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Neotropical Birds

BIRDS are a magnet that helps draw visitors to the Neotropics. Some come merely to augment an already long life list of species, wanting to see more parrots, more tanagers, more hummingbirds, some toucans, and hoping for a chance encounter with the ever-elusive harpy eagle. Others, following in the footsteps of Darwin, Wallace, and their kindred, investigate birds in the hopes of adding knowledge about the mysteries of ecology and evolution in this the richest of ecosystems. Opportunities abound for research topics. There are many areas of Neotropical ornithology that are poorly studied, hardly a surprise given the abundance of potential research subjects. Like all other areas of tropical research, however, bird study is negatively affected by increasingly high rates of habitat loss. This chapter is an attempt to convey the uniqueness and diversity of a Neotropical avifauna whose richness faces a somewhat uncertain future.

Avian diversity is very high in the Neotropics. The most recent species count totals 3,751 species representing 90 families, 28 of which are endemic to the Neotropics, making this biogeographic realm the most species-rich on Earth (Stotz et al. 1996). But seeing all 3,751 species will present a bit of a challenge.

When Henry Walter Bates (1892) was exploring Amazonia, he was moved to comment on the difficulty of seeing Neotropical birds in dense rainforest:

> The first thing that would strike a new-comer in the forests of the Upper Amazons would be the general scarcity of birds: indeed, it often happened that I did not meet with a single bird during a whole day's ramble in the richest and most varied parts of the woods. Yet the country is tenanted by many hundred species, many of which are, in reality, abundant, and some of them conspicuous from their brilliant plumages.

The apparent scarcity of birds in Neotropical lowland forests seems surprising because more species of birds occur there than in any other kind of ecosystem. Entire families, including cotingas, manakins, toucans, ovenbirds and woodcreepers, typical antbirds, and ground antbirds, are essentially confined to the Neotropics, as are such unique species as screamers, trumpeters, sunbittern, hoatzin, and boat-billed heron. Bates put his finger on the irony of birdwatching in the tropics. Even birds with glamorous plumages can be remarkably silent, still, and difficult to spot in the dense, shaded foliage. Patience, persistence, and keen eyes are required of the tropical birder. Birds often seem to appear suddenly, because a dozen or more species may be moving

together in a mixed species foraging flock (page 39), and thus the birdwatcher may face a feast-or-famine situation. One minute birds seem absent. Then suddenly they are everywhere. Bates described such an encounter:

> There are scores, probably hundreds of birds, all moving about with the greatest activity—woodpeckers and Dendrocolaptidae (from species no larger than a sparrow to others the size of a crow) running up the tree-trunks; tanagers, ant-thrushes, humming-birds, flycatchers, and barbets flitting about the leaves and lower branches. The bustling crowd loses no time, and although moving in concert, each bird is occupied, on its own account, in searching bark or leaf or twig; the barbets visiting every clayey nest of termites on the trees which lie in the line of march. In a few minutes the host is gone, and the forest path remains deserted and silent as before.

In this chapter, I survey Neotropical birds, their adaptations, and basic ecology. Without question, the most notable characteristic of the Neotropical avifauna is its extreme species (and subspecies) diversity (Haffer 1985; Stotz et al. 1996). New species are still being discovered. For example, the chestnut-bellied cotinga (*Doliornis remseni*) was unknown to ornithology until discovered in 1989 in Ecuador and subsequently described as a new species (Robbins et al. 1994). Recent taxonomic work indicates that certain species, particularly among the typical antbirds and ovenbirds, should be split into several species rather than counted as one. Even large taxonomic divisions are being reorganized, such as the recent split that divides the antbirds (formerly all in the family Formicaridae) into two families, the typical antbirds (Thamnophilidae) and the ground antbirds (Formicaridae), as described in Ridgely and Tudor (1994). Taxonomy of Neotropical birds is also being affected by analyses of DNA similarities among species (Sibley and Ahlquist 1990; Sibley and Monroe 1990) and other molecular-based studies. In this account, I follow the classification given in Parker et al. (1996). For a most up-to-date description and summary of the orders of birds, see Gill (1995).

The finest reference on Neotropical birds is the four-volume series by Ridgely and Tudor, of which two volumes (1989, 1994, both on passerines) are now in print. The other two volumes will be published within a few years. In addition, the volume by Sick (1993), though confined to Brazil, contains a wealth of natural history information on Neotropical birds. The most up-to-date list of Neotropical bird species is found in Parker et al. (1996), though this list omits common names and may thus prove awkward for the birder or student unfamiliar with scientific names. For a reasonably complete, though outdated, list of species, see Meyer de Schauensee (1966) or Howard and Moore (1980). Monroe and Sibley (1993) provide a checklist of the world's birds with a classification based on DNA analysis. Austin (1961) provides a dated but still useful survey of the natural history of the world's birds, including, of course, the Neotropics. Perrins and Middleton (1985) provide concise general natural history information on the world's birds. For detailed life histories of selected Neotropical species, see Skutch (1954, 1960, 1967, 1969, 1972, 1981, 1983). David Snow (1976, 1982) has written two books focusing on his studies of frugivorous birds. A comprehensive volume edited by Buckley et al. (1985) is invaluable for the serious student of Neotropical ornithology. For birders interested in identification, I include a list of regional field guides (page 316). The conservation of Neotropical birds is thoroughly treated by Stotz et al. (1996).

The dark, complex foliage of interior rainforest hosts the majority of tropical bird species, a diversity that increases markedly from Central America into equatorial Amazonia. From forest floor to canopy, hundreds of different species probe bark, twigs, and epiphytes for insects and spiders. Others swoop at aerial insects, follow army ants as they scare up prey, search for the sweet rewards of fruit and flowers, or capture and devour other birds, mammals, and reptiles. One bird, the harpy eagle (*Harpia harpyja*), stalks monkeys, sloths, and other large prey. A recent analysis suggests that there are currently 3,751 species of Neotropical birds (Brawn et al. 1996; Stotz et al. 1996), which represents about a third of all species of birds in the world. Even with such an abundance of diversity, patience and luck are needed to see birds well, especially when they may be 30 m (100 ft) or more above ground, or moving through dense vegetation.

