulence, making their flight silent.

Fish-eaters

Hunting in the water is the feeding behavior with the most variations. Fishing birds have evolved special bill structures and behaviors. A basic classification reveals the following general categories:

- Some trap fish between the two mandibles of the bill, while others use the bill as a harpoon.
- Some dive from the air, some float and dive from the surface, and some fly low over the surface of the water.
- Some may filter the water, or detect prey by touch with the bill, either in the water or buried in silt.
- Some move actively searching for prey, while others wait immobile for it to appear.

While the great majority hunt their own food, some steal it opportunistically. Kleptoparasitism is common among sea-gulls and Skuas (*Catharacta chilenses*) which pursue other birds and force them to drop their food. Sea-gulls, skuas, and Frigate birds are specialists in food-stealing, but other birds may attempt it from time to time.

The heron specializes in hunting fish or reptiles using its bill as a harpoon or tongs. It may actively search for food or wait immobile for the right moment to attack. It normally holds its neck folded back in an S-shape, only to extend it totally in the moment of attack. The kingfisher catches its prey with a blow of


White-necked Heron (*Ardea cocoi*)

its straight bill. Penguins, which are excellent swimmers, have protuberances on the tongue directed backwards toward the throat, to prevent captured fish from escaping. Many birds have adaptations of the palate, tongue, or bill to aid in feeding.

The Neotropical Cormorant (*Phalacrocorax brasilianus*) dives from a floating position. It has a hook at the tip of the bill to prevent the fish from slipping away. It stores what it has captured in a membranous sac in the throat or stomach. The anhinga (*Anhinga anhinga*), which belongs to the same order of Pelecaniformes, has a very sharp bill which it uses to pierce its prey like a harpoon. Unlike most fishing birds, which have water-resistant plumage, the feathers of the Pelecaniformes absorb water, which enables them to dive deeper. Later, they stand with their backs to the sun and their wings spread, to dry. The Emperor Penguin (*Aptenodytes forsteri*) carries stones in its belly which help it remain submerged. The Podicipediformes (grebes) empty their lungs and air sacs when they dive. The coots release air when submerged, leaving a ring of bubbles, in order to dive more deeply for food.

Sea-gulls use a hook on their bills, instead of a gular pouch, to transport food. The skimmer has an unusual bill with a longer lower mandible, the only bird with this characteristic. It flies low over the water with its lower mandible skimming the surface, snapping shut its bill when it detects its fish or crustacean prey.

Various groups of birds feed on small animals in the mud or sand or in low water. They bury their long, sensitive and somewhat flexible bills in the silt to detect and capture their food.

Two unusual cases are the Chilean Flamingo (*Phoenicopterus chilensis*) and the Roseate Spoonbill (*Platalea ajaja*). The flamingos have a complex feeding system. By means of laminate structures on the edges of the bill they filter water so that microscopic organisms remain trapped inside of their mouths. This is analogous to the feeding habits of certain whales. They feed in shallow water, stirring the surface with their feet and submerging their heads in the water, which they suck into their beaks. The Roseate Spoonbill feeds by sweeping its broad bill back and forth in low water, detecting its prey by touch. This form of feeding is also practiced occasionally by the White-faced Ibis (*Plegadis chihi*) which belongs to the same family of Threskiornithidae.

Great Kiskadee (*Pitangus sulphuratus*)

Invertebrates

Various birds eat land snails, but the Snail Kite (*Rostrhamus sociabilis*) is the most specialized for this purpose and feeds almost exclusively on snails. Its bill has a terminal hook for extracting the soft body of the snail from the shell. The Oyster-catcher (*Haematopus palliatus*) is a cosmopolitan coastal bird which feeds on bivalves introducing its strong flat bill between the shells to extract the meat.

The great majority of birds eat insects, which are abundant and a good source of proteins and carbohydrates. In temperate regions, insects proliferate in spring, coinciding with the reproductive season of birds. Insectivorous birds play an important role in the control of insect populations.

Birds may hunt insects on the wing, extract them from the bark of trees, search for them among the vegetation or by following larger animals which disturb them in passing. Some birds perch on the backs of large ruminants to extract parasites. Woodpeckers search for insects in or on the trunks of trees, and have a straight strong bill like a chisel. They drill holes in the trunks and extract larvae or insects with their long protractile tongue, which is equipped with barbs to capture and hold the insect. Woodcreepers can walk upside down on branches, extracting insects from narrow crevasses of the bark with their long fine curved bills. Swallows and most Tyrannidae such as Fork-tailed Flycatchers (*Tyrannus savana*) hunt flying insects on the wing.

Most of the Tyrannidae, after capturing a flying insect, will return to their perches to eat it, but swallows and night-jars (Caprimulgidae) eat as well as hunt on the wing. They have short bills and wide mouths, surrounded by vibrissae or "whiskers" which help them locate tiny flying insects. Many Passeriformes hunt on the ground, turning over leaves, or hopping through the undergrowth.

Leaves and stems

Feeding on the leaves and stems of plants requires a complex digestive system which is highly developed in ruminant mammals. Special enzymes, usually provided by bacteria, are needed to break down cellulose, and the weight of this digestive equipment makes it almost incompatible with flight. The only truly vegetarian bird known is the Hoatzin, a bird of the Amazon basin thought to be a member of the Cuculidae.

All other birds require foods rich in carbohydrates and proteins to provide the energy necessary to maintain their high rate of metabolism. Those birds which do consume young sprouts, poor in protein, carbohydrates, and fats, do so only occasionally and show no special adaptations for this function.

An exception to this rule is the Southern Screamer (*Chauna torquata*) a large but somewhat aberrant member of the order Anseriformes, which may consume a large quantity of leaves of low nutritive value, although leaves do not constitute its primary diet.

Flowers and nectar

Birds eat flowers only in the absence of more nutritious food. Plants do not benefit from flower-eating, but they produce nectar to attract pollinators, which may be insects, bats, or birds. Nectar, however, is of low nutritional value since it only contains water and carbohydrates. Birds which eat nectar must supplement their diet with seeds and insects.

Flowers and nectar are seasonal. Since insects do not perceive red, red flowers must have evolved this color to attract hummingbirds. The hummingbird is strictly endemic to the Americas, and the American forests contain more red tubular flowers than any other continent.

Hummingbirds feed by introducing their long, narrow, sometimes curved beaks into the corolla of the flower while hovering in the air. The tongue is long and tubular, sometimes with bristles at the tip to aid in sucking nectar. The beaks of the different species vary according to the flowers they prefer. This specialization guarantees that pollen will be transported to another flower of the same species.

Humans, and many birds, would succumb to "polidipsia" (intoxication by drinking excess water) if they drank close to their body weight in water. The hummingbird, however, may ingest between four and five times its body weight in nectar in twelve hours. It was speculated that they only absorb a fraction of this water in the intestines, but an experiment demonstrated that this is not the case. Hummingbirds fed with nectar "marked" with radioactive tritium were observed to absorb 80% of the water ingested in the intestines. This water therefore must be processed in the kidneys, which are adapted to eliminate large quantities of water. It is supposed that the rate at which the kidneys eliminate water puts a limit on the production of energy, that is to say, the bird can't consume calories in the form of nectar faster than its kidneys can eliminate the excess water. When the hummingbird is faced with cold weather, it can't consume enough energy to keep warm and maintain body weight. Many hibernate in winter.

Furthermore, the nectar of flowers is 20%-30% sucrose. If a human consumed enough sugar to raise his blood-sugar level to that of a fasting hummingbird, he would fall into a diabetic coma. But these birds do not suffer from diabetes. If we could understand how hummingbirds cope with the high levels of blood sugar, it could lead to advances in the prevention and treatment of diabetes.

Note: Birds of the order Apodiformes, family Trochilidae (hummingbirds) are adapted as pollinators. The scientific name, (from the Greek "apod") indicates that the hummingbird has very tiny feet, which are anisodactyl, that is, having three toes pointing forward and one backward. They can only perch, they cannot walk. They are endemic to the Americas. They have striking plumage with metallic glitter. They are the smallest warm-blooded animals. Their small size permits them to hover in the air and even fly backwards thanks to the conformation of the wing-muscles. The wing-beat is rapid (from 20-200 beats per second,) and requires a high consumption of oxygen (300 respirations per minute). Their diet consists of 90% nectar, which they suck with their long narrow bills and long tongue. They require large amounts of water, 150% of their body weight per day. Their metabolic rate falls sharply at night when they sleep.

Fruit-eaters

Fruit is highly seasonal. The best shape for the bill of a primarily frugivorous bird is short, flat, and broad. It may have some teeth at the border to permit the manipulation of fruit, but in general the adaptations are less specific than those of the nectar eaters. Fruit is poor in proteins and insects must be consumed to balance the diet.

The interrelationship between frugivorous birds and the plants they feed on is very important in the balance of nature. Angiosperms are flowering plants, and many of them have pulpy fruits which birds like. Since the seeds are not digested, these are dispersed in their droppings. On the other hand, some plants


White-necked Heron (*Ardea cocoi*)

protect themselves from being eaten by producing poisonous or bad-tasting substances. Plants of the genera Capiscum, red peppers, produce alkaloids which are irritating to mammals, but are harmless to birds. Some birds consume clay to neutralize these substances.

The principal means of dispersal of seeds is wind, but birds may carry them to sheltered places where the wind does not reach. There are two strategies used by plants in association with birds. One is to produce seeds too large for the birds to digest, which are regurgitated after the soft parts are consumed. The other is to produce large quantities of small, very resistant seeds which pass through the digestive system and are dispersed in the droppings. The seeds of some plants will not germinate until they have passed through the digestive system of the bird.

Grain-eaters

Granivorous birds require a high degree of specialization to deal with the resistant hull of the grain. The seeds or grain of grasses (gramineas) contain large amounts of fat and protein, but are low in water content, and birds which depend on them must include water in their diet. Some birds swallow stones which are retained in the gizzard to help grind up grain.

Many granivorous Passeriformes have short conical bills, with sharp edges to hold the grain. They perforate the hull with lateral movements of the lower mandible. Others swallow the grains whole. In general they supplement their diet with fruit and insects (except for Columbidae—doves and pigeons, which may be exclusively granivorous.)

Omnivorous birds

Many birds eat a great variety of foods. Some are known to raid garbage cans. Two special cases are geophagia, earth eating, and coprophagia, or eating the excrement of other species. Some insects are entirely coprophagic, such as certain beetles and flies, but this is rare among birds. Coprophagia enables birds to obtain vitamins from partly-digested food. The common House Sparrow (*Passer domesticus*), introduced into North America from Europe in 1851, spread rapidly due to its habit of feeding on horse manure at a time when horses were the primary means of transportation.

Various hypotheses have been suggested to explain the consumption of earth by birds. It was thought that they did it when food was scarce, but they have also been observed eating earth when food is plentiful. It is known that they swallow small pebbles to grind food in the gizzard, but at times they also eat earth too fine to supply pebbles. They may consume it to balance a diet too high in acid or too alkaline. Or they may absorb minerals from the earth to prevent diarrhea. Another possibility is that they eat earth to neutralize toxins and alkaloids which the fruit produces as protection against being eaten.

Great Egret (*Ardea alba*)

Narrow-billed Woodcreeper (Lepidocolaptes angustirostris)

Behavior

1 Flight

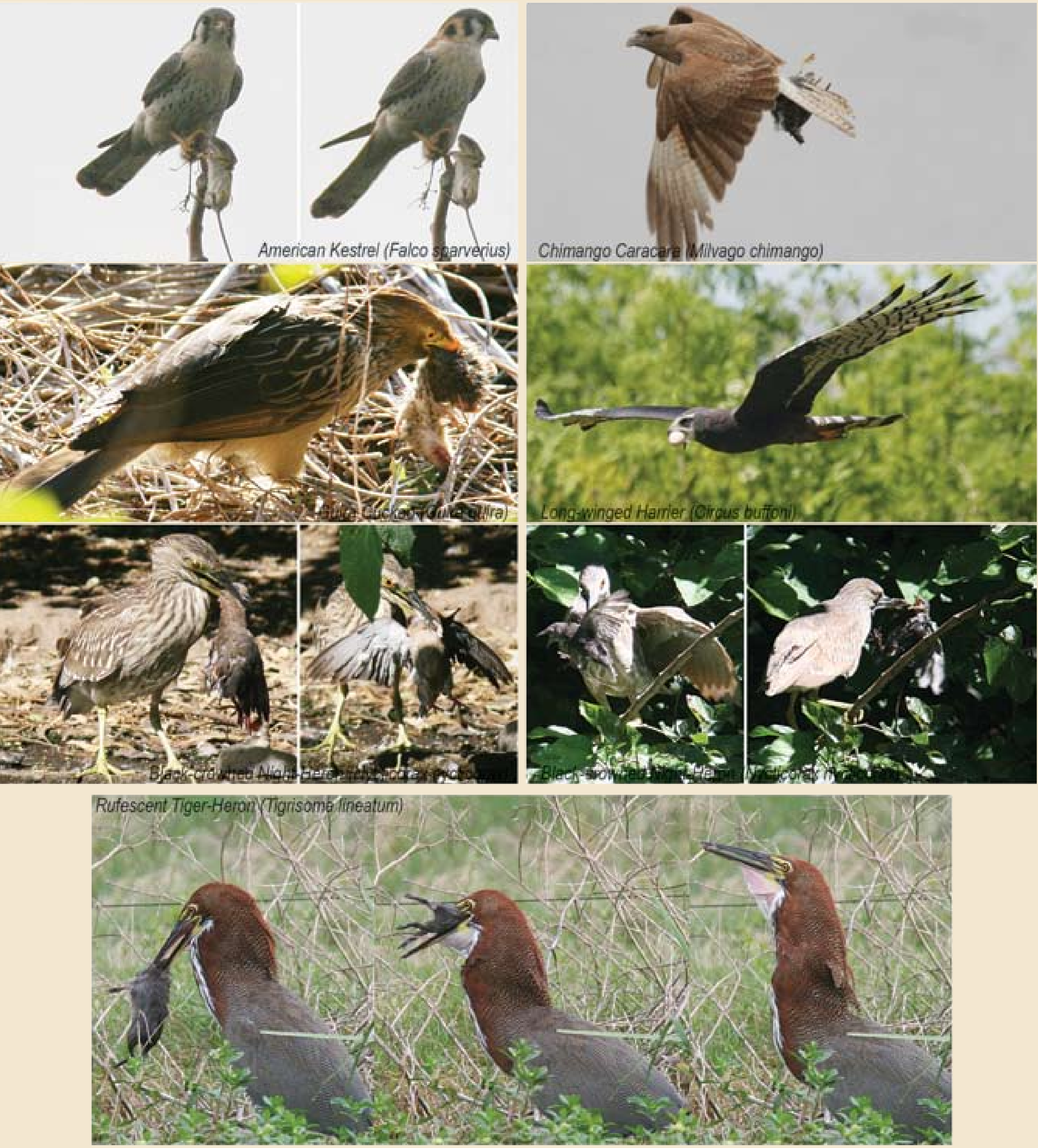
2 Feeding

3 Breeding

4 Agonistic

5 Emotional

The tail of the Narrow-billed Woodcreeper (Lepidocolaptes angustirostris) is graduated with a rigid rachis which projects inwards and serves as a support against the branch as the bird climbs in a spiral. They eat insects and small vertebrates which they capture with their long, narrow, curved bill.



Feeding on mammals and other birds. This Long-winged Harrier (Circus buffoni) is carrying an egg in its bill. The Black-crowned Night-Heron (Nycticorax nycticorax) has caught birds on two different occasions and holds them alive in its bill. Below, the Rufescent Tiger-Heron (Tigrisoma lineatum) is having trouble swallowing a large rodent.

Feeding on amphibians and reptiles. Once it has caught a snake, the bird manipulates it with its bill until it can swallow it head first.

Amazon Kingfisher (Chloroceryle amazona)

Ringed Kingfisher (Megaceryle torquata)

South American Tern (Sterna hirundinacea)

Royal Tern (Sterna maxima)

Great Grebe (Podiceps major)

Neotropic Cormorant (Phalacrocorax brasilianus)

Feeding on fish. Fish form the basic diet of many birds. They are always swallowed whole and head first, so that the fins don't interfere. Below, we see an anomalous situation, when a small bird is startled by a large fish which jumps out of the water trying to catch it.

Feeding on invertebrates. Various kinds of invertebrates are an important source of food. The Red-gartered Coot has caught a snail and breaks it with its bill before giving it to its young.

Feeding on insects. Most birds eat insects. Here, the Snowy Egret has accumulated food and delivers it semi-digested to its young by regurgitation. In this unusual case the adult has put its bill deep in the throat of the chick.

Great Pampa Finch (Embernagra platensis)

White-browed Ground Tyrant (Muscisaxicola albilora)

Black-capped Warbling Finch (Poospiza melanoleuca)

Long-tailed Meadowlark (Sturnella loyca)

Yellow-winged Blackbird (Agelaius thilius)

Austral Thrush (Turdus falcklandii)

Epaulet Oriole (Icterus cayanensis)

Feeding on worms and insects. Orioles (Oropendola) have an unusual way of finding food. The shape of the bill allows them to open leaves, stems, and flowers. The bill is inserted while closed and then opened to force open the stem. The Epaulet Oriole (Icterus cayanensis) demonstrates this technique opening the leaves of Pampas Grass (Cortadeira selloana) with his bill. Pampas Grass is a tall grass native to South America.

Feeding on fruit. Fruit is abundant but seasonal. The Fork-tailed Flycatcher (Tyrannus savana) must open its bill very wide to swallow a fruit almost too large for the size of the bird.

Feeding on flowers, grains, and leaves. Flowers are not very nutritious. Some birds feed on nectar. Grain is more nutritious, but harder to digest. Very few birds eat leaves. The Southern Screamer (Chauna torquata) and its chick are eating the leaves of floating plants.

Striated Heron (Butorides striata)

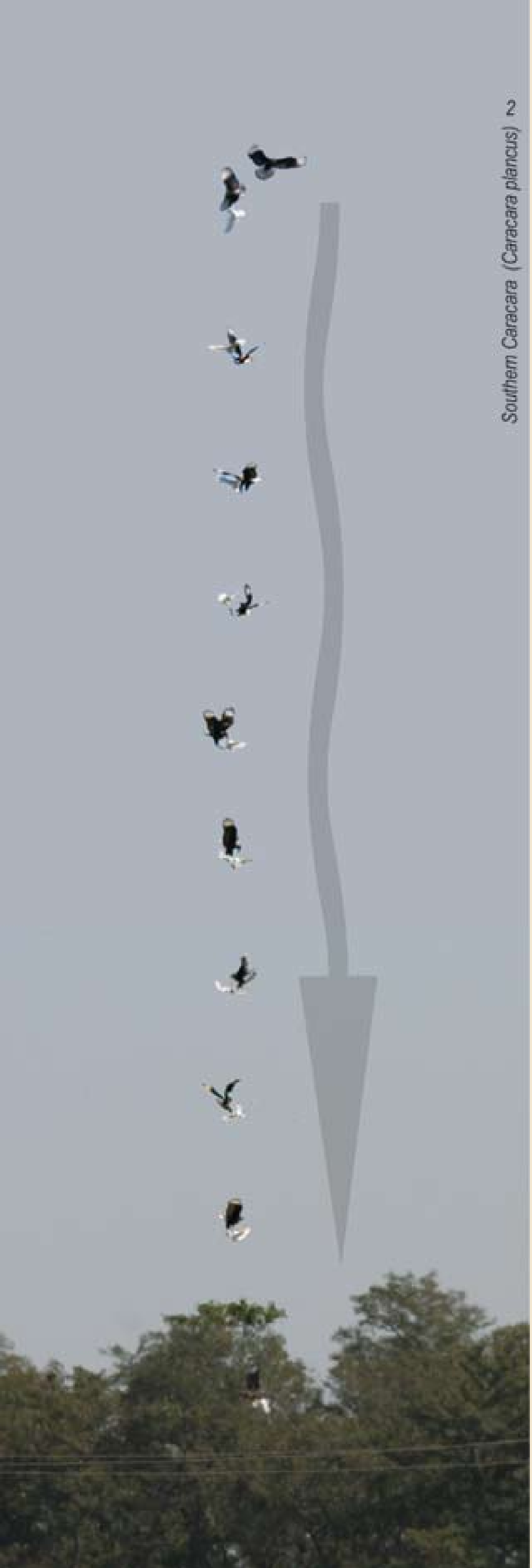
The Striated Heron (Butorides striata) sits on an abandoned coot's nest watching for fish, and leaps to the water to catch them. At the left, it catches a fish by the usual method of stretching his neck suddenly.

The Snowy Egret (Egretta thula) has various ways of feeding. Above, the usual method of catching a fish with a lightning blow of the bill. But, below, he takes advantage of very quiet water, stirring it slightly with his bill imitating the movement of an insect to attract fish (the arrow indicates the response.) Another way is to fly low over the water and catch fish with the bill. Finally, from the moving platform of a giant rodent (Hydrochoerus hydrochaeris) the heron watches for fish disturbed by the movement of the animal.

The hunting technique of the Rufescent Tiger-Heron (Tigrisoma lineatum) is passive and very methodical. It stands still or advances very slowly (1). When the victim (a small reptile) is detected, the bird waits for the right moment and seizes it with its bill (2-3). Then it holds it for a time while the victim exhausts itself with struggles before turning it head first and swallowing it whole (4-5). The bird has a sort of pocket under his lower mandible which stretches to allow the victim to pass. Finally it takes a sip of water to ease down the mouthful.

The bill of the Maguari Stork (Ciconia maguari) is adapted for hunting. This sequence illustrates the difficulty the bird has when the captured snake resists with determination. The first attempt to swallow it ends badly. Photos 1-4 show the snake wrapping itself around the neck of the stork forcing it to release it. The stork follows the snake through the grass for some minutes until it succeeds in capturing it again. In figures 4-8, it finally swallows it whole, with much difficulty. In 8 we see the stork with its crop so distended that it appears very uncomfortable and spends several minutes accommodating the victim inside it. In this case, the stork found a worthy opponent.

The Southern Caracara (Caracara plancus) is a hunter and carrion-eater with a varied diet. In this sequence we see it taking a dead cygnet of the Black-necked Swan (Cygnus melancorypha) from the water (1). In 2 a pair chases a Snowy Egret (Egretta thula) in flight. They force it straight down to the ground where they kill it. In 3, one steals the live chick of a Snowy Egret from a nest. In 4 it is seen carrying a dead chick in its bill. In 5, it has stolen an egg. In 6 and 7 it eats carrion of an already dead mammal and a bird.



2

Southern Caracara (*Caracara plancus*)

3

4

5

6

7

The ability to find food by touch is widespread. The South American Stilt (Himantopus melanurus) and the White-faced Ibis (Plegadis chihi) demonstrate their technique, moving their bills from side to side in the water. The ibis may either locate its food by sight and peck it, or it may "sweep" the water with lateral movements of its bill like the Roseate Spoonbill (Platalea ajaja), which shows their evolutionary relationship. The Roseate Spoon-bill (Platalea ajaja) finds its prey by brushing its half-open bill back and forth in shallow water. Spoonbills eat amphibians, small invertebrates, and insects. Wilson's Phalarope (Phalaropus tricolor) swims in muddy water and ducks its head to eat. It spins round and round touching the water with

White-faced Ibis (Plegadis chihi)

Hudsonian Godwit (Limosa haemastica)

Roseate Spoonbill (Platalea ajaja)

its bill 60 times a minute. In shallow water (in Argentina) it stirs up particles lying on the bottom, but in deep cold waters off Greenland it excites the mosquito larvae to make them more visible. The name Phalaropus (from the Greek) means "having a Coot's foot" due to its lobed feet

Black Skimmer (Rynchops niger)

Black Skimmers (Rynchops niger) are unique in several ways. The pupils of their eyes are vertical, enabling them to close them to a slit in bright sunshine and open them totally at night. The upper mandible of the bill is shorter than the lower, shaped like scissors and fits into a groove in the lower mandible. Skimmers have a very specialized method of fishing by touch. They fly low over the water with the lower mandible touching the surface. When they feel a fish, they bow their heads as they snap their bills shut. They live in groups and nest in colonies, laying 3-4 eggs in hollows scraped out of the sand. The males spend more time incubating the eggs and feeding the chicks than the females do.

