

Hummingbirds: their natural history

Extracted from the book "Hummingbirds of Colombia"

Introduction

Its small size and fleeting presence, its loud, iridescent colors—at times accompanied by extravagant ornament—its ability to hover and its association with flowers are just some of the characteristics that allow us to identify a hummingbird and to easily distinguish it from other birds. These are also the characteristics that have awed European explorers and naturalists since the discovery of the New World, and that continue to captivate the attention of scientists and observers.

Like hummingbirds, we too have a strong affinity for flowers—though for quite different reasons. Our flower gardens—for us a source of esthetic pleasure—are seen by hummingbirds only as a potential source of food. The garden is enlivened by a hummingbird, which, with its nervous flitting, breaks the calm and adds a splash of color. Even in the largest cities, where the primordial habitat long ago ceased to exist, certain species of hummingbird have adapted to seemingly inhospitable environments. In fact, they may be found in the smallest plot of city greenery, or even amongst the potted plants on the balconies of high-rises, breaking the monotony of endless concrete facades. Nonetheless, these hardy city dwellers are but a poor sampling of the abundant variety of hummingbirds to be found in less developed habitats.

Hummingbirds are counted among the more familiar birds—if what we mean by familiar is that most of us have seen a hummingbird at one time or other. They will not have failed to gain our admiration and even pique our curiosity. They become somewhat less familiar—though far more intriguing—once we begin to ask ourselves the myriad questions that come to mind after even the most cursory of observations. How are such striking colors produced? Why is its refulgent plumage dark and opaque one moment and scintillating the next? How is it able to approach a flower at full speed, only to stop instantly at the precise distance in order to introduce its beak in the corolla, without even moving the flower? How is it able to remain stationary in the air while it sips the nectar? How is it able to survive, this smallest of warm-blooded vertebrates, in the frigid nights of the high Andes?

Questions like these—among others—followed quickly in the minds of the many naturalists whose first encounter with hummingbirds was a source of deep admiration as they slowly uncovered the secrets of their natural history. The noted French naturalist Georges Louis Leclerc, Count of Buffon (1707-1788), described the hummingbird as “of all animated beings...the most elegant in form and most brilliant in colour. The stones and metals polished by art are not comparable to this gem of nature: she has placed it in the order of birds, but among the tiniest of the race...she has loaded it with all the gifts of which she has only given other birds a share.” Today, over two centuries later, hummingbirds are still a source of inspiration and admiration—as

well as the object of intense scientific inquiry. New questions are being asked, and more satisfactory answers sought to some of those posed by the hummingbird's earlier admirers.

Classification

A more rigorous look at hummingbirds in the entirety of their extensive range shows us that, despite our initial impression, these birds are quite heterogeneous—at least in some of their more obvious aspects. First of all, it is not true that all hummingbirds are small. Though they also include the smallest of birds: the Bee Hummingbird (*Calypte helenae*) of Cuba, weighing barely two grams, there is also the Giant Hummingbird (*Patagona gigas*) which tips the scales at a portly 20 grams. This is a good deal more than the weight of some of the more common birds such as the House Wren (*Troglodytes aedon*), weighing in at some 16 grams. Nor do all hummingbirds sport the blazing colors that characterize them as a group. The Giant Hummingbird, for example, is a stately brown. Others, such as the Speckled Hummingbird (*Adelomyia melanogenys*) and the Tawny-bellied Hermit (*Phaethornis syrmathophorus*), bear only the suggestion of a metallic glint down their backs.

Hummingbirds also show extensive variations in the form of the bill. We tend to think of them as long and straight, although this is not necessarily so. In fact, this impression is probably due to our familiarity with the most common (and least specialized) species of hummingbird, the Rufous-tailed (*Amazilia tzacatl*) and the Steely-vented (*Amazilia/Saucerottia saucerottei*). There are, of course, hummingbirds with very long, straight beaks such as the Sword-billed (*Ensifera ensifera*). But others have bills so short that one wonders how they can possibly gather nectar, such as the Purple-backed Thornbill (*Ramphomicron microrhynchum*). Yet others, such as Hermits (*Phaethornis* spp.) and Sicklebills (*Eutoxeres aquila* and *E. condamini*), sport long bills with a pronounced curvature.

Nevertheless, hummingbirds do share a number of superficial characteristics. They are extremely versatile when airborne, and their ability to hover with their whirring winglets is unparalleled. Hummingbirds are also characterized by their weak, thin legs—barely able to sustain them while perched. Thus, the majority of hummingbirds take to the air even when moving just a few centimeters—as when shifting around in their nests.

Hummingbirds belong to the Trochilidae (or simply “trochili”)—a numerous and varied family exclusive to the New World. There is controversy, however, regarding their nearest winged relatives. Some taxonomists assert that hummingbirds are more closely related to swifts (*Apodidae*) than to any other family. Consequently, they classify hummingbirds in the same order—Apodiformes. This classification is based on their peculiar wing structure, in which the bones of the hand are longer than those of the arm and forearm combined.

Although swifts are both fast and versatile, they are incapable of hovering—nor can they fly backwards. Swifts, furthermore, sport a dark, opaque plumage— rather unlike the exuberantly clad hummingbird. They form stable couples in which both the male and female incubate the eggs and take turns feeding the chicks—in striking contrast to the free-spirited hummingbird. For these reasons, most taxonomists prefer to classify hummingbirds as a separate order—that of the Trochilidae.

