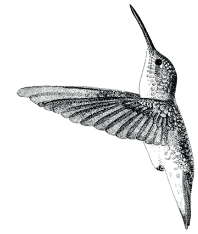
Contents



BirdLife INTERNATIONAL

The names of the hummingbirds and the taxonomy used throughout this book follow BirdLife International (see *page 239*).

All the images shown are males unless captioned otherwise.

The location given for each photograph indicates where it was taken. For information on the distribution of a particular species, see the relevant entry in *Taxonomy: The BirdLife List of Species* (*page 239*).

Bills and feeding

As shown on the previous page, hummingbirds exhibit a tremendous variety of bill shapes and structures, reflecting their close association with a range of different flowers. In some cases, hummingbird and flower appear to have coevolved, leading to specializations that now force a hummingbird with a very long or very strongly curved bill to feed from, and therefore potentially pollinate, just one or a few particular types of flower. Many hummingbirds, however, have a a relatively short 'all-purpose' bill which enables them to feed from a much wider range of blossoms, or even to pierce the base of the flower to access the nectar.

FACING PAGE The **White-tipped Sicklebill** *Eutoxeres aquila* has a sharply downcurved bill that is perfectly adapted for feeding from a limited range of plants that have long, curved flowers, such as this *Heliconia*. | Peru

ABOVE Most short-billed hummingbirds, such as the **Purple-backed Thornbill** *Ramphomicron microrhynchum* (*left* | Colombia) and **White-crested Coquette** *Lophornis adorabilis* (*right* | Costa Rica), have a rather generalized feeding strategy, taking nectar from a wide range of small flowers.

BELOW Some hummingbirds, such as this **Reddish Hermit** *Phaethornis ruber*, have the right-sized but wrong-shaped bill to feed from certain flowers and sometimes have to be creative in order to reach the nectar! | Brazil

Not all hummingbirds hover to feed: many perch or cling onto vegetation close to the flower, thereby conserving energy. Examples of species that often feed in this manner include **Green-crowned Brilliant** *Heliodoxa jacula* (♀, *above left* | Costa Rica), **Velvet-purple Coronet** *Boissonneaua jardini* (*above right* | Ecuador), **Tourmaline Sunangel** *Heliangelus exortis* (*below* | Ecuador), and **Shining Sunbeam** *Aglaeactis cupripennis* (*facing page* | Colombia).

Anna's Hummingbird *Calypte anna*

Chestnut-breasted Coronet *Boissonneaua matthewsii* | Ecuador

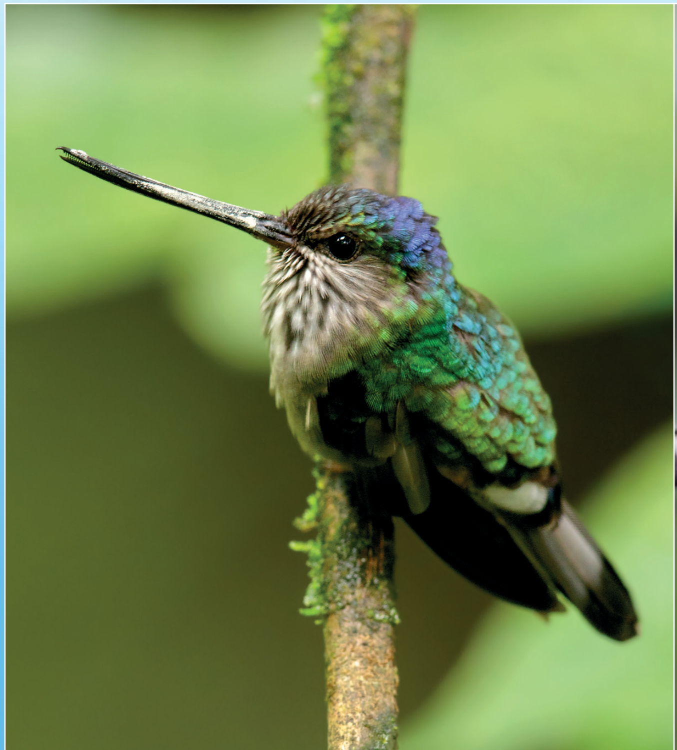
Dietary supplements

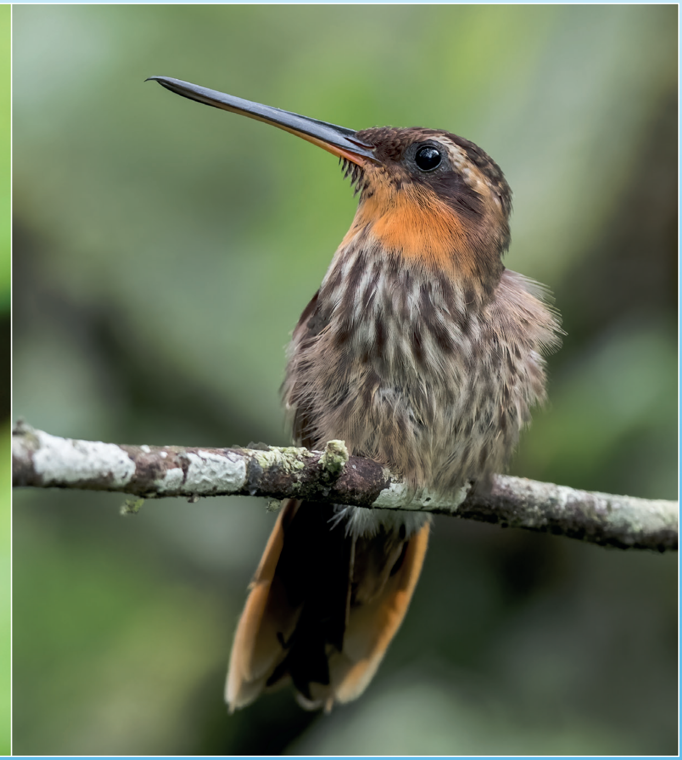
In addition to nectar, hummingbirds need to eat insects and other small invertebrates (arthropods) in order to obtain protein (which nectar lacks) and calcium for eggshell production. Females supplement this small amount of calcium intake by licking up bits of soil, sand, or even wood ash, as they hover over the forest floor. Insects are generally caught in the air, especially by short-billed and straight-billed hummingbirds; species that have a very long or curved bill are unable to do this and instead take insects and other small invertebrates by picking them from leaves. Unlike nectar, which is diverted straight to the intestines, where it can be processed rapidly, arthropod food is processed in the stomach, the hard parts being ground in the gizzard.

Like the swifts and treeswifts, their closest relatives (see *page 12*), hummingbirds are able to see insects at close range and catch them in their bill or wide-open mouth in flight. In order to achieve this, they have evolved specially adapted neck muscles, allowing a fast and accurate sideways movement of the head, as well as a quick snap of the bill, both of which are essential for this feeding technique to be effective. Short-billed hummingbirds can open their gape particularly wide (as shown by the Chestnut-breasted Coronet, *above*) and take in flying insects at the back of the mouth, rather than catching them in their fine and delicate bill. In North America, some hummingbirds have adapted to visiting the holes made in tree bark by sapsuckers (fairly small woodpeckers), feeding not only on the resulting sap runs but also on the insects that these attract. Ruby-throated Hummingbirds, for example, may do this before the full range of nectar-bearing flowers is in full bloom in spring (see also *Epic migrations*, *page 174*).

The various species of hermit, which live in the understory beneath a dense forest canopy, will sometimes hover around spiders' webs, snapping up not only the spiders' catches but also the spiders themselves. The Saw-billed Hermit (*facing page, top right*) has a particularly heavy, thick bill with a hooked tip that appears to be an adaptation to feeding on such invertebrates. Similarly, the uniquely serrated bill of the Tooth-billed Hummingbird (*facing page, top left*) is believed to be an adaptation to catching insects and other invertebrates, although it may also have a function in territorial defense and possibly when preening.

'Typical' hummingbirds 'flycatch' more frequently than do hermits, hawking insect prey in the air. Brown Violet-ear and occasionally Anna's Hummingbird (illustrated *above left*), for example, feed in this manner, catching insects by sallying out from a perch like a flycatcher, or by hovering for longer periods and darting to-and-fro, in effect using the hover as its 'perch'. Another species that is especially known for eating invertebrates is the Fiery-tailed Awlbill (*facing page, bottom*), which has a slender bill that, unusually for a hummingbird, tilts upwards at the tip. Although it feeds mostly on nectar, taken from many flowers along regular routes, it will also take insects, either hawking them in flight or picking them or other invertebrates from the undersides of leaves, this perhaps explaining its unique bill shape.





ABOVE LEFT **Tooth-billed Hummingbird** *Androdon aequatorialis* | Colombia; ABOVE RIGHT **Saw-billed Hermit** *Ramphodon naevius* | Brazil; BELOW **Fiery-tailed Awlbill** *Avocettula recurvirostris* ♀ | Colombia

El Jardín Encantado in the village of San Francisco de Sales, at an altitude of 1,500m (4,900 ft) just 47km (29 miles) from Bogotá, the capital city of Colombia, is an amazing hummingbird spectacle.