Large Ground Dwellers

Tinamous

Though treetop species can be a challenge to see, even ground dwellers can be elusive. Forty-seven species of tinamous comprise the order Tinamiformes, a peculiar group of birds endemic to the Neotropics. A tinamou is somewhat chickenlike, a chunky bird with a short, slender neck, a small, dovelike head, and thin, gently downturned beak. Plumage ranges among species from buffy to deep brown, russet, or gray, often with heavy black barring. Some tinamous inhabit savannas, pampas, and mountainsides, but most live secretive lives on the rainforest floor, searching for fallen fruits, seeds, and an occasional arthropod. Forest tinamous are much more often heard than seen. One of the most moving sounds of the rainforest is that of the great tinamou (*Tinamus major*), a clear, ascending, flutelike whistle given at dusk, a haunting sound that heralds the end of the tropical day. One bird begins and soon others join in chorus. Evening twilight is the hour of the great tinamou senenade—they rarely sing during full daylight or dawn. Basically solitary, the tinamou may use their chorus to signal each other as to their various whereabouts.

The best way to see a tinamou is to walk a forest trail quietly (!) at dawn. You may suddenly come upon one foraging along the trail, and it will probably stare blankly at you for a moment before scurrying into the undergrowth. Tinamous are generally reluctant to fly but may abruptly flush in a burst of wings, landing but a short distance away. They cannot sustain flight for long distances because, even though their flight muscles are well developed, they are not well vascularized, and the limited blood flow greatly restricts their effectiveness (Sick 1993).

Though superficially resembling chickens, tinamou anatomy and DNA analysis show that they are closely related to ostriches, rheas, and other large, flightless birds. They are considered both an ancient and anatomically primitive group. Their rounded eggs are unusual for their highly glossed shells and

range of colors, from turquoise blue and green, to purple, deep red, slate gray, or brown. Only the male incubates the eggs, another characteristic shared with ostriches and rheas.

Chachalacas, Guans, and Curassows

Figure 151

The fifty species of chachalacas, guans, and curassows (family Cracidae) are similar in appearance to chickens and turkeys and used to be classified with them but are now placed in their own order, Craciformes. They are found in dense jungle, mature forest, montane, and cloud forest. Though often observed on the forest floor, small flocks are also often seen perched in trees. All species nest in trees. Delacour and Amadon (1973) provide a detailed overview of the cracids plus individual life history accounts.

The nine chachalaca species are each slender, brownish olive in color, with long tails. Each species is about 50 cm (20 in) from beak to tail tip. A chachalaca has a chickenlike head with a bare red throat, usually visible only at close range. Most species form flocks of up to twenty or more birds. The plain chachalaca (*Ortalis vetula*) is among the noisiest of tropical birds. Dawn along a rainforest edge is often greeted by a host of chachalaca males, each enthusiastically calling its harsh and monotonous "cha-cha-lac! cha-cha-lac! cha-cha-lac!" The birds often remain in thick cover, even when vocalizing, but an individual may call from a bare limb, affording easy views.

Twenty-two species of guan and thirteen species of curassow occur in Neotropical lowland and montane forests. Larger than chachalacas, most are the size of a small, slender turkey with glossy, black plumage set off by varying amounts of white or rufous. Some, like the horned guan (*Oreophasis derbianus*) and the helmeted curassow (*Pauxi pauxi*), have bright red "horns" or wattles on the head and/or beak. Others, like the blue-throated piping guan (*Pipile pipile*), have much white about the head and wings and a brilliant patch of bare blue skin on the throat.

Spix's guan

Female great curassow

Guans and curassows, though quite large, can be difficult to observe well. Small flocks move within the canopy, defying you to get a satisfactory binocular view of them. Like chachalacas, guans and curassows are often quite vocal, especially in the early morning hours.

Both New World turkey species occur in the Neotropics. The wild turkey (*Meleagris gallopavo*), which graces the Thanksgiving table with its domesticated cooked presence, once ranged south to Guatemala. Now only domesticated individuals are found throughout the tropical portion of its range. The spectacular ocellated turkey (*Agriocharis ocellata*) ranges, still wild, from the Yucatan south through Guatemala. Smaller than the common turkey, the ocellated has a bright blue, bare head with red tubercles. Its plumage is more colorful than its relative, particularly its tail feathers, which have bright blue and gold, eyelike markings that give the bird its name. Ocellated turkeys are easy to see at Tikal National Park in northeastern Guatemala and Chan Chich Lodge in Belize.

Trumpeters

Figure 150

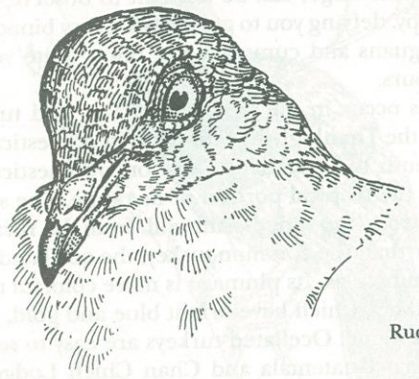
Nothing looks quite like a trumpeter except another trumpeter. These oddly shaped, rooster-sized birds of the rainforest floor are uniquely humpbacked, with long legs, slender necks, and a chickenlike head. There are only

three trumpeter species in the world (family Psophiidae), and each is confined to a different region within Amazonia. Species are distinguished by the wing coloration, ranging from white to very dusky. Otherwise the birds are blackish but with iridescent violet and greenish colors when in direct sunlight.

