

HYLOPHYLAX, *HYPOCNEMOIDES* AND *MYRMODERUS*
(AVES, FORMICARIIDAE) AS ARMY ANT FOLLOWERS

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ABSTRACT

Hylophylax naevia of moderately dense forest undergrowth and *H. punctulata* of open swamp undergrowth tend to sally for arthropods in low foliage rather than sally to the ground among large ant-following antbirds. They and related *Hypocnemoides melanopogon* of swamp understory edges are also limited by their microhabitat niches in following ants. *Myrmoderus ferrugineus* and *M. loricatus*, ground-walking small antbirds seemingly derived from *Hylophylax*, follow ants infrequently, probably because ants, large ant-following birds, and predators would attack them if they did so.

Some antbirds of the genus *Hylophylax* regularly capture flushed arthropods over swarms of army ants (Willis, 1972; Willis & Oniki, 1978; Willis, in press). Here, in the nineteenth report of a series on occasional ant followers, I note observations of related species of the genera *Hylophylax*, *Hypocnemoides*, and *Myrmoderus*

RESULTS

1. *Hylophylax naevia* (Spot-backed Antbird) was recorded at 37 scattered ant raids (1 Umbria, Putumayo, and 6 Mitú, Vaupés, Colombia; 1 Zatzayacu, 5 Limoncocha, 3 Yaapi, and 2 Putuimi, Ecuador; 2 San Alejandro and 1 Andoas, Loreto, Peru; 6 Coatá, 9 Maloquinha, and 1 Miritituba, Brazil). All were raids of *Eciton burchelli* except for a *Labidus praedator* raid with 2 birds at Putuimi and 3 such raids with a total of 4 birds at Mitú. *E. burchelli* raids with 2 birds each were these: 1 Zatzayacu, 1 Limoncocha, 2 Yaapi, 2 San Alejandro, 1 Andoas, 4 Coatá (plus 1 with 3 birds), and 2 Maloquinha (plus 1 with 3 birds). Occasionally *naevia* were irregularly present over 6 hours, but most wandered past and left raids within a few minutes.

This species, which weighs only 13.6 g (male at Maloquinha; cloacal temperature 42.7° C) in contrast to 17.5 g for *H. naevioides* across the Andes, rarely follows ants. It wanders low (27-9-3-1 records 0-4 m up, by 1-m intervals, in various regions) on slender (4-1 records at 0-2 cm diameter) vertical (6) or inclined (2) sprouts and bushes in the moderately open forest understory, retreating to nearby denser cover when disturbed. Unlike *naevioides*, it infrequently sallies to the ground for

prey: in various regions, there were 4 such records for *naevia* in contrast to 10 records to above-ground sites (4 foliage, 3 lianas, 2 air, 1 log). It sometimes flies a short distance and pecks prey off low foliage (8 records), a liana (1), trunk (1), or other (1) vegetation. Short periods of standing and looking about lead to flights to nearby prey above the ground, a prey-searching method that requires an understory that is neither dense enough for gleaning relatives (such as *Myrmotherula huxwelli*) nor open enough either for the long-distance sallies of other relatives (notably *Hylophylax poccilnota*) or for significant reduction in prey density. At Maloquinha, a *poccilnota* supplanted a *naevia* and a *Rhegmatorhina berlepschi* displaced one, while a *R. hoffmannsi* plus a *poccilnota* displaced a *naevia* at Coatá. Active competition from numerous species of Amazonian ant-following antbirds may keep *naevia* from becoming such a ground-sallying and regular ant follower as *naevioides*, thereby forcing *naevia* to maintain its small size and short-distance flycatching abilities. Little prey is flushed by ants up on the shrubs of the forest understory, perhaps accounting for the fact that *naevia* follows ants infrequently.