Hummingbirds and feeders

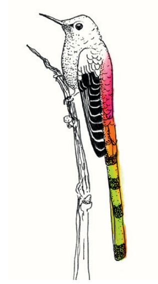
Hummingbirds' almost total dependence on sugary food means that they are readily attracted to special feeders that allow them to sip sugar-rich solutions in place of nectar. In many instances, these feeders may attract just a handful of hummingbirds, but in some cases the numbers visiting during the course of a day may be quite amazing. One spectacular example is El Jardín Encantado (the 'Enchanted Garden') in the village of San Francisco de Sales, near Bogotá, in Colombia, where 40 feeders are maintained and 27 species of hummingbird have been recorded. The total number of individual birds visiting is estimated to be more than 1,000 each day, consuming up to 450 kg (1,000 lbs) of raw sugar every month! As a general rule, it has been suggested that the normal number of birds visible at any one time at an individual feeder or group of feeders should be multiplied by six to arrive at the daily total.

As mentioned on *pages 15* and *34*, it seems likely that hummingbirds use their color vision to find flowers, and that red flowers seem to be particularly favored as they are most easily visible against a background of green. For this reason, many hummingbird feeders are colored red. Studies undertaken to try to establish whether hummingbirds have a color preference have, however, reached very different conclusions. Even the most sophisticated studies have been unable to discriminate between real preferences and memory, and it may simply be that red, as it stands out, is recognized as a good source of food, and that, once a red 'flower' is found, hummingbirds simply become conditioned to feeding from it.

While the use of hummingbird feeders may be beneficial for the hummingbirds, and for people who wish to see them at close range, it may not necessarily be a good thing for flowering plants. Hummingbirds using feeders carry far less pollen than do other hummingbirds, suggesting that the flowers in the vicinity could possibly be losing one of their chief pollinators. Nevertheless, whether at a backyard feeder, at feeders in a remote forest reserve, or when naturally visiting wild flowers, hummingbirds are endlessly fascinating to watch. Although not all aspects of a hummingbird's extreme physical adaptations can be seen, their more obvious anatomical features and their incredible abilities in flight can all be appreciated at close range as they concentrate on doing what they must do to survive, often oblivious to the presence of a human admirer. Such encounters provide endless joy to those who are prepared to take the time to watch and wonder about the marvels of the natural world, and they also provide an ideal opportunity to appreciate a hummingbird's coloration, another fascinating adaptation of these remarkable birds.

ABOVE Feeders provide an ideal opportunity to watch hummingbirds at close quarters and to observe how far they are able to extend their tongue beyond the tip of their bill. This is a female **Anna's Hummingbird** *Calypte anna*. | Canada

BELOW The feeders at the Fundación Jocotoco **Buenaventura Reserve** in the province of El Oro, in southern Ecuador, attract good numbers of a range of hummingbirds: in this case mostly **Green-crowned Brilliants** *Heliodoxa jacula*, a few **Green Thorntails** *Discosura conversii* and a couple of **Violet-bellied Hummingbirds** *Amazilia julie*.



Color and Iridescence: Flashes of Brilliance

Perhaps what is most captivating about hummingbirds, aside from their amazing flying abilities, is their incredible colors and, in many species, stunning iridescent plumage. Seemingly, in the blink of an eye, a bird that at first appears dull black or green can be transformed, as if by magic, into a profusion of shimmering hues. And while this transformation is not magic, but instead simply the effect of waves of light interacting with feathers, the reality is arguably even more amazing.

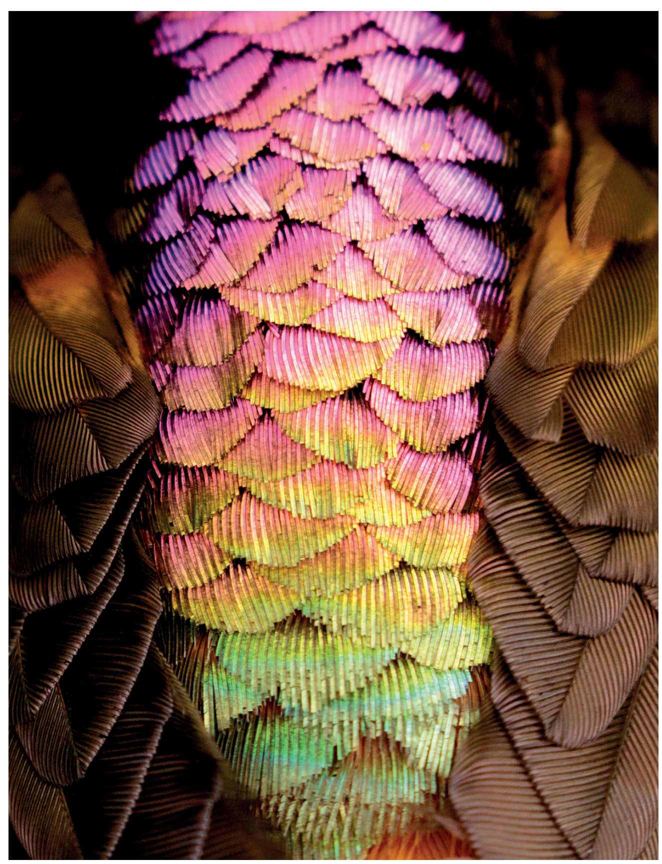
Although hummingbird feathers are capable of presenting the full spectrum of colors, it is red, orange and yellow that are the least commonly encountered. When it comes to greens, turquoise, blues, purples and purple-reds, however, the hummingbird palette runs wild. All of these colors have clearly long been important to us in our appreciation of these little jewels, as demonstrated by the delightfully evocative English names given to many species. These names reflect not only their color but often a particular quality or manifestation of that color, as well as gemstones or metals, or include celestial terms (as summarized in the table *below*).

As stunningly beautiful as hummingbirds are, their fast movements and the physics that might allow only a glimpse of their iridescence often make them difficult to appreciate fully. A brief view of a hummingbird might enable us to get some idea of size and shape or flight action, but not so much of that all-important color. A dark shape, or perhaps a flash of white may be all that can be perceived if the hummingbird is simply zooming away into the distance. But sometimes these spectacular birds are obliging enough to return to feed at a flower, or perch on a twig, or visit a special feeder, giving the lucky viewer a chance to truly enjoy the bird. And in those sublime moments when they are caught by a ray of sunshine breaking through foliage at a precise angle to the viewer, the hummingbird is transformed into a creature beyond compare—as illustrated by the portfolio of images of aptly named species on the *following pages*.

Hummingbird names (note: the names of some species, *e.g.* **Coppery-headed Emerald**, use more than one term)

TYPE	TERMS
GEMSTONES* **53 names using**	amethyst, beryl, emerald, garnet, gem, ruby, sapphire, topaz, tourmaline
METALS **33 names using**	bronze, copper, gold, metal, steel
CELESTIAL TERMS **59 names using**	comet, lucifer, rainbow, star, sun
MANIFESTATIONS OF COLOR **33 names using**	brilliant, fire, glittering, glowing, scintillant, shining, spangled, sparkling, velvet
COLOR **109 names using**	azure, blue, brown(s), green(s), hyacinth, indigo, lazuline, magenta, orange, pink, purple, red(s), turquoise, violet

*Hummingbirds' gem-based names are due more to human wonder than to accurate mineralogy, as many gemstones occur in a range of colors. Sapphires are a good example, being generally regarded as blue, but in reality occur in any color except red (which would make it a ruby). Narrow color ranges are found in emeralds (always a bright blue-green), rubies (pure red to slightly purplish-red) and amethysts (reddish-purple to purple). Wide color ranges are found in, for example, tourmaline, which can be anything from blue-black to blue, red, yellow, green and pink, and beryl, which ranges from red to blue-green; the two can also be colorless.