Trumpeters amble along the forest floor in small flocks, feeding on such diverse items as large arthropods and fallen fruits. They are also reputed to chase snakes. The name trumpeter comes from their curious vocalization, a ventriloquial, muffled hoot, rather like the sound of air blowing over the opening of a bottle (Sick 1993). Trumpeters will occasionally run around in circles, strutting and prancing with wings outstretched, apparently a courtship or excitement display. They roost in trees and nest in tree cavities. They are generally considered to be weak fliers.

Doves and Pigeons

Doves and pigeons (order Columbiformes) are much alike in anatomy, but, in general, doves are more birds of edges and open areas (with some notable exceptions such as the quail-doves) while pigeons are found mostly in closed forest. Doves and pigeons feed heavily on seeds and fruits, and some species can be important seed dispersers. There are just over 300 species in the world, of which about 64 occur in the Neotropics (Parker et al. 1996). Some Old World doves are extraordinarily colorful, but Neotropical species tend toward a plumage of muted colors such as grays, tans, or rich brown. Some of the larger species make low, deep, cooing vocalizations that suggest the hooting of an owl. Doves and pigeons of various species are relatively common throughout Neotropical habitats. Skutch (1991) surveys the general natural history of the group.



Ruddy quail-dove

The Gaudy Ones

Several groups of Neotropical birds are known for their bright colors. Among them are the trogons, motmots, toucans, cotingas, manakins, parrots, and tanagers. The ecology of many of these birds is closely associated with their habit of eating much fruit.

Trogons

There are thirty-nine species of trogons (Trogoniformes) found in the world's tropics and subtropics, and twenty-five are Neotropical. The family is well represented in Middle America as well as South America, and two species are found in the Greater Antilles. A trogon is a chunky, squarish bird with a long, rectangular tail and short, wide bill. Brilliantly colorful, males have iridescent green and blue heads and backs, and bright red or yellow breasts. Females resemble males but are duller in color, often quite grayish. The pattern of black, gray, and white on the tail and the color of the eye-ring (a patch of colorful skin circling the eye) are important field marks to identify various species. They range in size from about 23 to 38 cm (9–15 in).

Trogons tend to sit upright with tail pointed vertically down. They remain still, and so they are often overlooked. The easiest way to spot one is to look for its swooping flight, flashing the bird's bright plumage, and note where it lands. Most trogons vocalize throughout the day, often a repetitive "cow, cow, cow," or "caow, caow, caow," varying, of course, from one species to another. Sometimes the note sounds harsh, but in some species it's softly whistled and melodious. A good way to see a trogon at close range is to try to imitate its call. If the imitation is good, trogons will "come in" to investigate. Some species are common along rainforest edges or successional areas. Look for their characteristic upright shape perched in cecropia trees.

Trogons are cavity nesters. Some species excavate nest holes in decaying trees, others dig into termite mounds. The violaceous trogon (*Trogon violaceous*), common from Mexico throughout Amazonia, utilizes large wasp nests. Alexander Skutch (1981) observed how a pair of violaceous trogons took over a wasp nest. The pair excavated their nest over several days in the cool early morning hours before the wasps became active. Skutch observed the trogons attack the wasps. Perching farther from the vespiary than they had done while watching each other work in the cool early morning, they made long, spectacular darts to catch the insects, sometimes seizing them in the air, sometimes plucking them from the surface of their home. A sharp tap rang out each time a trogon's bill struck the vespiary in picking off yet another wasp. The two trogons never eliminated all of the wasps but did successfully nest, snapping up fresh wasps daily. Oddly, considering that they are often very aggressive, few wasps attempted to sting the trogons or drive them away.

Trogons feed on fruits from palms, cecropias, and other species, which they take by hovering briefly at the tree, plucking the fruits. They also catch large insects and occasional lizards, swiftly swooping down on them or snatching them in flight. Trogon bills are finely serrated, permitting a tight grip on food items.

The most spectacular member of the trogon family is the resplendent quetzal (*Pharomachrus mocinno*), which appears on Guatemalan currency and is said to be the inspiration for the legendary phoenix (the Guatemalan currency is the *quetzal*). Quetzals inhabit the cloud forests of Middle America, migrating to lower elevations seasonally. Peterson and Chalif (1973) describe the quetzal as "the most spectacular bird in the New World," a debatable point (my favorite is the Guianan cock-of-the-rock), but you get the idea. The male

is "intense emerald and golden green with red belly and under tail coverts" (Peterson and Chalif 1973). The male's head has a short, thick crest of green feathers (kind of an avian mohawk) and a stubby, bright yellow bill. Most striking are the male's uniquely elongated upper tail coverts, graceful plumes that stream down well below the actual tail, making the bird's total length fully 61 cm (24 in). Females are a duller green and lack the elaborate tail plumes.

Motmots

Motmots (family Momotidae) consist of nine species, all Neotropical. They are most closely related to certain kingfishers (page 215) and the todies (Todidae), a group of five species of small, brilliantly colored, kingfisher-like birds that inhabit various islands of the Greater Antilles. All of these birds share a similar foot structure, in which the outermost and middle toes are fused together for almost their entire lengths. Motmots are slender birds whose back and tail colors are mixtures of green, olive, and blue with various amounts of rufous on the breast. They have a wide, black band through the eye, and some species have metallic, blue feathers at the top of their heads. They range in size from the 18-cm (7-in) tody motmot (*Hylomanes momotula*) to the 46-cm (18-in) rufous motmot (*Baryphthengus martii*).

