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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 in-

terested 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

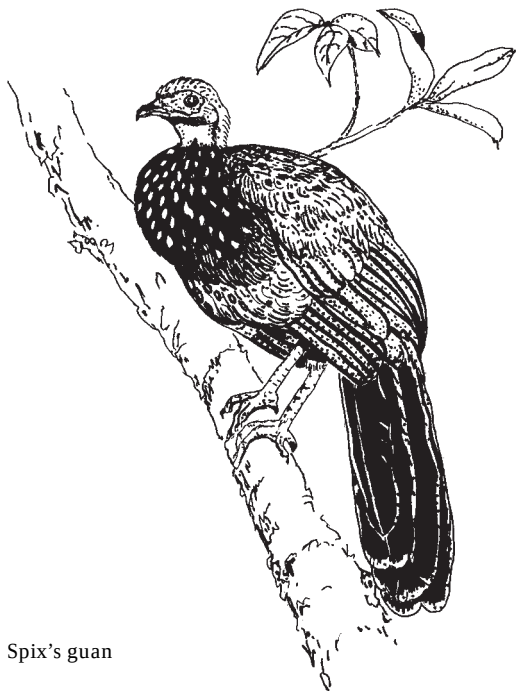
range of colors, from turquoise blue and green, to purple, deep red, slate gray, or brown. Only the male incubates the eggs, another characteristic shared with ostriches and rheas.

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 51 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 Neo-



Spix's guan

Female great curassow

tropical 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.

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, eye-like 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*

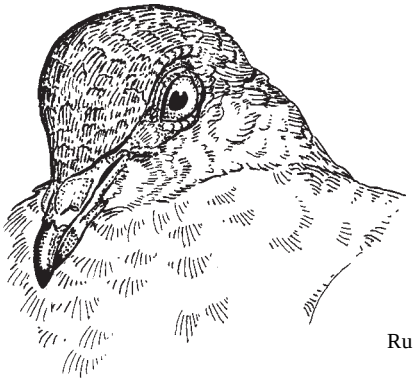
Nothing looks quite like a trumpeter except another trumpeter. These oddly shaped, rooster-sized birds of the rainforest floor are uniquely hump-backed, with long legs, slender necks, and a chickenlike head. There are only

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, raquet-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 "raquet 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

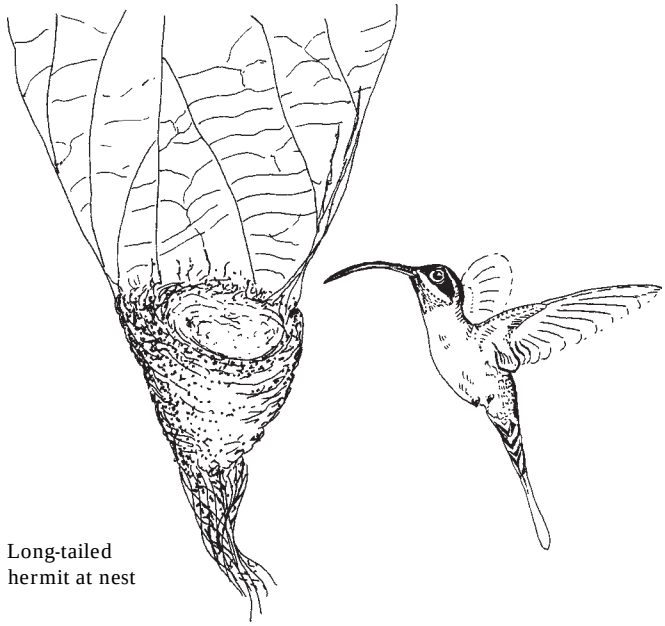
in their names: berylline, emerald-chinned, magnificent, garnet-throated, sparkling-tailed, ruby topaz, jewelfront, blossomcrown, and so on. Among the hummingbirds you'll meet trainbearers, sylphs, coronets, velvetbreasts, sapphires, hillstars, firecrowns, sabrewings, spatuletails, topazes, racket-tails, 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.

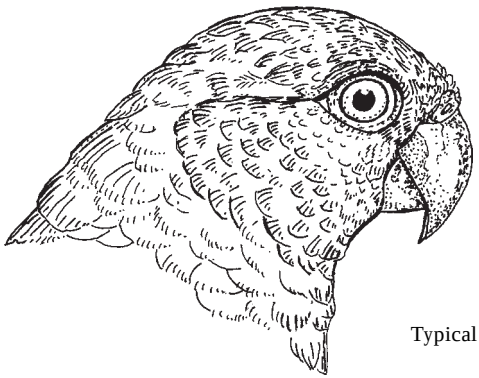
Robinson documented, however, that yellow-rumped caciques were occasional victims of nest piracy by other bird species. One, appropriately named the piratic flycatcher (*Legatus leucophaius*), harassed caciques until they abandoned their nests to the flycatchers. Russet-backed oropendolas (*Psarocolius 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.

Cotingas

Cotingas (family Cotingidae, order Passeriformes) are among the real glamour birds of the Neotropics. With names such as bellbirds, umbrellabirds, cocks-of-the-rock, pihas, fruiteaters, fruit-crows, and purpletufts, the sixty-six cotinga species are, indeed, a colorful and diverse family. They are birds of rainforests and, to a lesser extent, cloud forests, and they are described as "extreme fruit specialists" (Snow 1982). Large cotingids eat laurels (Laura-

ceae), incense (Burseraceae), and palms (Palmae), while smaller species eat smaller, sweeter fruits, sometimes plucking fruits while hovering. Cotingas typically have wide, flattened bills, shaped well for accommodating rounded fruits. Cotingas feed only on the flesh of the fruit and not the seeds and thus can be effective seed dispersal agents. Some species, such as the fruit-crows and pihas, mix insects among their fruits, but most cotingas feed exclusively on fruit.

Cotingas are diverse. Some, such as the umbrellabirds and cocks-of-the-rock, are large and colorful or have ornate plumage, while others, such as the fruiteaters and pihas, are smaller and relatively drab. Some are sexually monomorphic, the males and females looking alike, while others represent extreme cases of sexual dimorphism. Some form pairs and occupy territories, while others are highly polygynous, cocks mating with many hens. In a few species, such as the cocks-of-the-rock (genus *Rupicola*) and screaming piha (*Lipaugus vociferans*), males gather to court females in mating areas called leks. Bellbirds (genus *Procnias*) are known for their piercing, bell-like call notes, pihas for their loud scream, cotingas for their shiny metallic plumage, cocks-of-the-rock for their golden-orange or orange-red coloration and fan of head feathers, and umbrellabirds (genus *Cephalopterus*) for their extraordinary, umbrellalike head plumes and inflatable air sac on the breast. Cotingas generally make small, inconspicuous nests, incubate but a single egg, and have a prolonged incubation period. Bellbirds typically incubate for approximately thirty days, and cocks-of-the-rock for forty or more days. This long incubation period is probably related to feeding nestlings almost exclusively fruit, which is low in protein but high in fat and carbohydrate. Cotinga natural history is thoroughly reviewed by Snow (1982), and cotinga examples of sexual selection will be given below.

Manakins *Figures 139, 140*

The fifty-three species of the family Pipridae (order Passeriformes), the manakins, are small, chunky, fruit-eating birds, most of which inhabit lowland forests. All are confined to the Neotropics. Manakins are extremely close evolutionary cousins of the cotingas and tyrant flycatchers, and recent taxonomic analysis has suggested that manakins of several generi (ex. *Schiffornis*) are not true manakins but intermediates between cotingas, tyrant flycatchers, and manakins (Prum and Lanyon 1989). Males of most species are quite colorful; females, drab olive green and yellowish. Manakins have short tails, rounded wings, and a short but wide bill with a small hooked tip. They pluck fruits on the wing, supplementing their largely frugivorous diets with occasional arthropods.

Manakins have among the most elaborate courtship displays of any birds. Like some of the cotingas, many manakin species are “arena birds” and court in concentrated leks, assemblages of males that display to transient females. Others court in dispersed leks, while still others have a unique cooperative courtship behavior in which several males display together in an extraodinarily coordinated manner. Manakin courtship is detailed in the next section. Only females build the nest, incubate, and feed young. Clutch sizes are typically

small, one to two birds per nest. Manakin courtship is reviewed by Sick (1967), Lill (1974), Snow (1976), and Prum (1994) and is discussed further below. For a general review of courtship behavior among arena birds, see Johnsgard (1994).