Diversity and geographical distribution

With slightly over 320 species, hummingbirds are exceeded in diversity only by the neo-tropical flycatchers, of which there are some 370 species. Hummingbirds are found throughout the Americas, from Alaska to Patagonia, and habitats ranging from the tropical rainforest to the driest desert and from sea level to altitudes of 5,000 meters (15,000 feet)—the edge of perpetual snow in the Andes. Hummingbirds are also to be found in the most remote islands of the American continent, from the sultry islets of the Caribbean to the blustery Juan Fernández Archipelago, over 600 kilometers (375 miles) off the coast of Chile.

However, the distribution of hummingbirds throughout this domain is far from even. As with other birds, more than half the species is concentrated along a narrow band extending five degrees of latitude to either side of the equator. In Colombia, for example, whose territory extends from 4° south latitude to 12° north, and whose total area covers slightly over a million square kilometers, one finds over 150 species. Mexico, though almost twice as large, has but 51 species. The United States, with over nine million square kilometers, has just 13 species. As one leaves the temperate zone and moves farther north—or south—the number of species continues to drop. In Canada, there are only four species while at the Straits of Magellan, at the very southern tip of the continent, there is but one.

There is no simple explanation to the pronounced concentration of hummingbird species near the equator. It is not improbable, however, that the concentration of hummingbirds in that area goes hand-in-hand with the greater evolutionary diversity of flowers in the tropics. On the other hand, there is the greater variety of habitats to be found at equatorial latitudes—from the lush tropical rainforests at sea level to the perpetual snows of the Andes, at elevations of some 5,000 meters. In between, one finds an intricate climactic and topographical mosaic composed of valleys and foothills, plains and plateaus. These diverse habitats favor the evolution of a far greater number of species than one finds in regions whose characteristics show little variation.

Plumage and coloration

No other bird rivals the extraordinary design characteristics and versatility of the hummingbird's plumage. Far from a simple body covering, feathers are the source of many specialized functions. Despite their light weight and apparent simplicity, they enable birds to maintain high body temperatures—with far-reaching consequences for their metabolism. In the case of hummingbirds, their feathers account for its complex flight characteristics, coloring and communications system—including the production of sounds. The gaudiest color schemes include bright, iridescent splashes across the crown, throat and chest, whose sheen calls to mind a polished gem or highly reflective metal surface. In fact, the color schemes of hummingbirds have been their main source of nomenclature, providing taxonomists with an obvious way to classify and distinguish the various species. In the case of *Heliangelus exortis*, the generic name signifies angel or messenger of the sun; *exortis* (from the Latin *ortus*, or rising sun) refers to the large patch of iridescent pink about the bird's throat, recalling a sunrise. There are many such examples of imaginative nomenclature. *Coeligena helianthea* can be translated as “flower of the celestial sun” and *Aglaeactis cupreipennis* as “copper-feathered ray of resplendent sun”. In fact, the student of Greek or Latin can find ample amusement in translating the names of the many species of hummingbird.

The colors we perceive in an object are simply the reflection of different portions of the chromatic spectrum as they bounce off the surface of the object. For example, the green of foliage is due to the chlorophyll in the leaves, whose wavelength corresponds to green. The bright yellow, orange and red colors of birds are due to the carotene they absorb from their food and deposit in their feathers. Another pigment, melanin, absorbs most of the chromatic spectrum to produce black, gray and dark brown.

Not all colors, however, are produced by pigments. In many cases the colors we perceive are produced by the dispersion of light by particles whose size is similar to the wavelength of the reflected light. For example, the blue of the sky is due to the dispersion in multiple directions of the light that strikes the air molecules of the atmosphere, whose size is similar to the wavelength of blue light.

In birds, for example, those of a blue color owe their hue to the absorption of all wavelengths of light except blue light, which is reflected by small particles of melanin within the feathers. If we take a feather from a Bluebird and look at the light it reflects, we perceive the feather as blue. But if we then hold the feather up to the light and look at the light that passes through it, we perceive only a dark gray color. This is because the blue portion of the light is reflected upon striking the feather, and the remainder is absorbed by the melanin. This is an example of “structural coloring”.

Actually, the bright colors of hummingbirds have two components—reflection and iridescence. The amount of reflection is simply the “shininess” of an object, while iridescence depends on the relative angles of object and observer. As an iridescent object changes position, or our own position changes with respect to the object, then the color values of the reflected light also change. In the case of hummingbirds, we are treated to

bright, fleeting bursts of color which are extinguished as quickly as they appear, only to appear yet again the next moment.

The colors of hummingbirds are mostly structural in nature—both in the dorsal area, where their metallic sheen is more generalized, and in the actually iridescent areas. Pigmentation, however, also plays a role for it is the melanin within the feathers which is responsible for the wide range of grays and browns.

The metallic luster of a hummingbird's plumage is due to a complex interplay of factors as light passes through a series of minute structural elements within the feathers themselves. A sectional view of these elements, as seen through a microscope, reveals a number of small, hollow platelets of melanin, arranged in layers. Depending on the thickness of the plates and the number of layers, some wavelengths are reflected so as to be mutually reinforced—thus intensifying the color—whereas other wavelengths cancel out and the corresponding colors are not seen.