Other than in its foraging behavior, *naevia* closely resembles *naevioides*. The calls are similar (in *naevia*, the «song» is a descending *bee tiksee tiksee tiksee*, sometimes alternating with *peup* «chirps» as a «serpentine-song»; «chirring» is a rattling *de-e-e-e-ee*; «chipping» is a set of 1-6 *peep* notes at the fast rate of 4/sec; «bugling» is a *chwit* call; «snarling» is a nasal *wrieeeh*; young «peepsing» *chut-chut-chut pee pec pee pee* and «squeak» *chawaihh* notes), except that all the calls of *naevia* seem faint and sibilant or high-pitched compared to calls of its larger relative *naevioides*. In alarm, it flicks the tail up to the line of the body just as does *naevioides*. In disputes, the white back and white-tipped tail are spread as in *naevioides*, although the lighter *naevia* pivots back and forth more often. The white breast flashes with each *tiksee* phrase in a song, as in *naevioides*. Pairs chirp and «faint-sing» to each other as they wander separately near or away from ants.

H. naevioides is common in many forest types and understory types west of the Andes, for it forages largely on the ground. *H. naevia*, requiring moderately dense low foliage, is absent both in dry and relatively open forest and in dense ground cover or open flooded zones along swamps. I have seen it in mossy forests at 900-1100 m on the eastern slope of the Andes (Mera and Zatzayacu, Ecuador), and at scattered localities east of the Andes, but it is decidedly local and uncommon in most areas compared to *naevioides*.

2. *Hylophylax punctulata* (Dot-backed Antbird) attended 7 *Eciton burchelli* raids in the open seasonally-flooded understory of várzea swamps at Maloquinha, where *naevia* stayed in the nearby moderately cluttered *terra firme* forest understory. All records for *punctulata* were of a family of 3 birds except for at least 4 birds in a 2-pair dispute along a creek one day. They sometimes wandered near the ants for 3-4 hours, but deserted at once whenever the ants entered *terra firme* understory.

H. punctulata takes the flycatching tendencies of *naevia* a step further, for *punctulata* normally stands like a short-legged *Platyrinchus* flycatcher in or just below leaves at the high-water mark, sallying or fleeing by a descent through the open understory of the várzea. Horizontal (2) or slightly inclined (2 to 50°) perches of varying diameter (1-8 cm) at about 2 m up (4-4-1-2 records from 0-4 m up) were used, like a flycatcher rather than like its vertical-clinging relatives. One prey was pecked off a trunk, and 13 were taken by short-distance sallies (6 foliage, 4 air, 1 each liana, stem, and ground). It darts long distances from one perch to another, especially when alarmed. Its alarm calls include a sharp *bee-bee-beet* and a loud *steeyou* descending call, the latter given with an upward flick of the tail. The «song» seems to be a set of 1-3 loud *weebeyou* phrases, reminding one of the song of the Traill's Flycatcher (*Empidonax traillii*). In disputes, the closed tail is jerked to 45° above the line of the horizontal body, and may be held upright like that of a wren to show the fluffed white undertail coverts. The white back patch is open, framed by the dots at the margins of the back. The head angles upward to show the throat at the opponent. Often the bird crouches during this head-and-tail-up display, but one female briefly stood high on her bluish-white legs as she displayed after fleeing. One male gave a faint *wrieeeh* «snarl» and flew at another, supplanting him in a flurry of *bee-bee-beet* calls.

The main pair at Maloquinha may have been unusually wary because they were feeding a nearly-grown young female out of the nest, 23-27 Feb 1966. The young female lisped *wheesp-yerp* every 10-20 sec or gave *riehh* faint squeaks, flicking her tail for each note; once she was silent and once she «squeaked» rapidly as fed. The male gave faint *peup* «chirps» to her and to the mate.

Flycatching through the open understory of seasonally flooded swamps restricts the ant following of this species to occasional raids that enter the swamps, while ants flush rather little prey on foliage. However, the swamp colony of ants at Maloquinha was attended rather persistently, so that the species may capture much prey over ants.