Leks and Lovers—Sexual Selection among Cotingas and Manakins

Charles Darwin (1859, 1871) devised his theory of sexual selection in part to account for why certain bird species, among them many of the cotingas and most manakins, display extreme differences in plumage between the sexes. This sexual dimorphism almost always involves brightly and ornately plumaged males compared with subtle-plumaged, more cryptically colored females. Why females are cryptic seemed an easy question to Darwin. Females undergo natural selection for cryptic plumage because such coloration aids in reducing the risk of discovery by predators. But why are males so colorful? Adding to this mystery was the fact that elaborately colored males often augment their already gaudy selves by engaging in bizarre courtship displays.

The Amorous, Glamorous Cock-of-the-Rock *Figures 135, 136, 137, 138*

The Guianan cock-of-the-rock (*Rupicola rupicola*), a large (grouse-sized) cotinga, provides an example of elaborate courtship and plumage. The courtship of this species has been studied by Snow (1982) and Trail (1985a, 1985b). Males are chunky, with short tails and bright, golden orange plumage with black on the tail and wings. In flight they resemble winged, day-glo orange footballs! Beaks, legs, eyes, and even the very skin are orange. And not just any orange: bright, vivid, magnificent orange. The first male Guianan cock-of-the-rock that I saw was some distance away, perched in the midlevel understory of thick Brazilian rainforest. I urgently asked Bob Ridgely, who had spotted the bird, to describe just where it was. He said something like "Just look for the orange beacon" and pointed in the general direction. He was right. It was not difficult to find the creature. The male's already striking plumage is further enhanced by delicate, elongated orange wing plumes and a crescent-like thick fan of feathers extending from the base of the bill to the back of the neck. Females are dull brown, with neither the wing plumes nor the head fan.

Males gather in the rainforest understory in confined courtship areas called concentrated leks. Each male clears an area of ground in which to display and defends perches in the vicinity of its display site. The lek can be a crowded place, with males as close to one another as 1.2–1.5 cm (4–5 ft) and several dozen males on the same lek. When a female approaches a lek, each male displays by landing on the ground and posturing to her. Each displaying cock strokes its wing plumes and turns its head fan sideways, so that the female sees it in profile, and stares at her with its intense orange eye set against flaming orange feathers. The object of the cock's bizarre display is to mate, presumably by suitably impressing the female. Females do not appear to be easily impressed. A hen will typically visit a lek several times before engaging in copulation. These visits, called mating bouts, always excite the males to display. Only

one male on the lek will get to mate with a visiting female, who may return to mate with him a second time before laying eggs (Trail 1985b). No extended pair bond is formed, only a brief coupling. The cock returns to the lek, continuing to court passing hens while the newly fertilized hen attends to nest building, egg laying, incubation, and raising the young. The basis of her behavior in choosing a male from among many potential contenders is one facet of what Darwin called *sexual selection*.

Darwin reasoned that, in some species, female choice was the dominant factor in selecting males' appearances. Put very simply, males are pretty (or musical or noisy or perform complex dances) because females have tended through generations to mate mainly with males having these unique features. Since plumage color is heritable (as are behavioral rituals), gaudy coloration was selected for and continually enhanced. Recent work in sexual selection suggests that females may learn much about the evolutionary fitness of males by signals communicated both by plumage condition and male courtship behavior (Andersson 1994). In other words, females are not being frivolous in driving male evolution toward more elaborate, gaudy plumage and exotic behavior but rather are looking intently for the best vehicles in which to place their precious genes for their journey into the next generation.

The other facet of sexual selection recognized by Darwin is that males must compete among themselves for access to females. This may be accomplished by dominance behavior, guarding females, active interference with other males' attempts to mate (see below), injury to other males, or merely being sneaky and mating before other males can react. Gaudy plumage may contribute to a male's success by intimidating other males and thus make it easier to gain the attentions of a female. Male / male competition coupled with female selection of the winner is what Darwin defined as sexual selection.

Sexual selection has costs for both males and females. Though the hen exercises the most choice in the mating process, she is left solely responsible for the chores of nest building, incubation, and caring for the young. These are risky, energy-consuming tasks. Males may at first glance seem the luckiest, rewarded by a life of lust in nature's tropical "singles bar," the lek. The combination of male / male competition plus dependency on female choice makes life surprisingly difficult for most males, however. Though some cocks are quite successful, mating frequently, others, the losers, spend their entire lives displaying to no avail. After a lifetime of frustration, they die genetic losers, never selected even once by a hen. Pepper Trail (1985a, 1985b), who studied the Guianan cock-of-the-rock in Suriname, documented high variability in male mating success. He found that 67% of territorial males failed to mate at all during an entire year. The most successful male performed an average of 30% of the total number of annual matings, and the lek contained an average of fifty-five cock birds! One of these fifty-five mated 30% of the time. Many never mated. Such is the cost of sexual selection for males. In reproductive terms, females are the most fortunate sex. Most females do mate, though success in fledging young may certainly vary considerably among females.

Trail (1985a) also discovered another interesting twist in the mating process of the Guianan cock-of-the-rock. Some males were sore losers and habitually disrupted the mating of others. Trail found that aggressive males that

disrupted copulations by other males fared better in subsequent mating attempts. He learned that males that were confrontational "were significantly more likely to mate with females that they disrupted than were non-confrontational males." He hypothesized that only the cost of confrontation in terms of energy expenditure, loss of time from the aggressive bird's own lek territory, plus risk of actual retaliation kept direct confrontational behavior from becoming even more manifest among the birds. On the other hand, Trail (1985b) found adult fully plumaged males remarkably tolerant of juvenile males that were still plumaged in drab colors, resembling females. Yearling males would actually attempt to mount adult males as well as females in a crude attempt at mating. Adult males did not respond aggressively to these misguided efforts, possibly because yearling plumage, being drab, does not stimulate an aggressive response.

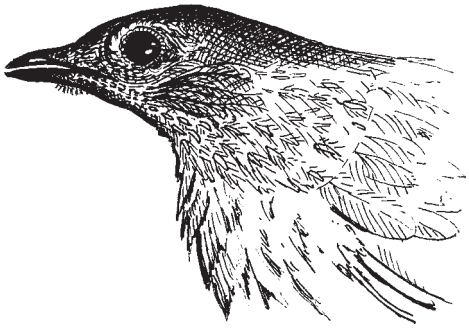
Screaming Pihas and Clanging Bellbirds

Sexual selection has evolved in various ways, and thus courtship patterns differ among species. The screaming piha (*Lipaugus vociferans*), a common bird throughout much of Amazonia, courts on leks that are much larger in area than those of the Guianan cock-of-the-rock. These dispersed leks, as they are termed, are possible because it is not the plumage of the bird that matters, it is its voice, and its voice is mighty. The piha differs from the cock-of-the-rock in that it is downright nondescript, being a slender, robin-sized bird light gray on the face and breast and dark gray-brown on wings, back, and tail. Though certainly attractive (at least to human eyes), it is by no means the glamour bird that its cousin is.

Male and female screaming pihas look alike and thus would not seem to fit with Darwin's concept of sexual selection, focused as it is on sexual dimorphism. It is with voice, however, and not looks, that a male screaming piha attracts a female and tells other males that he is doing so. Piha leks are composed of up to thirty males, and David Snow (1982) reports that males' calls are "one of the most distinctive sounds of the forests where these birds occur, its ringing, somewhat ventriloquial quality seeming to lure the traveller ever onwards into the woods." Ringing indeed. To me it sounds like a strident, clanging "peeh-HE-hah!" reminding me vaguely of the cracking of a whip. And it really carries.

Barbara Snow studied the screaming piha in Guyana and found that one male spent 77% of his time calling on the lek, usually from a thin horizontal branch well below the canopy. (Screaming pihas, though understory birds, can be surprisingly hard to see, as they are so nondescript and their voice is so ventriloquial.) An excited male called at the rate of twelve times per minute. Calling seems to replace plumage and display behavior as the signal to the females. Sexual selection has occurred, but for characteristics of voice, not appearance.

Bellbirds (genus *Procnias*), like the screaming piha, rely heavily on voice as part of the courtship process. There are four species, each shaped generally like a starling though larger in size, ranging throughout lush montane forests of northern South and Central America. They tend to migrate vertically,



Female bearded bellbird

breeding in highland forests and moving downslope to lowland forests when not breeding. Unlike pihas, bellbirds are sexually dimorphic, the males having much white on the body along with ornate wattles about the head. In one species, the white bellbird (*P. alba*), the male is entirely white with a fleshy, wormlike wattle dangling from its face above the bill. The male bare-throated bellbird (*P. nudicollis*) is almost all white but has bare blue skin on the throat and around the eyes. The male bearded bellbird (*P. averano*) has black wings and a chestnut head with a heavy "beard" of black, fleshy wattles hanging from its throat, and the male three-wattled bellbird (*P.tricarunculata*) is chestnut on body, tail, and wings, but with a white head and neck, and three fleshy wattles hanging from the base of the bill. Females of all four species are similar greenish yellow, darkest on the head, with streaked breasts.