Two remarkable features of motmots are a long, racquet-shaped tail (present on most but not all species) and heavily serrated bills. The tail, which in some species accounts for more than half the bird's total length, develops two extraordinarily long central feathers. As the bird preens, sections of feather barbs drop off, leaving the vane exposed. The intact feather tip forms the "racquet head." One may first sight a motmot as it sits on a horizontal branch in the forest understory methodically swinging its tail back and forth like a feathered pendulum. Another distinctive motmot characteristic is its bill, which is long, heavy, and strong, with toothlike serrations. I have held motmots and can testify as to the strength of their bite. They feed on large arthropods such as cicadas, butterflies, and spiders and will often whack their prey against a branch before eating it. They also take small snakes and lizards and frequently accompany army ant swarms (see antbirds, below and page 40). Motmots also eat much fruit, especially palm nuts, which they skillfully snip off while hovering in a manner similar to trogons.

All motmots are burrow nesters, another characteristic they share with kingfishers and todies. They excavate a tunneled nest along watercourses or occasionally within a mammal burrow.

Motmots are vocal at dawn. The call of the common and widespread blue-crowned motmot (*Momotus momota*) may have given the family its name. The bird makes a soft, monotonous, and easily imitated "whoot whoot; whoot whoot." Often a pair will call back and forth to one another.

Toucans, Aracaris, Toucanets, and New World Barbets

Perhaps more than any other kind of bird, toucans symbolize the American tropics. With an outrageous boat-shaped, colorful bill almost equal in length to its body, the toucan silhouette is instantly recognizable. As it flies with neck outstretched, a toucan appears to follow its own oversized bill. *Toucan* comes from *tucano*, the name used by Topi Indians in Brazil. Altogether, there are fifty-nine species in the family Ramphastidae, including toucans, aracaris, toucanets, and New World barbets, all Neotropical. Their anatomy and DNA indicate a close alliance with woodpeckers (and thus they are in the same order, Piciformes), and both groups share certain characteristics of foot anatomy (two toes face foward, two face to the rear), as well as the habit of roosting and nesting in tree cavities. Rhamphastids occur in lowland moist forests and montane cloud forests. Toucans, aracaris, and toucanets range in body size from 31 to 61 cm (12–24 in). Barbets (see below) are smaller.

Toucans' seemingly oversized bills are actually very lightweight. The bill is supported by bony fibers beneath the outer horny surface (which is not very different from a fingernail). The upper mandible is slightly down-curved, terminating in a sharp tip. Highly colorful patterns adorn most ramphastid bills.

Toucans have rather slender bodies with relatively short tails. Like their bills, their bodies are colorful, including patches of green, yellow, red, and white. One major group has ebony body feathers offset by white or yellow throats and scarlet on the rump or under the tail. Most species have a colorful patch of bare skin around each eye.

The 51-cm (20-in) keel-billed toucan (*Ramphastos sulfuratus*) is one of the larger species, ranging from tropical Mexico through the upper Amazon. It is black with a bright yellow throat and breast, a white rump, and scarlet under the tail. The bill is green with an orange blaze on the side and blue on the lower mandible. The tip of the upper mandible is red, and there is bare, pale blue skin around the eye. Both male and female look alike, a characteristic of most rhamphastids. The keel-billed toucan has a call remarkably like a treefrog: "preep, preep, preep" (see below). Like most toucans, keel-bills associate in flocks of up to a dozen or more individuals. Typically, when one toucan flies, soon another follows, and then another. A loose string of toucans will move from one tree to another.

Toucans are primarily frugivores, taking a wide variety of fruits from many genera, including *Cecropia* and *Ficus*. They show a preference for the ripest fruits, selecting black over maroon and maroon over red, the precise order of ripest to least ripe. Toucans are relatively large, heavy birds and prefer to perch on strong branches, reaching out to snip food with their elongate bills. Toucans are gulpers (page 139). A bird snips off a fruit and holds it near the bill tip. It then flips its head back, tossing the fruit into its throat. Though this may seem awkward, the birds seem to have little difficulty. The long bill may be adaptive in permitting the relatively heavy toucan to reach out and clip fruits from branch tips, which its weight would otherwise prohibit. In addition to fruits and berries, toucans eat insects, spiders, lizards, snakes, and nestling birds and eggs, all of which contain more protein than fruit.

Some sympatric species of toucans bear a close anatomical resemblance and are best identified by voice. For example, in northeastern Amazonia, the Cuvier's toucan (*Ramphastos cuvieri*) and the yellow-ridged toucan (*R. culminatus*) are both black with white throats and chest and a yellow rump. But the Cuvier's toucan, which is a bit larger, vocalizes with a loud series of whistled yelps, whereas the yellow-ridged toucan makes a sound much like the monosyllabic

croaking of a frog (Hilty and Brown 1986). Many ornithologists and birders have noted that where two large and similar toucans co-occur, one typically is a yelper while the other is a croaker. The same vocalization pattern applies, for instance, in Panama, where the keel-billed toucan is a croaker and the similar chestnut-mandibled toucan (*R. swainsonii*) is a yelper (Ridgely and Gwynne 1989).

Aracaris (genus *Pteroglossus*) are 38–41 cm (15–16 in) long, mostly dark in color with banded breasts highlighted by bright yellow or orange red. Their bills are patterns of gray and black. They have longer pointed tails than typical toucans. Toucanets (genus *Aulachorhy1nchus*) are about 33 cm (13 in) long and primarily greenish, with rufous tails. Their bills are dark below and yellowish above. Both aracaris and toucanets are gregarious fruit eaters.

Toucans bear an anatomical and ecological similarity to Old World hornbills (family Bucerotidae). Both families consist of colorful birds with huge, downcurved bills and slender bodies. Both nest in tree cavities, and both include fruit as a major part of an otherwise broad diet. Hornbills and toucans are not evolutionarily closely related and thus represent an example of convergent evolution.