The Chilean Flamingo (Phoenicopterus chilensis) (next page) has webbed feet, like a duck, which permits it to walk on soft mud without sinking. They walk in circles, using their feet to stir up the mud where they feed. The neck is long to compensate for the length of the legs and permit them to reach the surface of the water. They feed by filtering water a few centimeters deep. The head is inserted upside-down into the water, with the upper mandible open. The tongue acts as a suction pump to pump water into the bill, and as they expel it they filter out the food with the filament-like "teeth" of the bill. The food which is retained will be swallowed during the next respiratory cycle. They filter about 120 liters of water in 24,000 mouthfuls daily in order to obtain enough food in the form of crustaceans, algae and microscopic organisms. They must feed for 15 hours a day. The salt-water shrimp provide the pigment (carotene) which colors their feathers. In the photographic sequence two members of the group are indicated, to show how they turn clockwise. The sinusoidal movement of the feeders shows that they turn in circles with the head in the center while they stir the bottom with their feet.

Chilean Flamingo (Phoenicopterus chilensis)

Fishing methods of the White-necked Heron (Ardea cocoi). 1. Using its bill like a harpoon, it spears the fish through the body, then opens its bill to keep it from escaping. It turns the fish head-first before swallowing it. 2. With a smaller fish, it simply snaps its bill shut on it. In 3, it turns the fish around using a maneuver common among herons. But in figure 4, it has difficulty with a larger fish provided by a fisherman.

The American Oyster-catcher feeds on bivalve mollusks. Its bill is adapted to cut the adductor muscle which keeps the shell closed. This is an example of learning, because birds of the Haematopodidae family have two methods of eating shell-fish. One consists of breaking them on the rocks, and the other is to open them with the bill as in the photos. The techniques are taught to the young, and form an example of cultural transmission. They also lead to "cultural isolation" since some birds do it one way and some do it the other.

Great Kiskadees (Pitangus sulphuratus) in two frustrating incidents, photographed 800 kilometers apart. Both birds have caught a rat, too large to swallow whole. For many minutes they beat it against a branch trying to dismember it without success, and at last have to abandon it. In the lower sequence we see a kiskadee regurgitating something it couldn't digest.

The White-tailed Hawk (Buteo albicaudatus) feeds on mammals, birds, and reptiles. (In the photograph it is seen eating a rodent.) It is solitary and hunts by diving to the ground or into low vegetation. The Snail Kite (Rostrhamus sociabilis) feeds almost exclusively on snails. It lives in swamps, salt marshes, and wetlands. It flies low over the water searching for food. Having caught its prey in the water or vegetation, it lands on a branch where it extracts the snail with its hooked bill, discarding the shell intact.

1 Wattled Jacana (Jacana jacana)

2 Black-capped Donacobius (Donacobius atricapilla)

3 Cattle Tyrant (Machetornis rixosa)

4 Snowy Egret (Egretta thula)

5a

5b

5c Yellow-headed Carcara (Milvago chimachima)

The Carpincho (Hydrochoerus hydrochaeris) of the order Rodenthia, at 50 kilograms is the largest rodent presently existing. It is peaceable and sedentary and many birds use it as a floating platform while hunting in water or aquatic vegetation. The movement of the rodent disturbs fish or invertebrates which come to the surface. But the mammal not only helps certain birds, it also takes advantage of them to eliminate parasites. In 5 we see the rodent stretching and rolling over to allow a Yellow-headed Caracara (Milvago chimachima) search it for ticks.

6. The heart and the brain

1. The circulatory system

1.1. Regulation of body temperature

Homeostasis is the ability of living things to maintain internal conditions stable. Birds, like mammals, are homothermic because they maintain their internal temperature constant and endothermic, or "warm-blooded" because they are able to generate their own heat. Birds function as high-capacity metabolic machines. Their body temperature is higher than that of mammals, between 38º and 45º centigrade, with an average of 43º. The average temperature for mammals is 38º, with a maximum of 44º.

The speed of chemical reactions is doubled with each increase of 10º in temperature. This is why birds have higher temperatures. The upper limit of temperature within which life can be sustained degrades rapidly above 45º. At this temperature proteins begin to break down and must be replaced. For example, at 40º C., less than 10% of proteins must be replaced daily, but 25% must be replaced at 45º, and at 48º up to 100% must be replaced. Above 46º proteins are destroyed more rapidly than they can be replaced.

Therefore, life is restricted to a range of between 0º and 45º internal temperature. Although fish and some invertebrates may survive lower temperatures if their tissues contain chemicals that act as "anti-freeze" and keep ice crystals (which break down cell membranes from forming.)

Among mammals, high metabolic rate is associated with rapid oxidation and a short life span. Birds, however, may live a long time, between 1.5 and 2.5 times a mammal of the same size. Larger birds (like larger mammals) live longer (dozens of years) than smaller ones, which generally live 2 to 5 years. Naturally, the reproductive rate is the inverse of the life span, that is, short-lived birds reproduce more rapidly. The chemistry which permits birds to live longer than mammals while having a high metabolic rate is not understood.

The hypothalamus gland and the circulatory system are the keys to homeostasis. The hypothalamus is located beneath the brain. It is the thermostat of the vertebrates. Some sensors of temperature are within the hypothalamus itself, and others are distributed


Red-gartered Coot (Fulica armillata)

Control of body temperature (i). Compact groups allow aggregations of birds to keep each other warm. This large flock of coots has stayed close together all night on a sea beach, but the group opens out in the morning as the sun warms them. Studies of the Emperor Penguin (Aptenodytes forsteri), which incubates its eggs during the eternal night of the Antarctic winter, show by means of thermometers placed under the feathers that the birds share access to the center of the flock (the warmest and most protected place.) By means of this behavior they maintain a body temperature of 37.5° C, with an ambient temperature of 20° C inside the group while the surrounding temperature outside the group is -17° C.


Coscoroba Swam (Coscoroba coscoroba)

in the skin. Birds control their interior temperature through metabolism (by shivering, and by increasing or diminishing the circulation of blood to the skin) and by behavior (staying in the sun or in shade, panting, and urinating on their feet, among other things.)

Birds do not have sweat glands in the skin as do mammals to help them cope with high temperatures, perhaps because sweat could dampen and dirty the feathers and interfere with flying. Mammals can withstand very high external temperatures, provided they have an ample supply of water for evaporation. If the supply of water is cut off, the mammal starts to consume water from the tissues and the organism collapses.

Every time a bird takes off in flight, its metabolism increases sharply. For example, a pigeon consumes 0.5 kcal per hour in repose and 38 kcal per hour in flight. Flight and feeding produce excess heat which is eliminated during respiration. But in some cases it requires energy to maintain control of body temperature. When the external temperature is very high, birds prefer not to fly and remain quiet in the shade.

Some birds, such as Ciconiiformes (storks) use another device. First, they increase their rate of respiration in order to cool themselves by evaporation. If this proves insufficient, they urinate on their legs (up to once per minute) so that the evaporation, in this region not insulated by feathers, may help to cool them. Sometimes their legs appear white, due to the uric acid in the urine.

When temperatures are low, birds increase their metabolism by shivering, or warm themselves in the

Control of body temperature (ii). Guira Cuckoos spend the night in closely-packed groups to conserve heat, but in the morning they warm themselves in the sun. They spread their wings and expose their backs to the sun. On their backs they have small feathers which can be moved to expose the bare skin to the sun.

sun. Shivering releases energy from the ATP stored in the muscles. They fluff out their feathers, increasing the volume of insulation between the body and the exterior, and holding in the air warmed by their bodies. The feathers are most efficient insulators when they are clean and well-oiled, so birds invest considerable time in preening.

Nevertheless, when it is extremely cold, some birds (hummingbirds and night-jars) become hypothermic. Their body temperature drops and so does their metabolism. If the hypothermia is extreme, activity is minimal and they hibernate. Night-jars have been known to remain in this state (with low body temperatures and not responding to external stimulation) for several months. Hypothermia may also occur during periods when food is scarce, to conserve energy.

To maintain the high temperature necessary at the center of the body, birds have reduced the needs of other zones, particularly in the feet. They are composed of bone, tendon, and a thick skin. The thigh contains a network of capillaries called the rete mirabile ("Marvelous net" - the name comes down to us from the Renaissance 500 years ago) which acts as a heat exchange. The blood coming in to the body from the feet is warmed, while the out going blood is cooled in the capillaries as it flows in opposite directions.

Water conducts heat, so warm-blooded animals may lose much heat when they dive. To avoid this, diving birds have efficient thermal insulation in the form of clean, impermeable feathers. (Swimming

Control of body temperature (iii). A barefoot man wading in cold water would not survive for long, but birds do it all their lives. The legs of the American Wood Stork are 50 centimeters long. When the air temperature is 13^o C. and the water 10^o, the temperature of the blood passing through the counter-current of the "rete mirabile" (the "marvelous net" in the thigh) drops from 40^o C. to 16^o C. The temperature remains constant in the leg until at the foot it drops to the temperature of the surroundings. Without this temperature exchange, the long legs would radiate heat. In the second photograph, the White-necked Heron stands in a peculiar position to warm itself, using its wings to reflect sunlight on to its body.

mammals, on the other hand, generally depend on a thick layer of fat.)

The plumage of Pelecaniformes, (cormorants and anhingas), nevertheless, absorbs water, which helps them to dive. In spite of the possibility of losing heat, they are successful, being distributed almost world-wide, and they do not require more food than other birds. Careful analysis of the plumage shows that the outer feathers absorb water, but a middle layer is very impermeable. This conserves a thin layer of air against the skin, reaching a balance between float-ability and thermoregulation.

1.2. The circulatory system

Because of their high metabolic rate, birds require a highly developed circulatory system, like that of mammals. The birds' heart is larger and stronger, and beats faster, than that of mammals. The heart of the hummingbird, which is the bird with the highest rate of metabolism, occupies 30% of its body weight.

Birds have a four-chambered heart and the circulation is separated into two circuits. The pulmonary circuit carries blood to the lungs where it is oxygenated, after which the systemic circuit carries it to the rest of the body where the oxygen is consumed. The oxygen-rich blood enters the arteries which branch out and narrow until they reach the capillaries where the interchange of gasses is produced. From there the blood goes to the veins and is returned to the heart.

The circulatory system of fishes, amphibians, and reptiles is less efficient, because the oxygenated blood mixes to a certain extent with the de-oxygenated blood returning from the tissues. The advantage of separate circuits is considerable: since the incoming blood is not mixed with the outgoing, the body receives blood with a higher concentration of oxygen, and at the same time the interchange of gasses in the lungs is more effective because the blood reaching the lungs has a high concentration of CO_2. Furthermore, each circuit can operate at a different pressure.

There are some differences between the blood circulation of birds with respect to mammals. One equally functional anatomical difference illustrates a case of independent evolution from a common ancestor: the reptiles. The aortic archs (right and left) present in reptiles have evolved differentially in mammals and birds. In birds persisted the right arch, while mammals have only the left arch.

As was mentioned above, the birds' heart is stronger and relatively larger than that of mammals, and beats more rapidly. Also, the heart of a small bird is relatively larger than that of a large bird, and may beat faster. The blood pressure varies inversely with respect to the size of the animal, and is almost always higher than that of a comparable mammal. The heart of a human weighs 0.42% of his body weight, while that of a pigeon weighs 1.71%. The human heart beats 72 times per minute, that of the pigeon 135. A Hummingbird's heart may reach up to 615 beats per minute.

The lymphatic system consists of the lymph vessels and ducts, the lymph glands, and the lymphatic tissues. It forms part of the immunological system, and also may activate it. It also collects wastes high in fat content from the intestines. The lymphatic system is not highly developed in birds. Only the ducks have lymph glands, two in the thorax and two near

Snowy Egret (*Egretta thula*)

the kidneys. The lymph vessels are less numerous than those of mammals, they have valves, and empty into the veins.

Hemoglobin and oxygen

Hemoglobin transports oxygen from the lungs to the body and returns with carbon dioxide. In the lungs (pulmonary circulation) oxygen is absorbed and carbon dioxide is released and in the systemic circulation (capillaries of the rest of the body) oxygen is used in the oxidation of digested food releasing water and carbon dioxide.

Hemoglobin is a large molecule based on the protein globin and four groups of hemo. Each hemo group is formed by a molecule of porphyrin bonded to an atom of iron. The red color of blood is due to the iron, which bonds weakly with oxygen. The hemoglobin molecule is similar to the chlorophyll of plants, except that chlorphyll contains magnesium instead of iron, making it green instead of red.

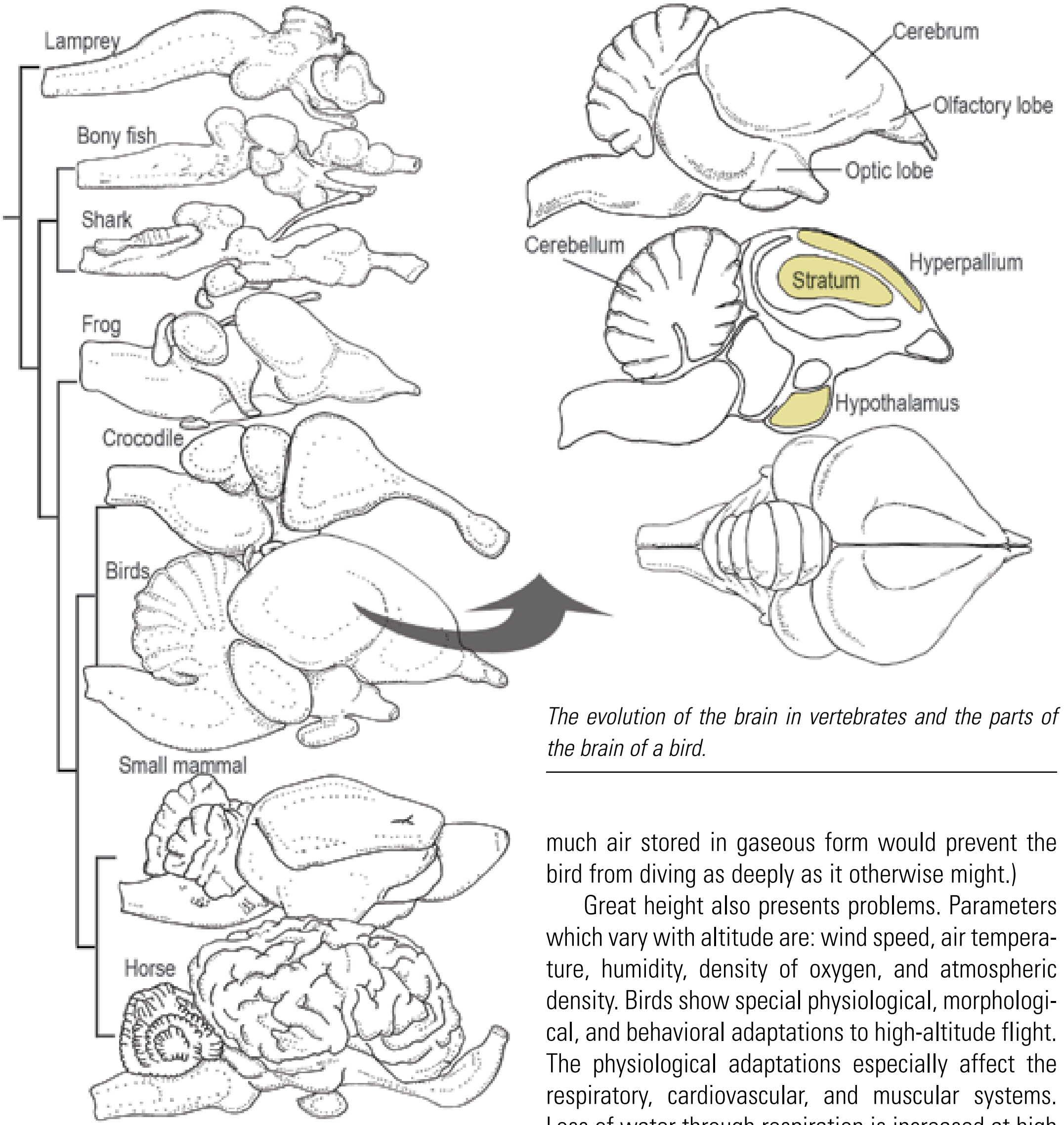
Carbon monoxide combines with iron in the same location the oxygen does, but the bond is 150 times stronger. This is why carbon monoxide is highly toxic when it competes with oxygen in the lungs. However, oxygen can also be dangerous. Oxygen oxidizes sugars and fats to release energy, but uncontrolled oxidation may break the chemical bonds of molecules necessary to life.

The reaction in which oxygen or carbon dioxide combines with hemoglobin is reversible, and depends on the pressure of the gas surrounding the hemoglobin. When the porphyrin absorbs an oxygen atom, it changes its three-dimensional shape in such a way that it increases the probability of absorbing another atom of oxygen (known as the hemo-hemo effect.)

The blood of birds contains somewhat less hemoglobin than that of mammals, but transports oxygen more efficiently. Oxygen is both essential and dangerous. Therefore nature designed very complex molecules for its transport (hemoglobin) and for storage (myoglobin). Myoglobin has only one hemo group and functions as a reserve of oxygen in the red muscles. Molecular analysis shows that myoglobin diverged from hemoglobin some 500 million years ago, and that all the vertebrates have similar molecules of hemoglobin. This demonstrates that nature is conservative, and a functioning system does not change easily.

Pushing the limits

Diving presents challenges. At 10º (as in fish) the metabolism is 1% of that which occurs in birds at 40º C. The concentration of oxygen in the water is 20-40% less than that of air, and the thermal conductivity is 25 times greater. Because of its low concentration, birds and mammals cannot obtain enough oxygen from water to sustain their high rate of metabolism. For every ten meters of depth, the hydrostatic pres-



The evolution of the brain in vertebrates and the parts of the brain of a bird.

sure of water increases by one atmosphere, and the concentration of gasses decreases.

Birds store oxygen in their muscles (in the myoglobin), in the hemoglobin of their circulatory systems, and in the air sacs of their respiratory systems. Diving birds have more hemoglobin and myoglobin than those which don't dive. As much as 60% of the reserve oxygen may be stored in the respiratory system. An exception is the King Penguin (*Aptenodytes patagonicus*) which stores 17% in the respiratory system and 50% in the muscles. (Perhaps because too much air stored in gaseous form would prevent the bird from diving as deeply as it otherwise might.)

Great height also presents problems. Parameters which vary with altitude are: wind speed, air temperature, humidity, density of oxygen, and atmospheric density. Birds show special physiological, morphological, and behavioral adaptations to high-altitude flight. The physiological adaptations especially affect the respiratory, cardiovascular, and muscular systems. Loss of water through respiration is increased at high altitudes due to the decrease of relative humidity. Flight is influenced by low barometric pressure and variations of wind speed.

2. The senses and the nervous system

2.1. The intelligence of birds

The brain of the bird

The demands of the nervous system of birds are somewhat less than those of mammals. The ability to fly frees them from a lot of tension.

The brain of all vertebrates follows a single line of evolution. According to the "three-brain theory" of P. Maclean, evolution added three successive brains, each one maintaining its own identity and memory. The first is the "reptilian brain," located in the lower part of the cranium. It regulates the vital functions such as respiration. The second is the "paleo-mamalian" brain. It occupies the center of the cranium and regulates the emotions. The third is the "neo-mammalian" brain located above the other two. It is the seat of reasoning and language. The three work simultaneously and independently.

Are birds intelligent? The word "intelligence" comes from Latin *intus* "between" and *leggere*, "To read." It might be interpreted as "reading between the lines." Intelligence is a capacity acquired by evolution. Therefore, human beings cannot have acquired "intelligence" by fiat without previous intermediate states. It is a capacity which permits the animal to make decisions which improve its conditions of life.

The most simple form of intelligence is based on hereditary (that is, genetic) instinctive reactions. It takes advantage of reactions based on the hormones or the nervous system. But only organism with advanced intelligence can base their behavior on learning. The quicker the ability to learn, the more intelligence we attribute to an organism.

The analysis of the brain of birds reveals that the cerebral cortex is smaller than that of mammals, but they are not therefore necessarily less intelligent. Rather, they use a different part of the brain. Birds demonstrate their intelligence by their ability to navigate (and learn) in migration, in the construction of complex nests, in their care of the young, and in their ingenious solution of new problems.

To understand the degree of intelligence of birds, we suggest the study published in Scientific American vol. 218, no.6, "The Brain of Birds," by L. Stettner and K. Matyniak. It will serve as the base of reference for some of the following comments.

Before describing the results of studies made under controlled laboratory conditions, I will relate a simple field experiment with the Golden-billed Saltator (*Saltator aurantiirostris*.) Its song was recorded while it sang from the top of a tree, and then played back. On hearing it, the bird became alert, quickly moved to another tree, returned to the original one, and then to a third, until it triangulated the source of the recorded song. It then dived at the recorder, and realized that there was no rival bird there. Then it retired more tranquilly to another near-by tree where it continued singing, ignoring further attempts to trick it.

This bird resolved a new problem (I doubt whether it had ever before encountered a similar experience) in no more than 20 seconds, by simple and effective means. Two things which had always been paired

Snowy Egret (Egretta thula)

(song and rival bird) were separated. This is intelligence, but of what degree?

Comparative intelligence

An elementary laboratory experiment is based on "recurrent inversion." It is a test of mental flexibility which measures ability to solve a problem by modifying behavior. The animal learns to choose between two symbols (a square and a circle) to obtain a reward of food. Then the symbols are reversed, and the animal must learn to change its behavior. Fish show no sign of learning, rats and pigeons learn after one or two attempts. Crows and magpies learn faster than pigeons.

A second experiment consists of "learning to learn" the answer. Subjects are shown two objects, one of them with a reward, and their position is changed. The subject must choose without regard to the position. Then, it is shown series of two distinct elements to which it must apply the same recognition. The chimpanzee is the best among the primates, while lower animals show very poor results. Pigeons and chickens do better than any other animal except primates.

A third experiment is that of the "discordant element." It consists of choosing the discordant element among three, two of which are identical. The discordant stimulus of the experiment is changed both in position and in form, for example A-A-B, A-B-A, B-A-B, etc. Monkeys learn after finding the solution to various problems. Cats need thirty attempts, and a canary learned on the first try.

The ability to count or to respond to the properties of numbers is very difficult in primates and still more for inferior mammals. Birds, on the other hand, can master difficult numerical problems. Crows, for example, after being shown a card with a certain quantity of dots (up to seven) can identify the quantity among various possibilities.

Recent investigations with parrots have demonstrated that they can not only imitate words, but may associate objects with them. They have been presented with problems which humans can only solve after achieving a certain age, for instance, using the image in a mirror to resolve the problem when a direct view is blocked. These studies have proved that the parrot learns faster if it sees another parrot solving the problem, without human intervention.

Cortex and striatum

How can the intellectual ability of birds be explained? Among mammals, the level of intelligence is related to the size and complexity of the cerebral cortex (the outer covering of nervous tissue covering the cerebrum.) Both in mammals and in birds, the cerebrum (the front of the brain) contains two types of structure: the cortex and the striatum. Both are inherited from reptiles, but they developed in very different ways. Among mammals, the cortex became dominant to such an extent that in humans it covers the striatum.