Male bellbirds establish calling and mating territories in the forest understory. Though not true lek birds, bellbirds have courtship territories that are closely spaced together. Each male spends most of his time on territory vocalizing to attract hens. Males take no part in nest building, incubation, or raising young. Two well-studied examples are the bearded bellbird in Trinidad and the three-wattled bellbird in Panama. Both court in a generally similar manner.

Male bearded bellbirds are among the first sounds one hears upon entering the Arima Valley in Trinidad. David Snow (1976, 1982) aptly describes their call as a loud "Bock!" The call carries amazingly well, and I thought the birds were nearby when, in reality, they were a quarter of a mile or more from me. The call definitely has a bell-like quality, though it is a muted clang, and the ventriloquial quality of the call note is evident. Even when very close to a calling male, it can be frustratingly difficult to locate him. Cock birds initially call from a perch above the canopy, often on a dead limb, but will drop down into the understory to complete the courtship. Females never call, and it is clear that male vocalizations are an essential part of sexual selection in bellbirds.

The object of calling is to attract a hen to the male's territory. Each cock bellbird has his own courtship site in the forest understory. The male "bocks" rather continuously, mixing the bocking with a series of "tock, tock, tock" notes. If successful in luring a female to his territory, the male initiates a series of courtship postures, performed from a horizontal branch upon which the female perches as his only audience. These postures include display of the

beard wattles, a wing display, and a display in which a bare patch of skin on the male's thigh is revealed. All bellbird species include a "jump-display" as part of courtship. A cock bearded bellbird will leap from one perch to another, landing before the hen with his body crouched, tail spread, and eyes staring at her. You can guess what happens next, assuming the male has performed satisfactorily.

The three-wattled bellbird takes the jump-display one step further. The cock jumps over to the place occupied by the hen while at the same moment the hen skitters along the limb to occupy the place the male just vacated. Called a "changing-place" display, the male then slides across the branch to be right next to the hen, emitting a close-up call virtually in her ear. Following the successful execution of this maneuver, more bellbirds come into the world.

The Dancing Manakins *Figures 139, 140*

Manakins carry the evolutionarily inspired art of courtship dancing to extremes. Male manakins are brightly colored, glossy black with bright yellow, orange-red, scarlet, or golden heads and/or throats, some with bright yellow or scarlet thigh feathers, and some with deep blue on their breasts and/or backs and long, streamerlike tails. A few species are sharply patterned in black and white. But fancy feathering notwithstanding, it is dancing in which these birds excel. Snow (1962a, 1976), Sick (1967), and Schwartz and Snow (1978) have made detailed studies of manakin courtship behavior and have provided much of the information outlined below, augmented by my own experience with these species.

The white-bearded manakin (*Manacus manacus*) courts on rainforest leks. I've observed its courtship in the Arima Valley in Trinidad. The male has a black head, back, tail, and wings but is white on the throat, neck, and breast. Its name comes from its throat feathers, which are puffed outward during courtship. Females are greenish yellow. Up to thirty or more males may occupy a single lek. Each male makes his "court" by clearing an oval-shaped area of forest floor about a meter across. Each court must contain two or more thin vertical saplings, as these are crucial in the manakin's courtship dance. The male begins courtship by jumping back and forth between the two saplings, making a loud "snap" with each jump. The snap comes from modified wing feathers snapped together when the wings are raised. When a female visits the lek, the snapping of many males is audible for quite a distance. In addition to the snap, the male's short wing feathers make a buzzing, insectlike sound when it flies, and thus active manakin leks can become a cacophony of buzzing, snapping birds. The intensity of the male's jumping between saplings increases until he suddenly jumps from sapling to ground, appearing to ricochet back to another sapling, from which he slides vertically downward like a firefighter on a pole. David Snow's film footage of the slide revealed that successful males slide down right to the female perched at the base of the sapling pole. Copulation is so quick that Snow only discovered the presence of the female in the film. He never saw her while he was witnessing the event!

Following copulation, the female leaves the lek and attends to nesting. The male starts to dance again. Male manakins spend most of their adult lives at the

Courtship dance of the white-bearded manakin. See text for details. From H. Sick (1967). Reproduced with permission.

lek. Some, as in the case of the cock-of-the-rock, are probably consistently successful and mate often. Others may never mate. Observations of banded males on Trinidad have revealed that life on a lek is usually fairly long for individual birds. Some live for a dozen years or more, a very long life span for such a small bird (Snow 1976). Males generally only leave the lek to feed on ripe fruits.

Another common Trinidad manakin that I have observed, the golden-headed (*Pipra erythrocephala*), is not a lek dancer, but rather each male displays in his own territory. As in the white-bearded, the dance begins when the male darts back and forth on selected twigs, calling "zlit" as he does so. Unlike the white-bearded, which dances close to the ground, the golden-headed usually displays about 3 m (10 ft) off the ground in an understory tree. The cock becomes increasingly vigorous in his dancing, crouching, his body at a 45-degree angle as he slides along a horizontal twig. His sparkling golden head and sleek black plumage are displayed very conspicuously, but more is yet to come. When a female arrives, the male skitters along the branch toward her, but *tail first*! As he advances, he bows, spreads his wings, and exposes bright red thigh feathers, all the while pivoting his body back and forth. The climax of the dance comes when the male suddenly flies from the dance branch and quickly returns, inscribing an "S-shaped" curve as he lands with wings upraised before the female. Various vocalizations accompany the performance.

If the white-bearded and golden-headed manakin performances amaze you, be warned that the blue-backed and swallow-tailed manakins (genus *Chiroxiphia*) seem to carry bird dancing to the point of incredulity. Blue-backed males

Blue-crowned manakin

have bright red on the top of their heads and shimmering turquoise blue backs on otherwise shiny black plumage. Swallow-tailed manakins, also called blue manakins, are similar but with blue on both back and breast and elongated central tail feathers. Even for male manakins they are extraordinarily beautiful, especially when seen in a burst of full sunlight as they dance in the forest understory. I say *they* because these manakins dance as a team. Two blue-backed males engage in a coordinated jump dance in which both birds occupy a thin horizontal branch, one jumping and hovering while the other crouches on the branch, the other jumping and hovering when the first lands. As they dance, they vocalize. The dance may occur in the presence or absence of a female, the males seeming to "practice" when a female is not present. The dance ends when one of the three cocks bows before the hen, head turned, exposing the bright red top, blue back upraised. In the case of the swallow-tailed or blue manakin, up to three males dance in perfect coordination before a single female. The three dancers align themselves horizontally on a thin branch, shoulder to shoulder before the female, each male facing in the same direction. The male farthest from the female jumps up, inscribes a 180-degree angle, and lands nearest the female, next to the other males. He immediately turns around, so once again all three dancers face the same direction. A second dancer, again the farthest from the female, repeats the first dancer's performance, and so on. The dance happens rapidly, and David Snow has described it as a spinning "Catherine wheel" of dancing males, jumping, displaying, and vocalizing in total coordination. No other case of such elaborate team dancing is known for birds. The termination of the performance occurs when one of the males vocalizes sharply, the effect of which is to "turn off" the other two males. The dominant male then erects his red head feathers as he perches before the female. She and he fly off into the underbrush.

One species, the wire-tailed manakin (*Pipra filicauda*), adds yet another element to the roster of manakin courtship techniques. Males, which are black with yellow breasts and a red cap, have stiff tail feathers that terminate in long, delicate filaments. Wire-tailed males dance in teams of two, rather like the blue-backed species. However, when the dominant male approaches a female, he performs a twist display in which he rotates his posterior side to side, gently touching the female on her chin with his tail filaments. Females apparently respond well to this maneuver, for a female will typically slide toward a male to receive the tail brushing. This is the only known example of tactile stimulation among manakins, and it appears that the unique tail is the product of sexual selection (Schwartz and Snow 1978).