Although we can perceive the shine of the dorsal plumage from any angle, and without much variation, actual iridescence is much more concentrated in certain specific areas such as the crown, the throat and the chest, depending on the species. The iridescent sheen of these areas depends on the precise angle of the incident light and on our position with respect to the hummingbird. Only at certain specific angles will we be able to appreciate the iridescence in all its brilliance. This phenomenon is explained by the curious arrangement of the structural elements within the feathers in the iridescent areas, which are arranged in a “V” pattern. The reflected light shoots out in a straight line, visible only through a narrow angle. By contrast, the structural elements in the feathers of the dorsal area are arranged so as to form a slightly convex mirror. Thus, the reflected light is seen through a wide range of viewing angles.

The wing feathers of hummingbirds are usually very dark and opaque rather than iridescent. No room here for iridescence, which would impose structural modifications incompatible with the strength and resistance of the feathers required for flight. At rest, though, the closed wing covers a minimal portion of the bird's body surface, and so its opaqueness hardly lessens the overall brilliance of a hummingbird's color scheme.

Many hummingbirds also sport specialized, highly ornamental plumage as part of their wardrobe. In the Spatule-tailed (*Loddigesia mirabilis*), native to the Peruvian Andes, the outside tail feathers—exceptionally long and thin—form two crossed arches, each with a large, black circular marking with purple specks. The diminutive Racket-tailed (*Ocreatus underwoodii*), common to the tropical forests, has similar ornamentation, though the tail feathers are somewhat shorter, straighter and thinner. So thin, in fact, that in faint light or against a dark background the “rackets” do not even seem to be connected to the rest of the body. In flight, it appears—especially to those unfamiliar with the species—that the hummingbird is being followed by two dark spots that it never seems to be able to shake off.

Other species, such as Sylphs (*Agelaiocercus kingi* and *A. coelestis*) and Trainbearers (*Lesbia victoriae* and *L. nuna*) sport long tails, easily twice as long as the rest of the body, though without the special modifications of the previous examples. In the Thorntails (*Popelairia langsdorffi* and *P. conversii*) the tail feathers—thin and pointed—get progressively shorter towards the mid-section of the tail. While hovering, their unfolded tail seemed rather lyre-shaped to the imaginative taxonomist. The Coquettes (*Lophornis delattrei*, *L. stictolopha* and *L. chalybea*), as their name implies, seem almost flirtatious with their brightly colored crests, necklaces and earrings.

In all these cases, ornamentation is exclusively a male characteristic. In females ornamentation is either less developed, less colorful or lacking altogether. This marked difference in the external appearance of the two sexes, called “sexual dimorphism”, has a rational evolutionary explanation. It is the female which is in charge of incubating the eggs and feeding the young. Were she more colorful, she would also be more noticeable to potential predators—a distinct disadvantage, both to mother and offspring. The male, on the other hand, needs his exuberant plumage in order to compete for the attention of the available females. For him, an extravagant coat confers the possibility of siring abundant offspring.

Flight

Marvelous enough in ordinary birds, the flight characteristics of a hummingbird represent the highest state of evolutionary development. Just a few moments of observation of hummingbirds in the vicinity of a flowering bush are enough to convince one of their extraordinary domination of the air. Zooming in at full speed, a hummingbird comes to a dead stop at just the right point to introduce its bill into the corolla—the while remaining absolutely stationary. It then flies to one side, then the other, then up, then down in search of more nectar-laden flowers. If attacked by a rival, the hummingbird quickly shifts into reverse and backs off, only to return to its former spot as soon as the aggressor has continued on his way. Once there, the hummingbird applies its brakes and resumes stationary flight. Having collected the nectar, it is off again at top speed — almost from the instant of departure. But however much we may marvel at the flight of hummingbirds, there is one activity they are incapable of: gliding. Their tiny wings simply could not support their weight, were they to keep them motionless. In this, birds of larger wingspan must find their only consolation.

The flight of a hummingbird is far easier to describe than to explain. In general, winged appendages do not permit rotation of the wrist and elbow. Movement is limited to flexion (or flapping). At rest, the wing folds into a “Z” position which straightens out during flight. The shoulder joint has a far greater range of motion in all directions, as well as some axial rotation. In a hummingbird, axial rotation is highly developed and approaches 180 degrees. That is, the leading edge of the wing can be rotated until it becomes the trailing edge. Its wrist and elbow joints, however, are far less flexible than those of most other birds.

Another prominent characteristic of a hummingbird's wing is its relatively large hand, which measures more than the arm and forearm combined. This dominance of the hand is reflected in the overall proportion of feathers. While the hand of a hummingbird has ten primary feathers, the feathers of the forearm (secondary feathers) are only six or seven. In the albatross, on the other hand, one finds nearly forty secondary feathers. These differences in feather covering correspond to differences in flight characteristics. The albatross is able to glide long distances just above the waves, thanks to its abundant secondary feathers which form an extensive surface area. In hummingbirds, on the other hand, flight is possible only through continual flapping—a function which is concentrated in the primary feathers.