The iridescent feathers on the back of the aptly named **Shining Sunbeam** *Aglaeactis cupripennis* contrast with the rather dull flight feathers. | Colombia

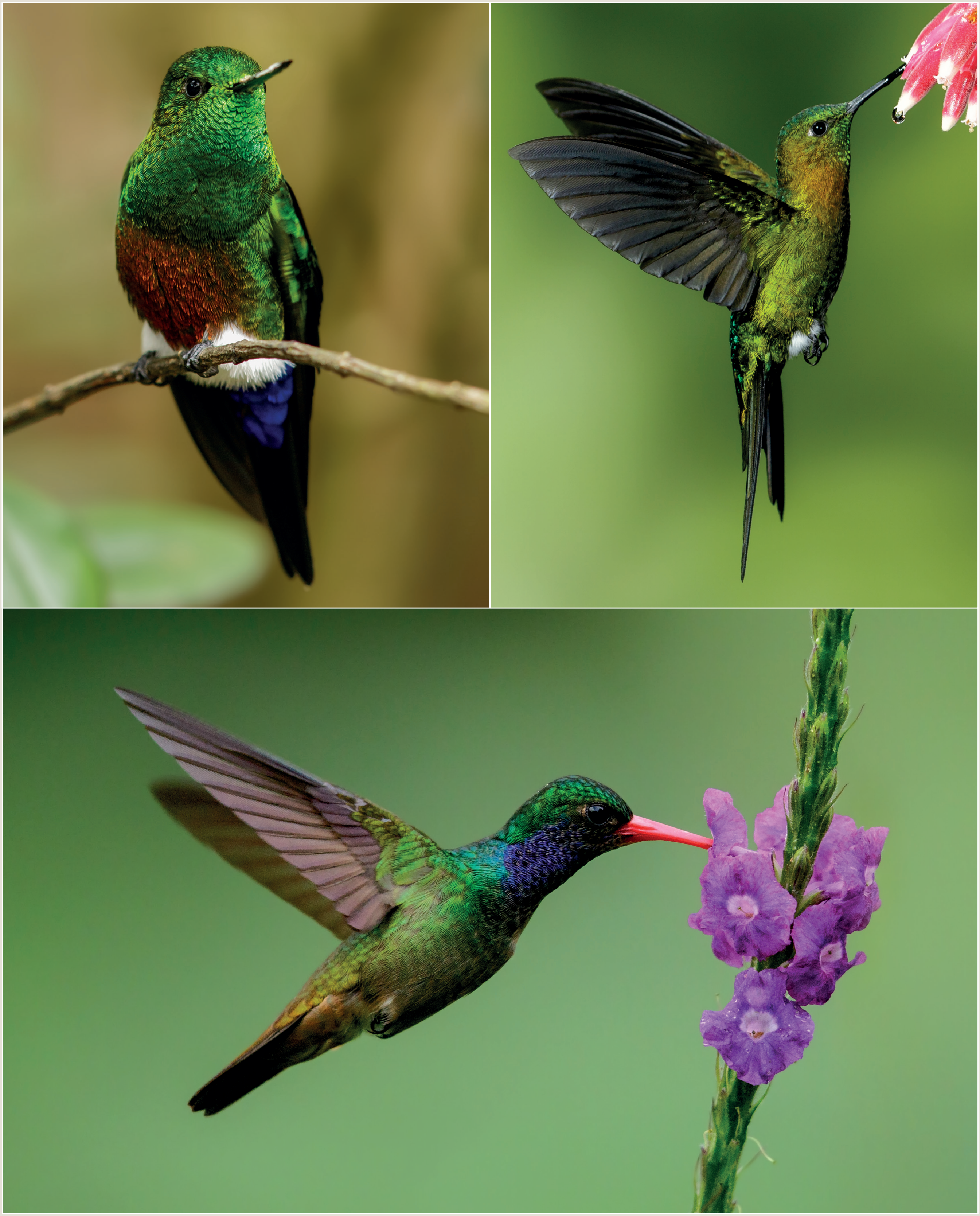
FACING PAGE **Red-tailed Comet** *Sappho sparganurus* | Bolivia

The true gems of the bird world

A total of 53 hummingbirds are named after precious or semi-precious gemstones, reflecting their scintillating iridescent plumage. Five are shown here: BELOW **Brazilian Ruby** *Clytolaema rubricauda* (*top left* | Brazil); **Emerald-bellied Puffleg** *Eriocnemis aline* (*top right* | Peru); **White-throated Mountain-gem** *Lampornis castaneoventris* (*bottom left* | Panama); **Amethyst-throated Sunangel** *Heliangelus amethysticollis* (*bottom right* | Ecuador); FACING PAGE **Sapphire-spangled Emerald** *Amazilia lactea* | Brazil.

Manifestations of metals

Thirty-three species of hummingbird have some reference to metals in their name, four of which are shown here: BELOW **Coppery-bellied Puffleg** *Eriocnemis cupreoventris* (*top left* | Colombia); **Golden-breasted Puffleg** *Eriocnemis mosquera* (*top right* | Ecuador); **Blue-throated Goldentail** *Amazilia eliciae* (*bottom* | Costa Rica); FACING PAGE **Coppery Metaltail** *Metallura theresiae* | Peru.



From the heavens

No fewer than 59 hummingbirds have been given English names that relate to celestial terms, reflecting their fantastic iridescent plumage—the words used most frequently being 'sun' and 'star'. A selection of the species that have been so named is shown here: BELOW **Rainbow Starfrontlet** *Coeligena iris* (*top* | Ecuador); **Blue-throated Starfrontlet** *Coeligena helianthea* (*bottom left* | Colombia); **Purple-throated Sunangel** *Heliangelus viola* (*bottom right* | Ecuador); FACING PAGE **Ecuadorian Hillstar** *Oreotrochilus chimborazo* | Ecuador.

Manifestations of color

Hummingbirds are frequently given wonderfully evocative names that relate to a manifestation of color or to their overall appearance, some examples of which are shown here: BELOW **Magnificent Hummingbird** *Eugenes fulgens* (*top left* | Costa Rica); **Snowcap** *Microchera albocoronata* (*top right* | Costa Rica); **Glittering Starfrontlet** *Coeligena orina* (*bottom left* | Colombia); **Shining Sunbeam** *Aglaeactis cupripennis* (*bottom right* | Colombia); FACING PAGE **Velvet-purple Coronet** *Boissonneaua jardini* | Ecuador.

Why be colorful?

The colors of a hummingbird's plumage, as with other birds, either help an individual to 'hide', by making it less conspicuous, or do the opposite and help it to show off in territorial and courtship displays. Furthermore, while some predatory birds have a cryptic coloration in order to be less easily detected by their prey, hummingbirds, being chiefly nectarivores (nectar-consumers), do not have the need for such subterfuge.

Most species of hummingbird are sexually dimorphic (see *pages 82–85*), the females typically having much duller plumage than the males as they need to be camouflaged when incubating their eggs or feeding young in order to avoid detection by predators. Many male hummingbirds, on the other hand, and particularly of those species that occur in open habitats, have bright, colorful plumage that makes them particularly conspicuous. It has been suggested that the amount of energy and effort that an individual male puts in to ensuring that his feathers are maintained in prime condition may signify his level of fitness. In such instances, a male hummingbird could be balancing the risks of drawing attention to himself (when defending a feeding territory or searching for a mate, for example) against the benefits of looking super-fit (or simply beautiful) and, therefore, extra special in the eyes of a female. In any case, male hummingbirds will never give away the location of a nest, because they usually have nothing to do with constructing the nest, incubating the eggs, or caring for the young, and at no time do they pay a visit. There is, however, another line of thought that, in some species at least, males may be brightly colored in order to attract the attention of predators and draw them away from the females, nests and young. While this may seem a very risky strategy, in evolutionary terms it may actually be effective as it increases the chances of the male perpetuating his genes.

There is some evidence to suggest that the color intensity of a hummingbirds iridescent feathering is influenced by diet. A high-protein diet has been shown to create brighter colors on the crown of male Anna's Hummingbirds, as well as a richer yellow-green on the tail feathers. This perhaps provides an additional indication that there are visual clues when showing off their colors in courtship and aggressive display as to which are the 'fittest' males. Although, to us, all male Anna's Hummingbirds may look pretty much the same, from a hummingbird's perspective they are likely to be recognizable as individuals, especially when taking into consideration the additional colors and hues that hummingbirds are able see that we cannot (as explained in the diagram on *page 62*).

Coloration may play a part also when a male is trying to maintain sole control of a patch of nectar-rich flowers—bold colors acting as a warning signal to other males and reducing the chances of an aggressive interaction, with all its inherent risks. As well as using color on its own, some hummingbirds show color patterns and areas of contrast in their plumage. A male Collared Inca, for example, has no bright colors but nonetheless is visually striking owing to an intensely black area surrounding a spotless white collar. On the whole, though, the males of forest-dwelling species are not particularly brightly colored, presumably because not much sunlight, an essential requirement of iridescent color, penetrates down into their dark and gloomy habitat.

The need for camouflage to reduce the risk of predation is another important aspect of hummingbird coloration. A subtly constructed pattern of contrasting streaks and spots can break up a bird's outline and help it to blend into its surroundings. An alternative is to rely on countershading, whereby light from above makes a bird's dark upperside appear paler and its pale underside (in shadow) look darker. This essentially reduces contrast and 'flattens out' the appearance of the three-dimensional bird, making it harder for a predator to spot.

It would seem logical that a hummingbird's bright, iridescent plumage has an extra impact compared with the 'ordinary' bright, pigment-based colors seen on many other birds. When a hummingbird really wants to show off, it can, by turning its head or spreading feathers in a particular way, 'turn on the lights' and send a strong directional signal that will be visible only from a certain angle (as explained in the diagram on *page 68*).