Why do several male manakins cooperate in courting a single female? Only one will get to mate with her. Some evolutionary theorists believed that the males were perhaps brothers, sharing the majority of each other's genes. Cooperative behavior could result in reproduction of many of one's own genes, which happen to be shared with one's brother, a example of possible kin selection (page 100). However, Mercedes Foster (1977), who studied *Chiroxiphia linearis*, found little evidence for a close relationship among cooperating males. Foster found that one male was consistently dominant over the others. Though the assemblage remained together throughout the breeding season and even from one year to the next, cooperating males were not brothers and did not behave altruistically toward one another. Rather, subordinates were biding their time until they could replace the dominant male. Foster hypothesized that one male, acting alone, could never succeed in attracting a female. Only by being part of a pair or trio could a male hope eventually to succeed. When a dominant male dies, it is quickly replaced by a subordinate who "trained" under it.

Why Do Pihas Scream, Bellbirds Clang, and Manakins Dance?

The bizarre results of sexual selection in cocks-of-the-rock, pihas, bellbirds, and manakins are evident, but what sorts of selection pressures were responsible for their evolution? Both David Snow (1976) and Alan Lill (1974) have suggested possible scenarios for the "release" of males from postcopulatory reproductive chores, thus initiating the male/male competition and pattern of female choice that resulted in both the gaudy plumages and elaborate courtship behaviors.

Snow emphasizes the importance of a diet almost exclusively of fruit. He points out that both bellbirds and manakins feed so heavily on fruit that they are easily able to secure adequate daily calories with only a small percentage of their time devoted to feeding. Fruit is both relatively abundant and easily collected. It does not have to be stalked or captured and subdued. The male bellbird or manakin has lots of time in which to clang or dance.

Lill, who studied manakins, agrees that a fruit diet is significant in the evolution of sexual selection in these birds. He places his emphasis, however, a bit more on nest predation. A largely frugivorous diet has metabolic costs as well as benefits (Morton 1973). Incubation time is relatively long and nestling growth rates slow in highly frugivorous birds because fruit is nutritionally not well balanced for a baby bird (low in protein but high in fat and carbohydrate). Lill argues that because of the slow development time brought about by a diet of fruit (recall oilbird, page 140), nest secrecy is of paramount importance. Heavy egg and nestling predation are best minimized by having only one bird, the cryptically colored female, attend the nest. A male's presence at the nest could actually be detrimental to raising young, since one bird can easily find sufficient food for the small brood (usually two nestlings), and a second bird might inadvertently reveal the presence of the nest to potential predators. Lill argues that it is to the advantage of both female and male for the male to stay away because male absence actually increases the probability of egg and

nestling survival. Males are dispensable, not needed for raising young. Lill concludes that this "male liberation" was followed by sexual selection and male "chauvinism" in the odd and varied forms described above.

Why Leks?

Given that a combination of factors have "released" males from attending nests, why have some species organized their courtship bouts in leks, especially the tightly clumped leks that are typical of manakins and cocks-of-the-rock? Several hypotheses have been suggested. One, called the "female preference model," argues that females prefer groups of males when making their selections of whom to mate with (Bradbury 1981). A male that stayed away from the lek would not attract any female, thus males have no choice but to join a lek. Another suggestion is that males might associate in leks because the lek area happens to be a place where females, for whatever reason, frequently occur. This idea, termed the *hotspot model*, presumes that leks form rather accidently, as males gather where they are most likely to encounter females (Emlen and Oring 1977; Bradbury and Gibson 1983). Both hypotheses place strong emphasis on female choice as causal to lek formation.

Beehler and Foster (1988) have critiqued both the female preference and hotspot models and have concluded that neither is sufficient to account for the evolution of lek mating systems. They offer yet another model, dubbed the *hotshot model*, that emphasizes the role of male-male dominance and interactions between dominant and subordinate males on a lek. Hotshots are individuals that control leks. Subordinates occasionally benefit from disrupting leks (recall Trail's observations of subordinate cocks-of-the-rock cited above), but mostly they bide their time while slowly advancing toward dominance. Beehler and Foster argue that novice males have little choice but to begin as subordinates, working their way up through the ranks to attain dominance status before they can reproduce. Subordinate birds congregate around the dominant cocks, since they have no hope for mating otherwise (recall Foster's observations on manakins cited above). The hotshot model places extreme emphasis on male-male interactions rather than male appearance and female choice. Dominance among cocks can be subtle, but it is real, and females will almost always select a dominant male with whom to mate. Beehler and Foster offer several predictions from their model. For instance, if all hotshot (dominant) cocks are removed from a lek, disruptions among the remaining males will increase (because none is dominant) and the lek may break up into several smaller leks, as new dominance rankings are established. Removal of the hotshots also predicts that females will visit the lek less and mate less until the lek restabilizes. These predictions are testable, and both the female preference and hotspot models predict different outcomes.

No model for lek evolution has as yet been shown to be conclusive. Indeed, evolutionary biologists routinely refer to the "paradox of the lek," an admission that leks are not easy to explain. The lek is by no means exclusively a tropical phenomenon. Leks occur among some shorebirds that nest in the arctic, among grouse that nest in grasslands, and among various other birds as well as some mammals.

Both the hotspot and hotshot models outlined above depend on proximate selection pressures operating now from within the environment. Prum (1994) has argued that evolutionary events dating back perhaps 14–35 million years ago, when frugivory may have permanently released males from parenting duties, may have set in motion an evolution of lek behavior such that lekking is now more readily explained by phylogenetic history than by any immediate selection pressures. Prum, perhaps a bit tongue in cheek, writes, "For manakins and a large majority of the lekking birds, the proximate answer to the 'paradox' of why they breed in leks is because their parents did; the ultimate answer lies in the ancient past when these behaviors initially evolved." For a general review of lekking, see Hoglund and Alatalo (1995).

Suboscines and Oscines

Of the more than 3,700 species of Neotropical birds, approximately 1,000 species are classified taxonomically as "suboscines." There are only about 50 suboscine species in all of the rest of the world, thus the Neotropics are unusual in harboring so many members of this group. The suboscines are part of the huge order of Passeriformes, or perching birds. Most passerines in the world are true oscines, which means that they have a complex musculature of the syrinx, the part of the trachea that produces elaborate sounds, such as the flutelike songs of various thrushes and solitares or the warbling of a canary. Suboscines, however, have a considerably less complex syringeal musculature and typically have far more limited singing abilities than true oscines.

Neotropical suboscines have undergone two major adaptive radiations, with the tyrant flycatchers, cotingas, and manakins representing one, and the woodcreepers, ovenbirds, true antbirds, ground antbirds, gnateaters, and tapaculos representing the other (Ridgely and Tudor 1994; Gill 1995). No one knows why suboscines have fared so well in the Neotropics, but the reason may simply be historical. At any rate, I have already discussed the tyrant flycatchers (page 102) as well as the cotingas and manakins (above). It is now time to turn our attention to the other major groups.

Insect-Arthropod Feeders

Several major groups of suboscine passerines utilize insects and other arthropods as their major food sources. These groups are among the most species-rich found anywhere. For instance, there are 218 species of ovenbirds (Furnariidae), 250 species of typical antbirds (Thamnophilidae) and ground antbirds (Formicariidae), 45 species of woodcreepers (Dendrocolaptidae), and an astonishing 393 species of tyrant flycatchers (Tyrannidae) (Parker et al. 1996). Of the above groups, only a few of the tyrannids venture to North America to nest. All others are entirely Neotropical.

Tyrannids, ovenbirds, and antbirds each represent a notable case of species diversification and adaptive radiation (chapter 4). Their primarily arthropod diets have probably provided major impetus in producing such diversity over evolutionary time. Eating insects per se does not cause species diversity nor speciation. It does, however, promote specialization, which produces

divergence and can, therefore, be a factor in speciation. Insects require catching; they do not seek predators, but, on the contrary, are well adapted to avoid predation through either cryptic or warning coloration or escape behavior. Each insect-eating bird tends to develop a particular pattern of feeding, and its size, behavior, and bill shape become refined to focus on a particular size range and type of prey (Fitzpatrick 1980a, 1980b, 1985). Prey characteristics provide major selection pressures in shaping evolution among avian predators.

Second, species compete against each other. The presence of many other insect-eating species could generate continuous diffuse competition within a species assemblage, keeping each species ecologically focused on doing what it alone does best.

Insect eaters can roughly be categorized by overall feeding method. These are (1) flycatching (tyrant flycatchers, puffbirds, and nunbirds), (2) bark probing and drilling (woodcreepers and woodpeckers), (3) foliage gleaning (ovenbirds and many antbirds), and (4) ant following (some antbirds, others).