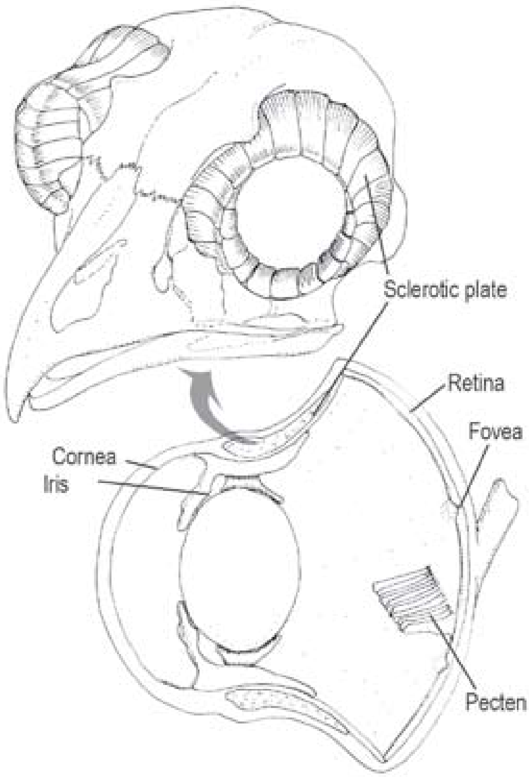
The classical description of the brain of birds indicates that the striatum was greatly augmented, while the cortex became a thin layer of tissue covering the upper and lateral surfaces of the cerebrum. The striatum is a mass of nervous nuclei and highly organized and integrated conductive fibers. The upper part of the striatum (hyperstriatum) is a structure which is not present in mammals. The function of the cortex is related to the sense of smell and since birds do not depend on this sense, the cortex shrank in size and importance.

Comparative analysis of brains leads us to the conclusion that the organ of intelligence is the hyperstriatum. The more intelligent the bird, the more highly developed the hyperstriatum. Among crows, parrots, and canaries, the hyperstriatum is most prominent. Another piece of anatomical evidence which supports this theory is the fact that the hiperstriatum receives the same type of neural connections for vision that the cortex of mammals receives. Removing the cortex of birds does not affect their sensory or motor abilities, while removing the hyperstriatum does.

Recently, a new distribution of the brain of birds has been proposed, in which the external position, formerly occupied by the hyperstriatum, becomes the hyperpallium. In either case, the brain of birds is well-developed.

Hypnotism and sleep

Birds can be hypnotized. Already in the XVII century it was known that chickens could be put into a cataleptic state by drawing a line on the ground beginning from the bill. The same hypnotic state can be induced by turning it over on its back. The bird's muscles become rigid, the cardiac and respiratory



The eyes of birds. The sclerotic plate protects the eye and holds it in shape, while the pectin oxygenates the interior of the eye.

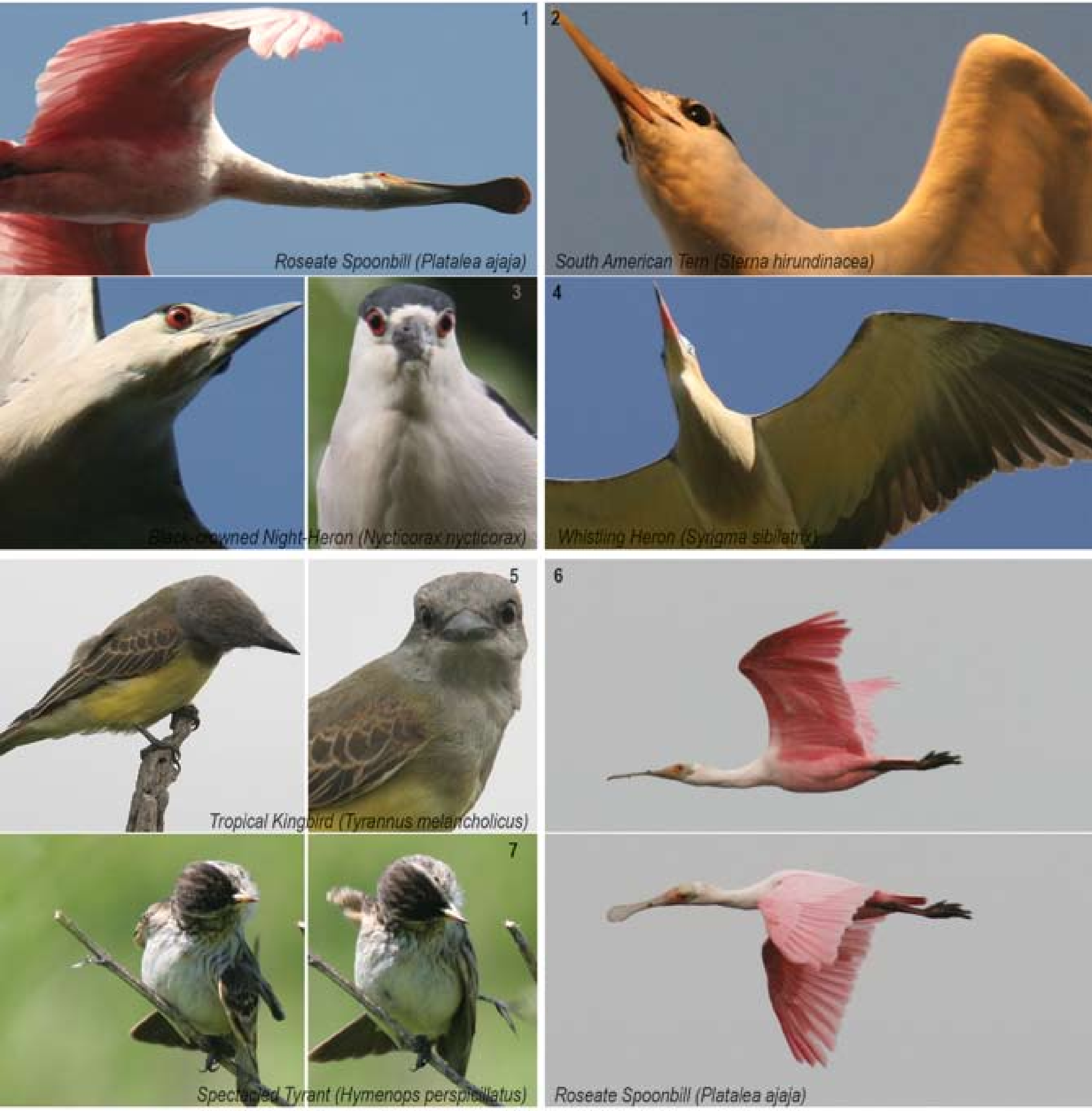
rhythms change, the bird is immobile and its responses to external stimuli are reduced.

Some reptiles and birds of prey seem to hypnotize their prey, which feel incapable of escaping. This phenomenon includes the "technical immobility" which occurs when the animal freezes when an enemy is near. The predator becomes more aggressive when the victim moves, but is inhibited when the victim is still.

Another peculiarity is that birds, like mammals, are capable of a hypnogogic state. This state, which precedes deep sleep, produces dreams which may be remembered. It is characterized by rapid eye movements, muscular twitches, and cerebral activity. Due to the wide-spread occurrence of this state among animals, it is supposed that it must have developed before the separation of birds and mammals.

2.2. Vision
The sense of sight

Vision is the most highly developed sense in birds. It is the source which can convey the greatest amount of information in the least time. In some species it is highly perfected. Hearing is also very acute, but on



Position of the eyes (i). Photographs 1-4 show the location of the eyes, which permits them to see below them as they fly. But they often turn their heads to focus better on the fovea of the retina (5-7).

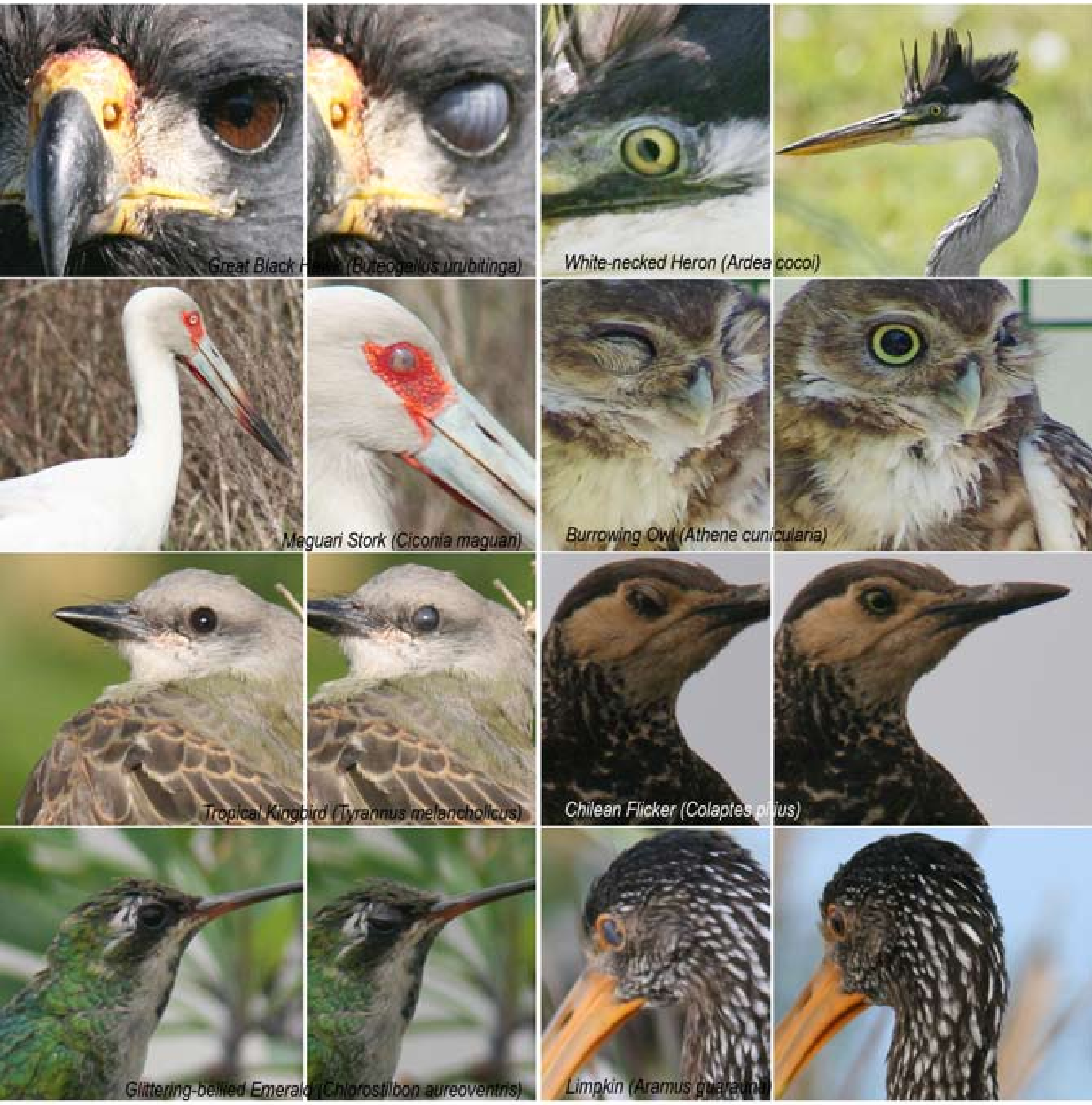
the other hand the senses of smell, taste, and touch are poorly developed.

The protein rhodopsine is the base of photodetection in all higher animals. This protein is contained in the membrane of the photoreceptive cells. When stimulated by light, rhodopsine changes its shape and

Position of the eyes (ii). Photographs 8-11 show the eyes of birds located at the sides of their heads as usual, but in many cases they are located more forward to provide better three-dimensional vision. However, the eyes at the sides enable them to see behind them better (12-13). The neck joint is such that they can turn their heads almost 360° (14-15).

after various intermediate steps facilitates the passage of sodium ions through the cell membrane. The cells specialized in the detection of light are the rods and the cones, located in the retina of the eye. This system is similar in the eyes of all animals.

The photoreceptive cells are formed by a series



The eyelids of birds. The nictitating membrane is translucent. The outer eyelid is similar to that of mammals.

of folds in the cell membrane, loaded with rhodopsine. This increases the volume and the probability of detection of photons in the successive layers of folds. The cones, furthermore, contain droplets of fat in which pigments are suspended for the detection of colors.

The eyes of birds are very large in proportion to their bodies. They occupy around 15% of the mass of

Some birds when walking keep their vision fixed in order to see better. Then they can be observed moving their heads in a very specific "zig-zag" synchronized with their steps.

the cranium (while in humans they occupy 2%). The eyes of eagles and falcons are as large as those of humans. The visual acuity of the falcon is eight times that of a human (as if it were using binoculars with a power of 8) and the owls' eye is ten times as sensitive to light as a human's, giving it better nocturnal vision. They are adapted to the hunting habits of their respective species.

Amazon Kingfisher (*Chloroceryle amazona*)

Great Kiskadee (*Pitangus sulphuratus*)

Amazon Kingfisher (*Chloroceryle amazona*)

Spectacled Tyrant (*Hymenops perspicillatus*)

When they are perched on a branch which is moving in the wind they may move their heads in a contrary direction to maintain the eyes fixed on a particular point.

Roadside Hawk (Buteo magnirostris)

Green Kingfisher (Chloroceryle americana)

Lesser Yellow Legs (Tringa flavipes)

Wattled Jacana (Jacana jacana)

When they want a better three-dimensional image, they move their heads although the body remains still.

The palate of many birds has a series of grooves pointing inwards to prevent live prey from escaping.

The position of the eyes in the cranium determines the angle of vision. When the eyes are located at the sides of the head, they permit a broad angle of visual field. This is useful for detecting enemies, and during migrations to obtain information about movement with respect to the sun and stars.

Birds which hunt live prey have their eyes at the front of the head, which gives them binocular vision (like that of humans) by super-imposing the visual fields of both eyes. It provides a three-dimensional image which permits the estimation of distance. A few birds (such as the snipe (*Gallinago paraguaiae*) have eyes located in the upper part of the head, the better to see the sky. Other birds (especially owls) have eyes located so as to allow them to see below as they fly.

The anatomy of the eye may be divided into the front (cornea and lens), and the back (retina). In certain modern birds, these are separated by a bony ring. This sclerotic ring is formed by twelve to fifteen small bones called ossicles. The shape of the eye is oval, due to the tension produced by the ring. Striated muscles are joined to this ring and help focus the eye. The ring also gives the eye greater resistance to pressure of wind and water.

Cornea, lens, and eye-lids

Birds' eyes in general have little mobility within the socket, and owls have none at all. The flexibility of the neck compensates for this. Owls can turn their heads almost 360º. The structure of the eye is similar to that of mammals. There is an iris to adjust the quantity of incoming light, and a lens to focus it on the retina, where the photo-receptors are located. In repose, the eye is adjusted for distant vision, and muscles adjust the lens and cornea for close focus. Two muscles are involved. One contracts to increase the curvature of the cornea (the refractive power) and the other adjusts the lens. The pupil is almost always round.

Land-dwelling vertebrates need eyelids to prevent the eyes from drying out and to protect them from dust. Birds have two types of eyelids, an upper and lower one. The lower eyelid is larger and more mobile. The upper one is only closed while sleeping. But besides these outer eyelids, they have an interior nictitating membrane which cleans and moistens the surface of the eye.

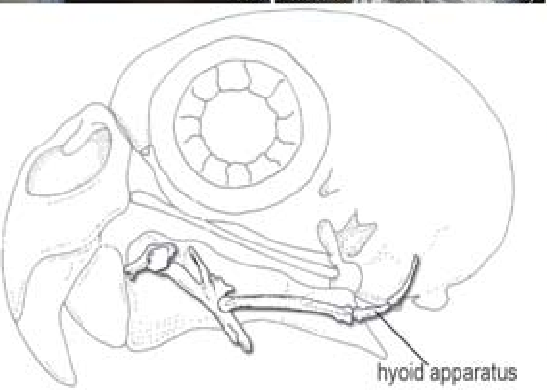
This membrane is almost transparent, so that it cleans and protects almost without affecting vision.


Southern Lapwing (Vanellus chilensis)


Cattle Tyrant (Machetornis rixosa)


White-necked Heron (Ardea cocoi)


Snowy Egret (Egretta thula)



Golden-breasted Woodpecker (Colaptes melanolaimus)


Glittering-bellied Emerald (Chlorostilbon aureoventris)

The tongues of birds have many forms according to the type of food they eat. The hyoid apparatus sustains the tongue. In some birds the muscle which retracts the tongue is attached inside the skull.

This membrane closes regularly in blinks which last about one-third of a second. In birds which submerge the head, it acts as a contact lens, correcting for the refraction of the light under water. Birds of prey close their eyes at the moment of attack, to protect the eyes from injury.

Retina and fovea

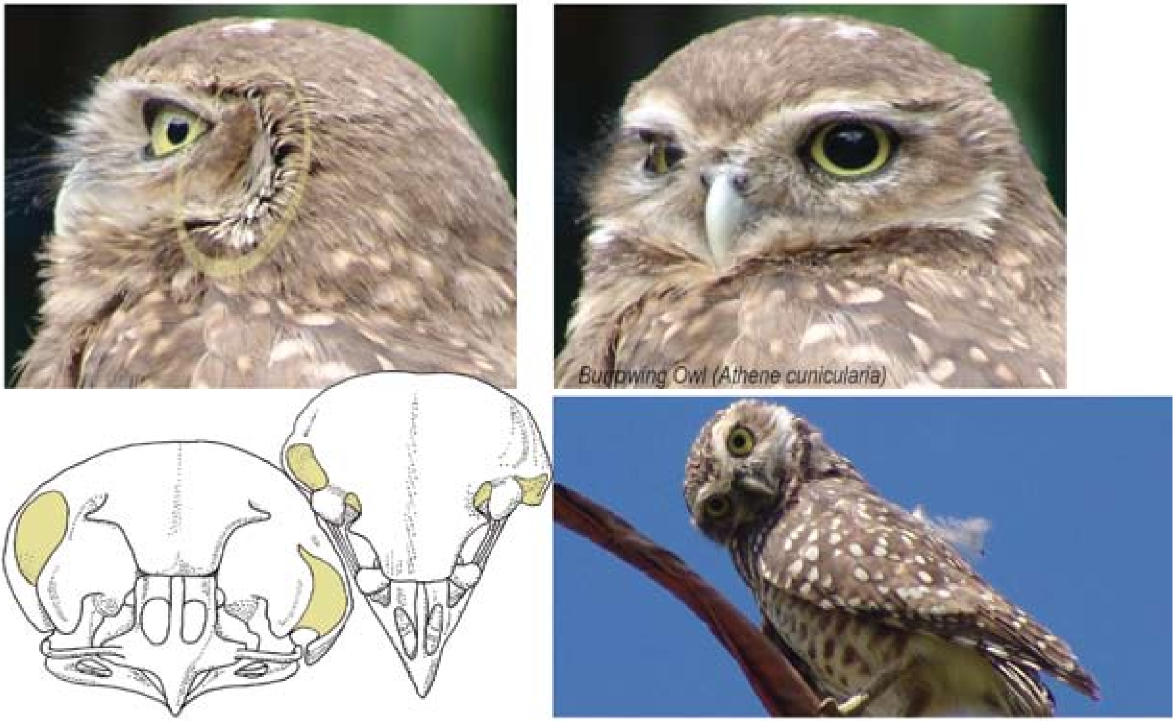
The retina contains a large quantity of photo-receptive cells per square millimeter. We can deduce from this that birds have excellent vision, superior to that of mammals. Humans have 160,000 receptors per square millimeter in the fovea, while a falcon has a million, and the digital camera used for the photographs in this book has 30,000 pixels per square millimeter in the optical sensor.

Birds have no external ear. The ear may be covered with feathers which can be moved to permit air to enter freely.

The fovea is a concave depression in the retina, where the greatest quantity of cones (photo-receptors) are located. It is the point of sharpest vision. Birds, besides having clear vision in all parts of the retina, have two foveae. The two foveae are useful for making continuous adjustments in distance. The temporal fovea receives binocular images and the central one receives monocular ones. Horses have a long vertical fovea so that when startled they raise their heads to see the nearest object below them. In birds, the position of the fovea causes owls to look sideways or down, and other birds to turn their heads.

The structure of the retina is highly sensitive to the perception of movement. Humans have a limit of 60 Hertz cycles per minute, while birds perceive 100 Hertz. The high quantity of cones indicates good perception of colors. Most mammals see only two colors, blue and green. Humans see three, red, blue, and green. Birds see four colors, because in addition to red, blue, and green, they perceive ultraviolet.

The retina, together with the forebrain region, seem to play an important role in magnetic compass orientation. These two areas, most active during magnetic compass orientation, form part of a visual processing stream. Cryptochromes, sensor molecules found in the retinal neurons which possess the required biophysical characteristics, have been suggested to provide information about the geomagnetic field which allows birds



Owls, which hunt at night, use their hearing to locate preys. It is known that they pinpoint the source of the sounds with more precision than any other animal ever recorded. This ability is based on the asymmetrical position of the ears (the right one is located slightly higher than the left one), which allows owls to triangulate sounds. The right ear is more sensitive to sounds coming from above.

to perceive the reference compass direction. This activation has only been observed in night-migratory birds and when they have their eyes uncovered, suggesting that some night vision specialization in night-migratory birds is involved in the process.

The pecten

Birds and reptiles possess a pecten, absent in mammals. It is a fan-like projection of folded parallel crests, which gives it a large surface area with a minimum of volume. It is near the optic nerve and projects into the eye. It forms a blind point on the retina.

The accepted theory is that the pecten provides nutrients and oxygen to the eye, because it is highly vascularized. It is also thought to collect metabolic wastes. The retina of mammals has abundant blood vessels, but that of birds does not. It is speculated that the pecten may interfere less with the visual functions than a network of capillaries within the retina. Another hypothesis is that this comb-like structure creates a zone of light and shadow which is used to follow movement in part of the visual field.

2.3. The other senses

Hearing

The ear is a highly-developed mechano-receptor. Birds depend on sound (songs and calls) to communicate among themselves, locate prey, defend their territories, find a mate, and perceive threats of danger. Structurally the ear of the bird is similar to that of mammals, and consists of three parts, the external ear, the middle ear, and the inner ear.

The external ear has no auricle or "porch" as in mammals. On the contrary, it is covered (and often hidden) by auricular feathers. The size and form of the covering varies with the species, the ear of the Rhea being free of feathers, while owls have an elaborate structure. These feathers are generally subject to muscular control to permit them to guide sound to the auditory canal. In aquatic birds, a fold of skin covers the ear when they dive, to avoid damage from water pressure.

The middle ear has a single bone, the columella, which conducts sound from the tympanic membrane to the inner ear. The inner ear contains receptors for the perception of movement and position. Cells with tiny hairs (cilia) receive vibrations and transform them into nervous impulses. These impulses are carried by the auditory nerve to the center of hearing in the middle brain.

Birds perceive sounds within a range of one to five kilohertz, less than humans, which perceive from one to fifteen kilohertz. Perception of high (ultrasonic) and low (infrasonic) sounds in birds is not good in most birds. A few exceed these limits, such as pigeons, which may perceive the infrasonic sounds of storms at a great distance. Owls perceive sounds at higher frequencies than humans.