Barbets are smaller than toucans but are colorful, frugivorous birds with prominent, wide bills. There are twenty-six barbet species in the Old World and eighteen in the Neotropics. Anatomically, except for plumage differences, they appear quite similar. However, analysis of DNA indicates that New World barbets are less closely related to Old World barbets than to New World rhamphastids (Sibley and Ahlquist 1983, 1990). Work on mitochondrial gene cytochrome c also supports this view (Barker and Lanyon 1996). Look for barbets in small flocks in fruiting trees. A barbet flock can be extremely territorial when defending a fruit tree, driving away larger birds such as pigeons.

Fruit and Nectar Feeders

Toucans are but one of several major bird families that concentrate on fruit for their diets. Throughout the tropical year there is at least some availability of both fruit and nectar. Though seasonality exerts important effects on animal communities (chapter 1), it is nonetheless generally true that some plants are fruiting or flowering every month of the year. In the temperate zone, fruits tend only to be abundant from midsummer through autumn. Many birds, including migrating species, switch over from predominantly insect to fruit diets at that time. In the tropics, however, no such dramatic switch need be made. The *constant* availability of at least some nectar and fruit has made it possible for several major bird groups to specialize and feed on one or the other (or both).

Hummingbirds

Nectar feeders consist almost exclusively of hummingbirds (family Trochilidae, order Trochiliformes). There are 322 species of these small, rapid fliers, all restricted to the New World. Most are tropical, but 16 species do migrate to breed in North America. The iridescent beauty of their plumage is reflected

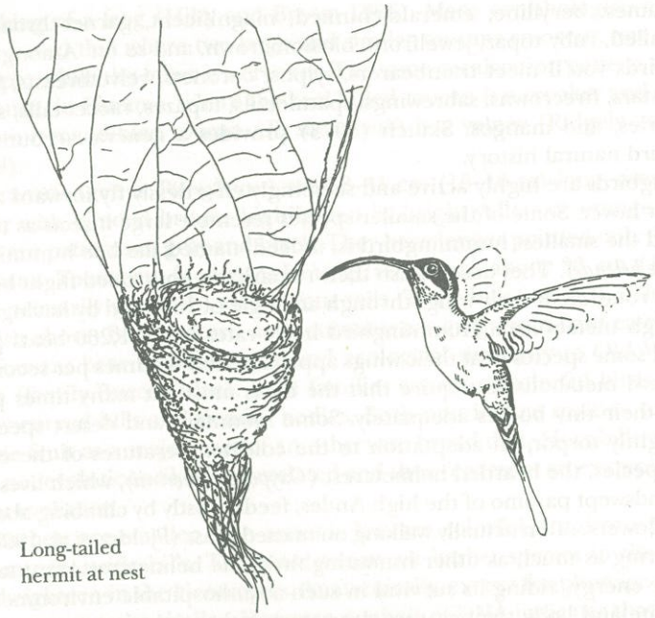
in their names: berylline, emerald-chinned, magnificent, garnet-throated, sparkling-tailed, ruby topaz, jewelfront, blossomcrown, and so on. Among the hummingbirds you'll meet trainbearers, sylphs, coronets, velvetbreasts, sapphires, hillstars, firecrowns, sabrewings, spatuletails, topazes, racket-tails, starthroats, fairies, and mangos. Skutch (1973) provides a general account of hummingbird natural history.

Hummingbirds are highly active and seemingly effortlessly fly forward and backward or hover. Some of the smaller species resemble large insects as they buzz by, and the smallest hummingbird is, indeed, named the bee hummingbird (*Calypte helenae*). They accomplish their remarkably controlled flight both by a unique rotation of their wings through an angle of 180° and by having an extemely high metabolism. Hummingbird heart rates reach 1,260 beats per minute, and some species beat their wings approximately 80 times per second! Hummingbird metabolisms require that the birds must eat many times per day to fuel their tiny bodies adequately. Some mountain and desert species undergo nightly torpor, an adaptation to the cold temperatures of the evening. One species, the bearded helmetcrest (*Oxypogon guerinii*), which lives in the cold, windswept paramo of the high Andes, feeds mostly by climbing about on *Espeletia* flowers, often actually walking on matted grass (Fjeldsa et al. 1990). By not hovering as much as other hummingbirds, the helmetcrest must save considerable energy, aiding its survival in such an inhospitable environment. Metabolic rate and body temperature drop during the nighttime hours, and the bird is thus able to sleep without consuming an inordinate amount of energy and literally starving itself.

Hummingbirds are both thrilling and frustrating to watch because they move so quickly. Suddenly appearing at a flower, its long bill and tongue reaching deep within the blossom to sip nectar, a bird will briefly hover, move to a different flower, hover, and zoom off. Others will come and go, and some will occasionally perch. The best way to see hummingbirds well is to observe at a flowering tree or shrub with the sun to your back so that the metallic, iridescent reds, greens, and blues will glow. In those hummingbird species that are sexually dimorphic, the male has a glittering red, green, or violet-blue throat patch called a gorget. The gorget is part of the male's display behavior when courting females. Depending on the sun's angle relative to the bird and observer, the gorget may appear dull, partially bright, or utterly brilliant and sparkling. When a male is courting, he positions himself such that the female is exposed to the gorget at its utter brightest.

All hummingbirds are small, the tiniest being the bee hummingbird found only in Cuba and the Isle of Pines. It weighs about as much as a dime. The largest is the 23-cm (9-in) giant hummingbird (*Patagona gigas*) of the Andean slopes. This bird is sometimes first mistaken for a swift as it zooms past.