3. *Hypocnemoides maculicauda* (Band-tailed Antbird) attended 7 várzea raids of *Eciton burchelli* at Maloquinha and 17 at Belém. Pairs were at all raids but 3 at Maloquinha (2 with 1 bird, 1 with 4) and 3 (with 1 bird each) at Belém. In all regions they stay near or over water in swamps. Like their relatives, they seldom move into sunlight; one in a sunny treefall at Belém twitched one wing out spastically as if starting «sunning» behaviour. At Belém, they hopped low (35-17-4-2 records 0-4 m up, by 1-m intervals) on mostly horizontal (19-7-2-4-3 records from 0° to 100° with the horizontal, by 20° intervals) twigs to palm fronds (17-6-6-0-1 records from 0-5 cm diameter, then 2 records to 15 cm diameter). Long bills, which barely separate this genus from *Hylomyza*, suggest that *maculicauda* peck prey rather long distances from semiopen perches; and at Maloquinha they did glean prey twice from debris and once from a trunk. However, I recorded even more short sallies both there (2 to ground, 1 to a trunk for a moth, 1 to foliage) and at Belém (3 to ground, 3 to foliage, 1 to air, 1 to a liana).

The Band-tailed Antbird hops and peers actively in low lianas, palms, and other somewhat cluttered vegetation. Jerking or flicking the tail from 10° up to 50° above the line of the body every second or two as if to display its pale tip, the bird may give sharp *peep-peep* or similar «chipping» in alarm (once to a Gray Hawk, *Buteo nitidus*). At a human, it gives a *de-e-e-e-e* «chirr» or «rattle» or a faint *wrieeh* «snarl». The tail waggles rapidly as pairs «sing» rapid series of *peet* notes ending in several snarling *pry* notes. One male at Maloquinha posed with bill up and throat, remiges, and rectrices spread at an opponent male, which hopped around jerking its spread tail rapidly from 30° up to 50° above the horizontal. Most records at Belém were of a color-banded pair (male 14.7 g, cloacal temperature 43.0°C; female 14.0 g) that kept for themselves a swamp zone about 300 m long. Restriction to moderately cluttered water edges in swamps prevents them from following ants regularly, as they never move into the more vertically oriented seedlings of *terra firme* forest even if the ants move there from seasonally flooded areas. The *maculicauda* are somewhat subject to attacks by regular ant followers as they hop near ants: at Belém, *Pyriglena leuconota* twice supplanted and once displaced a *maculicauda*, while *Dendrocincla merula* twice supplanted one. At Belém, they prefer seasonally flooded semiopen pools to forest channels or to cul-de-sacs flooded twice daily by tides. At Maloquinha, they used stream or backwater edges and low vines or roots, as much as 2 m below the rarely-flooded leafy understory «roof» preferred by *H. punctulata*.

4. *Myrmoderus ferrugineus* (Ferruginous-backed Antbird) followed 1 *Eciton burchelli* raid at Nappi Creek, Guyana (Oniki & Willis, 1972) and 58 raids at Reserva Ducke, Brazil. Pairs were at the Guyana raid and at 19 raids at Reserva Ducke. Most visits were brief, but a few birds were irregularly present 200-280 min.

This long-tailed walking antbird seems at first very different from *Hylophylax*, but is linked to that genus by short-tailed *Dichrozona cincta* (Banded Antbird), which is little more than a walking *Hylophylax*. (Behaviorally, *cincta* strikingly resembles unrelated nightingale wrens, *Microcerculus* species). I presume that *Dichrozona*, *Myrmoderus*, *Myrmorchilus*, and *Myrmornis* represent a ground-walking radiation (extended to leaf-tossing in the case of *Myrmornis*) from ancestors related to *Hylophylax* and *Hypocnemoides*, which themselves have radiated more toward flycatching or ground-sallying niches.

Neither *Dichrozona*, *Myrmorchilus* nor *Myrmornis* are yet recorded with ants, although I have seen all but *Myrmorchilus* near ants; but rarity of ant following is characteristic of nearly all small ground-foraging insectivores, including *M. ferrugineus*. Two problems are that small walking birds are easily attacked by ants, hence have to circle them warily, and that large birds tend to dominate prey-rich areas near ants, forcing small birds even further out. A third problem is that groups of birds near ants attract predators, and ground birds in general avoid bird flocks. *M. ferrugineus* normally walks on the ground and over roots or logs 5 or more m from ants, and deserts them readily.