Only by resorting to sophisticated photographic apparatus and wind tunnels has it been possible to study and describe the wing movement of a hummingbird in all its aerodynamic complexity. In forward flight a hummingbird follows the general pattern of other birds. Flapping is initiated with the wings in the extreme upper position, with respect to the longitudinal axis of the body. The wing then moves downward to provide both forward propulsion and lift. Once the wings reach their lowest point they initiate the motion that brings them back to their initial position, ready to begin a second flap cycle.

There is an important difference, however, which distinguishes its flight from that of other birds. While in the majority of birds the wing folds partially during the recovery flap in order to minimize air resistance, in a hummingbird this movement takes place with the wing totally extended. Furthermore, during the recovery flap the wing rotates backwards in such a way that it continues to provide lift. Upon completing a cycle, the wingtip will have described a narrow, flattened ellipse.

Hovering, which allows the hummingbird to survive on a nectar-based diet, is somewhat more complex. With the body in an almost vertical position, the wingtip describes a trajectory in the form of a horizontal figure 8 (or ∞ , the mathematical sign for infinity). The flap cycle is begun at the extreme backward position, from whence the wingtip moves forward and slightly downward until it reaches the extreme forward position, directly in front of the body. At this point the wing rotates and the leading edge moves backwards and slightly upwards, then down again until it reaches its starting point. The effect of this complex motion is to provide lift during both parts of the flap cycle—thus maintaining the bird absolutely stationary in apparent defiance of gravity.

The high-precision flying of a hummingbird does not seem to be related to the velocity of its wings. The smaller hummingbirds may flap their wings at perhaps 80 cycles per second (a cycle being a complete downward flap together with the corresponding recovery flap). In larger hummingbirds—from 5 to 7 grams in weight—wing flapping diminishes to some 30 cycles each second. In the Giant Hummingbird, the largest of the species, wing flapping frequency is down to about 8 or 10 cycles per second—far below the wing

flapping rate of the passeriformes, whose weight is far greater and whose flight is decidedly conventional. Even with its relatively slow flapping, however, the Giant Hummingbird is able to hover just as well as the smaller species and appears to be at no disadvantage whatsoever. It could be that we tend to attribute greater speed to the wings of a hummingbird simply because we are able to appreciate its whirring while the bird is stationary in mid-air. Other birds also have rapid forward motion, and so we are perhaps not as aware of their wing flapping, though it might well rival that of a hummingbird.

Metabolism

The intense vitality displayed by hummingbirds is quite genuine. In fact, all the specialized physiological characteristics that define birds in general, and that enable them to fly and achieve such a widespread geographical distribution, find their highest level of development in the hummingbird.

Like other birds and mammals, the hummingbird is both homeothermic and endothermic. That is, it maintains a relatively constant body temperature through its own metabolic processes. Amphibians and reptiles, on the other hand, exhibit wide temperature variations. As poikilotherms, they require external heat (ectothermic sources), such as direct solar radiation and contact with hotter surfaces, in order to maintain the temperature they require for their vital functions.

All the activities associated with living things, such as the production of heat, movement, a nervous system, digestion, growth, tissue repair, secretion, accumulation of reserves and reproduction, require that energy be freed through the oxidation of fats, carbohydrates and proteins obtained from food. A hummingbird's body temperature is higher than that of any other bird (102 to 108° F), in keeping with its extreme vitality and which in a human being would constitute a rather high-grade fever. The velocity of its chemical reactions and the resultant production of energy are directly related to this temperature. A high body temperature also means a more highly responsive nervous system, and stronger muscular contractions. Furthermore, the hummingbird's feverish state assures a quick response to sensory stimuli such as hunger, or detecting the presence of predators or intruders.

A constant body temperature has other advantages as well. The organism is able to maintain a constant level of activity, despite large variations in ambient temperature. Its rapid muscular contractions and rapid metabolism being the main source of heat, a hummingbird can venture safely into areas completely out of bounds to more lethargic organisms. Thus, birds in general have been able to occupy far larger areas of the planet than amphibians or reptiles, and among birds the hummingbird is particularly well adapted to climactic variations.

A high body temperature, however, is something of a mixed blessing. Even in the warmest of regions occupied by hummingbirds, the ambient temperature seldom approaches that of the hummingbird—a warm-blooded animal indeed. The hummingbird is thus called upon to continually generate extra body heat—and lots of it. However, the hummingbird's small mass, relative to its total area, means that the heat it produces dissipates very quickly. It is as if every gram of body weight were exposed to the external environment through a relatively large surface, resulting in a faster heat loss than would occur in a more massive animal under identical environmental conditions.

How then do hummingbirds solve the problem of generating sufficient heat at temperatures just above freezing? The answer lies in the feathers. The hummingbird's plumage traps and holds a layer of warm air directly in contact with the skin. This air, being a poor conductor of heat, forms a sort of thermal underwear for the hummingbird, keeping heat loss to a minimum. The hummingbird's plumage, however, is more than a simple pair of long johns. By adjusting the angle the feathers make with the skin, a hummingbird is able to increase or decrease the thickness of the insulating layer of air—and thus control the dissipation of heat. This also explains the hummingbird's apparent change in size with changes in ambient temperature. When the weather is warm a hummingbird seems thinner, for its plumage is flush with its body. In cold weather, especially if there is a high wind, the hummingbird's feathers are ruffled—making the bird look stouter than it really is.