The diversity of bill anatomy, plumage, and tail characteristics among hummingbird species represents a fine example of adaptive radiation (page 98). The Andean sword-billed hummingbird (*Ensifera ensifera*), which lives high among Andean dwarf forests, has a body length of 13.2 cm (5.2 in) plus an almost equally long bill! This extraordinary length is a probable case of coevolution since the Andean swordbill feeds on *Passiflora mixta*, a flower with a very long, tubelike corolla. The booted racket-tail (*Ocreatus underwoodii*), also



Long-tailed hermit at nest

a cloud forest dweller, has two long, central tail feathers with bare shafts but feathered at the tips, somewhat like a motmot. The ruby topaz (*Chrysolampis mosquitus*), a lowland forest and open area generalist species, is certainly one of the most beautiful hummingbirds. Males have glowing, orange throats and bright, metallic, crimson heads.

Though most hummingbirds are brilliantly colored, not all are. The subfamily Phaethornithinae includes the twenty-nine hermit species, some of the commonest hummingbirds in lowland forests. Most are greenish brown with grayish or rufous breasts. Unlike most species where males are brighter than females, hermits have similar sexes. All hermits have a black line bordered by white through the eyes and a long, often downcurved bill. Hermits inhabit the forest understory and edge, and their more subdued plumage seems to fit well with the dark forest interior. Male long-tailed hermits (*P. superciliosus*) are both abundant and vocal throughout Central and South America. Males gather in courtship areas called *leks* (see manakins, this chapter) and twitter vociferously at each other as each attempts to entice a passing female.

Hummingbirds are attracted to red, orange, and yellow flowers, and a single flowering tree or shrub may be a food resource for several species. When a tree is abundantly covered by flowers, it is neither economical nor practical for a single hummingbird to try to defend it from others. Nonetheless, hummingbirds are generally pugnacious, and it is easy to observe both intra- and interspecific aggression among them as they jockey for a position at their favorite flower. This competition is exacerbated because, though a plant may have many flowers, very few may be nectar-rich (see below). Some hummingbirds are highly territorial, defending a favored feeding site, while others seem to

circulate along a regular route visiting several flowers. The latter, which include some of the hermits, are called "trapliners."

Wolf (1975) reported a curious example of hummingbird territorial behavior for the purple-throated carib (*Eulampis jugularis*). Like many hummingbird species, males are pugnacious and territorial, defending favored flowers and dominating access to the nectar-rich food. Some females, however, employ a behavioral strategy that permits them to circumvent male dominance and gain access to desired flowers. Females court males, even during the nonbreeding season (when they cannot become pregnant). Both during and after the courtship process, a normally aggressive male will permit the "cooperative" female to feed on "his" flowers. Males inseminate females, though to no avail. Wolf reasoned that the behavior is adaptive for females, since they gain access to food that otherwise they could not hope to acquire, but he was unable to identify any clear advantage to the male, since courtship and copulation use energy and no offspring result. Wolf titled his paper "'Prostitution' Behavior in a Tropical Hummingbird." Hmm.

Hummingbirds sometimes have a mutualistic relationship with plants, feeding on nectar but facilitating cross-pollination. Hermits, for instance, often feed on the nectar of heliconia flowers. Many heliconias produce relatively constant amounts of nectar per flower. However, one heliconia studied in Costa Rica, *Heliconia psittacorum*, exhibits a "bonanza-blank" pattern of nectar production (Feinsinger 1983). Some flowers contain abundant nectar (bonanzas), some essentially none (blanks). Many other tropical plants, especially those in open successional areas, also are bonanza-blank flowerers (see below). Hermits must visit many flowers in order to encounter one with high nectar content, thus the bonanza-blank pattern presumably aids *Heliconia psittacorum* in accomplishing cross-pollination

In a comprehensive study of ten successional plant species and fourteen hummingbird species at Monteverde cloud forest in Costa Rica, Feinsinger (1978) documented that flowering was staggered among plant species, resulting in a constant nectar supply to hummingbirds. In five plant species that were closely measured for nectar volume, the bonanza pattern was evident. Feinsinger speculated that plants may conserve energy by producing large numbers of "cheap" nectarless flowers and a mere few "expensive" bonanza flowers, forcing hummingbirds to visit many flowers to find satiation. By visiting many flowers, cross-pollination is promoted.

Hummingbirds display a range of foraging patterns. Feinsinger and Colwell (1978) identified six patterns evident in how hummingbirds exploit flowers: high-reward trapliners, which visit but do not defend nectar-rich flowers with long corollas; territorialists, which defend dense clumps of somewhat shorter flowers; low-reward trapliners, which forage among a variety of dispersed or nectar-poor flowers; territory-parasites of two types (large marauders and small filchers); and generalists, which follow shifting foraging patterns among various resources. Large marauders are species with large bodies that can intimidate normally territorial smaller species. They move in and take what they want. Small filchers are species with small bodies that "sneak" in to feed quickly, before being detected by a territorial bird. High-reward trapliners such as the hermits have a regular route that they visit and are most common

in the forest understory. The other types of foraging are evident in the canopy and open, successional areas.

The complexity of interactions between hummingbirds and plants is further complicated by the fact that species of nectar-eating mites (*Rhinoseius*) depend entirely upon hummingbirds for their dispersal among flowers (Colwell (1973, 1985a, 1985b). The mites are transported in the nasal cavities of the birds! Mites are therefore dependent on the *mutualistic* interaction between birds and plants. This complex tapestry of ecological interdependence involves two mite species, three hummingbirds, one flowerpiercer, and four hummingbird-pollinated plants.

One other group of birds, besides hummingbirds, feeds principally on nectar. The eleven species of flowerpiercers, all members of the large tanager family (see below), do not probe into the center of the flower, as hummingbirds do, but instead snip a minute hole through the petal at the base. The bird pokes its bill in, sips nectar, but receives no pollen. Flowerpiercers are therefore nectar parasites. A few hummingbirds have occasionally been seen employing a similar behavior.