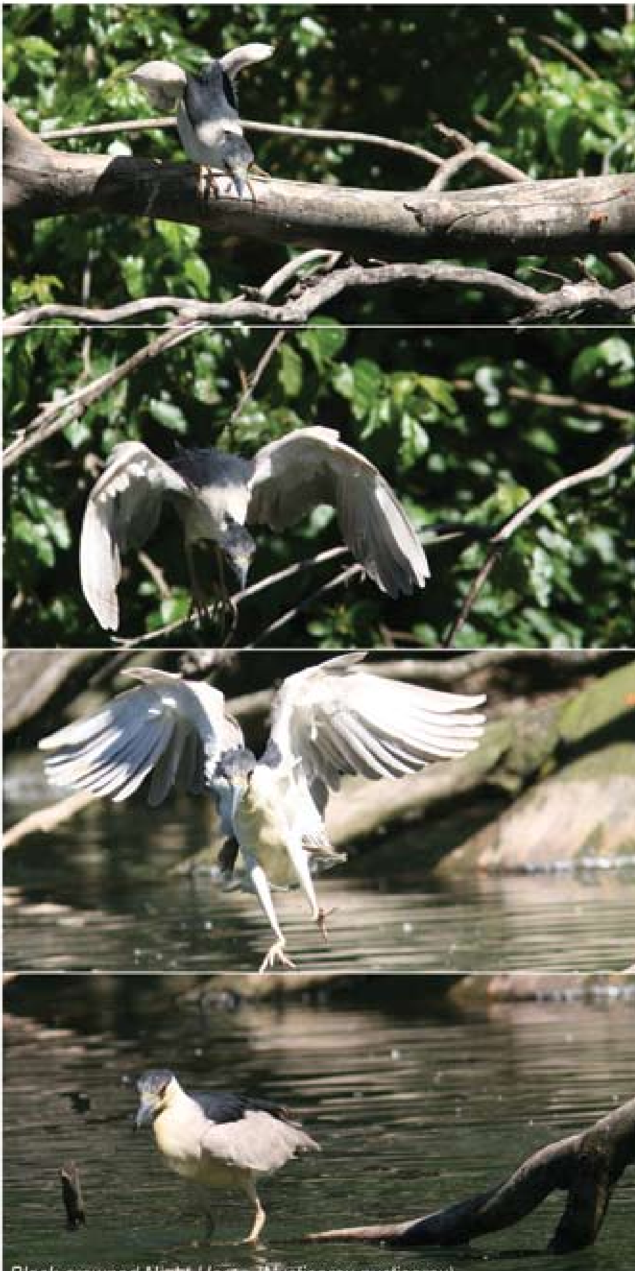
As in other vertebrates, the inner ear has a vestibular window in which the sense of balance is located. (Balance was the original evolutionary function of the ear.) The vestibular window is composed of cells with hairs which are immersed in a layer of gelatinous substance containing particles of calcium carbonate, called otoliths or otoconia. Gravity or acceleration causes these particles to change position in the liquid, moving the hairs and generating nervous impulses in the cells, which are transmitted to the brain. This is the way the brain obtains information concerning the body's position in space and direction of movement.

Taste

Chemoreception is the oldest and most widespread sense in the animal kingdom, but in birds it is of secondary importance. Although the sense of taste is little developed, birds evidently can perceive some types of tastes. Some birds have less that 70 taste buds on the tongue (humans have 10,000). Most of a bird's taste buds are on the roof of their mouth or deep in the oral cavity and none near the tip of the tongue. Human beings can sense a wide variety of tastes, thanks to the combination of taste and smell.

Smell

In many groups of animals the sense of smell mediates most life's processes (food location, mating cues, individual recognition.) This is not the case for most birds. The weak olfactory sense has been related to the small size of the olfactory lobes in the birds' brains. Most birds have little sense of smell and make use of other mechanisms to carry out all these processes. Vision is of primary importance, and since both senses compete for space in the cephalic region, the olfactory structures have been reduced to a mini-



Black-crowned Night-Heron (Nycticorax nycticorax) mum. The internal structure of the nostrils is adapted to flight, it is sensitive to air speed. This structure responds to air pressure and resistance during flight.

Among the species with large olfactory lobes we find the Turkey Vulture (*Cathartes aura*) which locates the prey by smell. Snipes probably feel and smell worms with their bills. Procellariiformes such as petrels, shearwaters and fulmars are said to locate the odor released by plankton. Some have been found to perceive social odour. They can recognize their nests, their chicks by scent and it is believed they use this ability for sex discrimination as well.

Touch

The sense of touch is somewhat developed in the feet and in the bill. Some water birds use the sense of touch in the bill to detect food. The technique consists of wading in shallow water with the bill submerged, in order to capture small aquatic animals. This method is rather wide-spread, with variations depending on the species and the medium in which the hunting takes place, water, sand, silt, etc.

Certain coastal birds (sandpipers) can locate crustaceans under wet sand by inserting the bill for a few seconds. This capacity seems to be based on a hydrodynamic principal. This was demonstrated by an experiment in which small pebbles were hidden in sand. The birds shouldn't have been able to detect the pebbles, because they don't move, they have no special smell, they don't generate a magnetic field, and their temperature is the same as the surrounding sand. Nevertheless, the birds were able to find them. They must have located them due to a special sensitivity in the bill to changes in water currents in the wet sand, caused by the pebbles or crustaceans.

Beneath the horny layer at the tip of the bill, these birds have clusters of ten to twenty Herbst corpuscles, which are sensitive to changes in pressure. When the bird inserts its sensitive bill into the sand at low tide, a pressure wave is produced due to the inertia of the water in the interstices between the sand grains. The pattern thus created indicates the presence of larger objects than the sand grains. The nodes in the bill can perceive the disturbances in the field, and perhaps even amplify them somewhat. Rapid vertical movements loosen the grains of sand, displace the water in the interstices, and create residual pressure around the object.

This explains why shore-birds only forage in wet sand. In dry sand, the sensor in the bill does not function. The sensors are not capable of distinguishing between buried pebbles and crustaceans.


Wattled Jacana (*Jacana jacana*)

7. Reproductive behavior

1. Procreation

1.1. The reproductive system

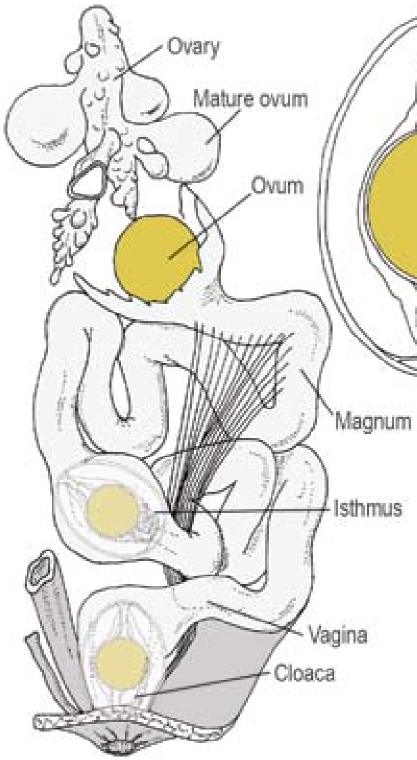
The origin of sex is still obscure and may go back 1,500 million years. “Sexual reproduction” is the opposite of “reproduction.” A cell reproduces itself when it divides in two, producing two identical cells. But in sexual reproduction two cells join to produce a single cell with a slightly different genetic pattern. Sexual reproduction is costly due to the necessity of finding a mate. Added to this is the cost to the female of producing males which do not produce descendants. The advantages of sexual reproduction are not to be found in the benefit to the individual, but elsewhere.

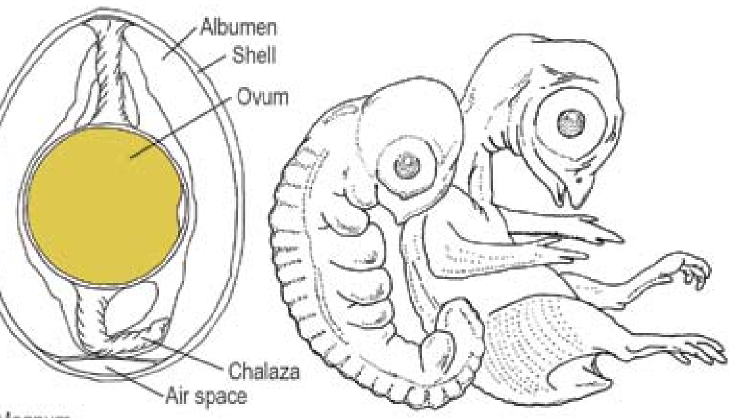
Instead, sexual reproduction benefits the entire population, by permitting variation and natural selection. But this requires a changing environment, in which a sexual population has an advantage over an asexual one. A long-term advantage like this throws doubt on the origin of sex, although it helps explain the persistence of the sexual strategy through time. If asexual females have short-term advantages over sexual ones, they should logically replace them. But to produce sexually differing progeny is like buying a lottery ticket. It is better to buy fifty different tickets than to buy 100 identical ones.

The reproductive apparatus of birds is reduced in weight for most of the year, an adaptation specific to the requirements of flight. Females have only one active ovary and the testicles of the males function only in the mating season. For example among the European Starlings (*Sturnus vulgaris*) the sexual organs weigh 1500 times more during the mating season than during the rest of the year.

The testes are small and oval-shaped and are located on the upper side of the kidneys. Hormones secreted by the pituitary start the growth of the testes, where sperm is produced at night, when metabolic activity is at a minimum. It is stored in seminal vessels at the body surface and is released during copulation. Only in passerines is there a prominent protrusion of the cloacal region. This cloacal protuberance is a clear indication that the bird is a male in breeding condition.

Among primitive species such as ducks and





The reproductive system of birds, the egg, and two stages in the development of the embryo.

ratites, the cloaca is equipped with a small erectile penis. But most species lack this organ for sexual contact. The equivalent of the penis is in the internal-ventral part of the cloaca. It consists of a pair of lateral phallic organs with an intermediate tubercle. They form a groove which receives and channels the ejaculation. During copulation, the cloacal orifice is everted and the phallus presses against the cloacal mucosa of the female, then the sperm is transferred by contact of the everted cloaca with the male on the back of the female. It has been described as "the kiss of the cloacae". Among the females, only the left ovary develops during mating season. In some birds of prey, both ovaries develop, but only the left one functions. The ovary is composed of follicles and looks like a cluster of grapes. It is close to the left kidney and may have thousands of follicles (from 500 to 20,000 according to the species,) far more than the few dozen eggs that the animal may produce.

The semen ejaculated at copulation is stored in receptacles in the oviduct, sometimes for months before the egg is actually fertilized, though the probability of fertilization drops rapidly a few hours after copulation. The egg is fertilized in the upper oviduct which then supplies nutrients and membranes and builds the shell around it as it passes down to the cloaca.

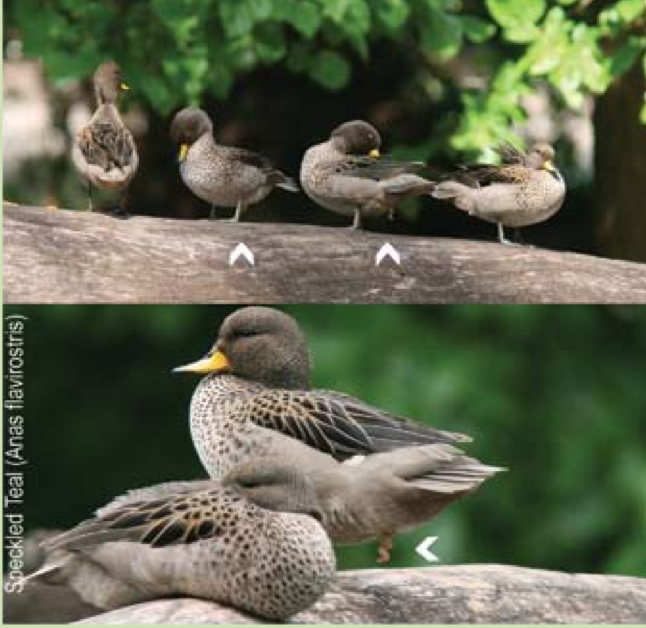
The oviduct is divided into several regions with specific functions. The first region is shaped like a funnel and receives the ovum as it proceeds from the ovary. Once fertilized, it passes to the magnum, which covers it with layers of albumin. Towards the end, the uterus produces another thin layer of albumin and the exterior shell, sometimes adding mimetic colors which help conceal the egg. Finally it reaches the vagina, which contains the mucus glands and muscular walls necessary to expel the egg when it is laid through the cloaca.

1.2. The egg

Birds are oviparous. The embryo, although outside the body of the mother, is still protected by the egg. This frees the mother during the time the embryo is developing so that she does not lose the capacity to fly. The eggs are laid early in the morning so that the bird does not have to carry extra weight while flying during the day.

The structure of the egg

The egg of the bird is amniotic, since the embryo is surrounded and covered by various membranes. The most important is the amniotic sac full of liquid in which the embryo develops. The evolution of the



The external reproductive organs. To the left, a pair of Great Egrets (Ardea alba) just before mating. The cloaca of the male is very similar to that of the female. To the right, two pairs of Speckled Teal (Anas flavirostris), in which by chance the penis of the male is visible.

Aggressiveness and forced copulation among birds

Except among Anseriformes (ducks and geese) forced copulation is rare among birds. This is due to the biology of the sexual organs and the mating conduct which puts fertilization under the control of the female. Since in 98% of the species the males do not have a penis, insemination requires the cooperation of the female. If forced copulation does occur, the female can still use her cloacal muscles to expel the semen.

The female also has the power to store the semen. The cloaca of birds is like a sac with three compartments. The three sections are separated by muscles. The male deposits semen in the urodeum, the intermediate compartment, with the cooperation of the female.

Ducks, however, do possess a rudimentary penis and forced copulation may occur. Nevertheless, the structure of the cloaca of the female is such that it reduces the possibility of fertilization. It might seem that a larger penis would increase the probability of reproductive success. However, the oviduct of the female, instead of being simple as in most birds, has sacs and spirals. The species with larger penis also have more elaborate oviducts, so that if the male does penetrate the female, she can still choose not to receive the semen. It seems to be a case of complimentary evolution in males and females, through which the female continues to maintain control of fertilization.

Forced copulation in order to perpetuate the species is not an effective genetic strategy among birds because of the selective power the female has over the semen.

The Code hypothesis stipulates that forced copulation creates a dangerous environment for the female, which reinforces the monogamous relationship, in which the female offers sexual access in return for protection. This theory predicts unusual situations. For example, forced copulation should be more common among birds where the male is larger than the female or has a powerful bill or claws with which to grasp her. It also ought to be more common among captive birds and birds which build closed nests where the female may be trapped, and among birds which nest in colonies.

Female control of fertilization may be assumed to be a "modern" evolutionary development, since only the oldest orders of birds (Ratites, Tinamiformes, and Anseriformes) have a rudimentary penis.

Chimango Caracara (Milvago chimango)

Baby birds are very vulnerable if they fall from the nest. They may fall prey to carrion eaters or be consumed by insects.

amniotic sac marks a disruptive step in evolution, because it permits eggs to be laid out of the water, without danger of desiccation. It is the essential evolutionary step from amphibians to reptiles.

Another membranous sac, the allantois, functions as a receptacle where waste products are deposited to avoid the intoxication of the embryo.

A newly -laid egg contains two substances, one of them transparent- the white or albumin, and the other yellow or reddish, the yolk. The yolk is a mixture of proteins, fats, and carbohydrates suspended in water, enclosed in a vitelline membrane. It provides the embryo with nutrients during its development. The yolk is formed of layers, pigmented red or yellow, depending on the bird's diet (alternating with white layers). Since these layers are deposited alternately

Sexual isolation of species

How do birds maintain sexual isolation between closely related species? Why do they not cross to produce hybrids? Sometimes hybrids occur, but they are very rare. Various studies devoted to the family Laridae, principally seagulls of the genus Larus, have made this genera one of the best-understood. Among seagulls the differences between species are slight, and in some cases, the seasonal changes in plumage minimal. Nevertheless, species distinguish among themselves even in those places where they nest side by side.

Geographical isolation is one of the factors which contribute to differentiation between species. Isolation prevents genes from passing freely from one population to another, and when the populations reencounter, they may be sufficiently differentiated to put hybrids at a disadvantage. Among seagulls it was the advance of the Pleistocene glaciers which cut off populations and allowed speciation.

Recognition of subtle visual signals maintains reproductive isolation among species of seagulls. In experiments with seagulls, external characteristics were artificially changed. Oil paint was applied to change periocular color, and black or white ink was applied to change wing markings, after washing the feathers with alcohol to allow the ink to penetrate.

Females which had already formed couples but had not laid eggs, on returning in changed form to the nest, were accepted but did not mate and abandoned the colony. Males with altered markings were not rejected by the females. It seems that the external appearance of the female stimulates mating. For the formation of couples, the females choose the male on the basis of eye-head contrast. This shows that coloration functions in two ways. The color of the male determines the formation of the couple, and the color of the female stimulates copulation.

Copulation is preceded by tactile, and possibly also by auditory, stimuli. A female seagull stimulates the male by rubbing his tail in the anal zone. But the principal stimulus is visual. The posture of the female when ready to mate is illustrated later on in this volume in the case of the South American Stilt (*Himantopus melanurus*), the Golden-breasted Woodpecker (*Colaptes melanochloros*), and the Southern Caracara (*Caracara plancus*).

The principal component of the bond is visual at first, but after the eggs are laid the nest and the eggs become the basis for bonding. It has been observed that when the size of the testes of the male exceeds a certain critical weight, he will respond to the female on a daily basis (the light ones deposited at night and the darker ones during the day) it is possible to determine how long the yolk took to form.

On the upper part a white spot appears, called the blastoderm, which contains the ovum from which the embryo develops. As soon as the mature ovum enters the oviduct it is fertilized or not and starts its descent downwards adding layers of albumin and membranes. The vitelline membrane surrounds the yolk and keeps it from mixing with the albumin.

The white or albumin is gelatinous, transparent, and composed of proteins. It serves as a defense against microorganisms, delivers water and proteins to the embryo, and protects it from blows. Within it are two protein structures (chalazae) like twisted cords which keep the yolk in the center of the egg and prevent it from bumping against the shell.

The outside of the egg consists of two membranes and a shell. The membranes which surround the albumin and yolk are fibrous elastic layers made up of proteins and lipids. The shell is the outer covering composed of calcium carbonate which forms crystals like irregular pillars of calcite. This irregularity permits the formation of pores through which the embryo breathes. The shell, together with the oval shape of the egg, keeps the birds' eggs rigid, unlike the eggs of reptiles which are somewhat soft. The mother bird accumulates calcium in her bones as a reserve for the production of the shell. When birds are lacking calcium in the diet, they eat their own eggs to replace it.

The egg contains all the components necessary for the development of the embryo, except oxygen. To hatch it only requires warmth and periodic turning to prevent the embryo from sticking to the shell membrane.

The shell and the membranes permit a limited interchange of gasses with the exterior environment through the pores. This interchange must be sufficient to allow the passage of oxygen and carbon dioxide (in opposite directions) yet at the same time, to prevent

even when her periocular color has been altered. But, if it is altered before the testes reach this threshold, they will not continue to develop.

The formation of colonies permits the synchronization of the reproductive cycle. The seagulls which nest in the center of the colony lay more eggs, lay earlier, and have more reproductive success. For this reason, space at the center of the colony is fiercely contested. It has also been postulated, but with less evidence, that colonies enable the birds to regulate the quantity of young according to the available food supply.

How do birds choose a mate like themselves if they can't see themselves? It is known that many birds become imprinted with an image of their parents when very young, and that they search for a similar mate. When eggs are interchanged among nests of seagulls of related species, the young hatch and are raised without difficulty. The changelings become imprinted with their adoptive parents and live and migrate with the adoptive species. But at mating time, these birds demonstrate the isolation of the species when the males attempt to mate and the females select for species. Nevertheless, there are birds which parasitize the nests of other birds, laying eggs in nests of other species. These young birds never see their biological parents, but nevertheless do not become imprinted with the image of the adoptive parents.

the loss of water, since this cannot be replaced. It is a delicate balance. The rate of interchange depends on external conditions. It may not function at high altitudes with very low atmospheric pressure, or in very dry environments, which limits the geographical distribution of nesting species. The microscopic structure of the egg-shell varies according to the habitat of the species.

The chemistry of the egg-shell is affected by pesticides such as DDT or its derivative DDE, which the bird accumulates through its diet. DDT and DDE cause a change in the concentration of magnesium and phosphates in the shell, increasing the danger of breakage and causing failure in the development of the embryo.

The embryo develops lungs, but these do not function at first. Gasses are interchanged between the venous and the oxygenated blood in the internal membrane of the shell. The lungs begin to function a day before hatching, and for a short while both systems function simultaneously.

Eggs vary in shape, size, and color. They may be solid-colored or speckled to blend with the environment. The color pattern is species-specific and also slightly variable between individuals, allowing the parents to distinguish their own eggs from those of others. The shape depends on the nest. They may be spherical, ovoid, or pointed. Pointed eggs, shaped like tops, are laid by birds which nest on cliffs so that if the egg rolls, it simply rolls in a circle without falling over the edge.

The sexual chromosomes

Among some reptiles, such as crocodiles and turtles, the sex of the embryo is determined by the temperature at which the egg is incubated. Among snakes and lizards, sex is determined by sexual chromosomes. Among mammals, the spermatozoa contain XY chromosomes, while the ova have identical XX chromosomes. At fertilization, one gene of each pair unites and the new pair determines whether the embryo will be male (XY) or female (XX). Since the female always supplies an X chromosome, it is the male spermatozoon which determines the sex.

Among birds, the situation is the reverse. The male is homogametic, that is, he supplies two identical chromosomes (ZZ) while the female is heterogametic, having ZW chromosomes. Therefore, the sex of the descendants is determined by the female.

The Y chromosome of mammals is about one third as long as the X, and transmits only one-hundredth the amount of genetic information. Among birds the situation is variable. In the order of Struthioniformes (Greater Rhea, *Rhea americana*) the Z and W chromosomes are almost the same and are considered the oldest. The order of Tinamiformes (Tinamou, *Nothura maculosa*) occupies an intermediate position with respect to the other orders of birds (Neognaths), which have well-differentiated sex chromosomes.

This genetic evidence coincides with other characteristics. The Rhea is a flightless running bird. It has no keel on its sternum and has a primitive palate (it is Paleognathic.) All species of the family of Rheidae are thought to have had a common ancestor, that is to say, it is a monophyletic group, about 100 million years old. It evolved in what is now South America when it was still united with Africa and Australia forming the supercontinent of Gondwana and spread into the other southern continents before they separated.

In December of 2004 it was announced that the complete genome of the domestic chicken (*Gallus gallus*) was analyzed for the first time. It was revealed

Mating displays are very frequent in mating season. A common ritual is to spread the tail like a fan (this and next page).

that the genome is only one-third the size of a mammalian genome, because it has fewer repetitions, pseudo-genes, and duplicated segments. It has between 20,000 and 23,000 genes. A large block of 70 mega-bases is closely aligned with the human genome, by which it is calculated that the lines diverged about 310 million years ago.

Genetic studies of birds, especially of DNA, have revealed much about their sexual customs. Species which appear to be faithful to one mate for life, such as swans, often mate with other birds. In most species of birds, mating outside the couple is common. A very detailed two-year study of paternity in House Sparrows (*Passer domesticus*) has verified the hypothesis referring to parental factors associated with mating conditions. Forty-five out of 419 baby birds (11%) were fathered by birds other than the "mate" and they occurred in 33 of the 126 nests (26%).

The incidence of "extra-marital" mating could not be correlated with synchronicity or with population density during mating, although it was more common towards the end of the mating season. Nor did secondary sexual characteristics of the male -body size and the size of the bib, in the case of sparrows- seem to influence frequency. The secondary sexual characteristics of dominant males did not insure paternity. Neither did age. It occurred as often among yearlings as among older birds.

No evidence was found that the female seeks to mate with strange males to avoid endogamy. Such matings occurred with equal frequency whether the mates were closely related or not. Neither did these matings supply rare genetic alleles in the population. Many studies are now underway which seek to explain the mating behavior of birds with the help of genetics.