Flycatching

Tyrant flycatchers have been discussed (page 102). There is, however, another group, less diverse but deserving of mention here. The puffbirds and nunbirds (family Bucconidae, order Piciformes) consist of thirty-two species, all Neotropical, that feed on insects and spiders captured by darting from a perch and snatching them in midair. They are not passerines but are most closely related to jacamars (page 217), toucans, and woodpeckers. The black-fronted nunbird (*Monasa nigrifrons*) is typical of the group. Ranging throughout the Amazon Basin, this ubiquitous, robin-sized, forest-dwelling bird is easily recognized by its black upper plumage and tail, gray breast, and tapered, slightly drooping, bright red-orange bill. It perches in the understory, upright on a horizontal limb, and, typical of "sit and wait" predators, hardly moves a muscle until it spots potential prey, at which time it springs into the air in pursuit. Nunbirds often form noisy groups and typically join large, mixed foraging flocks and often follow army ant swarms.

Puffbirds are large-headed, heavy-bodied birds so named for the puffed appearance of their feathers. Though some species are boldly patterned in black and white, most species are brownish or tan. Their cryptic plumage plus their stationary behavior when perched in the shaded forest understory make them easy to overlook. The white-whiskered or brown puffbird (*Malacoptila panamensis*) is a common bird of the forest understory from southern Mexico through Ecuador. It is dark brown above and has a tan breast with brown streaking. Close examination reveals red eyes and white feathering around the bill. Higher in the canopy is the white-necked puffbird (*Notharctus macrorhynchos*), a larger bird with bold black and white plumage that ranges all the way from southern Mexico to Argentina. Both species have large rictal bristles, hairlike feathers around the base of the bill, which probably aid in capturing aerial insects. These two puffbird species are generally segregated vertically, the white-whiskered in the understory and the white-necked in the canopy. Such a distribution may reflect the outcome of both specialization for food capture

Brown puffbird

(canopy insects are not the same as those of the understory) and interspecific competition (since each species inhabits a different vertical area, they do not directly compete with each other).

Nunbirds and puffbirds excavate nests in termite mounds or in the ground. A puffbird pair seems undisturbed by the presence of an observer when the two birds excavate a termitary and tolerate termites crawling over them as they incubate. Those that burrow make very long nest tunnels (Skutch 1983).

Bark Drillers and Probers—Woodpeckers and Woodcreepers

Woodpeckers (family Picidae, order Piciformes) both probe and drill bark, extracting insects, mostly larval, by using their extremely long, extrusible, barbed tongues. They hitch vertically up tree trunks, their bodies supported by stiff tail feathers that act as a prop. The world's woodpeckers are treated by Short (1982), and Skutch (1985) provides a general natural history of woodpeckers.

Woodpeckers occur globally (except Australia) wherever there are trees, and thus many are temperate zone species. Neotropical woodpeckers vary in size from the 35.6-cm (14-in) ivory-billed types (genus *Campephilus*) to the diminutive 8.9-cm (3.5-in) piculets (genus *Picumnus*). The world's largest woodpecker is the 55.9-cm (22-in) imperial woodpecker (*Campephilus imperialis*), now possibly extinct from persecution and extreme habitat loss (Collar et al. 1992), but which formerly ranged through montane oak-pine forests of the Sierra Madre Occidental in western Mexico. Tropical woodpeckers range in color from bold black with red crest, to greenish olive, to soft browns and chestnut. Some species have horizontal black and white zebra stripes on their backs with varying amounts of red on the head. One species, the brilliant cream-colored woodpecker (*Celeus flavus*) of varzea forests in northern Amazonia, is bright yellow-buff with brown wings and a black tail. Another species, the boldly patterened yellow-tufted woodpecker (*Melanerpes cruemtatis*), named for its distinct facial stripe, is widespread and commonly seen along forest edge.

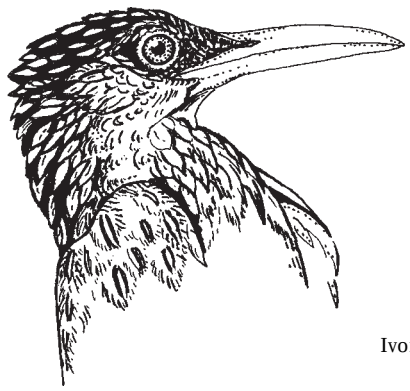
Neotropical woodpeckers excavate roosting and nesting cavities that are often usurped by other species. Skutch (1985) observed a group of collared aracaris (*Pteroglossus torquatus*) easily evict a pair of pale-billed woodpeckers (*Campephilus guatemalensis*) from their nest cavity. Skutch also reports that two

tityra species steal cavities from several woodpecker species. Skutch portrays the 17.8-cm (7-in) tawny-winged woodcreeper (*Dendrocincla anabatina*), which attacks and forces several woodpecker species from their cavities, as "the most consistently aggressive bird that I have watched in tropical America."

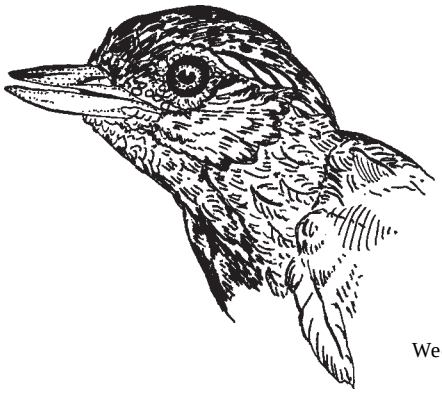
Woodcreepers (family Dendrocolaptidae, order Passeriformes) look superficially like woodpeckers but bear no close evolutionary relationship to them. The anatomical similarity is a case of evolutionary convergence brought about by similar ecologies. Like woodpeckers, woodcreepers have stiff tail feathers that prop them vertically against a tree trunk. They tend to climb upward, often spiraling around the trunk. Woodcreepers evolved from the ovenbirds (Furnariidae), to which they are so closely related that some authorities consider them to be a subfamily (Dendrocolaptinae) within the Furnariidae (Raikow 1994). All woodcreepers have become bark-probing specialists that feed quite differently from woodpeckers. A woodcreeper moves methodically around the trunk, probing into crevices, poking its bill into epiphytes, and generally removing insects, spiders, and even an occasional tree frog. They rarely peck into the trunk, instead using their long bills as forceps to pick off prey. Woodcreepers may also join mixed flocks that follow army ant swarms (see below).

Like furnarids, woodcreepers are colored soft shades of brown and rufous. Many have various amounts of yellowish white streaking on breast, head, and back. The overall size of the bird, its bill size and shape, and its streaking pattern usually separate one species from another. The smallest is the 15.2-cm (6-in) wedge-billed woodcreeper (*Glyphorynchus spirurus*), which has a very short but sharply pointed bill. Several species reach about a foot in length, and the largest, the long-billed woodcreeper (*Nasica longirostris*), a sensational inhabitant of varzea forests, reaches just over 35.6 cm (14 in). Among the oddest of the group are the five species of scythebills (genus *Campylorhamphus*), whose extremely long, downward-curving bills are used to probe deeply into bromeliads and other epiphytes.

Many woodcreepers are ant followers, joining antbirds and other species to feed on insects and other animals disturbed by the oncoming army ants. With differing body sizes and bill shapes, several species of woodcreepers coexist and feed with little or no apparent competition. At one army ant swarm in



Ivory-billed woodcreeper



Wedge-billed woodcreeper

Belize, I observed six woodcreeper species. Two were large, three medium-sized, and one small.

Woodcreepers are common not only in rainforests but also along forest edges, disturbed jungle, and dry forests. Although suboscines, some species are highly vocal, their songs consisting of pleasant, melodious, whistled trills.

Foliage Gleaners—Ovenbirds

The ovenbirds (family Furnariidae, order Passeriformes) are "little brown birds" of the American tropics. All ovenbirds are generally nondescript, their plumage basically brown, tan, buffy, or grayish. Identification of individual species can be very difficult, since differences among species are often subtle and hard to see in the field. This highly diverse family occurs not only in lowland forests but in all types of habitat ranging through cloud forest, Patagonian pampas, Andean paramos and puna, and coastal deserts and seacoast. Many kinds, especially the spinetails, are common along forest edge and disturbed areas, and many are found in dry forests. The family takes its common name, ovenbird, from several species (most notably the horneros, genus *Furnarius*) that construct ovenlike, dome-shaped mud nests. Not all ovenbirds build such structures. Some species nest in natural cavities or in mud banks, and some make basketlike structures of twigs and grass. The thornbirds (genus *Phacellodomus*) construct large and conspicuous globular nests of sticks that are easy to see in dry forest. The evolutionary trends of furnarids are analyzed by Fedducia (1973). For a general natural history of the group, see Skutch (1996).