Tanagers

Tanagers are a group of unusually colorful, small, perching birds. *Tanager*, like the word *toucan*, comes from the Topi Indian language of Brazil. The diverse subfamily Thraupinae (part of the huge family Emberizidae, order Passeriformes) consists of 242 species of tanagers, euphonias, chlorophonias, honeycreepers, dacnis, conebills, and flowerpiercers. Most species are brilliantly colored and feed on fruit (mashers, page 135), nectar, and insects. All occur in the New World, and they are found abundantly from lowland forests to high montane and cloud forests. They are particularly common around forest-edge habitats and are easy to see at fruiting figs, palms, cecropias, and so on. Though four tanager species migrate to North America to breed, the remainder are all confined to the Neotropics. Storer (1969) reviews a general taxonomy of tanagers, and Isler and Isler (1987) provide a comprehensive field guide illustrating all species, with much discussion of natural history. Also see Ridgely and Tudor (1989). For a good general account of tanager natural history, see Skutch (1989).

In most Neotropical tanagers, males and females have similar plumage. The common names of tanager species reflect their multicolored, exotic feather patterns. On a trip to southern Central America, for instance, one may encounter the crimson-collared, scarlet-rumped, flame-colored, blue and gold, golden-hooded, silver-throated, and emerald tanagers, a list that is far from exhaustive. One of the most common and widely distributed birds of the tropics is the blue-gray tanager (*Thraupis episcopus*), which is well described by its name. Chlorophonias are bright green and yellow, highland tanagers. Among the most exotically colored tanagers is the paradise tanager (*Tangara chilensis*) of South America. Like a mosaic of neon colors, this incredible bird has a golden green head, purple throat, bright scarlet lower back and rump, black upper back, and turquoise breast. As if that were not enough, paradise tanagers travel in flocks, so you get to see more than one! Euphonias (genus *Euphonia*) are a group of small tanagers, also multicolored, that tend to feed heavily on mistletoe berries (family Loranthaceae). They are important seed dispersers of mistletoe, as their sticky droppings, deposited on branches, contain the seeds that begin life as epiphytes, before becoming parasitic. Euphonias often nest in bromeliads (Bromeliaceae).

Honeycreepers, which include dacnises and conebills, are nectarivorous, though they also include ample amounts of fruit and arthropods in their diets. Warbler-sized, they have fairly long, downcurved bills. One of the most common and widely distributed of this group is the bananaquit (*Coereba flaveola*). This small bird with a dark back, white eye stripe, and yellow breast is among the most ubiquitous of tropical birds. It is found in virtually all habitats from lowlands to cloud forests and often becomes quite tame around gardens. Like the flowerpiercers, bananaquits are prone to poke a small hole at the outside base of a flower and drink nectar without contacting pollen.

Some tanagers, such as the ant-tanagers (genus *Habia*), are army ant followers, and many tanagers, euphonias, and honeycreepers move with antbirds, woodcreepers, and other species in large, mixed foraging flocks.

Studies have revealed the high diversity and intriguing complexity of behavior within both canopy and understory mixed species flocks in the Peruvian Amazon (Munn 1984, 1985; Munn and Terborgh 1979). Each flock type consists of a core of five to ten different species, each represented by a single bird, a mated pair, or a family group. Up to eighty other species join flocks from time to time, including twenty-three tanager, euphonia, and honeycreeper species, a remarkably high diversity. Mixed foraging flocks occupy specific territories and, when another flock is encountered, the same species from each flock engage in "singing bouts" and displays as boundary lines are established. Adult birds tend to remain flock members for at least two years. Nesting occurs in the general territory of the flock, the nesting pair commuting back and forth from nest to flock.

Munn's work revealed an odd twist on interactions within mixed foraging flocks. One long-held hypothesis about mixed flocks is that being part of one serves to help protect against predation (Moynihan 1962). With so many eyes looking, predators have difficulty going undetected. Munn showed that actual sentinel species are part of every mixed flock. One species of shrike-tanager and one antshrike (an antbird, see below) aided the flock by giving general alarm calls when danger threatened. Both sentinel species, however, also gave "false alarm calls," a behavior Munn described as "deceitful." False alarm calls are exactly that: alarm calls uttered when no danger is present. The hypothesized reason for the false alarms is that the alarmist has a better chance of capturing food that is also being sought by another bird. When a white-winged shrike-tanager (*Lanio versicolor*) and another species were both chasing the same insect, the shrike-tanager's false alarm would cause momentary hesitation by the other bird, allowing the shrike-tanager to capture the insect.

Orioles, Oropendolas, and Caciques

The large avian family Icteridae (order Passeriformes) includes the blackbirds and their relatives. Among those occurring in the Neotropics are thirteen oropendola species, nine cacique species, and twenty-four oriole species. Oropendolas and caciques are colonial and make long, hanging, basketlike

nests. An oropendola nest tree is easy to spot because it is out in the open and adorned with numerous pendulous nests. The isolation of the nest tree affords some protection against predation by monkeys, since the simians are usually loathe to leave the canopy and cross open ground. Oropendolas are large birds (some almost crow-sized), and caciques are robin-sized. In shape, both caciques and oropendolas are relatively slender, with long tails and sharply pointed bills. Oropendolas come in two color types. One group of species is mostly black and chestnut, with yellow on the bill and tail, and the other is quite greenish. Caciques are mostly sleek black but with bright red or yellow rumps and/or wing patches, and yellow bills.

Both caciques and oropendolas tend to locate their colonies near bee or wasp nests. Because these colonial insects can be very aggressive toward intruders, this behavior helps reduce the probability of predation by mammals. Robinson (1985a, 1986) learned that yellow-rumped caciques (*Cacicus cela*) employ other strategies that would also seem to protect the colony. Caciques often nest on islands in a river or lake, affording added security from both mammals and snakes, for would-be predators would have to cross a water body patrolled by otters and caimans. Caciques tend to mob potential avian predators, and unused, abandoned nests remain in the nest tree along with active nests. The presence of the unused nests may confuse a predator. Not surprisingly, each cacique attempts to locate its nest in the center (where protection is maximized), rather than the more risky periphery of the colony. For caciques, colonial nesting and group defense is a significant adaptation against nest predation.