2. Courting, mating, and raising the young

2.1. Reproductive groups

Males and females have different roles. The male attempts to mate with all possible females, while the female attempts to select the male with which she mates. This is interpreted as a manifestation of the relative cost of producing spermatozoa (many, small and cheap) and ova (few and expensive). The reproductive success of the male is increased if he mates with many females, but the reproductive success of the female depends not on how many males she can mate with, but on the quality of genes the male supplies, the resources he controls (territory and food

supply) and the help he gives her while she is raising the young.

If the female insists on certain qualities when selecting a mate, naturally the males will evolve to supply them, whether they consist of melodic song, showy plumage, elaborate courtship rituals, or food offerings. The latter is common among the Southern Caracara (*Caracara plancus*).

It has been demonstrated that the females may choose mates with the showiest coloration. A group of males was covered with a substance which blocked rays of ultraviolet light, while a control

Inverted Sexual Roles

Many species of birds exhibit sexual dimorphism. Usually it is the male which is dominant and brightly colored, but among phalaropes, the situation is reversed. The female is larger, brighter-colored, and more aggressive, driving away other females. When approached by another female, she lowers her head, draws back her neck, swims toward the intruder, stretches her neck and flings herself at her. If they are ashore, she stretches her neck with her bill partly open.

Before mating, the couple faces each other with the heads raised and the bills pointing to the upper part of the head. This posture is sustained for a few seconds, indicating lack of aggressivity. If the female is receptive, she lowers her body, the male jumps on her back, and copulates.

After laying the eggs, the female abandons the nest to the care of the male. It is the male who develops the "incubation patch" and incubates the eggs. O. Höhn reports on the physiological and hormonal factors in "The Phalarope," in Scientific American, Vol. 220, No. 6.

Androgens -testosterone- are responsible for the nuptial plumage and the greater aggressiveness of the female. Injection of this hormone into the male, after plucking the feathers from his shoulder, caused them to be replaced with nuptial plumage. This did not occur with the injection of estradiol, a female sex hormone which together with prolactin causes the development of the incubation patch. The female phalarope produces large quantities of androgens. In other species, where the male is dominant, the testosterone in the testes is five to ten times greater than that in the ovaries. Among phalaropes, the quantity of testosterone in the ovaries is equal to or greater than that in the testes.

Among phalaropes, the combination of androgen and prolactin induces the formation of the incubation patch in the male. The pituitary gland of the male secretes three times as much prolactin as that of the female.

The Wattled Jacana (*Jacana jacana*) also has reversed sexual roles. The female mates with up to four males, and each male incubates and raises young which may or may not be his own. DNA studies have shown that about 40% of the young are not descended from the "father" which raises them. This custom assures the reproductive success of the female, but contradicts the traditional view in which the male is a jealous custodian of the paternity of his young.


Wilson´s Phalarope (*Phalaropus tricolor*)

group was covered with a similar but transparent substance. The females chose their mates from the latter group, because the ultraviolet light made the colors brighter.

The reproductive groups

Birds band together in groups according to the season and the availability of food. The great flocks of ducks in autumn separate into couples in spring and then live as families with their progeny until autumn, when once again they flock together.

The most common reproductive unit among birds is the monogamous couple. The temporal duration of the couple is variable. It offers advantages, because the female does not have nutritional reserves sufficient to nourish the young. She does not nurse them as mammals do and therefore requires the participation of the male. The pair-bond of the monogamous couple may last for life, or only for one reproductive season. There are examples of both kinds of behavior.

But monogamy does not necessarily signify absolute sexual fidelity. Some species have been demonstrated to copulate outside of the couple. Others may change mates with each new reproductive season. However, species which practice absolute monogamy for life may exist.

About 90% of bird species form couples for reproduction, but females frequently mate with males outside the couple. This strategy enables them to lay eggs with some genetic diversity. It may also be an attempt to secure the tolerance of males in neighboring territories to allow them to search for food. Nevertheless, to raise the young successfully requires the collaboration of a bonded couple.

DNA analysis has proved that the eggs in a single nest almost always belong to one female (birds rarely lay eggs in the nests of others) but frequently they reveal the DNA of males other than the "official" mate. Few socially monogamous species are also genetically monogamous (less than 40 of 130 species studied.) The monogamous relationship in birds is sustained by a delicate equilibrium. A male which is too possessive may frighten away potential mates.

The family bond is closest when territory and resources are limited. When food is abundant, the young fledglings may drift away, requiring no help. But if the family controls a fixed territory it is more likely that the juveniles will remain with the group, since it is easier to inherit a territory than to establish a new one. In some species the juveniles may help their parents raise a second nest of siblings if the season is favorable. Mutual aid within the family group contributes to persistence of the genetic pattern, since the siblings are genetically very similar.


Rock Dove (*Columba livia*)

If the reproductive group contains more than two

Parasitism

Various species (like the proverbial European Cuckoo) deposit their eggs in the nests of other species. Parasitic birds are found in various groups, including certain ducks, mocking-birds, and the Shiny Cowbird (*Molothrus bonariensis*).

Parasitic birds have developed various adaptations. They lay their eggs very quickly, so that they don't have to stay long in the nest of the host. Sometimes, the mate helps by harassing the owner of the nest. The female has a protractile cloaca which enables her to lay in small nests or hollows. The eggs often imitate the coloration of the host's eggs, and the color pattern of the mouth and palate of the young is like that of the host, although the adults may be very different. In some cases (the cuckoo) the parasite hatches before the young of the host, and pushes the others out of the nest.

Parasitism is a very convenient way of life, enabling the parasite to produce many descendants in a short time. But the possibility of success of a parasite is always limited, because if it is too successful it will eliminate its own host. Some hosts develop defenses against it, such as recognizing the parasite eggs and eliminating them, or abandoning the parasitized nest. Or they may simply cover the parasite egg with more nesting material and lay their own eggs on top of it.

Some birds lay eggs in the nests of others of their own species. This is called intraspecific parasitism. It is common among aquatic birds (seagulls and diving birds) and in Passeriformes. This behavior is more frequent when population is dense and nesting sites lacking.

Investigators have studied how young parasites learn to identify their species in order to mate. A group of male parasitic birds kept isolated and seeing only their hosts, when released later did not mate successfully. Another group was raised in the presence of females of their own species, but at mating season they were rejected by the females. Only when they were raised in a mixed group of males and females did they "learn the language". It was concluded that parasitic birds must leave their adoptive parents and join a mixed group of their own species in order to learn the art of courting and mating.

members, it is called polygamy. There are two variants of polygamy, polygyny and polyandry. In polygyny, the male mates with several females, sometimes keeping them together in a "harem" as do Rheas. Others, such as hummingbirds, mate with various females but do not help to raise the young. Polyandry is much less frequent. The female mates with various males and may even keep them in a "harem." The cases of the Phalarope and the Jacana are described elsewhere.

Some polygamous birds maintain and defend territories dedicated to courting and mating, which are later abandoned until the next mating season. These territories are called "leks" (the word is Swedish and means something like "arena of display"). The lek is established by the dominant sex, generally the male. The territorial individual places himself in a visible place, to watch for intruders and defend his space. The methods of defense are various. Some species may sing a warning, many display their plumage, and in some cases they may actually fight.

An extreme variation of polygamy is promiscuity. This occurs when various monogamous couples lay eggs in a single common nest. The young are cared for by all the parents. The Guira Cuckoo (*Guira guira*) raises its young this way.

2.2. The reproductive cycle

At the end of the reproductive season the reproductive organs begin to change. The testes no longer produce sperm and sexual behavior ceases. Many species which form families in the reproductive season now band together in flocks for the winter. When spring approaches, the neural and endocrine apparatus once again become sensitive to external stimuli in the environment. The sexual organs develop, territories are claimed, construction of the nest begins, followed by mating, laying of eggs, and raising the young. Ovulation and insemination are the chronometers of the sexual cycle and must be perfectly synchronized.

The right place and the right time

The claiming of territory and the nuptial display are the activities which synchronize and direct reproductive behavior, both in space and in time. Aggressive conduct is sublimated and gives way to courting, which has similar characteristics but a different orientation.

During the reproductive season, the physiology of the bird is changed as well as its song, and the nest is constructed. The physiological changes are initiated by environmental factors such as the length of the day or the rainy season. In tropical regions, the changes in duration of the day are minimal. Birds may nest several times during a year. The factors which regulate the cycle may be the rains or other stimuli. Nesting must be synchronized with environmental factors which guarantee the food supply—fruit, insects, or seeds—for the young.

The hormones of the hypothalamus stimulate the

White-rumped Swallow (*Tachycineta leucorrhoa*) sexual organs. The testes increase in size, the ovarian follicles grow, and the gonads begin to produce hormones which stimulate courting, singing, and nesting. The hormones are balanced between accelerators and inhibitors. Light (diurnal length) is an accelerator, cold is an inhibitor. Other inhibitors are lack of a safe nesting site and fear, while the presence of the mate is an accelerator.

Birds must assure themselves of a safe territory for the nest near an adequate food supply. The size of the territory depends on the species and its specific needs. In birds such as seagulls which nest in dense colonies, the territory may only be large enough to allow the bird to sit on its nest without its bill touching the next bird, while birds of prey need vast territories.

Many species nest in colonies. The colony offers distinct advantages. It serves as a center of information. Predators are more readily detected by hundreds of birds than by a single one. (However, a large colony cannot be hidden and tends to attract predators.) The colony synchronizes the reproductive season of all its members. On the other hand, it allows the build-up and spread of parasites. It increases the probability of infidelity of the mate (this may be an advantage for the female and a disadvantage for the male) and requires time and energy to defend the nest.

Courting rituals serve as signals which enable the birds to find mates and copulate. They may include song, specific postures, dances, flights, noises produced by wings, tail, or objects, and the offering of gifts. This is called display. Ducks court in the water, swimming according to specific patterns. Some Falconiformes court in flight, and the culmination of display is the offering of a gift of prey to the female. Differences of courting patterns help to distinguish species, avoiding hybridization.

Among some hummingbirds, courting takes place in a small territory where several males meet to perform acts of display. The females watch and mate with the male which performs best. The dominant male mates with various females. Other males may have a second chance to mate at another time.

The nest and laying of eggs

The construction of the nest is the key to the success of most bird species. The nest is the center of all activity, and must be safe from predators, accidents, and bad weather.

The nest may be constructed by one or both members of the couple. Some species (such as woodpeckers and ovenbirds) are hard-working and may require one or two weeks of work to complete the nest. Other species may use nests abandoned by other birds. The Ovenbird (*Furnarius rufus*) builds a new nest each season, and its abandoned nests are used by other

American Wood Stork (*Mycteria americana*) species. But some birds take advantage of natural formations -cavities or hollows in trees, rocks, and even in buildings. The nest is constructed of available materials (mud, twigs, leaves) and covered inside with feathers, hair, or straw to insulate it.

Ovulation is controlled by the Hypophysis or pituitary gland, which is stimulated by hormones. It becomes active in the dark of night, and ovulation occurs six to eight hours later, that is, early in the day. Twenty-four hours later, the egg is complete and ready to be laid. Eggs are laid at fixed and regular intervals of a day or a few days, from the time the nest is completed until the bird is ready to incubate.

The size and quantity of the eggs varies according to species. In general the size of the egg is correlated with the size of the bird, but small birds lay somewhat larger eggs in relation to their size than do large ones. And birds which produce self-sufficient (precocial) young lay larger eggs with larger yolks than do birds which produce helpless (altricial) young.

The number of eggs laid depends on the way the species has evolved. Many birds lay as many eggs as they can raise, and the number is determined by the available resources. The number of young a pair can raise also depends on the time and energy needed to care for them, which may be very great in the case of large birds. Birds which live a long time usually lay fewer eggs, sometimes only one egg per season, and even in some cases (Albatross) only nest every two years. Obviously this is a factor which puts them at risk of extinction.

The female responds visually to the number of eggs in the nest and ceases to lay when it is complete. However, she can replace eggs which are lost. Under experimental conditions, a woodpecker has laid up to seventy eggs in one nest, as eggs were removed.

Incubation and hatching

During incubation birds transfer heat from their bodies to the egg, to facilitate development of the embryos. At the beginning of the reproductive season, a large quantity of the hormone prolactin is released into the blood. This causes an "incubation patch" to develop. Feathers on the breast are lost, while the skin thickens and more blood-vessels develop. This patch keeps the eggs warmer. During incubation, the temperature of the eggs is maintained between 37º and 38º C. Outside of this range the embryo may cease development and damage may occur.

In many cases, incubation begins only after laying is completed, and all the young hatch at the same time. But in other species, incubation begins with the first egg and the young hatch at different times. In about 25% of species, only the female incubates the eggs. In about 5%, the male incubates. But in the majority of species, both parents share the task. The time of incubation varies, generally lasting from three to five weeks. To insure that the eggs are evenly warmed, they are regularly turned over with the feet or the bill.

When both parents incubate, they perform ceremonies at the "change of shift" which may include touching bills, ruffling feathers, offering food, etc. The Emperor Penguin (*Aptenodytes forsteri*) is an extreme case. After the single egg is laid, the male cares for it for two months, incubating it between his feet and his breast during the Antarctic winter, while the female feeds to recuperate the weight lost with the laying of the egg. The male cannot leave the egg during this time. When the female returns, the baby has hatched. She relieves the male in caring for the young. Both parents feed the baby from their crop.

When the young is ready to hatch, it has an "egg tooth" on the point of its bill, on one or both man-

Speckled Teal (Anas flavirostris)

dibles. This is used to break the egg, and is lost a day or two later. There is also a special "hatching muscle" which helps to press against the egg-shell to break it. The young already exhibit social behavior even before hatching. It has been shown that among partridges, the tapping of the embryos inside the adjacent eggs stimulates the others and synchronizes hatching.

First care of the young

Some chicks are born with open eyes, a thick covering of down, and can already walk and feed themselves. These are called precocial. Those which are born helpless and must remain in the nest being fed by the parents are called altricial. The young of oyster-catchers, for example, are precocial. The parents guard them from predators, watch over them, and teach them how to locate food.

The Passeriformes have helpless young. They must be protected both from heat and from cold, and fed by the parents. Certain signals stimulate the parents to feed them, generally a large open mouth, which may be marked with bright colors or patterns.

Most birds feed insects to their young. Birds of prey feed pieces of meat, and sea-birds regurgitate partly-digested fish. Flamingos and pigeons produce a "milk" which is a mixture of half-digested food with substances produced in the crop.

The young compete to obtain the maximum amount of food. Among herons, which lay two eggs per nest, the larger and stronger chick may receive such a large proportion of the food that the smaller one dies. This behavior insures that in times of scarcity, at least one chick will survive.

Larger birds must care for the young longer than small birds. Care must continue at least until the young can fly.

Though they may be tiny and helpless when hatched, birds grow with amazing speed. It is supposed that this is a characteristic inherited from their dinosaur ancestors. The great quantity of blood-vessels in the marrow of bones of dinosaurs allows us to deduce that they grew very fast, perhaps even faster than birds. Lizards, which are cold-blooded and farther back in the evolutionary chain, grow very slowly.

Great Egret (Ardea alba)

Behavior

1 Flight

2 Feeding

3 Breeding

4 Agonistic

5 Emotional

The courtship ritual of the Chilean Flamingo (Phoenicopterus chilensis) includes rubbing together of necks and bills. Among adults neck-rubbing may indicate courting, while juveniles do it as a form of competition. These birds are highly social and travel in large groups. The males are somewhat larger than the females and during mating the female keeps her head under water. They nest in colonies and the young are fed in common.

Chilean Flamingo (Phoenicopterus chilensis)

Reproduction in Black-necked Swans (Cygnus melancoryphus). *The reproductive cycle lasts about five months. It begins with a face-off between couples trying to claim more territory in the lake (1). The straw nest is constructed among the weeds. The female incubates the eggs, while the male remains constantly nearby (2). Although they are very discrete and protective, they are known to mate outside the couple frequently. The new-born cygnets are carried on the backs of their parents (3) even until they are rather well-grown (4). The parents defend them from neighboring species in the lake (5). They exercise strict discipline to keep the group closely united during the whole period. At the age of about three months, (7) the young are independent enough to find themselves harassed by neighbors. Figure 8 shows a three-month-old swan compared with an adult.*

Reproduction in Coscoroba Swans (Coscoroba coscoroba). *Both parents help build the straw nest. The female incubates the eggs while the male remains nearby, but not as close as the Black-necked Swan (Cygnus melancoryphus) (2). If the female leaves the nest to feed, she covers the eggs with feathers (3). Discipline of the cygnets is more lax than among Black-necked Swans, so that in 4, the cygnet of one family becomes isolated in another until the parents separate it with pecks and aggressive runs. They do not carry the young on their backs, but at night they shelter them beneath their wings in the nest (5). They grow more slowly (6) and when larger sleep in a closely-packed group to protect themselves from the cold (7).*

Reproduction in Snowy Egrets (Egretta thula). *The reproductive cycle lasts less than three months. They reproduce in colonies which consist of dozens of couples, and include other species of herons. The courting exhibition begins with cycles of raising the head (1). The nest is built in trees, using twigs from last-years' nests (2). Mating occurs on the nest. (3). They lay two or three eggs and care for them for five or six weeks. Both parents incubate the eggs (4). The young can move about as soon as they hatch, and in a few days they begin to explore (5). They are fed regularly by the parents (6). Their wings are developed by the time they are three weeks old (7) and they start to practice flapping movements. Soon afterwards they may be seen attempting to feed themselves (8) on the shore of the water or on land.*

Reproduction in Coots. *The couples put on aggressive displays with neighbors (1) during the entire reproductive period. Both members of the couple build the nest (2), incubate the eggs (4) and feed the young (8). Mating occurs on the edge of the nest, which is constructed on a mound in the water. The young rarely ride on the backs of their parents (5). The parents must defend the young from competitors for food such as the Coscoroba Swan (Coscoroba coscoroba) in 6, and predators such as the Southern Caracara (Caracara plancus) (7). Coots are devoted parents and closely united as a couple. Here we see a couple which began their first nest in autumn and due to the loss of the young built two successive nests until at last they were able to raise two chicks successfully in spring.*

Three activities which begin the reproductive cycle of Great Egrets (Ardea alba). *The upper sequence (1) shows the mating exhibitions of the male. They consist of spreading his plumage (egrets) and stretching his neck almost vertically, then swiftly retracting it. The central sequence (2) shows the couple gathering twigs nearby to build the nest. This activity, besides being necessary for raising the young, re-affirms their pair bond, because it continues during the period of incubation. In the lower sequence, we see them mating. The male perches on the back of the female (3b) and the cloacae touch (3c).*

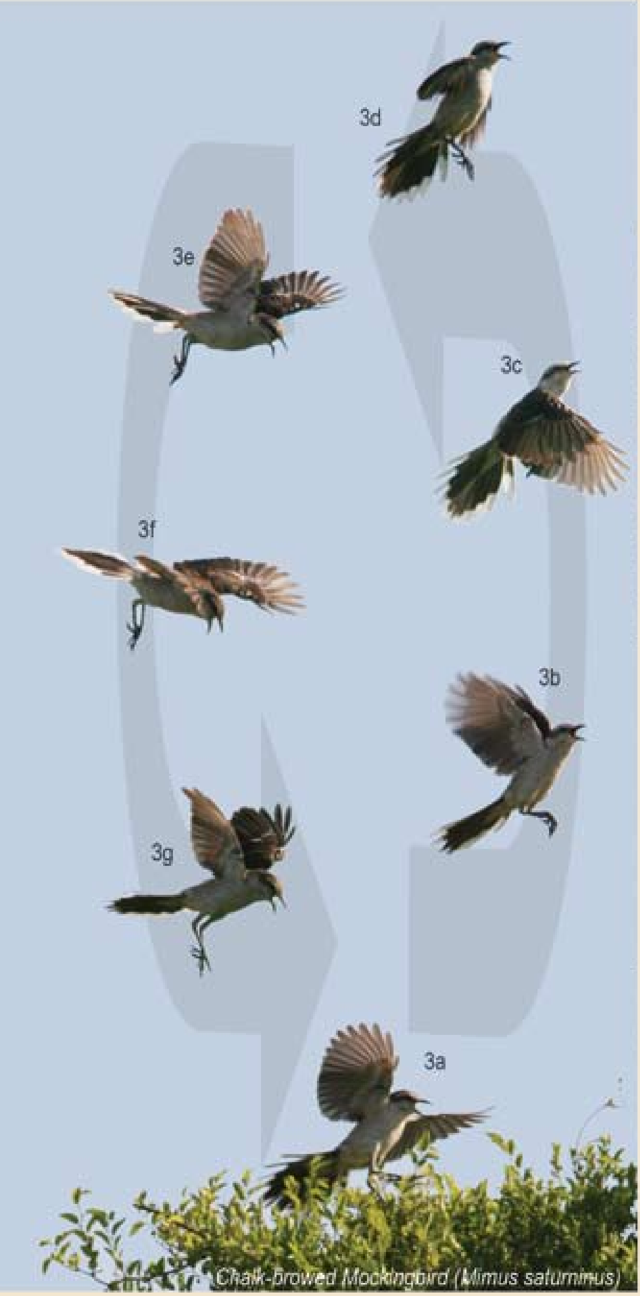
The reproductive cycle of the Great Egret lasts some three months. After the initial phases (see previous page) the couple remains together during the nesting (3) until the young are born. After four weeks (4) the wing-feathers are grown. The young are fed by the parents with semi-digested food (5). They compete actively for food to the point that some of them fall from the nest, and wander on the ground until they die (6). At six weeks of age the wings are completely developed and they begin to strengthen their muscles by exercising in the trees (7). The first attempts at flight show their clumsiness when they attempt to turn in the air. Like a person learning to ride a bicycle, they are fine as long as they are going straight -the problem is when they attempt to turn.

Mating of the Southern Caracara (Caracara plancus). *These Falconiformes have a very strong pair bond. They usually remain together all year, and are always seen near each other. The reproductive cycle begins with demonstrations of affection and bonding. One of them brings gifts (1). The male brings the female something he has caught. Then he "shows off" throwing back his head and emitting a guttural sound (2). The female also does this, but does not throw her head as far back. When the female is receptive, she raises her tail, lowers her head, and opens her wings (3). The nest*

is built of twigs high in a tree. It is saucer-shaped, large and conspicuous (4). At mating time, they engage in energetic acrobatics. The males fight in the air (5), whether for possession of gift offerings (as in 1) or just before mating in a frenzy produced by the availability of the female. Mating occurs in the tree (6 and 7) where the female incites the male (as in 3) and the male, after mating, emits a cry of victory (as in 2). The young caracaras show their plumage (8), which is partly similar to that of the adults.

Plumbeous Rail (Pardirallus sanguinolentus) Whistling Heron (Syrigma sibilatrix)

These two couples perform a ritual to reaffirm their pair-bond. To the left, the Plumbeous Rail (Pardirallus sanguinolentus). These birds are timid. They inhabit the borders of rush-beds. When they feel themselves observed, they quickly hide in the thickets. Their pair-bonding ritual consists of a series of loud deep cries, emitted simultaneously. It is easy to hear the song, which carries a great distance, but it is difficult to see them emitting it. They move in circles around each other with the bill at mid-level. To the right, an interesting and unusual incident. Two Whistling Herons (Syrigma sibilatrix) feel themselves threatened by a solitary Whistling Heron, who has approached them evidently in search of a mate. The male of the couple flies to the female, and the two of them dance to reaffirm their bond. They raise their bills and then lower them to the ground, while they walk in circles with the feathers of the head erect.