Ovenbird species have among the oddest common names of any birds. One may encounter a xenops, a recurvebill, a foliage-gleaner, and a leafscraper (not to be confused with leaftossers). There are also woodhaunters, tree-hunters, treerunners, palmcreepers, and earthcreepers (not to be confused with streamcreepers). There are barbtails, spinetails, tit-spinetails, softails, and thistletails (not to be confused with prickletails). Finally, there are thornbirds, miners, cinclodes, horneros, and canasteros. You will need patience and skill to sort out ovenbirds, as they are a challenging group.

All ovenbird species are basically insectivorous, but as a family they do not show the bill diversification that is so evident in woodcreepers. Rather, ovenbirds tend to be habitat- and range-specific and develop specialized feeding behaviors. Some, like the ground-feeding leafscrapers and leaftossers, systematically probe among the litter. Their bodies are chunky and almost thrushlike in shape. Others, like the slender foliage gleaners, search actively among the leaves, ranging throughout canopy and understory. Spinetails dart quickly from bush to bush while the small xenopses hang chickadee-like, searching the underside of a leaf. Ovenbirds of various species are common members of mixed foraging flocks.

Ant Followers—The Antbirds *Figures 141, 142*

Antbirds (families Thamnophilidae and Formicariidae, order Passeriformes) include the antbirds, antshrikes, antwrens, antvireos, antthrushes, and antpittas. Until recently, all antbirds were placed in the family Formicariidae, but analysis of DNA patterns in the group resulted in splitting the family into two. About 75% of the antbirds are placed in Thamnophilidae, referred to as typical antbirds, while the other 25%, the anthrushes and antpittas, are placed in Formicariidae, the ground antbirds (Ridgely and Tudor 1994). Antbirds reach their peak species richness in Amazonia, where up to thirty or forty species may occur together. The name antbird, or formicarid, comes from the army ant–following behavior of some species. However, most antbirds do not follow army ant swarms. Some never do, some occasionally do, and some virtually always do. The latter group is often termed the "professional antbirds." For an introduction to the natural history of antbirds, see Skutch (1996).

Typical antbirds (Thamnophilidae) are more colorful than ovenbirds, with many sexually dimorphic species. Males are often boldly patterned in black and white. Some, like the widely distributed and common barred antshrike (*Thamnophilus doliatus*), are zebra-striped. Others are grayish black with varying amounts of white patterning on wings, breast, and flanks. Still others are chestnut or brown. Females tend to be rich brown, tan, or chestnut. Some antbirds have an area of bare blue or red skin around the eye, and in some species iris color is bright red.

Most antbirds are foliage gleaners, picking and snatching arthropods from

Great antshrike

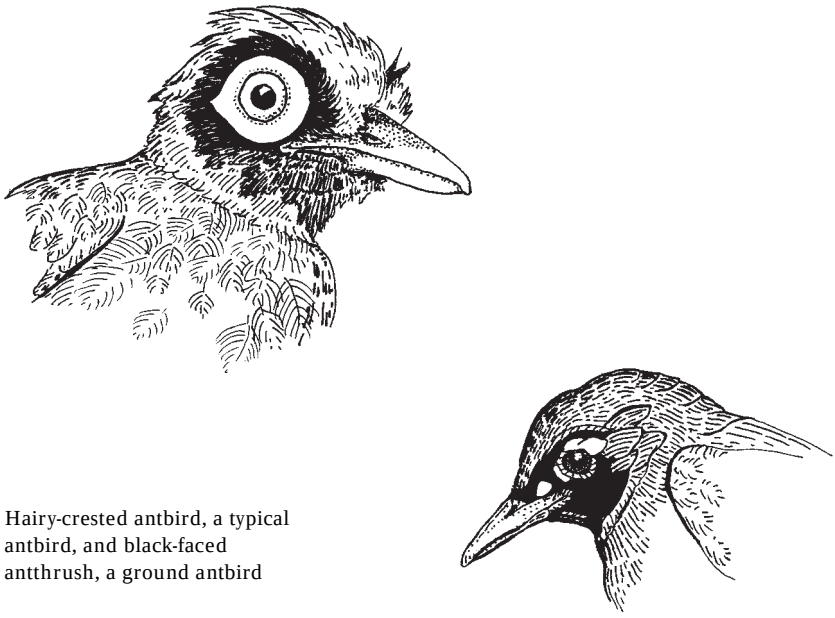
foliage, and some capture insects on the wing. They forage at all levels from the canopy to the litter on the forest floor. They typically form mixed species flocks with other birds, and various antbird species tend to feed at specific heights above the forest floor. Mixed flocks of up to fifty bird species move through Amazonian lowland forests, of which twenty to thirty species may be antbirds. Certain species such as the flycatching antshrikes (genus *Thamnomanes*) occupy the role of "central" species in the flock (Willis and Oniki 1978). These antshrikes are highly vocal and act as sentinels, warning the others of impending danger should they spot a forest falcon or other potential predator (see above, tanagers). Willis and Oniki describe the relationship among the various mixed flock species as a "casual mutualism." They each benefit somewhat from the other's presence.

There are twenty-eight species of professional ant-following birds, each of which makes its livelihood by capturing arthropods scattered by advancing fronts of army ants. In addition, other bird species frequently, but not always, can be found accompanying the ants. There are even some butterflies that associate with army ants to feed on the bird droppings (Ray and Andrews 1980). In northern Amazonia, the white-plumed antbird (*Pithys albifrons*) is among the commonest professional antbirds. This bird is unmistakable, its face dominated by a tall white crest, its head black, its back and wings blue-gray, and its breast and tail rich chestnut in color. The spotted antbird (*Hylophylax naevioides*), the bicolored antbird (*Gymnopithys leucaspis*), and the black-faced antthrush (*Formicarius analis*) are among the most devoted ant followers in Central America. Where these three are found together, there are surely army ants about (Willis 1966, 1967).

Ant followers rarely feed directly on army ants. It is suspected that the high formic acid content of these insects deters birds from eating them. Instead, antbirds feed on anything from insects to small lizards scared up by the oncoming ant columns. Two army ant species, *Eciton burchelli* and *Labidus praedator*, are the ants most frequently followed. Birds such as woodcreepers, ovenbirds, motmots, certain tanagers, and other "less professional" antbirds come and go as part of the ant-following avian assemblage, but the professional antbirds always stay with the ants. Only when breeding do they become territorial and cease to follow ants for a time. Even then, they will quickly orient to army ant swarms within their territories.

Species such as the spotted and bicolored antbirds feed actively in trees and undergrowth, while the black-faced antthrush walks sedately on the forest floor. With the stature of a small rail, the black-faced antthrush, which can be found throughout lowland forests in Central and much of South America, walks with its short tail cocked upward and head held up and alert. It is easy to imitate its whistled, downscaled "chew, chew, chew, chew" call. In Trinidad, I called one almost to my feet as I whistled and it answered.

Antbirds tend to mate for life. Both male and female are active nest builders (Skutch 1969, 1996). One species, the ocellated antbird (*Phaenostictus mcleannani*), forms clans. Sons and grandsons of a pair return to the breeding territory with mates to form clans, and a clan will occasionally attack another intruding clan (Willis and Oniki 1978). Antbirds also sometimes intimidate migrant thrushes that attempt to gather at antswarms (Willis 1966).



Hairy-crested antbird, a typical antbird, and black-faced antthrush, a ground antbird

Birds of Prey

Birds of prey are diverse and abundant in the Neotropics. They range in size from the tiny bat falcon (*Falco rufigularis*) and pearl kite (*Gampsonyx swainsonii*) to the majestic harpy eagle (*Harpia harpyja*). Open areas, such as savannas, are excellent for searching out many of the larger species, since some habitually soar on thermal currents rising from the hot ground. Inside forests, birds of prey can be elusive. Many, such as the forest-falcons (genus *Micrastur*), sit motionless on a branch waiting for an opportunity to attack would-be prey.

New World Vultures *Figures 144, 154*

Five vulture species, the black (*Coragyps atratus*), turkey (*Cathartes aura*), lesser yellow-headed (*Cathartes burrovianus*), greater yellow-headed (*Cathartes melambrotus*), and king (*Sarcoamphus papa*), can often be seen in various combinations in the sky together over rainforests and savannas. Not strictly raptors, these birds rarely if ever kill prey (black vultures are alleged to kill small animals) but rather devour animals that are carcasses, already deceased.