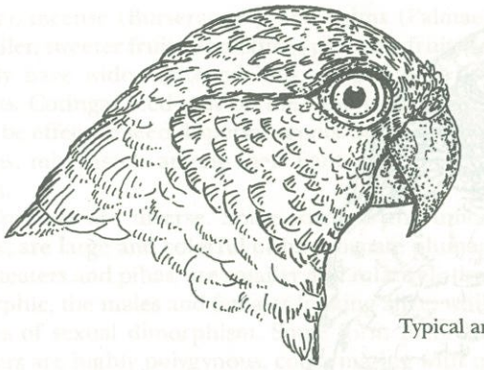
Robinson documented, however, that yellow-rumped caciques were occasional victims of nest piracy by other bird species. One, appropriately named the piratic flycatcher (*Legatus leucophaius*), harassed caciques until they abandoned their nests to the flycatchers. Russet-backed oropendolas (*Psarocolius angustifrons*) destroyed cacique eggs and killed young, leaving empty nests. Finally, troupials (*Icterus icterus*), which are large, aggressive orioles, both took over cacique nests and destroyed eggs and young. Robinson hypothesized that the piracy is not related to competition for food because each of the nest pirate species has a diet different from that of caciques. Instead, the creation of many nearby empty cacique nests serves to confuse potential predators and confer protection on the nest pirate species (Robinson 1985b).

Orioles nest as territorial pairs and are not colonial like the oropendolas or caciques. They are colorful, with various combinations of orange, yellow, and black. Several oriole species migrate to nest in North America, but most remain in the tropics.

Orioles, oropendolas, and caciques feed on fruit and nectar, mixing various arthropods into an otherwise vegetarian diet. Like the tanagers, these birds move in mixed flocks, foraging in fruit trees and drinking nectar from blossoms.

Parrots *Figures 102, 146, 147, 148, 149*

Like toucans, parrots are quintessentially tropical. Global in distribution, they occur mainly in tropical forests of the southern hemisphere. In the Neotropics, 136 species of the family Psittacidae (order Psittaciformes) can be



Typical amazon parrot

found, ranging from the spectacular large macaws (genera *Ara, Anodorhynchus, Cyanoliseus*) to the sparrow-sized parrotlets (genus *Forpus*). Among the most commonly encountered of the New World parrots are the chunky, short-tailed amazons (genus *Amazonia*). There are also moderate-sized, long-tailed parrots known collectively as parakeets (many in the genus *Aratinga*). Parrots are mostly green (though there are some dramatic exceptions) and can be remarkably invisible when perched in the leafy forest canopy, quietly and methodically devouring fruits. They reveal their presence by vocalizing, usually a harsh screech or squawk. Often a flock will burst from a tree like shrieking banshees, and it is amazing to see how many birds were actually in the tree when so few were readily apparent. Generally, there is little or no difference in plumage between the sexes. Forshaw (1973) has treated all of the world's parrots.

Parrots are gregarious frugivores. It is uncommon to find only one or two, though that may occur with large macaws. Flocks move about in forests and savannas searching out fruits, flowers, and occasionally roots and tubers. Parrots climb methodically around the tree branches, often hanging in awkward acrobatic positions as they attack their desired fruits. Their sharply hooked, hinged upper mandible is useful in climbing around in trees as well as in scraping and scooping out large fruits. Using their strong, nutcracker-like bills, they can crack many of the toughest nuts and seeds, which they eat with equal relish as the pulpy fruit itself. Their tongues are muscular, and they are adept at scooping out pulp from fruit and nectar from flowers. Because of their ability to crush and digest seeds, they are primarily seed predators rather than seed dispersers. The orange-chinned parakeet (*Brotogeris jugularis*) in Costa Rica is, for instance, a seed predator on the trees *Bombacopsis quinatum* and *Ficus ovalis*. Janzen (1983c) shot one bird, examined its crop, and found several thousand *Ficus* seeds, all of which were damaged in some way. Droppings from orange-chins contained no evidence of intact seeds.

The most spectacular Neotropical parrots are the nineteen macaw species, especially the larger species. These long-tailed parrots with bare skin on their faces range in plumage from the predominantly green chestnut-fronted (*Ara severa*), military (*A. militaris*), and great green (*A. ambigua*), to the bright red scarlet (A. *macao*) and red-and-green (*A. chloroptera*), to the brilliant blue-and-

Scarlet macaw

yellow (*A. ararauna*) and the deep indigo blue of the hyacinth (*Anodorhynchus hyacinthinus*). Macaws are most commonly seen flying to and from their roosting and feeding sites. Their slow wing beats and long tails make them distinctive in flight. Many macaws frequent gallery forests along watercourses or humid forests interrupted by open areas. They feed heavily on palm nuts, their huge bills being fully capable of crushing these dense fruits.

Unfortunately, forty-two species, or about 30% of the species of Neotropical parrots, are considered to be at some clear risk of extinction, principally from habitat loss and/or pet trade (Collar and Juniper 1992). In addition to threatened and endangered species, many, if not most, other species are also in decline for the same reasons. Nest trees are cut to procure the nestlings for the pet trade. Deforestation eliminates still more nest trees. Mortality rates among parrots shipped from Latin America for the pet trade are staggering. While it may prove possible to develop protocols to manage parrot populations such that there can be sustainable use for international trade (Thomsen and Brautigam 1991), doing so in countries where enforcement is at best problematic (and that would be most Latin American countries) suggests a dubious potential for success. Free-ranging large macaws may provide a unique opportunity for ecotourism, an example discussed in chapter 14.