

ANTTHRUSHES, ANTPITTAS, AND GNATEATERS (AVES,
FORMICARIIDAE) AS ARMY ANT FOLLOWERS

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ABSTRACT

Antthrushes (Formicarius, Chamaeza) sometimes walk around swarms of army ants and capture ground prey, but do not follow ants regularly. Among antpittas, only fast-leaping *Pittasoma michleri* and *P. rufopileatum* regularly follow ants. Gnateaters (Conopophaga) follow ants little. All these ground-foraging genera are poorly adapted for rapid flying, and failure to follow ants is perhaps due to inability to evade predators or outfly competitors near groups of birds attracted by ants.

Buffon (1841) reported that certain neotropical birds, which were named *Formicarius* and became the type genus of the Formicariidae or antbirds, associated with ants. In recent years, the *Formicarius* "antthrushes" and some of their relatives have often been found among groups of birds capturing arthropods flushed by army ants (Willis & Oniki, 1978). Here, in the twenty-third of a series of reports, I evaluate recent data on ant following by members of the genera *Formicarius*, *Chamaeza*, *Pittasoma*, and *Conopophaga*.

RESULTS

1. *Formicarius analis* (Black-faced Antthrush), reported with ants by Johnson (1954), Willis (1960), Skutch (1969), Oniki (1972), Oniki & Willis (1972) and Gochfeld & Tudor (1978), usually forages away from ants, but follows them often enough to have been recorded at 152 raids between 1960 and 1981. It was found north to Costa Rica (Golfito 3, including one with 2 birds) and Panama (Cerro Campana 3; Madden Forest Reserve 4; Escobal Road, 1 with 2 birds; Limbo Hunt Camp 1; Bohio Peninsula 1), west to Colombia (Remedios 4, Tukurá 1) and Ecuador (Zatzayacu 500 m, 2; Limoncocha 8, including 2 with 2 birds; Yaapi 3; Putuimi 4), south to Peru (San Alejandro 3, Andoas 2), and east to Trinidad (Simla 10, including 4 with 2 birds and 2 with 3), Guyana (Nappi Creek 8, including 1 with 2 birds; see Oniki & Willis, 1972), and Brazil (Reserva Ducke at Manaus, 1 plus 1 recorded by D. Wechsler; Maloquinha 1; Diamantina 2; Palhão 1; Bacabal 2, including 1 with 2 birds; at Belém 86, including 7 with 2 birds). All raids were of *Eciton burchelli* except for the following raids of *Labidus praedator*: Forest Reserve 3, Limoncocha 1, Diamantina 1, Belém 4, and Bacabal 2.

The bird or birds at many raids walked past or disappeared within a few minutes, but some birds followed for hours (510 min at one Simla raid, 317 min at one at Belém). Like regular ant followers, *analis* sometimes follows a line of ants to a swarm. *F. analis* struts along the ground and along low horizontal roots or logs, tail up in the air at 60° like a rail. At each step, the tail is pounded to 20° or so above the horizontal. At times *analis* wanders under dark logs or in dense seedlings, but usually it walks in the open or moderately dense understory. The bird is generally ahead of the ants, less often behind. Crossing through the ants, it often runs or hop-flutters as they attack its feet. It rarely captures food among ants, and generally pecks small prey from nearby leaf litter (43 records at Belém), runs to peck such prey (4), or tosses leaves on the ground (13). Small leaves are swiped away with

the side of the bill, but large leaves are pecked up and tossed away. One bird at Belém jump-sallied for prey to a leaf 0.3 m above the ground. Records in other regions were similar (82 records of pecking at the ground, 13 of run-pecking, 11 of leaf tossing, plus 2 pecks at low leaves and 1 at a low stem). At times the prey is crushed in the beak or carried away for dissection on the ground. One bird at Simla pecked at clumps of ants, trying to rob prey from them.

Two *analís* at a raid generally wander separately. One at Simla, 2 at Belém, and 1 at Escobal ran at other birds and sent them running off, the attacker giving either loud *di-dip* "chipping" or faint *fooh* "grunts". When one whistles the "song" (a *peh*, *pew-pew* normally in Costa Rica and Panama, and a longer *peh*, *pew-pew-pew-pew-pew-pew* or similar series elsewhere) the bird often approaches and sings a reply, head up but tail horizontal or below the horizontal. One attracted bird at Simla walked up with tail angled rigidly forward over the back, the rusty crissum fluffed out and prominent. Generally *analís* does not interact with other species at ant swarms, but one *analís* at Belém repeatedly (7 times) displaced White-blacked Fire-Eyes (*Pyriglena leuconota*), running at them with tail lifted and spread wide, crissum fluffed out, back feathers raised, wingtips spread, bill open, and head down, pirouetting as it gave faint grunts. The Fire-Eyes moved in and took over the site despite the rushes of the larger *analís* (60.3 g for one color-banded bird). At Simla, *analís* once supplanted and once displaced, with a "snap" of the beak, a woodcreeper (*Dendrocicla fuliginosa*), while an *analís* displaced 2 *Formicarius colma* at Nappi Creek. On the Escobal Road, an *analís* supplanted a *Hylophylax naevioides* and a *Gymnophithys bicolor*.