The plumage of 'typical' hummingbirds is more varied than that of the hermits, the males of many species showing extensive iridescence of red, orange, yellow, green, blue, purple or pink. These colors may be enhanced by various adornments, such as a fan-like gorget, a crest or long tail feathers. On the other hand, the plumage of hermits is predominantly a range of muted browns, grays and reds produced by pigments, with iridescence, if there is any, mostly limited to the upperparts—far less eye-catching than that of other hummingbirds. Most hermits are non-territorial and, as explained in the following chapter, *Breeding: Continuing the Line* (*page 87*), males display communally in what are known as leks, in which the color of the bill and open gape plays an important role in the display. Hermit leks are often in gloomy habitats where the lack of light makes a glowing plumage nearly impossible to achieve. The fact that the gape appears as a flash of color suggests that color must have a function, and leads to the conclusion that in hummingbirds, whether iridescent or not, color generally performs an important role in display.

As mentioned earlier, the finest coloration seems to play at least some role in attracting females, although exactly how a female makes her choice of mate is much

ABOVE **Collared Inca** *Coeligena torquata* | Ecuador; BELOW **Black-bellied Hummingbird** *Eupherusa nigriventris* | Costa Rica

more difficult to explain—and a topic that is still much debated—from the established 'finery = fitness' theories to the thought that perhaps beauty evolves simply for aesthetic reasons, for its own sake. It is, however, very unlikely that a female hummingbird chooses a male simply because he looks good, but rather that she chooses him because he is giving a message about his fitness to father a strong brood of chicks. A fascinating line of thought that springs from this is that, if females prefer these colorful males, then the evolution of such males puts them at greater risk of predation: in such cases it could be argued that evolution is reducing the chances of an individual contributing to a future gene pool, which would seem paradoxical. This does, however, provide the basis for the so-called 'honest signaling theory', which suggests that because certain traits, such as a colorful plumage, have a high maintenance cost and present a higher predation risk there is no real opportunity for individuals to 'cheat the system'. Only the highest-quality individual males can afford the risks associated with this type of signaling, and prospective mates or rivals can easily see a visual clue to the fitness of these 'honestly displaying' individuals.

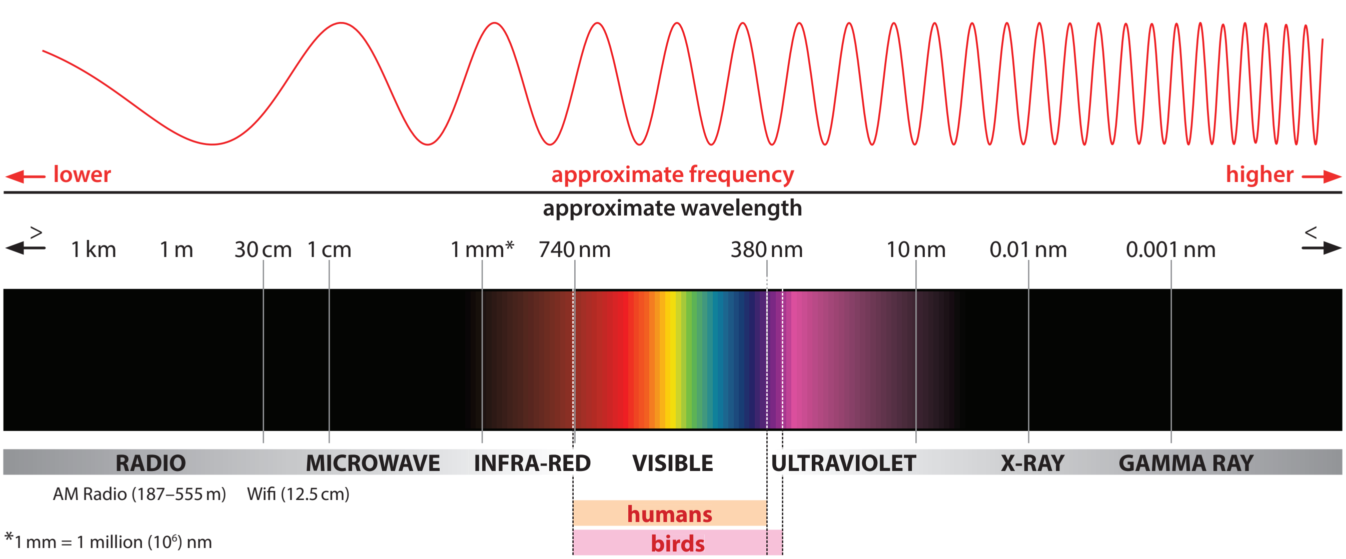
So the key question remains, why be colorful at all? Is it merely to look beautiful and to be appreciated, or is it, as most scientists believe, to relay some sort of message about fitness and willingness to risk the 'costs'? In other words, does coloration confer some competitive advantage with risks attached, or are colors merely arbitrary developments that offer little or no gain in an evolutionary sense? When considering this last point it is important to take into account the fact that sexual selection is the strongest driver of evolutionary traits in the natural world.

How does color work?

When contemplating how color works, it is important to put anthropocentric views to one side and to look at light purely as it exists, recognizing that color is merely an interpretation of wavelengths within the limitations of what we can actually see. Hummingbirds, like many animals, and indeed plants, are 'simply' taking advantage of the laws of physics relating to light. But the more one delves into the subject, the more one begins to realize that this simplicity is in fact quite complex and requires an astounding set of circumstances to make it happen.

Light is a form of energy (electromagnetic radiation) that acts as both waves and particles (photons), which is just a small portion of the electromagnetic wavelengths that range from very low-frequency radio waves, through sunburn-inducing ultra-violet, to extremely high-frequency gamma rays (see the figure *below*). Light (which on Earth means predominantly sunlight) is a beam of photons in the visible portion (between ultraviolet and infrared) of the electromagnetic spectrum. Sunlight appears 'white' unless refracted by some means—in which case the light splits into the familiar rainbow spectrum. The color that is actually seen by an observer depends on which wavelength is reflected back.

It is these waves that are fundamental to color, as our eyes perceive different wavelengths (measured in nanometers (nm)) of light and our brains interpret them as different colors. For example, a typical rainbow is created when sunlight passes through water droplets in front of a viewer at a precise angle of 42°. Sunlight is bent (refracted) when it enters the almost round, clear water droplet before being reflected by the back of the droplet and refracted once again upon exiting the droplet; whichever wavelength leaves the droplet is perceived as a color. The same principle applies when

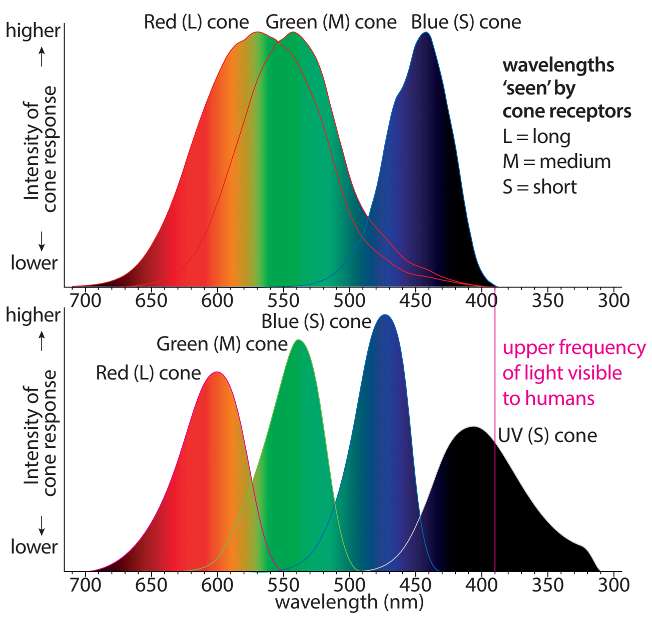


The electromagnetic spectrum showing the categorization of waves and the range of visible wavelengths for humans and birds.

Bright, often iridescent, colors are a prominent trait of hummingbird adornments: **Wine-throated Hummingbird** *Atthis ellioti* (*top left* | Guatemala), **Rufous-crested Coquette** *Lophornis delattrei* (*top right* | Peru) and **Long-tailed Sylph** *Aglaiocercus kingii* (*bottom right* | Ecuador). On hermits, vivid colors are confined to the bill and gape: **Long-tailed Hermit** *Phaethornis superciliosus* (*bottom left* | Brazil).

Color	Wavelength range (nm)
red	750–625
orange	625–590
yellow	590–565
green	565–500
cyan	500–485
blue	485–450
violet	450–380
ultraviolet	380–300 (birds, not humans)

Visible light wavelengths



The sensitivity and wavelength range of the cone receptors in a typical human eye (*top*) compared with that of a typical hummingbird (*bottom*).

viewing oil on water, or a soap bubble, although in this case, the color seen is a function of the thickness of the surface film, which affects the speed at which the light travels through and is refracted—the different thicknesses causing different wavelengths to reflect back, producing a distorted rainbow effect (see the box on *Interference colors* on *page 66*).