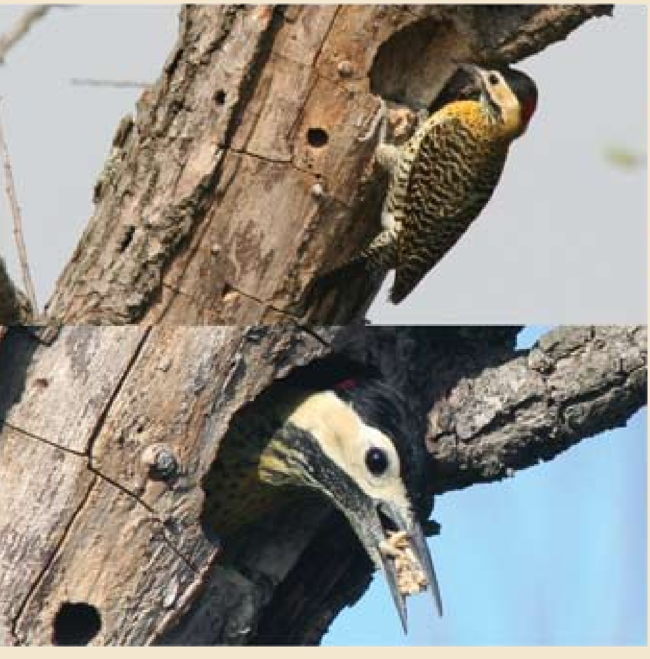


Chalk-browed Mockingbird (Mimus saturninus)

Snowy-crowned Tern (Sterna trudeaui)

Chalk-browed Mockingbirds (Mimus saturninus) sing beautifully, but have rather drab plumage. They perch on the highest twig while singing their varied songs. Then they fly into the air, glide for a moment, and land in the same spot, still singing. They do this repeatedly and continue for a long time. The male of the Snowy-crowned Tern (Sterna trudeaui) demonstrates that he is an expert fisher. He flies at medium height, dives into the water, and catches a fish which he offers to the female. She may refuse it if she doesn't like the male.

Golden-breasted Woodpecker (Colaptes melanolaimus)



Campo Flicker (Colaptes campestris)

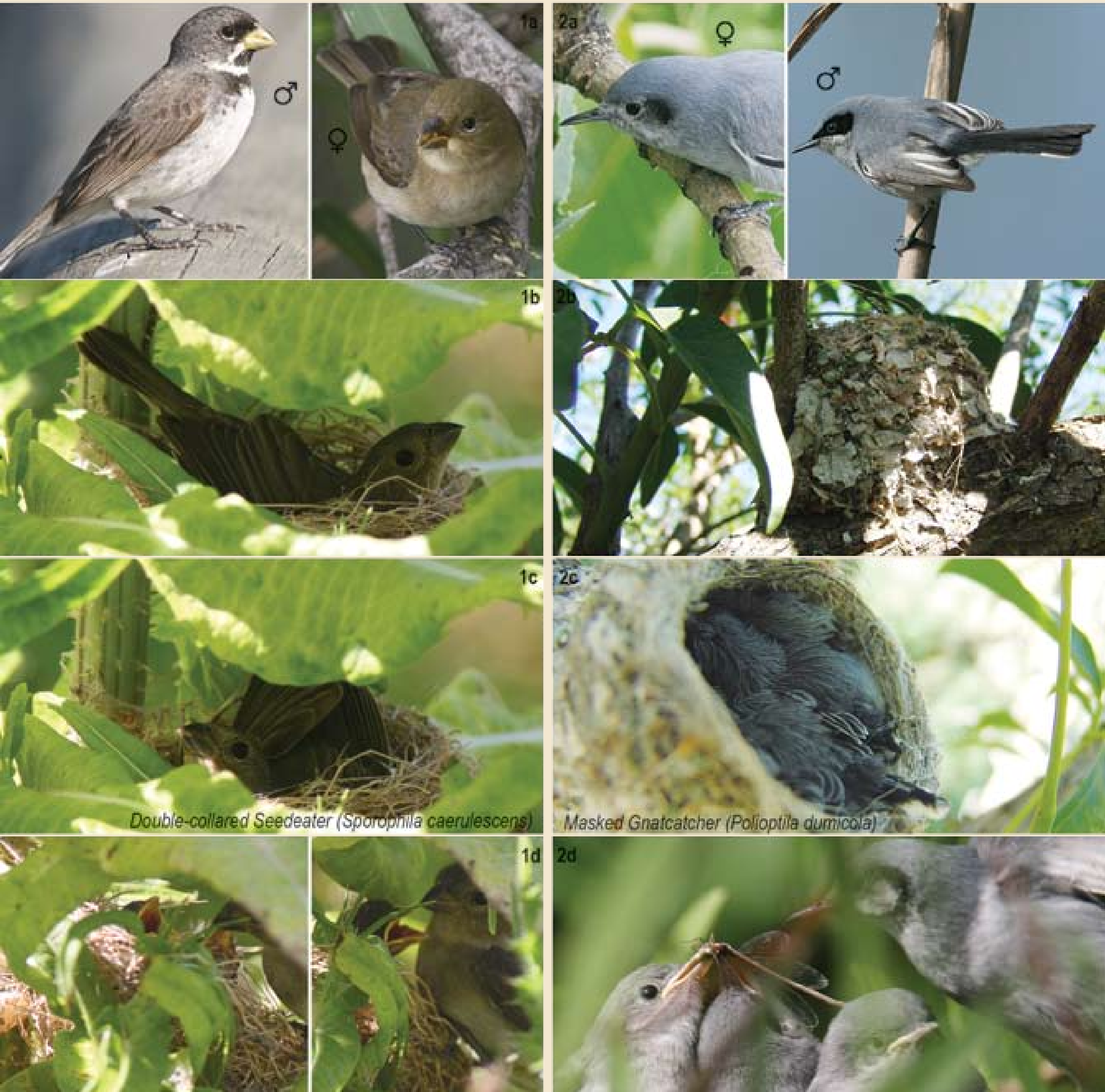
Woodpeckers are distinguished by their zygodactylous feet having two toes pointing forward and two backward, with strong claws for climbing. They usually have striking colors and slight sexual dimorphism. Their short robust legs are not ideal for walking on the ground, but they can climb vertical tree-trunks with the help of the stiff feathers of their tails, which give them a third point of support. They tap on tree-trunks to establish their territorial rights. During courting and territorial displays their posture includes: tail open like a fan, eyes half-closed, head erect, and wings held out from the body. In this position they move the head up and down and from side to side, emitting the typical call of woodpeckers (Quick! Quick! Quick!)

The male South American Stilt (Himantopus melanurus) courts the slightly smaller female by blowing into the water to produce bubbles, while erecting his lateral feathers. He does this first at one side and then other of the female, for about twelve seconds (2). The female demonstrates her receptiveness with her head stretched down and forward (1). This eliminates all possibility of mistaken aggressiveness. In mating (3), the male stands on the back of the female and mates for not more than two seconds. In (4), the female breaks off the submissive posture when mating is finished, but before separating, the couple touches heads and breasts, crossing their bills.

These two pages show various stages of the reproductive cycle. Number 1 shows the growth of the young of the White-necked Heron (Ardea cocoi). These herons are very discrete and it is difficult to observe them mating. The young have mimetic plumage which enables them to hide in the foliage. The Southern Screamer (Chauna torquata) (2) nests on open ground. The hen lays one egg every two days until the nest is complete. The couple is closely united and stays together all year around. The young remain close to the parents and feed on plants.

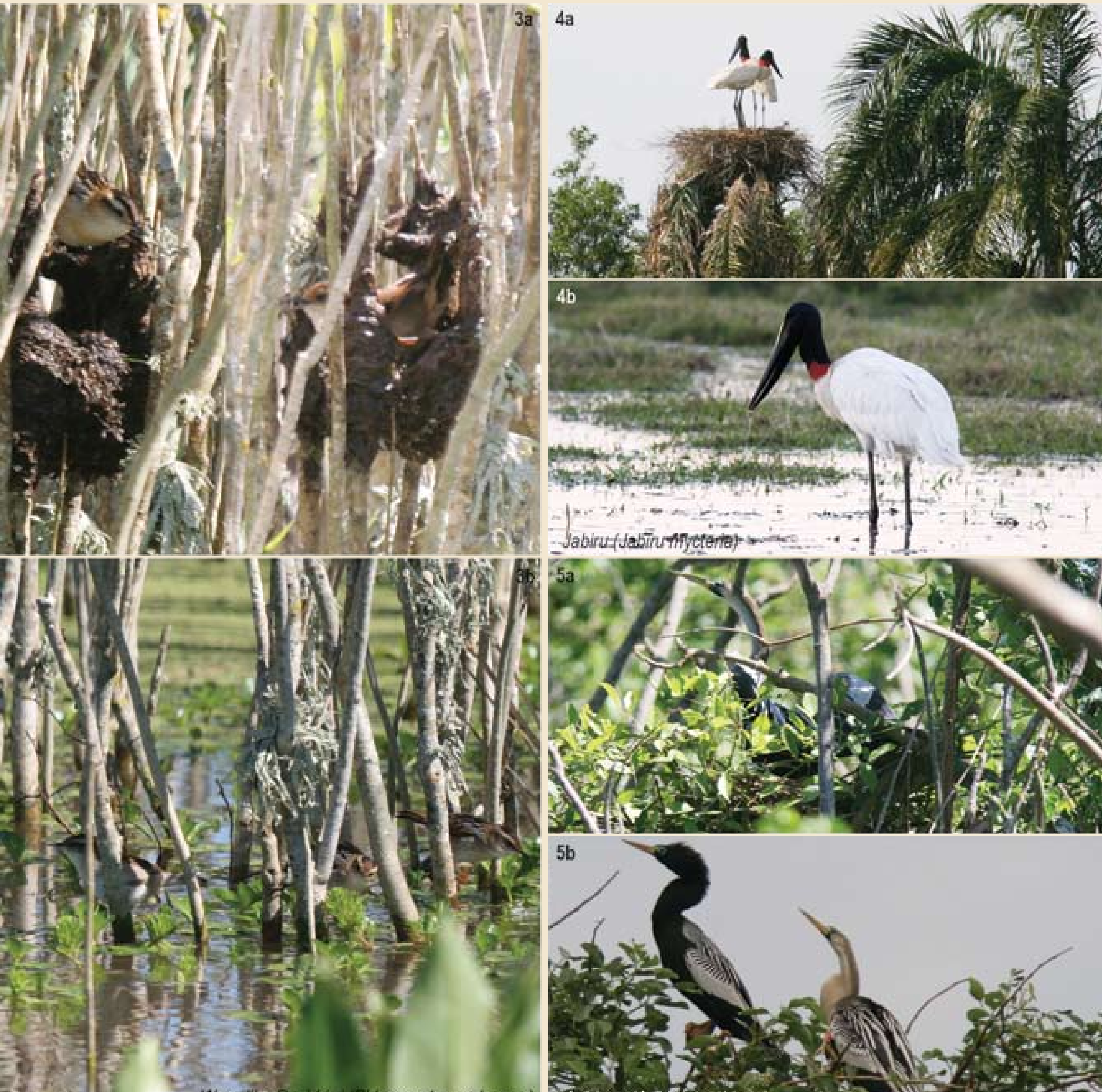
The Pied-billed Grebe (Podilymbus podiceps) (3) is an aquatic bird which prefers to dive under water rather than fly when frightened. They are not good flyers, but are excellent under-water fishers. The nest is rudimentary and little trouble is taken with its construction. The young leave the nest soon after hatching and are fed fish by the parents. The Wattled Jacana (Jacana jacana) (4) is polyandrous, one female mating with various males. The male incubates the eggs in open ground, defending them by leading enemies away from the nest. The plumage of the young is very different from that of the adults.

The male of the Rosy-billed Pochard (Netta peposaca) (with the red bill) joins the female in the water and they practice a simplified courtship ritual, circling around each other. Then the male mounts the back of the female, and she becomes completely submerged in the water except for part of her face. After mating, which lasts only seconds, the female splashes in the water, turning about. As a triumphal finish, first the female and then the male stretch and flap their wings while standing in shallow water. Finally, both members of the couple sit together on the shore. Like most ducklings, the young form a closely-packed group and feed for themselves at the surface of the water.



The male and female Double-collared Seedeater (Sporophila caerulescens) (1) have highly differentiated plumage. The nest is built among leaves and stems of small plants. The female brings fine straw while the male keeps guard nearby. The female puts the straw in the nest and sits on it, turning her body to mold it to her shape. The Masked Gnatcatcher (Polioptila dumicola) (2) builds a much more elaborate cup-shaped nest with various materials. Both parents feed the young both in and out of the nest, bringing small insects which they find among the foliage of near-by plants.

Various types of nests. *The Rufous Hornero (Furnarius rufus), an ovenbird, (1) is native to South America. It builds a new nest every year, using clay, roots, straw, manure, and other materials. Both the male and the female work on it, using their bills. It requires about five kilograms of clay and takes a week to build. The interior is divided by a partition into two zones, the entry and the nursery. Old nests*



Jabiru (Jabiru mycteria)

Wren-like Rushbird (Phleocryptes melanops)

Anhinga (Anhinga anhinga)

are occupied by other birds, in this case a Saffron Finch (Sicalis flaveola). The Firewood Gatherer (Anumbius annumbi) (2) builds its nest in low trees or in angles of posts, carefully interlacing dry twigs. Both members of the couple participate. The Wren-like Rushbird (Phleocryptes melanops) (3) builds a nest of straw supported by vertical stems low over the water. Both the male and the female work on the nest, in this case built among the vertical stems of Duraznillo (Ludwigia sp.) The Jabiru (Jabiru mycteria), a kind of stork, builds great high platforms, often on the tops of palm trees as in the photograph. The Anhinga (Anhinga anhinga) prefers to nest on hidden branches. It often nests with herons.

The Great Egret (Ardea alba) feeds its young using a fish as an embolus or plunger to bring up partly-digested food from deep inside its digestive system (l-3). It transports partly-digested food to the young this way. On rare occasions (4-6) it may give the fish directly to the young.

Many kinds of birds, such as the Great Egret (Ardea alba), cannot feed all the young they hatch. This obliges the stronger siblings to push aside the weaker at feeding time. In 1a, the parent stands by indifferently as one of the young attacks the other, taking it by the neck and pushing it until it falls. Once on the ground, the weaker birds will wander for a few days until their health deteriorates and they die. In other cases, such as the Masked Gnatcatcher (Polioptila dumicola) (2) the parents distribute the food among all the young. The three chicks have spent the night huddled close together to keep warm. Early in the morning, the parents search for small insects nearby, which they carry to the young. It can be observed that they feed each chick in turn until they are satiated.

Various ways of feeding the young. *The Grassland Yellow Finch (Sicalis luteola) (1) regurgitates partly-digested food to make it easy for the young to digest. The photographs show a sequence which took a rather long time (on the hyper-active scale of these little birds) while the adult (at the right) regurgitates various times, passing food in the form of a white paste to the young. Seagulls (5) also regurgitate food for their young. The Eared Dove (Zenaida auriculata) (6) regurgitates a "milk" composed of cells shed from the crop of both parents. Other birds, such as the Chestnut-capped Blackbird (Chrysomus ruficapillus) (3) feed the young on insects or whole worms.*

The White-rumped Swallow (Tachycineta leucorrhoa) feeds its young on the wing. The color of the young bird's palate is thought to function as a stimulus which induces the parents to feed them. Their wings are long and pointed, ideal for flight, but their legs are so short they cannot walk. The bill is wide and flat, adapted to catch flying insects. They eat, drink, and feed the young while flying. The Yellow-billed Cardinal (Paroaria capitata) is seen here teaching its young feed themselves. It shows them how to pick up small grains from plants or directly from the ground. Faced with the complaint of the young, it is less indulgent, scolding it with its mouth wide open.

8. Social behavior

1. Understanding Behavior

1.1. Classification of behavior

This chapter is devoted to aggression, resolution of conflicts, rituals, and pleasure. Behavioral patterns are not pure. Courting rituals include attack or feigned attack and flight, while preening shows elements of appeasement. Fixed patterns of behavior are often derived from other behaviors related to feeding or hygiene.

All behavior is adapted to survival. Behavior is a sensitive and powerful tool aimed at maintaining (or re-establishing) the status quo.

Experimental studies of behavior have tended to take somewhat opposed points of view, one deriving behavior from physiological mechanisms such as the nervous system and hormones, the other concentrating on what might be called "psychological" factors such as learning. In practice it is usually impossible to separate the two, especially in field studies. This book is devoted to observation of animal behavior in the wild.

Complex behavioral patterns

The difference between simple reflexes and complex behavior is not easy to establish. They have common characteristics and the difference may be in degree rather than in kind.

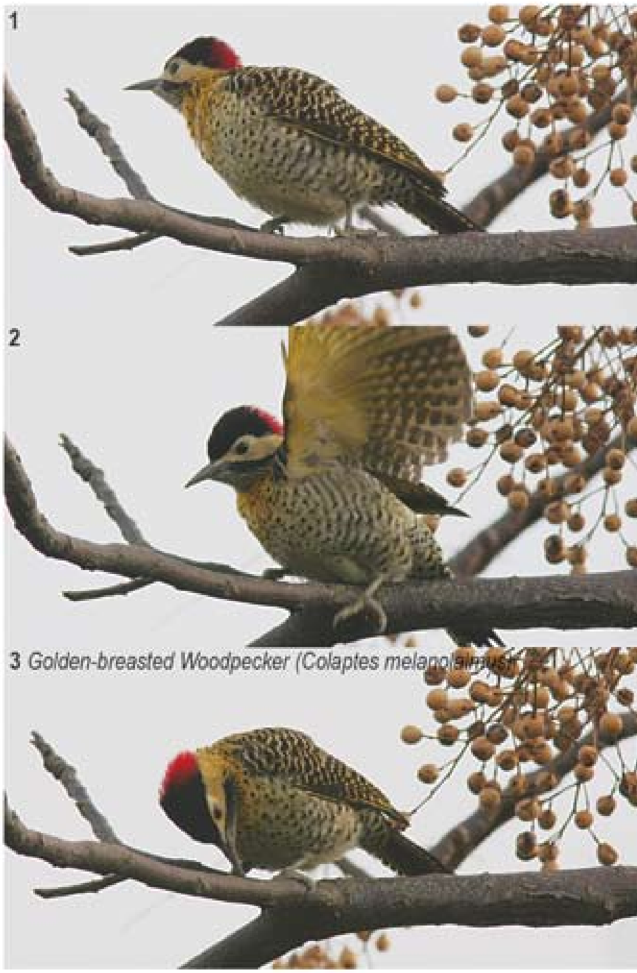
Latency is delay between stimulus and effect. This may be physiological due to causes in the nervous system, but it may also be determined by the threshold of reaction. Once activated, the behavior may be slow to disappear even when the stimulus is withdrawn.

Addition refers to stimuli received from various sources and possibly through various senses at different times.

Warm-up and fatigue. Some behaviors require a warm-up period. The intensity of the response increases with the time the stimulus is maintained. However, stimuli of great frequency or long duration may also lead to fatigue and a diminished response.

Inhibition permits an organism to control its conduct, so that the same stimulus does not always inevitably elicit the same response.

Much behavior is stereotyped. It is always repeated in the same way. It also may be specific, showing little variation among individuals of the same species. Nest-building and song are species-specific.



This Golden-breasted Woodpecker (Colaptes melanochloros) moved its left leg and slipped. Having recovered its balance, it examines the place where it slipped like a human who slips in the street. This shows that it is innate behavior of very ancient origin.

Instinct and Learning

Instinct is inherited and genetically determined by natural selection, while learning is based on the history of the individual. Instinct is rigid, difficult to change, and long-lasting. It is the result of many generations of evolution, useful for species with short life-spans, and with a short interval of parental care and therefore little opportunity to learn. Natural selection has favored inherited behavior in cases when the delay required for learning a response could be fatal.

But although behavior in birds has an inherited basis, the influence of the genes in complex behavior is not absolute. Learning does modify behavior according to circumstances. For instance, the basic pattern of bird-song is genetic, but young birds learn the "local dialect" from their parents.

W. H. Thorpe has formulated a scale of learning according to increasing complexity, with the following gradients:

- Habituation. This is the simplest, and consists of the loss of a reflex when the stimulus is repeated or constant. For example, birds become accustomed to a scarecrow in an orchard.
- Conditioned reflex. This concept was first demonstrated by Pavlov in his experiments with dogs.
- Trial and error. This is associative learning, in which behavior is modified to obtain a benefit.
- Latent learning. This is learning which yields no immediate benefit, but may be useful or essential for long-term survival. The exploration of territory is an example of latent learning.
- Intuitive learning. Intuition may resolve problems without trial and error or a process of deduction.

Imprinting is a special case, of particular importance in birds. Konrad Lorenz noticed that at certain brief periods in their early life, young birds are receptive and become imprinted with the image of the mother, which (in precocial birds) they then follow. Imprinting lasts for life and the bird when ready to mate will seek a similar mate. This reinforces species recognition and the separation of the species. However, birds raised by a surrogate will become imprinted with the surrogate and may attempt to mate with the wrong species. Thus, a white peacock raised in the reptile house of the San Diego Zoo "fell in love" with a large tortoise and performed its mating display before the reptile. For this reason, ecologists raising condors for later release in the wild use a puppet in the form of a condor to feed them, and avoid showing their human forms to the young birds.

Categories of Social Acts

Colonial species have special behavior patterns absent in solitary animals. Intra-species social behavior falls into four classifications. Behavior which

Scratching is an ancestral behavior. Most tetrapods use their hind legs to scratch their heads. This bird has lowered its wing to reach its head, like a dog.

benefits both the actor and the receiver is called cooperative. If it benefits only the actor, it is egoistic or selfish. If it only benefits the receiver it is altruistic, and if it is injurious to both, it is malicious.

This behavior is not assumed to be guided by a conscience, and terms such as "egoistic" and "altruistic" are not intended as value judgments. Altruistic behavior exists because it has survival value for the gene pool, if not for the individual. Therefore malicious behavior is rare.

Behavioral interactions between different species are also classified according to the benefit or damage produced to the individual. When two species struggle for the same resource, it is called "competition." When one species feeds on another, it is called a "predator" or a "parasite" depending on whether the victim as a rule survives, and the victim is called "prey" or "the host." When both species are benefited, the relationship is called "mutualistic." When one species is benefited and the other is not affected, it is called "commensualism" and when one is damaged and the other is not benefited, it is called "amensualism."

The results of these interactions depend on the availability of resources, which in turn may be changed by the interaction. Competition reduces resources. The human being is a strong competitor for the resources of many species.

The interaction of predator-prey is fairly predictable. An increase in the availability of prey leads to an increase of predators, which then cause a reduction in the quantity of prey and a consequent reduction in the predator population.

Absence of competition or absence of predators can lead to a population explosion of the prey. This often occurs when new species are introduced into habitats where they have no natural enemies. The new species may expand without limits, affecting the population stability of native species. The same may happen when the predator population is reduced by over-hunting or other factors.

An example of mutualism is the relationship of birds with those plants which depend on them to disperse their seeds. Most of the fruits which depend on birds as vectors of diffusion are red and odorless (which is attractive to birds but less so to other animals which might eat them). Some fruits are bad-tasting to mammals but not to birds. Another example of mutualism is the relationship between the hummingbird and the flowers which it pollinates.

1.2. Behavior and hormones

Behavior is influenced by the nervous system and by the endocrine system. The latter consists of various glands which release hormones directly into the extra-cellular liquids. The pituitary gland generates the principal hormones which affect conduct.

The hypothalamus produces dopamine which controls appetite and sexual responses. In laboratory experiments, when electrodes are connected to the hypothalamus of an animal and the animal learns a response which will activate the electrodes and thereby stimulate the hypothalamus, it will continue to respond until exhausted. The hormone released produces the state of excitement related to "search", whether for food or for a mate. The search itself is more rewarding than achieving the goal.

Hormones

Hormones comprise a system of chemical communication which causes physiological changes in the animal. For example, changes in the length of daylight stimulate the hypothalamus to release hormones which activate the reproductive system in birds.