The black vulture is one of the most ubiquitous birds of the Neotropics, ranging from Argentina well into North America. Black vultures commonly congregate in vast numbers around garbage dumps and are thus common city dwellers, urbanite birds that work as sanitary engineers thoughout much of Latin America. Turkey vultures are named for their red heads, giving them a superficial resemblance to turkeys. Turkey vultures fly with wings distinctly

upraised, in a dihedral pattern. One hawk, the zone-tailed (*Buteo albonotatus*), flies very much like a turkey vulture, a possible form of behavioral mimicry, since the plumage of the two species is generally similar. Perhaps a zone-tailed hawk can fly closer to potential prey if it's mistaken for a carrion-eating turkey vulture. Two other species, the greater yellow-headed and lesser yellow-headed, are closely related to the turkey vulture but have yellow-orange heads, not red heads. The greater yellow-headed is most common flying over forests and along watercourses. It is common throughout most of Amazonia. The lesser yellow-headed avoids closed forests, being common on savannas. The king vulture is the largest and most spectacularly plumaged Neotropical vulture. It is black and white, and its head is adorned with bright (but bizarre-looking) orange wattles.

Kites

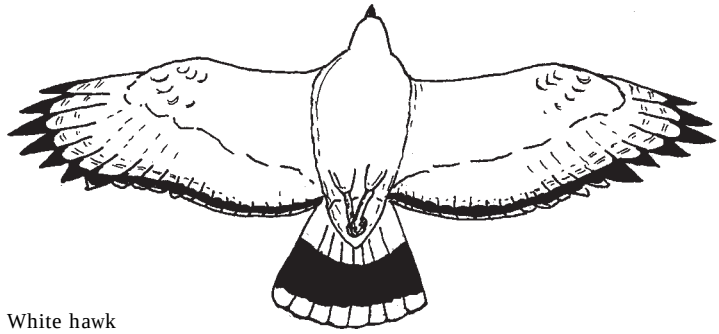
Eleven species of kites gracefully skim Neotropical skies searching out small animals such as mice, birds, lizards, and arthropods. Kites have sharply hooked bills, a trait particularly evident in the snail kite (*Rostrhamus sociabilis*) and the hook-billed kite (*Chondrohierax uncinatus*). The snail kite specializes on one food source, large marsh snails, which it adeptly removes from the protective shell with its sharply hooked bill. Another common kite is the white-tailed (*Elanus leucurus*), often seen hovering over open fields and savannas seeking its small animal prey. The most graceful flier among the kites is the swallow-tailed (*Elanoides forficatus*), a slender black and white kite with a deeply forked tail. The 22.9-cm (9-in) pearl kite (*Gampsonyx swainsonii*) is one of the smallest tropical birds of prey. Mostly black with white underparts, it has a buffy forehead and face, and a white or rufous neck. Like most kites, it frequents savannas.

Hawks, Falcons, and Caracaras *Figures 145, 154*

Forty species of hawks (family Accipitridae, order Falconiformes) can be found in the Neotropics. Included here is a mere sample.

The crane-hawk (*Geranospiza caerulescens*) is a slender, blackish gray inhabitant of wet savannas, mangroves, and swamps. The bird has exceptionally long, bright orange legs. It feeds both on the ground and in trees and has been reported to assume odd postures, such as hanging upside down, when probing epiphytes and branches for amphibians and reptiles. Another savanna species is the savanna hawk (*Heterospizas meridionalis*), which tends to be seen walking about on the open ground on its long yellow legs. It is largely rufous, with black tail and wing tips and dark barring across its breast.

The splendid white hawk (*Leucopternis albicollis*) is apt to be seen soaring on warm thermals over forests. As its name implies, it is virtually all white but for a black band across the tail and black on the wings and around the eyes. Other soaring hawks include the common black hawk (*Beautiogallus anthracinus*) and great black hawk (*B. urubitinga*). Both of these birds are almost all black but for white tail bands.



White hawk

The black-collared hawk (*Busarellus nigricollis*) is one of the most elegantly plumaged Neotropical birds of prey. Warm rufous in overall color, it has a white head and black throat, outer wings, and tail. This hawk has a distinct shape when seen overhead because its wings are quite wide and tail short. Found around marshes, it feeds mostly on fish.

The roadside hawk (*Buteo magnirostris*) is very well named. The hulking shape of this grayish rufous hawk can be seen perched on cecropias, palm trees, ceibas, and telephone poles all along tropical roads. This abundant and widely distributed species is also variable in plumage, and thirteen races have been recognized.

Falcons are small, speedy birds of prey known for their aerial agility. With long tail and sharply pointed wings, falcons are quick to pursue and capture rodents, small birds, and insects. One species, the diminutive bat falcon (*Falco rufigularis*), specializes in capturing bats at dawn and dusk. It is largely dark blue, with a white throat and orange on the thighs and lower belly.

The laughing falcon (*Herpetotheres cachinnans*) is often seen perched atop a snag along a forest edge, cleared field, or savanna. Very buffy on the head,

Bat falcon

neck, and breast, the laughing falcon has dark brown wings, back, and tail, with a black band through the eyes and around the back of the neck. Named for its penetrating loud call, these birds prey on snakes and other animals spotted by patiently sitting for long periods.

Forest falcons (genus *Micrastur*) are grayish falcons that skulk inside forests and are generally difficult to find. They are very inconspicuous, sitting motionless in the deep forest shade.

The yellow-headed caracara (*Milvago chimachima*) is common and conspicuous, often seen in groups along rivers and forest edges. Caracaras, like vultures, feed on carrion and, hence, are frequently encountered along roadsides. Yellow-headed caracaras are slender birds, buffy yellow on head, breast, and belly with blackish brown wings and tail. Several other caracara species also inhabit the Neotropics.

Crested caracara

Hawk-Eagles and Eagles

The largest Neotropical birds of prey are eagles and hawk-eagles. There are three species of hawk-eagles, each of which has a crest atop its head. The ornate hawk-eagle (*Spizaetus ornatus*) has a bright orange neck and a tall black crest. The black hawk-eagle (*S. tyrannus*) is uniformly dark, and the black-and-white hawk-eagle (*S. melanoleucus*) is black above and white below. Hawk-eagles are soaring hawks, usually seen above the canopy making circles high overhead.

The rare harpy eagle (*Harpia harpyja*) certainly ranks among the most splendid of Neotropical birds. In fact, I would argue that it is one of the most impressive avians on the planet. It ranges from southern Central America throughout Amazonia but is very difficult to find over most of that vast territory. This huge predator is just over a meter tall, with extraordinarily thick, powerful legs and feet. Mostly gray on face and belly, its wings, back, and upper breast are black. The head sports a tall blackish gray crest. No bird of prey equals the size of a harpy. Nonetheless, it is secretive, tending not to soar, and thus is difficult to

Harpy eagle

see well. Harpys feed on monkeys and sloths, including the largest species, captured by a swift pass, legs extended, grabbing the prey from its tree.

Strictly a forest dweller, now unfortunately quite rare over most of its range, the magnificent harpy eagle is a top prize for anyone seeking unique tropical birds. I visited a harpy nest at Imitaca Forest in Venezuela, seeing a nearly full-grown immature and an adult female. This forest was being heavily logged, and the long-term success of harpy eagle in this region is, I fear, dubious. Recent work done in the area with radiotelemetry, involving actually tracking the birds by satellite (Alvarez-Cordero et al. 1996), may aid in developing a management plan to ensure that harpy eagles have adequate protection and sufficient habitat. One promising result of this work is that some harpy eagles do not abandon an area even after years of selective logging.

Owls

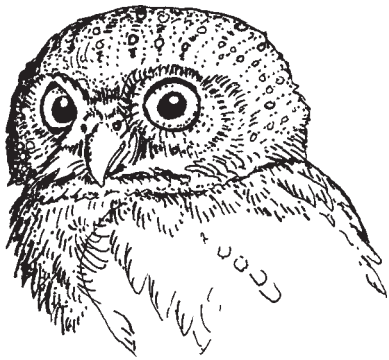
Owls (order Strigiformes, families Tytonidae [barn owls] and Strigidae [typical owls]) are nocturnal birds of prey. Over two dozen species occur in the Neotropics. Below are several of the most wide-ranging.

The spectacled owl (*Pulsatrix perspicillata*) is the largest Neotropical owl, reaching 48.3 cm (19 in) in length. It is buffy yellow on the lower breast and belly, with dark brown back, wings, tail, and head. A dark brown band crosses its upper breast, and its bright yellow eyes are highlighted by white, giving the bird its name. Spectacled owls make a deep, hooting sound and can be easily attracted to tapes of their voice.