What wavelengths (and therefore colors) can be interpreted is dependent on the receptors in an animal's eyes. Human eyes have three types of cone receptor (red, green and blue), whereas hummingbirds' eyes (as those of most birds) have four (red, green, blue and a fourth that is sensitive to some ultraviolet light). The visible light spectrum available to humans (as seen in a rainbow) has wavelengths between approximately 730 nm (red) and 390 nm (violet). The extra cone that a hummingbird possesses allows it to perceive wavelengths in the near ultraviolet zone (between 400 and 300 nm), and, as a result, it can see a broader range of colors than us, including nonspectral colors (see the graphs *left*). This ability of hummingbirds to see ultraviolet colors has been proven by testing their capacity to discriminate colors based on colored feeders containing either a sugar-rich solution or pure water. The results of these studies showed that hummingbirds could discriminate colors, including ultraviolet-influenced nonspectral colors such as purple, ultraviolet+green, ultraviolet+red and ultraviolet+yellow. While the ultraviolet+green feeders (sugar) and the green feeders (water) looked identical to the researchers, the hummingbirds almost unerringly showed a preference for the sugar-rich ultraviolet+green feeders. This suggests that the role of color and iridescence in hummingbirds may be even more important than currently thought and very likely serves a key role in both display strategies and foraging efficiency.

As well as the color-creating process of refraction (which is explained later in this chapter), there are two other aspects of light that also play fundamental roles in how colors are seen: absorption and reflection.

Black, brown, pink and white

Some materials, especially those that are matt black, absorb almost all light. This means that light hitting that surface is not reflected in any great quantity but is instead converted into heat energy (which is why, in sunlight, black surfaces feel warmer than white surfaces). Conversely, some materials, typically those that are opaque or highly polished, absorb virtually no light but instead reflect it. For example, on a sunny day, an open window or a car roof reflecting the sun can generate an intensely piercing, star-like spot of silver-white light that can easily be seen with the naked eye from miles away. Because so little light is absorbed by the glass or metal, the full spectrum of sunlight is reflected as a white beam (this was the basis of signaling by heliograph long ago). Many other colors that we commonly differentiate are a result of the brightness of the light reaching our cones. For example, black does not activate any cones at all; brown activates the red cone partially and the green cone slightly; and flesh (pink) tones are a result of the red cone being fully activated, the green cone a little less and the blue cone slightly.

Hummingbirds presumably have a similar method of color perception to us, although their additional UV-sensitive cone opens up an even wider range of both spectral and nonspectral color options. For example, the reflectance of the Broad-tailed Hummingbird's gorget starts at approximately 300 nm (or possibly lower). This is outside our perception range, but to another hummingbird will appear as colors about which we can only speculate. Also, any activation of the UV cone in combination with any of the other three cones in a hummingbird's eyes will result in a greater range of colors that humans cannot perceive—UV-Red, UV-Green, and UV-Blue.

Nonspectral colors—the magenta conundrum

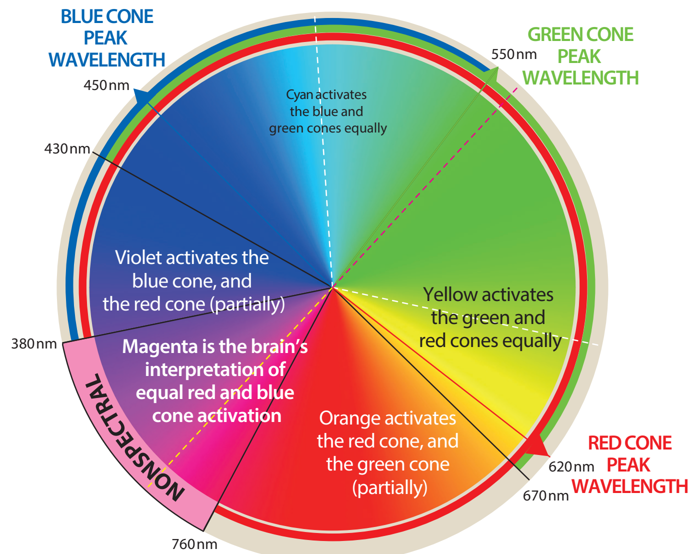
Look at a rainbow and ask yourself the question "Where is the pink?" The answer is that this 'color' is not actually there! This is because pink or, to be more accurate, magenta, does not exist in the spectrum as a spectral color (*i.e.* one with a wavelength as found in the rainbow) but instead exists as a nonspectral color, which is one perceived as a result of the simultaneous stimulation of cone types that are sensitive to different, even widely separated, light wavelengths.

When light is received by the various cones in an animal's eye, it is processed depending on the light wavelengths that the cone is stimulated by—with a higher or lower intensity of stimulation determined by the actual wavelength involved. If two cones are activated by the same beam of light, then the brain processes the cumulative effect of the wavelengths received. The graph *opposite* (*page 62*) shows that humans do not respond to 'darker' reds with as high an intensity as we do to more orange-reds, and that we are best at differentiating the subtleties of a range of yellow to green colors. This is because both our red-sensitive and green-sensitive cones overlap considerably in the wavelengths they receive, and in the intensity of cone response that those wavelengths create.

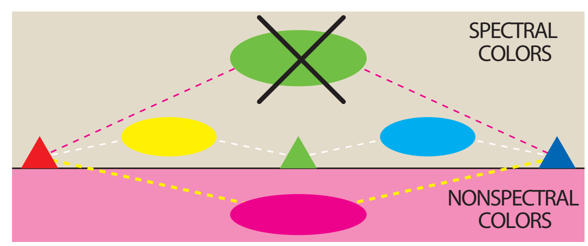
If both our red-sensitive and blue-sensitive cones are stimulated equally, we might expect the color mix perception to follow this same 'average' mix pattern and be midway between the two spectral wavelengths (*i.e.* green). However, we already have a cone that is sensitive to green, and therefore a mix of red and blue creating green makes no sense to our brain! So, instead, we perceive these mixed wavelengths of red and blue light as magenta to purple, colors that do not exist within the spectrum of light or as a result of spectral colors affected by the intensity of light, such as pink and brown. Put simplistically, our brain 'invents' these colors and the magenta and purples we see on many hummingbirds are an illusion (so-called 'chimerical' colors—as explained graphically to the *right*).

Hummingbirds, however, appear to be most sensitive to, and therefore respond to, relatively narrow ranges of red-orange, green and blue and, to a lesser extent, their ultraviolet range. This suggests that these limited colors are of importance, and that the ultraviolet component of their color vision is also significant.

The logical next question is that of how hummingbirds take advantage of the physics of light—and in particular the effects of absorption, refraction and reflection.

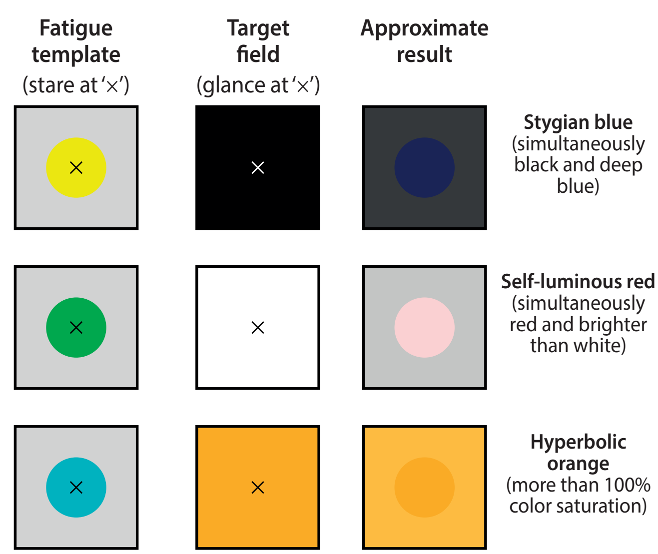


If the same 'equal mix rule' seen in other spectral colors was followed, then an equal mix of red and blue light should be seen as green …



… instead, the human brain 'invents' colors (magenta and purples) between the red and blue wavelengths.

How magenta is created in our brain
The midway points of equal stimulation of two cones (white dotted lines) give red + green = yellow, and green + blue = cyan. On that basis (magenta dotted line) red + blue = green; instead, we see magenta (yellow dotted line).



Chimerical color demonstration
Staring at the '×' in any of the fatigue fields above for 20–60 seconds will fatigue your color receptors; glancing at the associated target field '×' should result in some color-based strangeness!

The body and tail feathers of many hummingbirds are brightly colored, whereas the flight feathers are dark and dull, reflecting the presence of strengthening melanin pigment—as shown by this **Buff-winged Starfrontlet** *Coeligena lutetiae.* | Ecuador

How does feather color work?

Birds' feathers utilize the absorptive, refractive and reflective qualities of light to create colors in one of two ways: either through pigmentation within the feather or through a feather structure that has evolved to create certain colors. Although these two methods work in isolation, they can also work in combination.