Hormones and behavior interact. Behavior affects the release of hormones. The female pigeon does not lay eggs if the male is not present. The courting of the male stimulates the production of sexual hormones in the female. The presence of an actively courting male is more effective than the presence of a castrated male. The male pigeon does not incubate the eggs, but when the female starts to set, this action stimulates the release of the hormone prolactin which initiates the production of "pigeon milk" in the crop of the male.

Courting in social species helps to synchronize reproduction. All couples nest and raise their young at the same time. Birds which parasitize other birds are stimulated to ovulate when they see their host birds building nests.

Sexual Hormones of Birds

Territorial behavior changes with the season and depends largely on the testosterone level. Testosterone plays an important role in aggression during the reproductive season, but at other times territorial behavior may be independent of the control of the gonads. While the young are being raised, a conflictive situation arises between the need to defend the territory aggressively (which requires a high testosterone level) and the need to care for the young (which requires a low one.) The testosterone level is highest while territories are being established, then drops to an intermediate level while the young are being raised. It drops again to a minimum during the winter months when many species band together in large flocks and aggression may be counter-productive.

Testosterone is essential for sexual behavior of the male, territorial behavior, development of secondary sexual characteristics, muscular growth, and the production of sperm. Nevertheless, a high level of testosterone has its cost for the organism. It causes hyperactivity which requires more energy, it may be carcinogenic, it depresses the immune system, reduces the amount of stored fats, and causes the organism to take risks which may subject it to injuries. Excess testosterone also interferes with the care of the young.

Experiments with sub-cutaneous implants of testosterone in male birds show that female birds prefer them to birds with lower, normal levels of testosterone. But the implanted males were less attentive to the young. They visited the nest less often and

The Rufescent Tiger-Heron (Tigrisoma lineatum) is no threat to the group of Brown-headed Gulls (Larus maculipennis). Nevertheless, the birds closest to him are startled by an unexpected movement and take wing, causing the whole flock to fly. Early warning is an advantage of living in large groups.

supplied less food. They sang more, flew further, took more risks, attracted more predators, and suffered a higher rate of mortality. They produced more descendants, but the young were smaller in size and had a higher mortality rate. Evidently the correct hormonal balance is essential for successful reproduction.

Stress

The morphology, physiology, and behavior of birds respond to a predictable annual cycle. But unpredictable events elicit rapid changes in physiology and behavior. Environmental changes, the presence of predators, or threats to the social status influence the release of hormones in the pituitary-hypothalamus circuit. Long-term stress has damaging effects. Animals must control the stress level with other hormones which inhibit it. The concentration of hormones has three basic levels. The lowest maintains life. The intermediate level corresponds to seasonal fluctuations and is predictable. The highest level of hormones is related to stress level and depends on unpredictable outside stimuli.

Both the behavior and the physiology of birds respond to changes in the environment. These changes are well-documented with relation to the digestive system, but it has also been demonstrated that certain birds will change their flight patterns according to the risk of predation. In a controlled experiment, two groups of Turnstones (*Arenaria interpres*) were presented with the silhouettes of seagulls and of raptors. The silhouette of the raptor induced more flying activity. After a few days, the threat of predation caused an increase in the size of the pectoral muscles of about 3.6%. This shows that factors of risk may directly affect the size of organs.

2. Aggression and Ritualization

Aggressive behavior may be motivated by the need for security or by desire for conquest (of territory, a mate, food, etc.) Aggressive and defensive behaviors are indissolubly linked and universal in the animal kingdom. In nature much time is spent in vigilance, but actual conflicts rarely last more than a few seconds. Laboratory studies, however, are often devoted to situations of chronic conflict, with the purpose of extrapolating them to human behavior.

There are no clear limits to aggressive behavior. Aggression is defined as an offensive act which obliges the opponent to abandon what he has or is trying to obtain. Some ethologists group aggression under the heading of agonistic behavior (from the Greek word for combatant) which includes all behavior related to fighting, aggression, defense, submission, and flight.

Aggression can be divided into two types: predatory and emotional. Predatory aggression occurs because the predator likes to hunt. If an animal hunts only for pleasure and not only for food, there is a cost in energy, risk, and opportunity (i.e., the relation between alternative behaviors. A bird which is constantly hunting may lose an opportunity to mate, or a bird which does nothing but eat may lose its territory.)

Emotional aggressiveness, on the other hand, is related to anger. This is the aggressiveness by which dominance is affirmed and territories are claimed. Normally it occurs among males. It may also originate from emotions such as fear, pain, stress, or a combination thereof. Cases of pathological aggressiveness also occur.

Territorial aggression varies widely. The territory of a bird of prey may be several miles in extent, while

a seagull claims less than a square yard. Among gregarious animals aggression is sublimated or disappears, and distance between individuals is reduced to a minimum. When the individuals separate into pairs or families, aggression reappears.

Territorial behavior is usually related to feeding, but may have other functions such as keeping rivals away from the mate, controlling predators, and avoiding the introduction of parasites.

Territorial limits are not absolute. A bird will chase an intruding neighbor out of his own territory into the neighbor's, until at a certain point the intruder becomes the owner, turns, and chases the (now intruding) neighbor back to his own territory. Territory has fluctuating limits and a dynamic stability. It is balanced between attack and flight, where defeat is quickly recognized and the defeated bird will retire to a distance to avoid further attacks.

Fear, Pain, and Stress among Birds

Of course birds feel pain, but they conceal it to keep their weakness from being suspected. In nature, the weak cannot survive long. Temple Grandin in his book *Interpreting Animals* has advanced the hypothesis that although animals feel as much pain as humans, they suffer less. This may enable them to conceal the state of distress in which they find themselves. At the same time, he suggests that fear is worse than pain, but animals are prepared not to be more frightened than necessary.

There are many causes of stress. For example, the conflict between fear (desire to flee) and the need to protect the young. Overpopulation causes conflicts between groups. Adverse climatic conditions (extreme cold, heat, or drought cause stress as do many other factors.)

Fear and pain may make animals aggressive.

A Red-gartered Coot (Fulica armillata) approaches and menaces a competitor. The closer he gets to his opponent, the more insecure he is, and at last turns and flees as if surprised by his own temerity. Ancestral behavior may be inhibited by the balance of fear and aggression.

Frustration causes many conflicts. Birds submitted to chronic stress may sicken and die without visible injuries, due to excess hormonal levels. But they have also developed ways of dealing with stress. A posture of appeasement may minimize the threat without the need to flee.

Interspecies aggression has less in common with the attack of the hunter than with the counterattack of the prey originating in fear. Many small birds will attack or "mob" a predator trying to drive it away from the nesting territory. However, the principal threat to a species is not predation but competition for limited resources.

An interesting category of combative behavior is the "critical reaction." When the weaker party cannot flee and has no hope of mercy, he will fight to the finish. Tiny animals, when cornered, become very fierce. The Chinese general Sun Tse in his book *The Art of War* warns against surrounding the enemy on four sides, because if his retreat is cut off, he will then fight to the death.

Ritualization among Birds

Birds employ various strategies to avoid outright fighting, including flight and concealment. They may resort to camouflage, remain motionless, or "disappear" within the anonymity of a large flock.

Many birds can blend into their environment thanks to their remarkable mimetic plumage, often combined with specific postures, such as the bittern which stands with its neck stretched so that the stripes look exactly like the reeds among which it lives. Helpless young birds must be camouflaged. The juveniles often have mimetic coloration similar to that of the adult female. The males of many species develop striking plumage only during the breeding season.

Well-camouflaged birds usually remain immobile in the face of a threat. An extreme case is that of the Spotted Tinamou (*Nothura maculosa*) which only flies when the hunter is a few steps away, becoming easy prey to firearms. Migrating birds try to evade diurnal predators by flying at night.

Another way of "disappearing" is to form large colonies. Almost certainly, the first social organization, pre-dating the family unit, was the "anonymous crowd," exemplified by a school of fish. A flock of ducks is an aggregate of many family groups, while a band of seagulls is heterogeneous. It becomes difficult for a predator to single out an individual from a large flock. Studies have demonstrated that the rate of success of a predator diminishes as the size of the flock preyed upon increases. When the massed band flies together, the predator loses track of a single victim. A flock of seagulls reacts to a menace by flying in a chaotic fashion. Some species such as terns

Speckled Teal (*Anas flavirostris*)

Red Shoveler (*Anas platalea*)

Ducks use movements of their heads as a rudimentary means of communication. They stretch their necks and point the bill at the opponent. This is a sign of challenge and claim to territorial domination.

flee in wave-like movements, and others (ducks, for instance) scatter in small groups.

Many species of birds, like other animals, have a hierarchy of dominance when they gather in flocks. There will be a dominant "alpha" leader and perhaps a "beta" to reinforce him. Aggression, such as pecking, is controlled and once the hierarchy is established it can be reaffirmed by simply staring down a member of the group which infringes on the rules. But other species, such as the Common Tern (*Sterna hirundo*) outside of the mating season gather in seasonal flocks which show no hierarchical structure.

When faced with a threat, an animal has two options, fight or flight. Generally a bird flies or dives if it can. Fighting is not a good alternative.

Aggression has two phases: the preliminary face-off and the actual fighting. When the preliminary face-off is prolonged, it is transformed into a combat ritual. Various tools are exploited in the preliminary face-off. Many birds (such as the Cattle Tyrant - *Machetornis rixosa*) possess an erectile crest which is only visible in situations of extreme tension. Birds may fluff out their feathers to appear larger. Herons stretch their necks and point to the sky in an attempt to intimidate their opponent.

At the beginning of the XX Century, W. Huxley discovered that certain types of behavior may be transformed into symbolic ceremonies, which he denominated "rituals". Some basic aspects of ritualization are the following:

A ritual is derived from habitual patterns of behavior, but is no longer directed at the goal of that behavior. This pattern of behavior, which "emancipates" from its previous function, is known as "displacement activity." The ritual shows profound differences in form and emphasis from the behavior from which it is derived. When displacement preening becomes part of courtship it is more conspicuous than normal preening. It becomes a signal, it is not an aid in keeping feathers clean.

Changes in threshold and frequency are necessary to transform a behavior pattern into a ritual. The social signals must be clear and strong in order to function.

Ritualization must be prolonged, which demonstrates its long-term effectiveness.

One of the most elementary rituals is that of appeasement. Its function is to suppress or reduce aggression in situations in which flight is not feasible. An animal which lives in a large colony may not safely flee. In courting, hostile behavior of the prospective mate must be defused. A female shows her receptiveness through postures which include lowering the head (a non-aggressive position). Threat and appeasement may both be expressed in a single "nodding" movement: the head raised means aggression, the head lowered indicates appeasement. Seagulls do this. Ducks indicate aggression by pointing with the bill inclined forward and upward.

Natural selection has favored behavior which keeps the group united, while avoiding injuries. Appeasement reduces stress and allows the submissive individual to remain with the group.

Rituals of aggression are based on the premise of postponing actual fighting as long as possible, with the probability that one of the contestants will give up and retire. The longer the "combat" lasts, the more ritualized it becomes. Two herons challenging each other with necks outstretched, may do so for a long time without actually attacking. Without the ritual, fighting is inevitable. A characteristic of the ritual is that neither contestant is actually injured. Sometimes one of them will rush forward as if to attack the opponent and then suddenly retreat as if surprised by his own temerity.

Irrational Behavior among Birds

Supermarkets manipulate the choices of their customers when they change the range of products offered. If two competing brands are offered and a new one is introduced, about a third of the buyers will change brands. Similar behavior has been observed among birds.

The hummingbird feeds on nectar. It must eat almost constantly because of its high rate of metabolism, and returns to the same area in search of food. Investigators constructed hummingbird feeders having different concentrations of sucrose. The concentration was indicated by the color of the imitation "flower." Normally, the birds would prefer the feeder with the highest concentration of sucrose. Nevertheless, when a new "flower" was introduced, the birds would prefer it regardless of the sucrose concentration. This demonstrates that birds, like human beings, may exhibit "irrational" behavior and are less "programmed" than we might think. They are prepared to make a swift decision on the base of available information. This should be taken into account with regards to a wide range of biological problems which require an animal to make a choice, whether in the wild or in captivity.

3. Mathematics and Behavior

About Mathematical Models

The ornithologist Ernst Mayr has an interesting perspective on how we ought to regard biology. The study of living things has two well-defined viewpoints. One is mechanistic, physiological, and functional. It tends to ask the question, "How?" The other point of view is evolutionary and historical. It concentrates on the question, "Why?" The latter recurs to historical narrative and may be based on tentative evidence. The present volume tries to maintain an equilibrium between the two viewpoints.

According to Laplace, a complete knowledge of the world and all its processes should make it possible to predict the future without a time limit. But Mayr is careful to avoid biological determinism. Chance plays a very important role in living systems. Sexual reproduction introduces unforeseen variables, and natural selection, though it generally favors the strongest, is also subject to hazard.

Biology works with statistical generalizations, where exceptions to the rule are merely exceptions and do not refute the theory. Most of these theories are based not on laws but on concepts, such as the concept of speciation, phylogeny, competition, biodiversity, etc.

Therefore mathematical models can provide us with an approach, an aid to interpretation, but hardly a conclusive answer. The help they can offer must be carefully evaluated, but their usefulness is undeniable.

This is the case when we ask questions such as, "Why does an animal behave in a way which at first glance is not beneficial for the particular individual?" We are searching for an explanation of altruistic behavior when an individual sacrifices itself for the survival of the group. The best-known case is that of the worker bee in the hive, which does not reproduce but works for the reproduction of the queen. Ritualized combat is a variant of this question, where an individual who does not respect the rules would obtain the initial advantage. "Why has evolution favored behavior which seems to diminish the probability of winning a fight?" The males accept the conventional proceedings (the ritual) even though they would have greater probability of winning if they infringed upon them. Ritual exhibitions are much more common than actual fighting.

Is there a conflict between "group selection" and "individual selection"? The first favors conventional, ritualized aggression, while the second favors breaking the rules. Is that which is good for the individual bad for the group? Is it possible to achieve a pattern of behavior which favors both the individual and the group?

Choosing advantageous behavior

Games Theory is dedicated to studying situations of conflict between two or more players and has given some answers to these questions.

To apply this theory, we first need to understand the conflict of interests in question. A conflict occurs when that which is good for one individual is bad for the other. Here we make a list of possible strategies to follow. We specify what each player does in each situation, and assign points according to the result. This may be difficult, since it becomes very detailed. Besides, the point system may require us to assign a handicap, if the players play at different levels, for example, in the case of birds of different species.

When one contestant wins what another loses, the mathematical model calls it "zero sum." This applies, for example, in chess and in poker. But in nature, contests are normally non-zero sum. Both contestants may win or lose simultaneously. In a variation called cooperative play, clear strategies are negotiated which return mutual benefits. This is evident in business transactions among humans.

The application of Games Theory to biology may be attributed to John Maynard-Smith. The correct application is not based on the "rationality" of the decisions, as they would be in human games or business transactions, but on the "adaptation" of the species to achieve the optimum strategy. A strategy

which contributes to stability in time and the survival of the species is called an "Evolutionarily stable strategy." No other strategy can improve upon it, unless conditions change radically.

The Prisoner's Dilemma

Pierre Jaisson offers an interesting perspective on cooperative behavior among members of a species. He presents the case of "The Prisoner's Dilemma" and suggests a strategy which might be described as, "Risk what you receive, to win on the return."

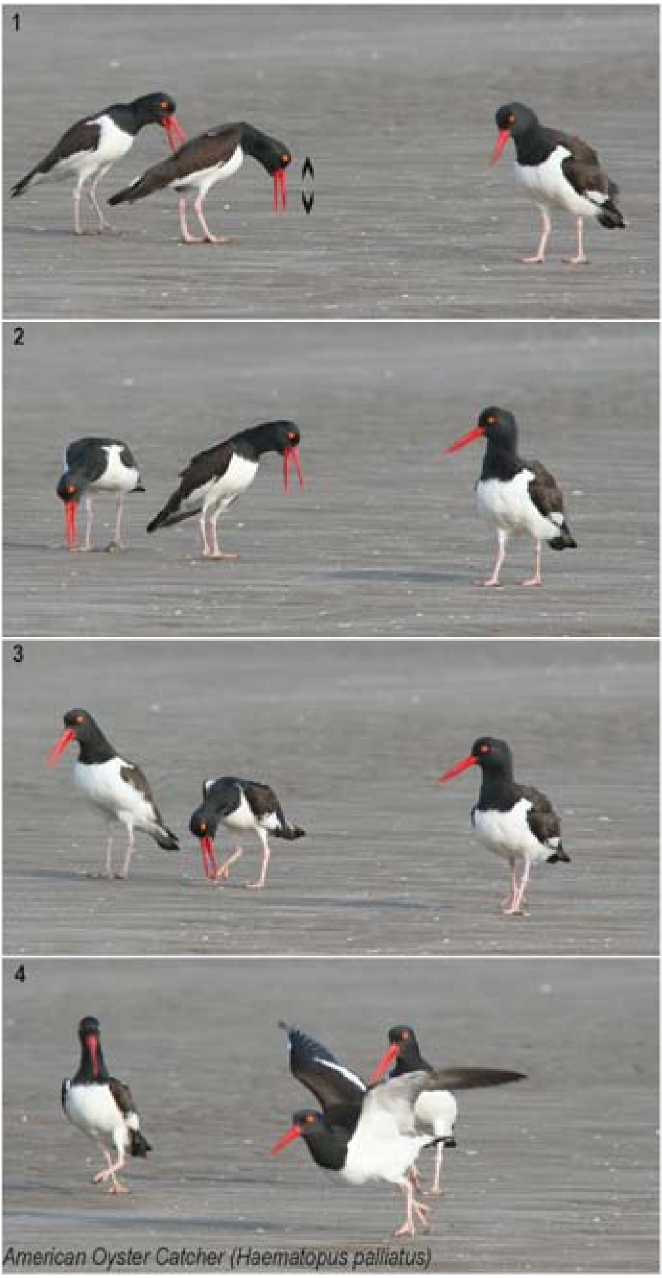
The Prisoner's Dilemma may be summed up as follows: Two prisoners, who have no means of communication with each other, are promised a reduction in their sentence if one incriminates the other. Only the first to do so will receive the reduced sentence. The best strategy for an individual is to confess before the accomplice does. Nevertheless, if both maintain silence, they will be released for lack of proof. What should they do?

This is a non-zero game with only two players. The two participants may cooperate (follow the rules or the ritual) or betray each other (violate the rules.)

If one player cooperates and the other betrays, they receive 0 and 5 points. If both cooperate, both take three points. If both betray, both take one point.

Obviously, it would be better to betray and receive the largest quantity of points, but it is unlikely that the opponent will continue to cooperate if he is continually betrayed.

Now, let us look at it in terms of "Evolutionarily Stable Strategy." This game has been examined by



informatic media and it has been demonstrated that the optimum behavior is:

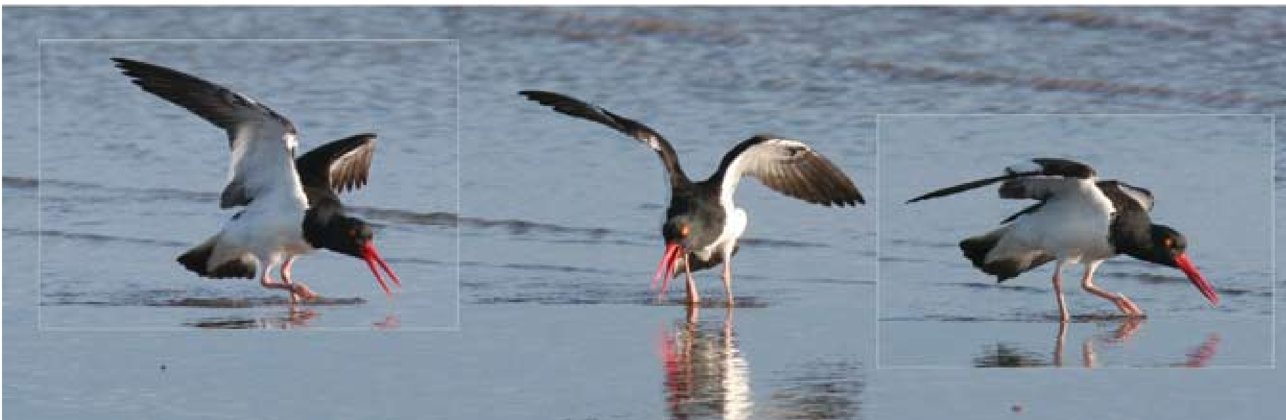
- To be nice (play fair) (not to be the first to betray.)
- To be indulgent (not to punish treason in order to teach the opponent a "lesson")
- To be reciprocal (to do what the opponent does.)

In other words, in the first game transaction, to cooperate. In successive transactions, to follow the lead of the opponent in the previous interchange. This strategy is an "evolutionarily stable strategy" and wins by a wide margin, even pardoning a hostile move.

4. Pleasure and Affection

Not all bird behavior can be explained as related to feeding, reproduction, and conflict. Birds also demonstrate pleasure and affection. Such behavior elevates birds to the level of organisms with very high intelligence. In the opinion of this author, pleasure, affection, and love are products of

American Oyster Catchers (Haematopus palliatus) perform their ritual dance curiously similar to the Bolivian "carnavalito" dance. They arch their necks with the bill down, moving in semi-circles and emitting strident cries. The dance is used both in courting and to confront competitors in their territory.



evolution like other biological phenomena, and if it makes sense to talk of them in relation to human beings, other animals must share them to a greater or lesser degree.

This section of the book is devoted to personal observations and opinions about pleasure and affection among birds, some of which we have been able to photograph.

Hygiene and Pleasure

Hygiene (that is, preening) is one of the most commonly observed activities among birds. It is aimed at generally maintaining health.

The plumage of birds exhibits some of the most beautiful colors and designs in the animal kingdom. It functions as a medium of expression during the mating season and during ritual demonstrations of aggression. The feathers must be kept clean and impermeable (only a few species have non-impermeable plumage.) But preening is an activity which exceeds the necessities of simple cleanliness and is linked to pleasure.

Impermeability is maintained in one of two ways: either through the disintegration of special powdery feathers, or by the use of oil produced by a gland at the base of the tail (the oil gland or preen gland). This secretes an oily or waxy water-repellant substance.

Some investigators doubt the necessity of the oil gland for water-proofing the feathers. They believe rather that the function of the oil it produces is related to the control of bacteria, parasites, and fungi which attack the keratin of the feathers. Traces of parasites have been found in fossil birds dating back 44 million years.

Whether the feathers are kept impermeable by oil from the preen gland, or by powder from the disintegrating "powder feathers", the product is carefully spread over the body by the bird when it preens. We may often see birds caressing the feathers of their bodies, back, and wings with their necks or their bills

Bathing is related to preening. Birds most often bathe in water, but also take "dust baths." Shallow water is preferred—even marine birds bathe in shallow water near the coast. They duck their heads and bodies, emerge, shake themselves, and beat their wings. They may submerge head first or first one side, then the other. Not only do they bathe in shallow lakes or puddles, but also "shower" in rain. Gardeners have often observed hummingbirds "shower" in the fine spray of a hose.

After bathing, the bird preens for a time, as if

Giant Wood Rail (Aramides ypecaha)

combing itself with its bill. It removes parasites and filth, and where it can't reach with its bill, it uses its feet. Hummingbirds, with a bill too long for preening, rely mainly on their feet.

By preference they preen in the sun. The Guira Cuckoo (*Guira guira*) warms its back in the sun, regulating the access of sun-rays with its feathers and wings. Birds of the Cormorant family need sun to dry their feathers, as they are not entirely waterproof.

Some birds "bathe" in fine dust. Domestic fowl are often seen doing this. They scratch an area of ground to loosen the dust, and then "soak" their feathers in it until they are covered with dust.