The following example illustrates the vast importance of thermal regulation in small birds. A swan may have a total of some 25,000 feathers capable of being ruffled, while a hummingbird may have about 940. If one compares the birds on a gram-for-gram basis, however, we find that the swan has only four feathers per gram while the hummingbird has 335!

The regulation of heat flow through its total body surface, however, represents only a partial solution to the problem of temperature conservation. A hummingbird must also generate sufficient energy for its rapid metabolic functions. In fact, a hummingbird is rather like a small internal combustion engine. It requires a fuel (food), an oxygen supply for burning the fuel (delivered through the respiratory system) and a pump (the heart) to deliver the fuel precisely where it is needed, and in the proper quantities.

Flight has a high energy cost for birds, and this is especially true of the hovering flight of the hummingbird. While at rest, a hummingbird may require some 3 to 4 milliliters of oxygen per hour, per gram of body weight. In flight, however, its requirements jump to 43 milliliters—fully ten to fifteen times as much. This rate of oxygen consumption is one of the highest among the vertebrates, per gram of body weight. We should also keep in mind that the hummingbird's tiny wings, relative to its body weight, preclude more economical forms of flight such as gliding.

The minute size of the hummingbird's digestive system does not permit the storage of large quantities of food. Furthermore, the bird's intense energy requirements does not allow for slow digestion processes, as well as foods containing large amounts of non-digestible residue. Therefore, the hummingbird is quite restricted as to its potential food sources, and must limit itself to a high energy diet. The only food source that satisfies these conditions is nectar. With its high sugar content and easily digestible ingredients, it seems a made-to-order fuel for this diminutive dynamo.

The ease with which hummingbirds can be attracted to man-made feeding stations, supplied with sugared water, makes it a simple matter to measure the bird's daily consumption of sugar. Although results differ according to the specific procedures employed by researchers, and because of variations in species and environmental conditions, the following example can be considered typical. A hummingbird weighing 4.3 grams was found to drink 10.6 grams of water per day, containing 22% sugar by weight. That is, the bird's daily intake was over twice its body weight and its daily sugar intake was fully 54% of its body weight. These data are considered more or less conservative, since they do not take into account any additional nourishment the hummingbird might have obtained from other sources during the day.

Nectar alone, however, is not a balanced diet for a hummingbird. Also needed is a source of protein. A captive hummingbird, besides gorging itself on sugared water, will also consume a considerable number of fruit flies—677 in a single day, by one count. These flies weighed in at 0.8 grams—some 27% of the total weight of the hummingbird itself. Although the protein content of these flies may have been only about 0.1 gram—we still find the hummingbird's appetite voracious.

At first glance, the bill of the hummingbird does not seem the most adequate when compared with that of other insectivores. Nonetheless, the hummingbird does a fine job of catching a sufficient number of fruit flies and small spiders to satisfy its protein requirements. It is common to observe hummingbirds alternating between static flight and fast, short displacements in all directions, within a small space and with no apparent purpose. But with the aid of a good pair of binoculars, one discovers that the hummingbird is flitting within a cloud of tiny mosquitoes—each flitting movement resulting in a tasty catch. Hummingbirds may also be seen pecking at insects amongst the foliage or in the walls of buildings—nor are they above stealing insects caught in spider webs.

The hummingbird's respiratory system is not unlike that of other birds—and mammals, for that matter—in that its basic function is to supply the organism with oxygen for its metabolic activity and to carry away the resultant carbon dioxide. The lungs of the hummingbird—small and rather stiff—are connected to an intricate system of air bags, some of which extend to the very marrow of the bones in the bird's extremities. Although these bags may contain more air than the lungs themselves, they lack the network of blood vessels necessary to affect the gas exchange function of true lungs.

What then is the purpose of these air bags? The lung-airbag respiratory system of birds represents an important departure from the respiratory system of mammals. While in mammals inhaled air enters the lungs directly, in birds the air first enters an airbag before proceeding to the lung. From the lung, the exhaled air passes to yet another airbag, before being vented to the outside. In other words, air flow in the lungs of a mammal is bidirectional (entrance and exit), while in birds it is unidirectional. In mammals, the exchange of O₂ and CO₂ takes place within the alveoli of the pulmonary cavity at the very end of an extensive bronchial network. In birds, the inhaled air flows continuously in a single direction along a network of “air capillaries”—highly irrigated microscopic passageways in which the interchange of gases takes place. It is of interest that in mammals approximately 20% of lung volume is “dead space”, representing air that never comes into contact with the gas exchange surfaces. Birds, on the other hand, cannot afford the luxury of pumping air that is not put to use. The totality of aspirated air passes through the network of capillaries, and so 100% of its volume is made available.

The above characteristics are indicative of the greater respiratory efficiency of birds. This is much in evidence by the capacity of birds to absorb sufficient oxygen at the very low pressures of high altitudes. Were it not so, they would not be able to fly much above 5,000 meters—an altitude which has been proven through experiment to immobilize most mammals due to oxygen deprivation. Another significant difference is the far higher respiratory rate of birds, in direct proportion to their size. While a twenty-two-pound turkey may have a rate of seven breaths per minute, a 2.5-gram hummingbird—at similar levels of physical activity—may have a rate of 143 breaths per minute. In flight, breath rates of 250 are not uncommon—although not all that air will be used for gas exchange. At very high levels of activity, the hummingbird generates a lot of heat. Its rapid breathing thus serves a ventilating function in order to dissipate excess heat, over and above its normal respiratory function.