Pigmentation

On most species of bird, the colors that we see are produced by pigments, deposited on the feather surface, which absorb and reflect particular wavelengths of light as a single color. Feather pigments fall into three main groups:

Carotenoids—which absorb shorter wavelengths while transmitting and reflecting longer wavelengths, producing bright yellow and orange. These pigments are found in plants and are obtained by birds either directly, by eating the plant, or indirectly, by eating something else (such as a caterpillar) that has eaten the plant.

Porphyrins—which produce pink, brown, red and green hues. Porphyrins are created from specific amino acids and fluoresce bright red in ultraviolet light, suggesting that they may have evolved to stimulate birds' UV-sensitive cones.

Melanins—these pigments have a high absorbance of visible light, the highest absorbance being of shorter wavelengths resulting in black or golden to rusty-red coloration. Two types of melanin are involved, eumelanin and phaeomelanin, respectively, and these can mix to produce intermediate colors, such as brown, and combine with carotenoids to produce shades of olive-green. Melanins are produced by the oxidation of the amino acid tyrosine in special cells found in feathers and skin.

Melanins are particularly important in birds' feathers, since not only do they produce colors ranging from intense black to reddish-browns and pale yellows but they also add strength and stiffness to the feather structure. For this reason, they are frequently present in flight feathers, or at least at the tips of the longest primary feathers, which have to withstand a lot of wear and tear. Hummingbirds possess both the blackish and rufous basic pigmented color types produced by melanins, and, since flight is so crucial to their lifestyle, the wing feathers are invariably melanin-rich—dark-pigmented and dull.

Feather structure

Notably absent from the list of colors produced by pigments is blue, a color very commonly found in birds. Blue is very difficult to achieve through pigmentation, but much easier to produce as a result of a feather's structure 'directing' the way light is absorbed, refracted and reflected. This is because blue light has a very short wavelength and so is more easily reflected than colors with longer wavelengths. The blue sky we see during the day (when the sun is at a steeper angle to the Earth) is caused by individual nitrogen and oxygen molecules scattering this easily reflected blue light, which effectively blocks out the other spectral colors. Conversely, in the evening, when the sun's angle is lower and light has to travel farther through the atmosphere to reach us, the wavelengths that are predominantly scattered are the longer reds and oranges.

The blue feather colors of birds make use of this scattering, reflective quality of blue light—not in a random way (as in the sky) but rather by having a feather structure that is designed to interfere with the light in an organized manner. This is known as 'structural coloration'. Blue feathers typically have a dark, melanin-rich layer (that absorbs the longer wavelengths), which, either as an arrangement of pure melanin or with small air cavities and/or keratin particles on its surface, reflects and scatters blue light.

White feathers also appear the way they do due to their structure. They reflect nearly all light by virtue of a complete absence of melanin combined with a microscopic surface topography that resembles cut glass or snow. The white feathers of some species also contain air pockets that increase the combined total reflection of all colors of visible light, making them appear even brighter. White feathers can be shown to lack any pigment as they become transparent when immersed in an effective light-blocking substance such as balsam.

Colors that result from structural effects of feathers, such as the intense blues displayed by many kingfishers worldwide, are termed semi-iridescent insofar as (unlike the perfect alignment of iridescent feather structures) the microscopic structures that create the blue color are imperfectly aligned, causing a narrower range of iridescence that can be seen from a wider range of angles. The intense brightness can be explained by two sets of reflected waves being in phase and hence effectively doubling up (as explained in the diagram on *page 66*).

The resemblance of some hummingbirds to sunbirds of Africa and Asia is mentioned in *An Introduction to Hummingbirds* (see *page 9*), but sunbirds, bright and beautiful as they are, usually have colors that are more constant, being less dependent upon the exact angle of view. The basic reds, greens and yellows of the sunbirds are for the most part visible all of the time by virtue of bright red or yellow carotenoid pigmentation (which hummingbirds lack), but sunbirds also have iridescent feathers more akin to the semi-iridescent feathers of a kingfisher or the head of a male Mallard duck.

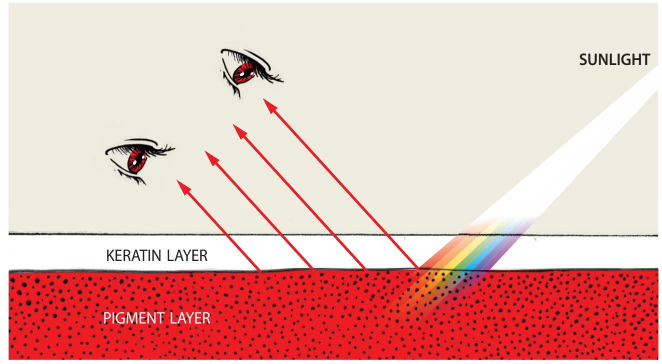
Although structural coloration has been broadly understood since 1665, when Robert Hooke observed that a peacock feather was iridescent in air but not under water, drawing the conclusion that pigments could not be responsible, the mechanisms of iridescence were not fully understood until the turn of the 19th century. It is only very recently, however, through the advances of technology, that we are really beginning to understand the complexities and incredible accuracy of the structures involved in order for iridescence to occur.

Iridescence

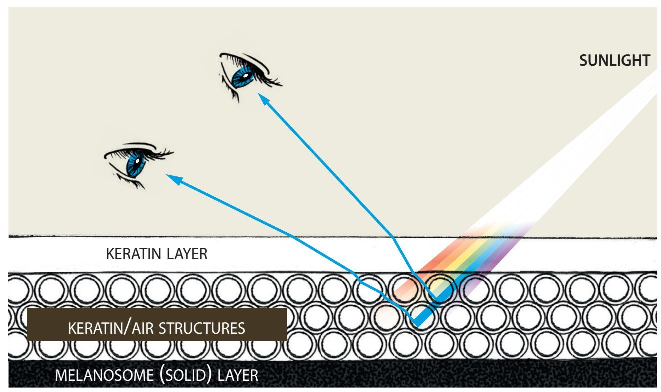
The particular shades of lustrous green on the body of various 'emerald' hummingbirds is pretty much the same on each and every individual of a given species. Similarly, the fierce shot of red on a Crimson Topaz (see *page 72*), seen full-on in good light, is always the same shade of pure crimson. In many hummingbirds, however, just parts of the plumage, such as a shiny gorget, are iridescent, looking bright red when viewed head-on, bluish when seen from slightly to one side, but dull black from a greater angle.

True iridescence is a combination of how light interacts with complex biological nanostructures that produce thin films or so-called 'diffraction gratings' in a constant fashion. In hummingbirds this is no random event but rather a result of astoundingly precise feather structures that are perfectly aligned and cause the light

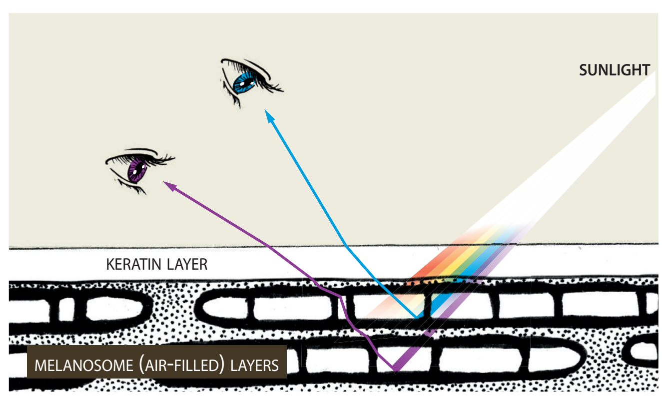
Different ways in which colors are created in feathers (the arrowed line indicates the feather's cross section from keratin to basal layer).



Pigmentation: pigment granules in a feather selectively absorb and reflect particular wavelengths. For example, carotenoid pigments absorb shorter wavelengths (such as blue) and reflect longer wavelengths (such as red). Light is reflected only as a single color and this color is constant no matter the viewing angle.



Structural—non-iridescent: spongy, air-filled pockets in a feather selectively absorb particular wavelengths and reflect/refract others, creating a scatter pattern of a single wavelength, and hence a constant color, when viewed from any angle.



Structural—iridescent: spongy, air-filled pockets in the melanosome layer of a feather selectively absorb some wavelengths and reflect/refract others. The complexities of the structures and air pockets (different thicknesses of melanin and air) mean that waves can either be reflected directly or be 'bounced around' by being refracted multiple times within the structure before exiting. If the wavelengths are in phase they add together to create a brighter, more intense version of the color; if they are out of phase they cancel each other out and no light is returned. At some angles a particular light wavelength may simply be reflected back on itself and be unable to exit the structure. The diagram above is highly simplified; in reality, multiple wavelengths interact both constructively and destructively to create different colors with a range of shimmering brightnesses and intensities (see *page 70*).

to refract and reflect in a variety of ways to produce waves that are termed interference colors (as seen randomly in, for example, a soap bubble—see box *below*). This accuracy of structure and the resultant coloration are seemingly critical from an evolutionary perspective, as they are highly significant in terms of breeding success.