Certain species kill ants and then rub them on their feathers. It is supposed that the formic acid of the smashed ants acts as a repellent of lice and parasites. Other birds will settle by an ant-hill and let the ants crawl over them. The ants probably clean them of parasites.

There are 2500 species in 40 families of microscopic mites or acarids associated with birds. They may live in the feathers or in the nests. Some feed on the feathers, but others may suck blood of the host. Some may be harmless or live in a relationship of mutualism with the bird, but many are parasitic and may spread disease among the birds or the nests.

Coscoroba Swan (Coscoroba coscoroba)

Affection

Pairs of White-faced Whistling Ducks (*Dendrocygna viduata*) are often seen preening each other (allopreening) for long periods. The two ducks sit face to face, nipping very gently at each others' plumage. One concentrates on the upper part of the head, while the other does the neck. Then they exchange positions and continue to preen. They close their eyes and seem to concentrate lovingly. It is a moving scene. Allopreening occurs with certain kinds of birds with strong social ties, such as parakeets and cuckoos.

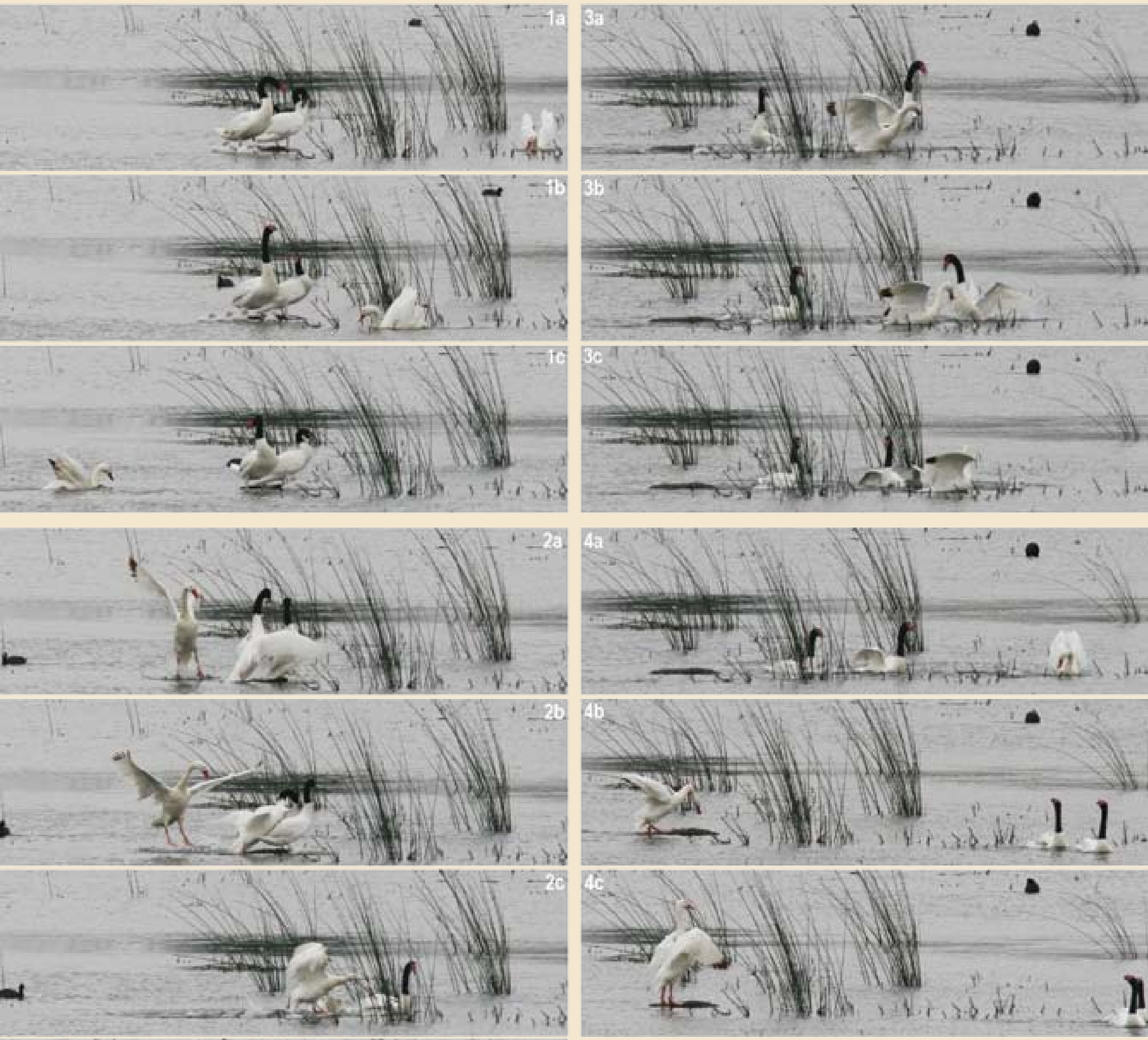
Two hypotheses have been advanced to explain allopreening. One of them suggests that mutual preening is a way of earning the gratitude of more dominant members of the community, as an investment in the future. This has not been born out by observations. The second hypothesis suggests that preening releases pleasure-producing hormones. This would supply an immediate reward for the activity. If human beings feel pleasure at being "preened" by another member of the species, why not a bird, since the hormonal chemistry is similar?

Hygiene includes bathing (besides preening) but in aquatic birds it also consists of distributing the water-proofing substance produced by the uropygial gland.

Striated Heron (Butorides striata)

Stories of the lake (I). *Two pairs of Ringed Teal (Callonetta leucophrys) compete for an apparently insignificant space. The challengers approach emitting threatening sounds, loud and clear, with the head down and the bill pointing. Finally the female occupies the disputed space, unopposed. Konrad Lorenz has pointed out the importance of this kind of behavior, where the couple acts together and reaffirms the pair bond.*

Stories of the lake (II). *In I, a pair of coots attempts to evict a pair of swans from a mound. Because of the difference in size, they don't succeed. At this point, a phenomenon occurs which, although strange, has been observed on more than one occasion. In one of the coots, the aggression becomes redirected, and it pursues and attacks the other coot. Unlike displacement activities, which emancipate from their original drive, redirection activities are caused by their usual drives but they are directed towards an object or animal other than the one releasing or directing them. In sequence 2, the coordinated attack of two coots succeeds in dislodging a single swan, by means of kicks in the air.*



Stories of the lake (III). *A family of Black-necked Swans (Cygnus melancoryphus) occupying a mound is approached by a Coscoroba Swan (Coscoroba coscoroba). The Coscoroba Swan decides to take possession of the mound by means of a direct attack on the group. The Black-necked Swans prefer the safety of the young to the possession of the mound, and retreat, carrying the young on their backs, while the Coscoroba Swan occupies the mound.*

Stories of the lake (IV). *The Case of the White-Faced Whistling Duck (Dendrocygna viduata), The following photo sequence shows an example of controlled aggression, interpreted in the light of Game Theory. Two groups of about a dozen individuals, meet in a lake. The face-off is ritualized. It begins with the members of both groups interchanging cries or whistles of "siriri, siriri" with the head lowered and bill extended. After a moment, ducks break formation and advance on the opposing group. While B keeps his wings folded, A shows more aggressiveness (also more fear) keeping his wings raised, and by a more violent attack and rapid retreat. While B meets with the opposition and they attempt to stare each other down, A crosses the scene diagonally with no clear goal. While A has not yet reached his destination, ducks intercepts him (still crying "siriri, siriri.") Ducks pursues A, to the hypothetical border between the two groups (although by this time the border is almost non-existent because the initial formations have broken up.)*

Stories of the lake (V). *The defense of the family group of Black-necked Swans (Cygnus melancoryphus) entails striking rituals. In the first picture we see one of the adults herding the young together so that they can be protected by the other adult. Then it swims rapidly to meet the intruder. On arriving, it submerges its head in the water as a symbol of defiance. Head-play is also used in rituals of defiance (2), and the ritual struggle is completed with flapping in the water.*

Stories of the lake (VI). *Fight sequence between Coscoroba Swans (Coscoroba coscoroba). The run, the initial blow (1-4) and a counter-blow and flight (5-8). The motive of this fight was complex and interesting. Shortly before these photos were taken, the presence of humans in the lake caused one young cygnet to become separated from its family, and it attempted to join the other family group. The parents of the host family tried to reject the intruder without success. Nevertheless, when one of the parents of the family which had lost the cygnet approached to recover it, the host family reacted by defending the entire group. Fortunately, a few minutes later the host family managed to separate the lost cygnet, and this, after wandering about a little, was able to return to its own family.*

Coscoroba Swan (Coscoroba coscoroba)

Coscoroba Swan (*Coscoroba coscoroba*)

Resolution of conflicts (I). *Herons use certain rituals and much dramatic action in their confrontations. The ritual consists of a dance with necks raised and heads pointing to the sky (1). But if one of them does not retire, the conflict escalates (2 to 4) as they try to peck each others' legs. Flight may be to one side, but it is also common to see them jump.*

Resolution of conflicts (II). *In a confrontation between coots, both contenders stretch themselves erect in the water (1). Each puts its feet on the breast of the other (2-3), trying to place them in the center. They push and try to sink each other in a sort of "arm-wrestling match". In breeding season, both members of the couple (5) may be seen engaged in combat. When they are able to sink their opponent, an unusual situation due to the great buoyancy of these birds, the winner attempts to teach his opponent a lesson by pecking at its head (6-7).*

Resolution of conflicts (III). *Two herons confront each other for several minutes at dawn, in 2006 in Punta Rasa. Ritual was brief and almost immediately they began to fight. This page shows the "aerial dance" during which both opponents strike at each other with their long legs in jumps of various meters high, face to face, without actually making contact. But the opposite page shows a five-second aerial chase, culminating when the dominant bird catches the other by the foot.*

White-necked Heron (Ardea cocoi)

White-necked Heron (Ardea cocoi)

Resolution of conflicts (IV). *The young in this nest of Great Egrets (Ardea alba) appear fairly well-grown, but are still being fed by the adults. When the parents are not near, they behave normally. But when one of the adults appears, they begin to behave like very young birds. The stronger ones attack the weaker ones at feeding time. On the next page we see two cases where the fighting is not ritualized and is lacking in elegance. The long thin legs are used as offensive weapons, but cause little damage. The battles consist of various successive altercations, chaotic and of short duration. They end when one of the*

South American Stilt (Himantopus melanurus)

Lesser Yellowlegs (Tringa flavipes)

birds retires a few meters, putting an end to close contact. But in the case of the South American Stilt (Himantopus mexicanus), we see an unusual sequence where one bird succeeds in seizing the neck of the other with its bill. Although it appears that no serious damage was done, the aggressiveness was striking. It was provoked when a solitary individual approached an already bonded couple.

Ritual and display (I). *The strategy is often not "to speak softly and carry a big stick," but to scream loudly and attack wildly, only to back down and run away if the opponent is not sufficiently intimidated. The primary importance of the display is to impress the opponent. In sequence 1, a Wattled Jacana (Jacana jacana) dances before the photographer*

3

Greater Rhea (Rhea americana)

4

White-winged Coot (Fulica leucoptera)

5

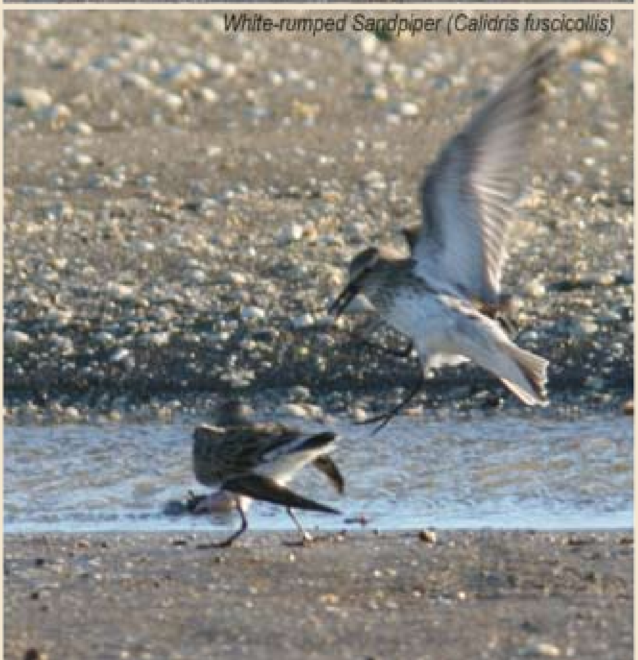
Coscoroba Swan (Coscoroba coscoroba)

when he intrudes on the tranquility of the territory, giving his mate time to flee with the young. The show of plumage, with the wings outspread, is a very common technique. In 3, a Greater Rhea (Rhea americana) flees running in a zig-zag with its wings open. Photos 4 and 5 show water birds with their wings erected to make them look bigger.

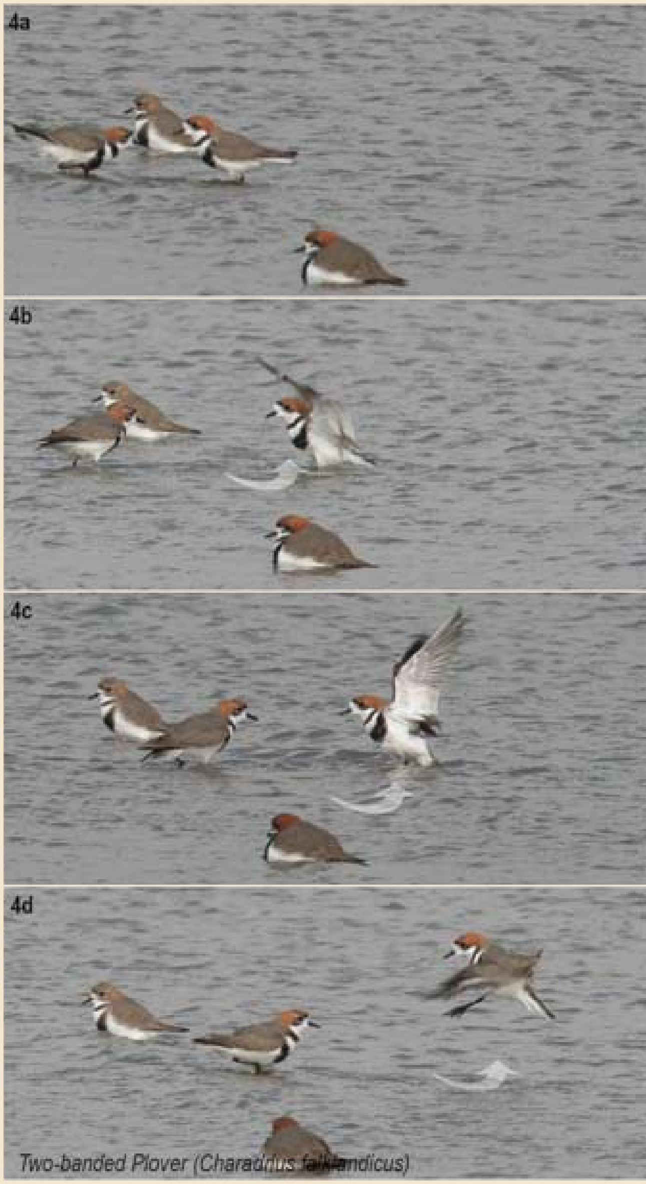
Ritual and display (II). *A Southern Lapwing (Vanellus chilensis - Tero in Spanish) performs frequently before his neighbors. Here, seven individuals have met in an open space (dominant birds are indicated). The incident lasted several minutes. The dominant birds may be identified by their slender, erect position. One by one they challenged each of the remaining birds until they ejected them from the "arena." They use an erect posture, as if "baring their chests", and show their red wing-spurs to intimidate their opponents. The spur is located on the carpometacarpus at the front of the wing. Once the last opponent (C) has been ejected, the dominant couple performs a victory dance, turning in a circle with the head down and the tail up. It is much more common to see a group of lapwings engaging in aerial combat among various couples.*

Ritual and display (III). *The "privileged position" of one coot (3) is claimed by another, which forces the first coot to move to a lower position on the submerged log merely by looking at it ("pecking order"). Social position in the group has been established previously by means of races on the water typical of this family of birds. Among many other species display is a form of resolving conflicts.*

Ritual and display (IV). *Gulls demonstrate how disagreements can be kept to a level of noisy screams (1). But Brown-headed Gulls (Larus maculipennis) use a ritual position which consists of the body tensed and stretched horizontally, with wings folded and head raised or horizontal. This may be a posture of challenge or submission depending on the position of the head, but in either case it inhibits attack (2a). If neither bird assumes the ritual posture, fighting occurs (2b).*



White-rumped Sandpiper (Calidris fuscicollis)



Two-banded Plover (Charadrius falklandicus)

Ritual and display (V). *Both sequences show one bird challenging another and forcing it to retreat a step each time. In 3, it attacks from the side and in 4 it attacks from the front.*

A Chalk-browed Mocking Bird (Mimus saturninus) versus a Southern Caracara (Caracara plancus). Caracaras are frequently mobbed, for obvious reasons. Here, the mockingbird attacks the Caracara from behind and so disarrays its plumage that the raptor is forced to fly away and land on a nearby mound to re-arrange its primaries. Below, we see the instant before and the instant after the blow from behind.

Southern Caracara (Caracara plancus) versus Chalk-browed Mockingbird (Mimus saturninus)

The female (left) of the Southern Crested Caracara (Caracara plancus) preens her young (distinguished by the vertical striations on the breast.) Then she rests her head on that of the young in a protective maternal gesture.

White-necked Heron (Ardea cocoi)

Guira Cuckoo (Guira guira)

Snail Kite (Rostrhamus sociabilis)

Long-winged Harrier (Circus buffoni)

Guira Cuckoo (Guira guira)

Turkey Vulture (Cathartes aura)

Preening the feathers occurs among all species of birds and is always performed in the same way. The purpose is hygiene, but it is done with such dedication that it suggests pleasure is associated with the activity.

Hygiene includes water baths (1) and dust baths (2). But in 3, we see an unusual case where a Great Kiskadee (Pitangus sulphuratus) repeatedly dives from a branch, hits the water with a splash, and returns to the branch to dry. Here we see bathing and play joined together. In 4, a Golden-breasted Woodpecker (Colaptes melanochloros) hollows out its nest and the female clears splinters from the interior. It would have been enough to take out the splinters and let them fall, but in most cases she prefers to toss the splinters into the air. There can be no doubt that it is being done for fun, and we would

Golden-breasted Woodpecker (Colaptes melanolaimus)

Rufous-collared Sparrow (Zonotrichia capensis)

Hepatic Tanager (Piranga flava)

Rufous-bellied Thrush (Turdus rufiventris)

hear her laugh—if she could. In 5 to 7 we see birds looking at their reflections in the rear-view mirror of a vehicle and in a window. They do this many times a day, with passion and dedication. It has been interpreted as facing a competitor, but my observation suggests that it is more closely linked with pleasure and curiosity. The excesses remind us of a human being playing video games or using a cell phone.

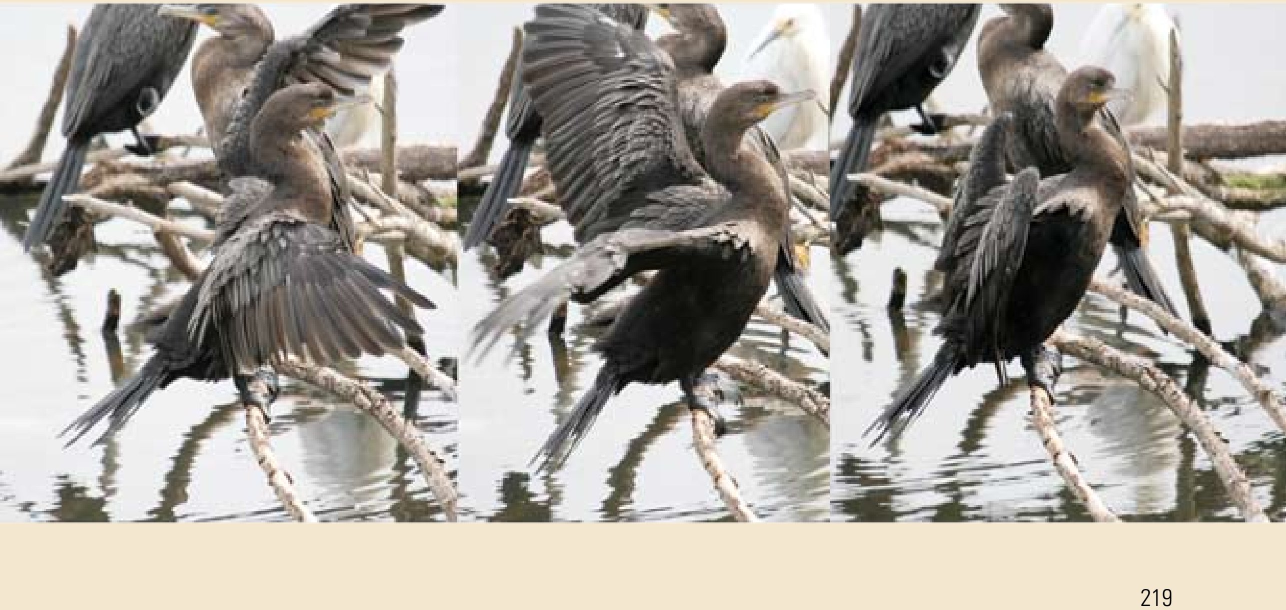
A Neotropic Cormorant (Phalacrocorax brasilianus) has a behavioral routine related to hygiene. On returning to the place where it sleeps, it normally lands in the water, skidding in first with the tail and then with the feet (1). It prefers the water because it likes to take a shower to clean itself (2). Then it jumps on to a branch and spreads its wings to dry in the sun. In photos 5 to 7 we see three rather disconcerting incidents which are difficult to classify. In 5, a cormorant is seen "playing" (is it enjoying itself?) with a stick, tossing it into the air and catching it repeatedly. In 6, another bird plays the same way with a feather found in the water. In seven, a cormorant is "playing" with a live fish before swallowing it. The bird releases it in the air and re-captures it twice. Is this a game, played for fun, or training? Is he enjoying himself?

5

6

Neotropic Cormorant (*Phalacrocorax brasilianus*)

7



Mutual preening. In 1, the mate of a rail indicates a difficult-to reach spot which needs cleaning. In 2, ducks gently nip each other as a sign of recognition and affection. The female is in the water while the male stands on a mound. The Monk Parakeets (Myiopsitta monachus) in 3 demonstrate how they preen each other and defend their privacy when a third parakeet approaches too closely on a near-by branch.

It is uncommon to observe mutual preening in birds. But among White-faced Whistling Ducks (Dendrocygna viduata) this activity is somewhat more frequent. They can be seen concentrating on this activity for long periods, with their eyes closed in evident pleasure. It is the best example we can offer of how mutual preening rewards both individuals, since it is a shared and reciprocal operation. While one preens the head of the other, the latter preens the neck of the first, complementing each other. This shows how preening contributes to the hygiene and pleasure of the species.

White-faced Whistling Duck (Dendrocygna viduata)

1 South American Stilt (Himantopus melanurus)

2 Ringed-Teal (Callonetta leucophrys)

3 Southern Screamer (Chauna torquata)

4 Pied-billed Grebe (Podilymbus podiceps)

5 White-necked Heron (Ardea cocoi)

Birds don't allow their misfortunes to show. Even when disabled they forge ahead. Photos 1 and 4 show broken legs, 2 shows a birth defect, and 3, a broken wing. Photo 5 shows a White-necked Heron (Ardea cocoi) which appears normal when standing, but when it takes off, we see that it has completely lost its tail, leaving only a few bare vanes of feathers. Since it was photographed in an area where alligators are common, it could be that it was injured when one of them attacked it. The feathers of the tail will be replaced at the next molt, but the shock will last.

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