The supply of oxygen and nutrients to the tissues of a hummingbird, and the elimination of waste products at a rate commensurate with its physical activity, require a highly efficient circulatory system and an especially powerful pump. In relation to its weight, the hummingbird has an enormous heart. In the Black-breasted Mango (*Anthracothorax nigricollis*), for example, the heart accounts for 2.7% of its body weight, compared with less than 0.1% for the stork. The hummingbird’s heartbeat is equally frenetic. In the Blue-throated Hummingbird (*Lampornis clemenciae*) of North America, the heart pumps at an incredible 1,260 beats per minute during flight. The seagull (*Larus argentatus*), on the other hand, clocks in at a lethargic 625 beats per minute. Man, of course, is no contender. Even with vigorous exercise, his heart rate will seldom surpass 180 beats per minute.

The above variables are merely indicative of the hummingbird’s accelerated metabolism and high energy consumption. In other words, this is why hummingbirds must eat a lot. This is also why night-time presents

the hummingbird with a new set of difficulties. Being a strictly diurnal creature, nighttime means 11 or 12 hours of compulsive fasting. Furthermore, its small size precludes storing energy in the form of fat or undigested food for future use. Add to this, the lower temperatures prevalent at night and you have one hungry bird in the early morning. How does a hummingbird tolerate these conditions in the biting cold of the Andean plains, where nighttime temperatures can drop to the freezing point—fully 70 degrees below the bird's normal body temperature?

In all diurnal birds, one observes a slight drop in body temperature during sleep, accompanied of a drop in energy consumption when in a state of rest. Hummingbirds, however, go further. During sleep they enter a state of quasi-hibernation in which their body temperatures drop to a cool 65° F. The ambient temperature, of course, remains substantially lower and so hummingbirds must continue to maintain their body heat, though at a somewhat lower level. It is not simply a matter of allowing body temperature to drop to that of the surroundings—as is observed in reptiles and poikilotherms. The ability to adjust body temperature to a substantially lower level, and which hummingbirds share with only a few other species of birds and mammals, is known as “heterothermia”.

By letting their body temperature drop during their nocturnal lethargy, hummingbirds are able to cut their energy consumption to just 15% of their normal daytime consumption. This energy saving allows them to pass the night without eating and to still have sufficient energy left to resume their feeding activities upon waking. Nocturnal lethargy is not exclusive to hummingbirds inhabiting high altitudes or other regions with low nighttime temperatures. Even those species inhabiting the hottest climates seem to display this capacity.

It is not known, however, whether nocturnal lethargy is a normal part of the hummingbird's daily cycle—whatever the food situation—or whether it is a defense mechanism brought into play when food is scarce. Lethargy, while advantageous for conserving energy, also makes a hummingbird vulnerable to potential predators—especially since the bird requires several minutes to awaken fully and to resume its normal state of activity. It would seem then that lethargy is not a good idea unless it is really necessary. On the other hand, hummingbirds are quite adept at taking refuge during the night in good hiding places or in hard-to-reach crevices—well out of the reach of all except the most determined predator.

Reproduction

Relatively little is known about hummingbird reproduction. This is unfortunate, for it is precisely at this stage of the life cycle that the mechanisms of adaptation are employed to greatest effect—not only to ensure that procreation actually takes place but also to guarantee the long-term survival of the species. Indeed, the natural history of a species cannot be considered complete if we are unable to provide at least the basic information with regard to its reproduction.

This lack of information is due to the remarkable diversity of species in the tropics—home to the greatest variety of hummingbirds—as well as to the general lack of observers. Of course, the same might be said of most other tropical bird species. But hummingbirds present their own peculiar difficulties. Their flight makes them extremely difficult to follow once they have left the immediate vicinity of their favorite flowers. Their nests—whose size is in keeping with their occupants’—are well hidden and ingeniously camouflaged.

As do other birds, hummingbirds exhibit courtship behavior or “gallantry”. This behavior is the series of activities that culminate in mating and fertilization. By means of this behavior the potential mates identify themselves with regard to species, sex and reproductive disposition. Courtship also serves to lessen the aggressive behavior of strongly territorial animals. Curiously, the female of a certain species of hummingbird from the Antilles (*Eulampis jugularis*) is amenable year-round to the advances of territorial males. This behavior gives the female access to flowers that would otherwise be off-limits. Such tactics have been termed—too bluntly, perhaps—“prostitution.”

The Sparkling Violetear—native to all three Cordilleras of the Colombian Andes at altitudes of 2,000 to 3,000 meters—provides us with the most readily observable characteristics of hummingbird courtship. A frequent visitor to both rural and urban gardens, this species’ outlandish behavior immediately draws our attention. We should note, however, that the many species of hummingbirds give rise to a correspondingly great variety of behaviors. The male favors high perches from whence he commands an unobstructed view of the surroundings. He then begins to emit a monotonous “chiip, chiip”, interrupted only occasionally to imbibe nectar or to expel an unwelcome intruder from his territory. He then returns to his perch and continues his incessant song. Around noontime, the male engages in a singularly curious dance. Every few minutes he rises several meters in the air, only to immediately descend—tail spread fan-like—with a rapid series of “chiips”. This dance probably serves the double function of warding off other males and of proclaiming to available females that the songster is ready for reproduction.