In the iridescent feather of a hummingbird, the basal two-thirds or so are unexceptional and look like a typical feather, but the tip (the part visible when the feathers are smoothed down) is where the highly specialized structures are located. Birds' feathers are made of keratin, which is the same substance as human hair and nails. The feather barbs that are attached to the main shaft (or rachis) have, in turn, tiny filaments attached to them called barbules. Each barbule of an iridescent hummingbird feather has a reflective surface layer of keratin seated above a mosaic of microscopic packets of melanin called melanosomes. In the iridescent feathers of most birds, these melanosomes are log-shaped and solid. In hummingbirds, however, they are typically pancake-shaped and filled with tiny air pockets, although in some feather tracts of some species there may be solid melanosomes, or a mixture of solid and air-filled. Astonishingly, in a hummingbird's feather there are around 1,500 of these 'bubbles' per square centimeter (about 10,000 per square inch). Depending on the species, feather keratin comes in a range of thicknesses; melanosomes vary slightly in shape, contain different air-bubble sizes and are stacked from seven to fifteen deep. This range of factors gives rise to a wide range of surface complexity and, as a result, the incredible variety of hummingbird iridescent colors that can be seen (see *pages 70–71*).

Light passing through the keratin, melanin and air will bend at slightly different angles, with the thickness of the granule and the depth of the air bubble each affecting the color of the reflected light. Thicker melanin with thinner air bubbles means that light with longer wavelengths (towards the red end of the spectrum) is reflected; thinner melanin and wider air bubbles means that light with shorter wavelengths (towards blue and violet) is reflected. This can happen, however, only if the reflected light is received by a viewer at the optimal narrow angle, as determined by the feather structure. Slight differences in angle will change the color seen, or its intensity or brightness, and, if viewed at the 'wrong' (or a suboptimal) angle, light within the melanosomes is all but fully absorbed, or undergoes destructive interference such that virtually no light is reflected and

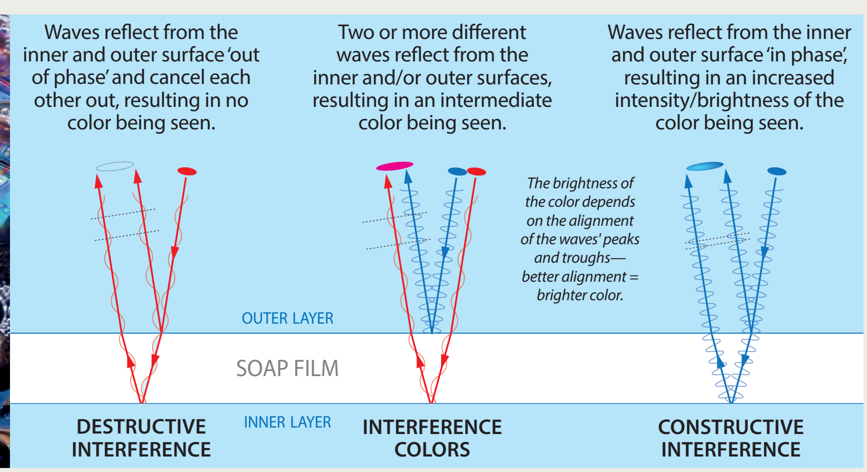
Interference colors—the soap bubble example

When light waves meet the thin film of a bubble, light is reflected from both the outer and the inner surfaces. However, this means that the light reflecting off the inner surface has slightly farther to travel than that reflecting from the outer surface. Different light wavelengths will behave differently depending on the distance they travel through the film, which itself is dependent on the angle at which the lightwaves hit the film and the thickness of the film. If the distance traveled through the film is equal to, or is a whole number multiple of, a particular wavelength of light, then that light will reflect from both surfaces in such a way that the waves' peaks and troughs align perfectly. These waves are described as being **in phase**, and the result is an increase in color intensity and brightness known as constructive interference.

Conversely, if the distance traveled is half the width (or odd number multiple of) the wavelength, then the two waves' peaks and troughs will be perfectly aligned, effectively canceling one another out. These waves are termed as being **out of phase** and no color is visible (destructive interference).

In the cases where the film thickness means that reflected waves are neither perfectly in or out of phase, the results range from brightish to dullish colors depending on how much the waves are in or out of phase.

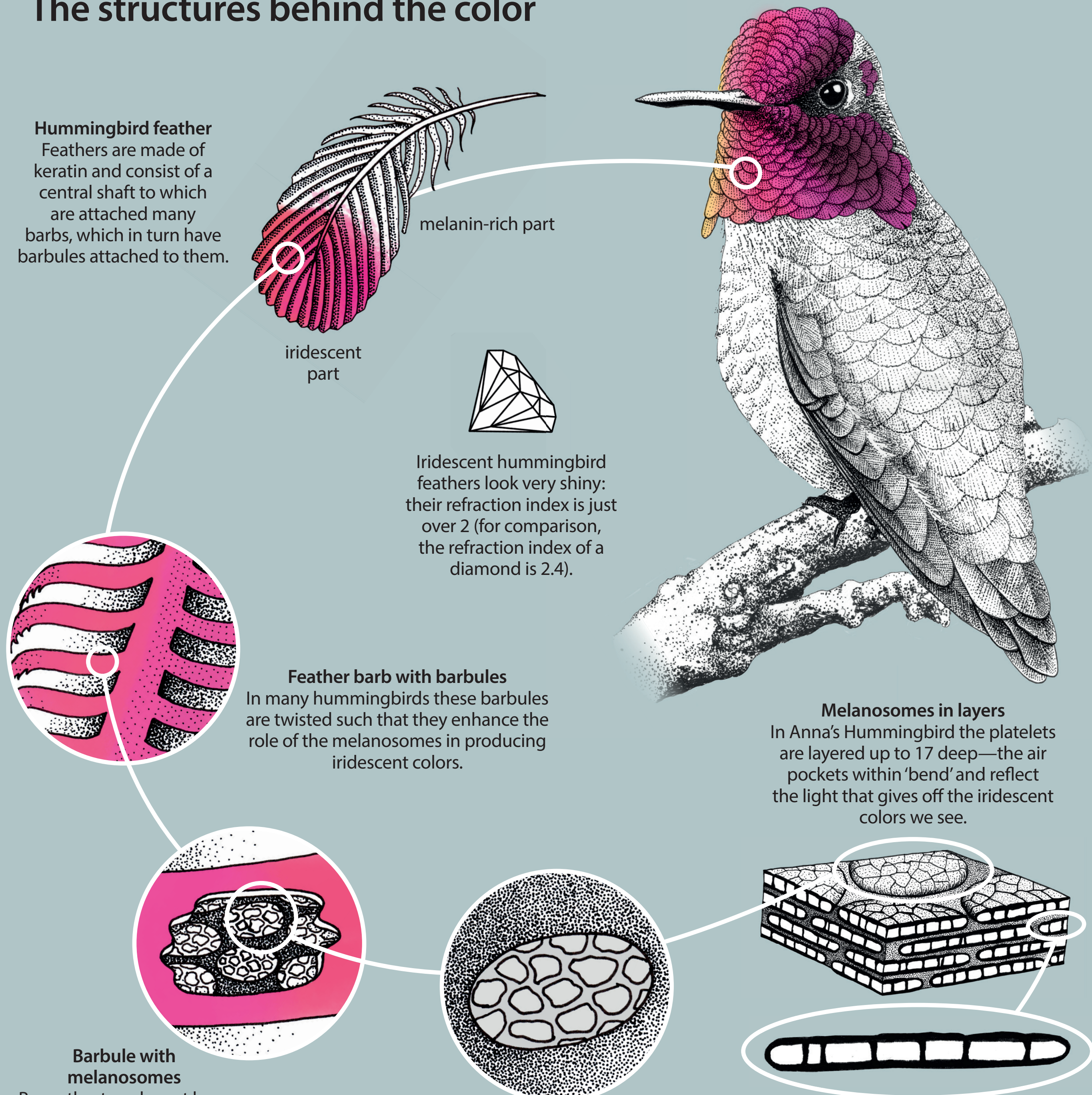
When all wavelengths are taken into account, then for any given thickness of film some wavelengths will be fully in phase, others fully out of phase and the remainder somewhere in between, mixing and matching to produce the familiar iridescence we see in bubbles. This is the essence of iridescence in hummingbirds' feathers, as the physics of interference colors is what hummingbirds have evolved to take advantage of via their complex yet precise feather nanostructures.



The constancy of coloration among individuals of the same species, such as these **Green Violet-ears** *Colibri thalassinus* (*above* | Costa Rica) and **Fiery-throated Hummingbirds** *Panterpe insignis* (*below* | Costa Rica), despite the effect of iridescence, is quite remarkable.