At sunny spots in the forest interior, *ferrugineus* is often replaced by lizards of *Ameiva* or *Kentropyx*; *ferrugineus* and similar antbirds are the «lizards» of shade. Few *ferrugineus* were seen to capture prey near ants: 8 pecked tiny items from the leaf litter, and one ran and jumped to snap small prey from the air. Only once was one supplanted near ants, by a Black-headed Antbird (*Percnostola rufifrons*).

Alarmed *ferrugineus* give dit-it or even longer series of «chipping» notes, also (at least at humans) a *dre-e-e-e-e-e* «rattle» or «chirr». They «flick their tails upward like *Hylophylax* rather than «pound» the tails downward like antbirds of the genus *Myrmeciza*. Pairs can be detected in dense ground vegetation by warbling «songs», series of 2-10 *tike* notes like a *Hylophylax naevia* from the male answered by infrequent *tee-tee-tee-tee-tee-tikee-tikee-tee-tee* songs from the female.

5. *Myrmoderus loricatus* (White-bibbed Antbird) followed 2 *Eciton burchelli* raids at Boa Nova, Bahia, 1 at Fazenda Três Pancadas (Ituberá, Bahia), and 1 at Sete Barras Reserve, São Paulo. Pairs were at both Boa Nova raids. Most visits were brief, for this species normally forages on the ground away from ants; but one Ituberá bird stayed near ants for 6 h. While *loricatus* resembles *ferrugineus* in plumage, foraging behavior, and in flicking the tail upward in alarm, it hops rather than walks on the forest floor. At Ituberá, 3 prey were pecked from the ground, 2 pecked off low trunks by jumping, and 1 each captured by short upward sallies to air, a leaf, and debris. Alarm notes include *psseek* «chips» and *de-e-e-e-e-ee* «rattles», while the «song» (at Boa Nova) is a *wee tivee tivee tivee tivee tivee* or similar series.

DISCUSSION

Regular ant following is recorded for two members of the genus *Hylophylax*, one a bird of Central American forests (which have relatively low ant-following diversity; Willis, 1972) and the other an Amazonian species with the unusual ability to cling inconspicuously to large trunks in the open forest understory away from larger competitors (Willis & Oniki, 1978; Willis, in press). Two other *Hylophylax* and one related *Hypocnemoides* are even smaller birds that have little chance to persist among large and aggressive birds over ants. These three species have radiated instead into other niches, flycatching low in moderately dense *terra firme* understory (*naevia*) and in open floodplain understory (*punctulata*) or moving low along moderately dense swamp edges (*maculicauda*). With restriction to specific microhabitats, they become even less able to follow nomadic ants, but in their microhabitats they sometimes follow ants persistently.

Another evolutionary line from the genus *Hylophylax*, if morphology (shape, spotted colors) and certain behavioral patterns (voice; flicking the tail upward in alarm) are good indicators, leads through *Dichrozona cincta*, a walking ground antbird very like *Hylophylax*, to longer-tailed ground birds of the genera *Myrmoderus*, *Myrmornis*, and perhaps *Myrmorchilus* (a tail-flicking antbird of bushes in dry areas). Ground-living

birds of small size cannot walk among aggressive ants, and tend to be excluded even from zones near ants by large ground birds (from rails, trumpeters, and ground-cuckoos down to zones more than about 5 m from ants reduces prey capture so much that *Dichrozona* and *Myrmornis* are not yet recorded with ants, while *Myrmoderus* are recorded only infrequently wandering around ant raids. Another problem for ground birds is that most avoid bird flocks, perhaps because subject to predation if in flocks. Probably ground antbirds of this evolutionary line find prey as well or better away from as near ants.

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