Upon approaching another hummingbird’s territory, visiting females are initially accorded the same reception as an intruding male: an immediate and occasionally prolonged chase. This is entirely rational, since an intruding female represents the same threat as a male with regard to the resources of nectar that are so jealously guarded. The intruding female must therefore take pains to announce her sex and her availability for reproduction.

After several attempts to enter the protected territory, the female will alight on an exposed branch and—upon being approached by the male—open and close her wings while remaining in place. The approaching male hovers at several points around the female, just a few centimeters away. As if to announce his intentions, he ruffles the brilliant violet auricular feathers on either side of his head. In response, the

female ruffles hers—but remains stationary. Then both male and female fly forward and backward, a short distance from each other and with bodies vertical. In a successful mating attempt, the female finally perches on a nearby branch while the male alights on her back. Mating proceeds as is in larger birds, tail to tail and with the cloaca in contact to allow the transfer of sperm.

Both genders of the Booted Racket-tail, inhabitant of the cloud forests, sport dense tufts of white feathers on their feet. To the casual observer these tufts—known as “tibial feathers”—do not seem to bear any relation to reproduction. Nonetheless, they form an important part of the male’s courtship dance. During courtship the male typically approaches the female from above, with his feet raised towards his head and with the tibial feathers ruffled to the maximum. The diminutive suitor appears as if he had two large tufts protruding from his neck. The male sometimes accompanies his courtship dance with brisk tail fanning and the occasional chirp.

It is much more difficult to observe the courtship of the various species of Hermits, given the dense foliage they favor for the mating ritual. Normally several males will congregate and hover over a small area of dense underbrush—either at the edges of the forest or deep within, and where only their persistent chirps reveal their presence. This communal breeding ground is known as a lek, a word of Swedish origin. With luck, the persistent observer may be rewarded with the sight of a Hermit, rhythmically waving its longish tail in time to the calls. Hermits frequently abandon their perches and suspend their mating rituals to chase one another or to take time out for feeding—usually amongst their favorite flowers, the blossoms of the diverse species of *Heliconia*.

One assumes that female Hermits are attracted to the leks by the persistent mating calls of the males. However, the similarity of the male and female plumage, together with the rapidity of their movement, makes it extremely difficult to establish whether a given individual is male or female. The subsequent chases, in which the individual birds fly out of view, might either be part of an elaborate mating ritual or simply one male driving off another from his territory.

In general, it appears that hummingbirds take partners only for the duration of the mating ritual. Unlike other birds, which often exhibit greater commitment on the part of the male, hummingbird homemaking is a decidedly female activity. It is the female that builds the nest, incubates the eggs and feeds the chicks— with no male participation whatsoever. Only occasionally is a stable male-female union observed. And even then, the male shows no great inclination for housekeeping chores. It is likely that alleged observations of male participation in homemaking activities are due to mistaken identifications of males in species whose sexual dimorphism is not readily apparent.

Hummingbird nests are as varied as the species that build them. Nests are generally cup-like, open at the top; the roof is not part of the nest structure itself. Sylphs, however, are the exception, as they generally place a dome over the cup and provide for a side entrance.

Nest placement is equally varied. The nest of the Black-breasted Mango looks much like a miniature tower arising from a thick, horizontal branch. The Rufous-tailed Hummingbird, on the other hand, attaches its nest to the slender branches of trees, bushes or garden plants that provide adequate shade. The nest of the Greenish Puffleg is invariably to be found beneath the low-lying frond of a fern—well protected from all but the most assiduous observer—and predator. The White-necked Jacobin is not quite as cautious, for it builds its nest on the upper surface of a horizontal leaf. Sometimes the leaf is hardly larger than the nest itself, although on occasion the bird chooses a spacious palm frond on which to build.

The nests of Hermits are perhaps among the most architecturally interesting. Indeed, every detail of their construction is worthy of note. First of all, Hermits generally chooses the underside of a Heliconia leaf or similar broad-leafed plant. The nest is thus well protected from the elements and from the roving eyes of potential predators. Only the protruding ends of the cobweb that the Hermit uses to affix its nest to the leaf could perhaps expose its presence. Even then, the nest's location is such that a predator could hardly come calling without alerting the occupants.

One's interest is also drawn to the general appearance of the nest itself. Unlike the nests of other hummingbirds, the Hermit's nest is quite unkempt. The many cobweb threads left dangling give it a rather ragged appearance. According to some observers, however, these loose ends serve a useful function. Rainwater that would otherwise be absorbed by the nest is drawn down to the ends of the cobweb and then drips off.

Some hummingbird species occasionally break their traditional nest-building rules to avail themselves of the supports provided by human dwellings and other man-made structures. One Green Hermit forsook the abundant Heliconia leaves in the area in favor of a palm frond that had been used to thatch a roof. A certain Green-fronted Lancebill even built its nest on the wall of a dwelling.

The materials used by hummingbirds for nest building are as varied as their architectural styles. The Greenish Puffleg usually collects ample fresh moss, whose color blends perfectly with the fern fronds under which the nest is built. Hermits resort to a great variety of long fibers, stems and roots. The Rufous-tailed Hummingbird and others of its genus plaster their nests with lichens long after construction has been completed—and even while chicks are being incubated within. This coating not only helps reinforce the structure of the nest but also assures a more effective camouflage. But whatever materials are used, they are always well interwoven and affixed to the supporting structure with abundant cobweb. Some species appear

to use a mixture of nectar and saliva as a mortar to further assure adequate adhesion between the disparate components of the nest.

