

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 genera (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 extraordinarily 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 Pihás 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 pihás 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 pihás, 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 pihás, 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.

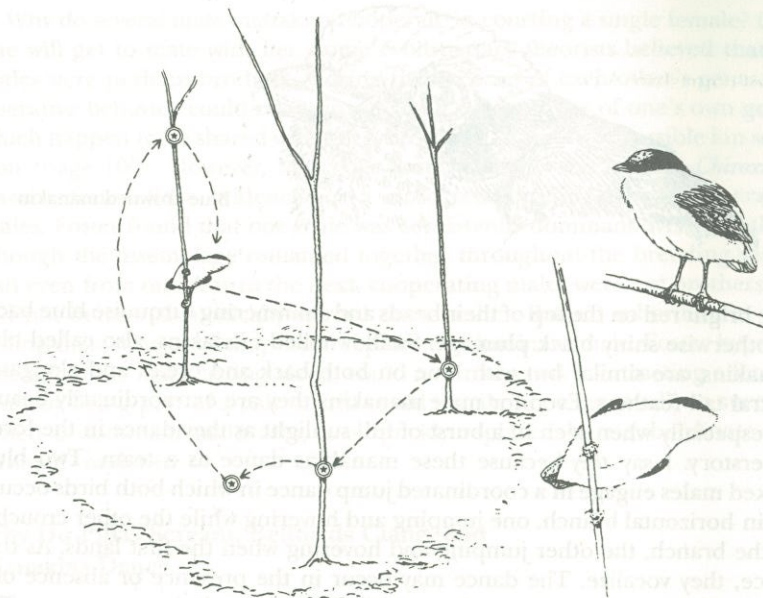
The Dancing Manakins

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 *Chiroxi-phia*) 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, an 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 Pihás Scream, Bellbirds Clang, and Manakins Dance?

The bizarre results of sexual selection in cocks-of-the-rock, pihás, 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 accidentally, 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 Høglund 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 solitaires 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 patterned yellow-tufted woodpecker (*Melanerpes cruentatus*), 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.”

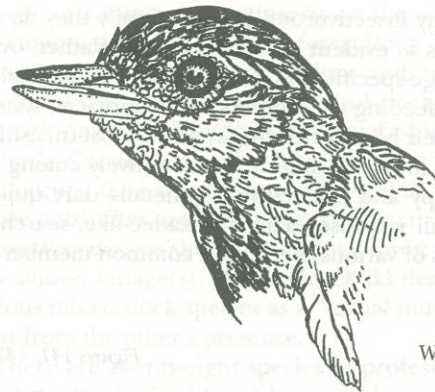
Woodcreepers (family Dendrocolaptidae, order Passeriformes) look superficially like woodpeckers but bear no close evolutionary relationship to them. The anatomical similarity is a case of evolutionary convergence brought about by similar ecologies. Like woodpeckers, woodcreepers have stiff tail feathers 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 (Rai-kow 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, treehunters, treerunners, palmcreepers, and earthcreepers (not to be confused with streamcreepers). There are barbtails, spinetails, tit-spinetails, softtails, 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 leaf-tossers, 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

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 antthrushes 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 formicariid, 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

Figures 141, 142

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 (*Hylomyphax naevioides*), the bicolored antbird (*Gymnopathys 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