The black-and-white owl (*Ciccaba nigrolineata*) is just that. Its breast, belly, back, and face are barred black and white. This species, which feeds heavily on bats, is also responsive to tapes of its voice.

The mottled owl (*Ciccaba virgata*) is warm brown and tan with dark brown eyes. Unlike its black and white relative, it does not tend to be attracted to tapes.

During the daytime, it is not uncommon to see a small pygmy-owl (genus *Glaucidium*) with its bright eyes staring as it perches atop a snag. Several species of these 15.2-cm (6-in) owls occur in the tropics, but the most common is the ferruginous pygmy-owl (G. *barasilianum*), so named for its reddish brown plumage.



Amazonian pygmy-owl

North American/Neotropical Long-Distance Migrant Birds

Within the past two decades, research has burgeoned on Neotropical migrant birds, species that migrate north to nest in North America and then migrate south to winter in the Neotropics. With the realization that some species of Neotropic long-distance migrants are experiencing alarming declines in population (Terborgh 1989; Askins et al. 1990), the need to study these birds thoroughly on both their breeding grounds and their wintering grounds (as well as the migratory route in between) became a rallying cry for field ornithologists, me included. Below, I summarize some of what we have learned. For additional information, see Keast and Morton (1980), Hagan and Johnston (1992), Rappole (1995), and DeGraaf and Rappole (1995).

During autumn, 338 species, or about 52% of all North American migrant bird species, fly to wintering areas in the Neotropics (Rappole et al. 1983; Rappole 1995). This influx may total somewhere between five and ten billion birds. The majority winter in Central America, but many also winter in South America and the Caribbean Islands, especially the Greater Antilles. The density of North American migrants is high in the Neotropics from November through March. Not only are there many yearling birds in addition to adults, but the actual land area of Central America is less by about a factor of eight, compared with available nesting area in North America. Migrants ranging from Swainson's Hawks (*Buteo swainsoni*) to Least Flycatchers (*Empidonax minimus*) are packed into tropical America, and their abundance is evident.

Many North American migrants are from families that evolved in the Neotropics. Tyrant flycatchers, hummingbirds, tanagers, orioles, and wood warblers all originated in the Neotropics, though their speciation patterns may have been much affected by their breeding ranges in North America. Long-distance migrant species represent the relatively few that ventured northward

into the temperate zone, extending their ranges, perhaps because the northern summer presents an abundance of proteinaceous insect resources for the rearing of young, longer days in which to feed, fewer predators, plus the availability of abundant nesting sites.

The host of Neotropic migrant landbird species, when on their tropical wintering grounds, use virtually all available habitat types. They can be found, often abundantly, in dry forest, mangrove forest, montane forest, and rainforest. Brushy successional areas are habitat for many species, such as gray catbird (*Dumetella carolinensis*), northern yellowthroat (*Geothlypis trichas*), and yellow-breasted chat (*Icteria virens*). Rainforests provide habitat for wood thrushes (*Hylocichla mustelina*), Kentucky warblers (*Oporornis formosus*), American redstarts (*Setophaga ruticilla*), and other wood warblers. But many of these species also utilize successional areas.

Some Neotropical migrants, like the black-and-white warbler (*Mniotilta varia*), range very widely in the Neotropics, occupying many kinds of wintering habitat. Black-and-white warblers, unique among wood warblers for their habit of foraging for arthropods on bark, somewhat like nuthatches, are extraordinary as they range widely and frequent virtually any terrestrial habitat. They can be found in oak-pine forests, in mangroves, in plantations, along any kind of forest edge and successional scrub, in dry forests, and in interior rainforests in western Mexico, Antilles and West Indies, all parts of Central America, and northern South America (Kricher 1995). In general, other migrants are more restricted (some much more so), putting them at risk should they suffer from habitat loss. An example is the cerulean warbler (*Dendroica cerulea*), which winters along a narrow altitudinal belt between 620 and 1,300 m (2,034–4,265 ft) in the eastern Andean foothills of Colombia, Ecuador, and Peru (Robbins et al. 1992). Unfortunately, this area has been and continues to be heavily deforested from conversion to agriculture, including cocaine fields, putting the future of this species at some risk.

Many North American migrants eat a diet high in fruit while in the tropics. Baltimore and orchard orioles (*Icterus galbula* and *I. spurius*) and scarlet and summer tanagers (*Piranga olivacea* and *P. rubra*) feed in cecropia and fig trees among mixed flocks of euphonias, Neotropic tanagers, and honeycreepers. Leck (1987) cites studies indicating that fruit availability is often high on disturbed habitats. Many researchers have noted that abundance of migrants is high in successional areas and young forests. Higher fruit availability may be one reason why migrants favor such areas. North American migrants are believed to be important fruit consumers and seed dispersers, especially for plants that typically grow in disturbed areas (Wheelwright 1988). Some Neotropical migrant species, such as the orchard oriole and Tennessee warbler (*Vermivora peregrina*), which feed on nectar, have been recognized as potential pollinators while on their wintering grounds.

Given that North American migrants spend perhaps the majority of their year in the Neotropics, it is not surprising to learn that some are relatively specialized when on their wintering grounds. For example, the worm-eating warbler (*Helmintheros vermivorus*) spends about 75% of its time foraging for arthropods that are hidden within dead leaf clusters, which abound in Neo-

tropical forest and forest edge. *Cecropia* leaves alone are huge and curl when they drop, forming ideal habitat for arthropods. This wood warbler is specialized to reach deeply into the cavelike curled leaves. On its breeding grounds it spends about 75% of its time gleaning insects from live leaves (Greenberg 1987a, 1987b).

The degree to which North American migrants interact with Neotropical resident birds is by no means certain and probably varies considerably depending on the ecology of the birds. Willis (1966), working on Barro Colorado Island, noted that North American thrushes are prevented by resident antbirds from access to swarms of *Eciton*. Many other researchers, however, argue that North American migrants may compete relatively little, if at all, with resident species. Much research remains to be done on this question.

My colleague William E. Davis, Jr., and I (Kricher and Davis 1986, 1987, 1992) have investigated winter site fidelity among migrant species in southern Belize. We, along with many others working throughout the Neotropics, have shown that such species as the wood thrush, ovenbird (*Seiurus aurocapillus*), Kentucky warbler, and gray catbird occupy exactly the same locations from one winter to the next. Although these birds migrate north to nest, they return in the fall to precisely the same local wintering area used the previous year, a behavior called winter site fidelity. We placed fine mesh nets (called mist nets) in selected locations in both successional areas and rainforest. We captured some of the same banded individuals in the same nets, at the same locations, over three succeeding winters.

As one might expect, winter site fidelity often means that the birds are territorial, defending winter sites. Work by John Rappole and others has shown this to be true, at least for some species. Wood thrushes, for example, establish and defend winter territories, using subtle vocalizations and body posturing. Each wood thrush has its own turf within the rainforest. Survivorship among "floater" wood thrushes, birds that have not succeeded in acquiring and holding a winter territory, is diminished (Rappole et al. 1989; Rappole et al. 1992; Winkler et al. 1990). In another example, observations suggest that male hooded warblers (*Wilsonia citrina*) obtain territories inside interior forest and females are territorial in disturbed, successional habitats (Rappole and Warner 1980). Other researchers have also reported high site loyalties and as well as winter territoriality for other migrant species (Hagan and Johnston 1992; Rappole 1995).

Though many North American migrant species inhabit disturbed areas and montane forests, many also inhabit mature rainforest, and the degree to which deforestation (see chapter 14) may be eliminating wintering sites is an increasing concern. Some migrant species are now rare in North America, possibly due to loss of their wintering areas. The Kirtland's warbler (*Dendroica kirtlandii*) nests only in successional jack pine forests in Michigan. The bird was once probably more widely spread and could possibly occupy a larger nesting area today, but winter habitat loss in the Bahamas gives it no place where large populations could winter. The Bachman's warbler (*Vermivora bachmanii*) is an extremely rare nester in southern hardwood swamps. Loss of cane habitat in Cuba, where the bird winters, is thought to have been responsible for its

populational demise. On the other hand, increase in second-growth habitat could actually favor such species as chestnut-sided warbler (*Dendroica pensylvanica*) and indigo bunting (*Passerina cyanea*). The effect of tropical deforestation on migrants eludes a simple answer. Like virtually all of tropical ecology, simple answers to complicated questions are just not there.

Male bare-crowned antbird