The interior walls of hummingbird nests are always lined with soft materials—the down that surrounds the seeds of the balsa, the ceiba or the thistles of various weeds. The materials, however, are really a function of what is locally available. The Booted Racket-tail, for example, pulls off the fuzz that covers certain arboreal ferns native to its habitat in the mist-enshrouded forests. Showing exceptional resourcefulness, one Sparkling Violetear lined its nest with the fur of a sheepdog, while another plucked threads from a woolen blanket left out to dry in the sun. But whatever the material, its function is the same—to protect the eggs and hatchlings from the onslaughts of the weather.

Hummingbirds generally hatch but two eggs. As might be expected, they are minute. Those of the Steely-vented Humminbird measure but 13.7 millimeters in length and 8.7 millimeters in diameter, one-half and one-third inches, respectively. Their weight is hardly more than half a gram. The eggs are generally laid early in the morning and on consecutive days—although sometimes there is a two-day interval between one and the other.

Incubation takes from 16 to 19 days, depending on the species. Hummingbirds whose habitats are located at exceptionally high altitudes, with low ambient temperatures, may have extended gestations. The eggs of Peru's Andean Hillstar, for example, take from 22 to 23 days to hatch. Unlike many songbirds, hummingbirds do not sit on their eggs for extended periods of time. Incubation is interrupted several times per hour for feeding, preening or simply stretching out. Even so, perhaps 80% of the daylight hours are devoted to incubation.

Upon coming to term, hummingbird hatchlings are still in a very rudimentary stage of development. Blind and dark in color, their plumage is limited to the mere suggestion of two rows of feathers running down the length of their backs. Their beaks and extremities are likewise barely discernible. In fact, they can scarcely be identified as hummingbirds at all. The offspring first movements are limited to stretching their necks and opening their mouths in response to a gentle nudge from the mother. She then introduces her beak deep in the gut of each hatchling and regurgitates a bit of nectar with partially digested insects. The sight of a long, sharp beak going down a slender neck inevitably brings to mind the spectacle of a sword swallower. By the time the hatchlings are three or four days old, their mother takes to feeding them while hovering motionless over the nest—a real exhibition in precision flying.

Although hard data are scarce, we are nonetheless able to outline the main events in the development of hummingbird hatchlings. Depending on the species, they open their eyes between the sixth and ninth days. At about this same time the wings sprout their first flight feathers. Shortly thereafter the hatchlings gain the

ability to maintain their own body temperature— thanks to their developing plumage. The mother then concludes her incubating activities and stops sitting on her chicks—even at night.

The hummingbird's flight feathers grow rapidly. By the fifteenth day they have completed their growth—the tufts having entirely emerged from the shafts. At this time the chicks begin to exhibit greater activity. They groom constantly and perch on the edge of the nest to stretch their wings. Little by little they learn to flap them furiously, but without yet taking to the air. The nest is now clearly too small for two frisky adolescents, and pieces often break off as the activity becomes ever more intense.

Hummingbird chicks abandon their nests anywhere from 19 to 26 days after birth, depending on the species. The greatest delay is observed in Peru's Andean Hillstar, whose young remain homebound for up to 40 days. Those of the Reddish Hermit, on the other hand, are the most precocious. Their small size notwithstanding (for they are the smallest of the entire genus), they take their leave a mere 15 days after hatching.

Chicks may abandon their nest at an earlier date if there is any unusual commotion in the vicinity—perhaps caused by the observers themselves. It is not then unusual for the young birds to take to the air several days earlier—an ability that has clear survival advantages in the face of approaching predators.

The older of two Violetear chicks was once observed to make its first flight directly to a thick bush some four meters from its nest. The following day the younger chick also abandoned its nest and was seen early that morning beside its older sibling. The two chicks remained in the bush for the following eight days, during which time the mother never failed to bring them nourishment. The chicks' dark plumage had not yet fully developed the characteristic violet markings along the sides and breast—which must have made it especially difficult for the mother to locate her brood in the dense foliage.

Over the following days the birds began to make exploratory flights to nearby shrubs, after which they always returned to the shelter of their home base. It was as if they had agreed with their mother that they would meet at that particular spot. Fully twelve days after abandoning their nest, they were still being fed by mother. The chicks disappeared from view shortly thereafter, having tasted their first nectar directly from the flowers of a nearby plant. It is probable, however, that mother continued to feed them for a few days more. Despite the scarcity of reliable observations, it appears that the chicks of the Sparkling Violetear continue to be fed by the mother for a full three weeks after leaving the nest.

We must keep in mind that the above anecdotal information is but an incomplete picture, fragmentary and excessively general. It does not do justice to a group of birds whose diversity is so great and whose geographic and ecological distribution is so extensive. Only a handful of species has been studied with anything resembling the necessary detail. Furthermore, the species studied in greatest detail are invariably

from the temperate zone. It is unlikely that much of the data can be extrapolated to include neo-tropical species. There remains ample room for the patient and dedicated observer, willing to delve deeply into the natural history of this most fascinating of winged creatures.