Iridescence

The structures behind the color



Hummingbird feather
Feathers are made of keratin and consist of a central shaft to which are attached many barbs, which in turn have barbules attached to them.

Iridescent hummingbird feathers look very shiny: their refraction index is just over 2 (for comparison, the refraction index of a diamond is 2.4).

Feather barb with barbules
In many hummingbirds these barbules are twisted such that they enhance the role of the melanosomes in producing iridescent colors.

Melanosomes in layers
In Anna's Hummingbird the platelets are layered up to 17 deep—the air pockets within 'bend' and reflect the light that gives off the iridescent colors we see.

Barbule with melanosomes
Beneath a translucent layer of keratin the barbules of an iridescent feather have layers of melanosomes.

Melanosome
Pancake-shaped melanin platelets about 100 nm thick that contains pockets of air (viewed from above).

Melanosome cross-section
The thickness of the melanin and the shape and size of the air pockets is variable. This variation is key to the absorption and the refraction/reflection of different wavelengths of light which produces the iridescence we see.

so, to the viewer, the feather appears very dark or black (see *below*). In many iridescent hummingbirds, as well as these complex, yet accurately arranged melanosomes, the barbules are flattened and twisted to create the maximum effect for the viewer (whether that is another bird or, incidentally, any watching human).

Hummingbirds—a rainbow of iridescence ...

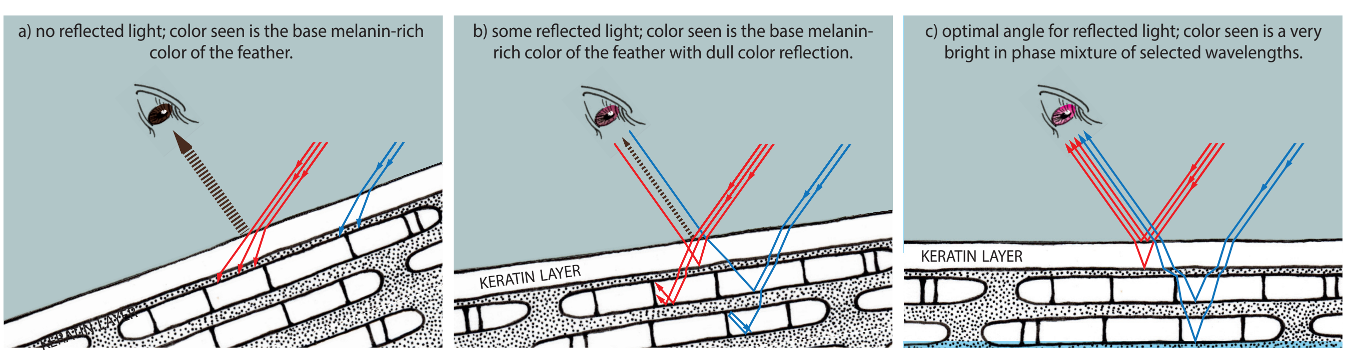
While observing a hummingbird, at any given moment we might see a brilliant cap, a vivid throat patch, perhaps a shiny back, or maybe a brightly colored rump. Viewing angle is fundamental to the colors we (or indeed another hummingbird or predator) perceive. While a white patch may be seen from any angle of view, a shiny back or bright rump is most likely to be visible to us only when presented within a certain angle of view depending on the nature of the structural reflection. The full impact of an iridescent cap or throat patch will be apparent only when seen from the optimal narrow angle.

Given that sunlight is a single-point, unidirectional light source, it is, by the laws of physics, impossible to see all of these colors at the same moment, and much of the body of a hummingbird often simply looks 'dark'. In most instances, hummingbirds generally reveal their visual riches just one or two at a time. A Ruby-topaz Hummingbird appears as little more than a black-brown shape, darting from bloom to bloom high above us in a treetop. Even when lower down, viewed at a shallower angle, it can seem merely dull and dark, perhaps showing a brighter tail. With the light reflected at the optimal angle, however, there will be a glimpse of a ruby-red cap, before the bird turns face-on and, for a brief and brilliant second or two, we may be treated to a flash of its glistening deep golden-yellow throat (see *page 70*). This presents great difficulties for an artist, who is torn between giving a realistic impression of the bird and wanting to show the full range of colors that could, at any moment in time, be seen. And, of course, it causes similar challenges for photographers, who, without multiple simultaneous sources of light, have no possibility of capturing all the colors in a single shot.

The color red is clearly important to hummingbirds as it often seemingly influences their choice of

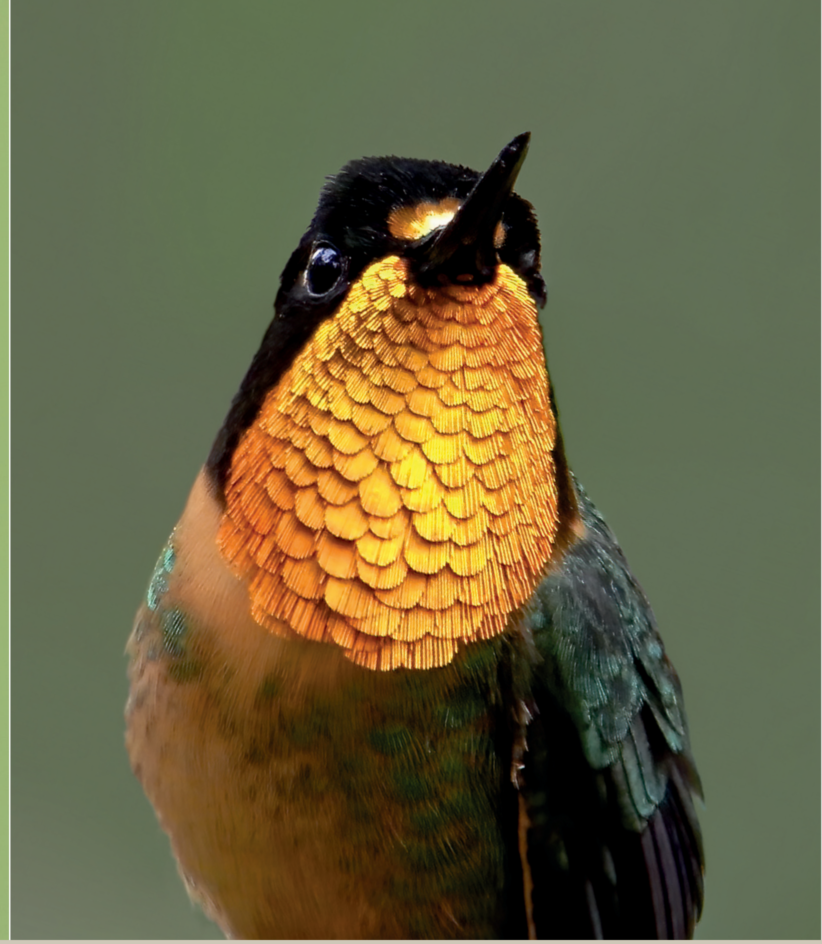
[continued on *page 78*]

These photos of an **Anna's Hummingbird** *Calypte anna* show the effect of iridescence as the bird turns its head. | Canada



Highly simplified illustration showing the effect of barbule angle on reflected light coming from the same direction
In Anna's Hummingbird, peak reflectance is in the red wavelength range (at approximately 670 nm), with a lesser peak in the blue wavelength range (480 nm)—the two combining to give a magenta iridescence (all other wavelengths are absorbed in the topmost layers of the barbule). In diagram a) the feather angle means that light does not reach any air pockets and is absorbed, such that the viewer sees only the melanin-rich base color of the feather. In diagram b) a slight change of feather angle means that some light reaches the air pockets, is 'bounced' around and a little is reflected, such that the viewer sees a magenta tint to the melanin-rich feather base color. In diagram c) the feather is at the optimal angle to allow the two wavelengths to be in perfect alignment with different air pockets and multiple waves are reflected in phase, such that the viewer sees a bright, intense mix of red and blue light (appearing as magenta) that obliterates the dark base color of the feather.

A rainbow of iridescence



Ruby-topaz Hummingbird *Chrysolampis mosquitus* (*above left* | Trinidad); **Orange-throated Sunangel** *Heliangelus mavors* (*above right* | Venezuela); **Magnificent Hummingbird** *Eugenes fulgens* (*below left* | Costa Rica); **Sapphire-throated Hummingbird** *Amazilia coeruleogularis* (*below right* | Panama)

(continued...)

Index

This index includes the English and, in *italics*, *scientific* names of all the hummingbirds covered in this book. The English names of species that are illustrated with a photograph are highlighted in **bold** text.

Alternative English names used by taxonomic authorities other than BirdLife International are shown in grey text.

Bold italicized numbers refer to a page where a photograph appears; regular *italicized* numbers indicate illustrations; blue numbers are used for the genus (**bold**) and species entries in *The BirdLife List of Species*. Regular figures refer to pages where other key information can be found.