F. analís pounds the tail rapidly when disturbed, infrequently or not at all when tame. Ones that suddenly noticed me sometimes lifted their heads high, sometimes lowered their heads or bodies jerkily as if on ratchets, and peered at me briefly. Usually they walk away silently and quickly, but at times one flushes a short distance with chipping calls or gives series of chipping notes as soon as it reaches the cover of ground vegetation. Series of chipping calls from a distant bird sometimes elicit songs or chipping notes from another bird. *F. analís* usually avoids forest-falcons (*Micrastur ruficollis*) at ant swarms, foraging at the far ends of a raid or deserting the ants whenever a falcon arrives. One *analís* flushed when a dog passed. Occasionally an *analís* flutters to cross a small cliff or log, or flies off downhill, even when undisturbed.

8 Dec 1961 at Simla, a grown young bird, giving clicking faint *peep* notes at 3/sec, followed one of a pair of adults persistently despite the *krawk* grunts of the adult. Skutch (1969) records young out of nest giving loud *chip* calls.

One at Belém bathed in a tiny pool in the forest, dipping its breast and fluttering the wings, and then scratched its head indirectly (over the wing). In the Amazon, as indicated for the following species, *analís* tends to be restricted to floodplain or second-growth forests, and *F. colma* replaces it in any well-drained or slightly hilly region.

2. *Formicarius colma* (Rufous-capped Antthrush) normally walks away from ants on the floor of hilly forests from the Andes eastward, but followed ants persistently enough to be recorded at 219 raids. It was found north to Guyana (Nappi Creek 3, including 1 raid with 2 birds; Oniki & Willis, 1972) and Colombia (Mitú 2), west to Ecuador (Yaapi 1, Putuimi 1), south to Peru (Cashibococha 2; Andoas 1), and east to Brazil (Carauari 2; Borba 1; Coatá 3; Maloquinha 4; Diamantina 4, including 1 with 2 birds; Palhão, 2; Serra Negra 1; Santo Amaro 4, all with 2 birds; Reserva Ducke near Manaus 145, including 1 with 3 birds and 19 with 2; D. Wechsler found it at 32 raids there, including 4 with 2 birds). All raids were of *Eciton burchelli* except for 4 of *Labidus praedator* (Mitú 1, Putuimi 1, Diamantina 2, including 1 with 2 birds). Unless noted, single birds were at raids. Absence at Belém is attributed to nearly complete recent destruction of upland forests there, for *analís* often

replaces *colma* in floodplain forests where the two species occur together. At Reserva Ducke, *analís* was found only near the main creek and *colma* elsewhere, including minor swampy creeks on incised or flat hilltop topography.

F. colma often deserts ants rapidly, although one pair followed a raid 226 min at Manaus. It pounds the tail, turns back and forth, raises the head, gives one or more *keup* alarm "chips", flits the tips of the wings, and walks off or flushes to a log or other horizontal perch to 2 m up when it sees a human. A few birds lowered their tails and heads near the horizontal and froze briefly, looking like thrushes, before running or (from a high liana) flying off. They hide in dense or log-blocked parts of the forest understory, and are difficult to detect except by an occasional series of chips or ghostly, trilling upscale "songs" (*re-e*). On days when forest-falcons (*Micrastur ruficollis*) follow an ant colony, *colma* generally disappear or follow at the opposite end of the raid from the falcon.

Unalarmed foraging birds pound their tails mainly when walking, and often use the open understory. They sometimes follow an ant trail in to the swarm or wander near an inactive ant nest, but usually follow a given colony on some days and not others — as if they stumble on ants rather than search for them. At Manaus, they ordinarily walked back and forth ahead (248 records) of ants, less often to the sides (right 29, left 25) of a swarm or at the rear (23). They ran quickly across swarms, hence seldom (6 records) were at swarm "centers". Records of *colma* walking on the ground (470) far outnumbered records on low logs (9). One on a log peered back and forth like a chicken before hopping off. At Manaus, *colma* normally pecked tiny prey from the ground (97 records), ran to peck prey (7), or tossed leaves (19) to peck prey. One *colma* pecked debris 0.1 m, up and another pecked at a spider on a low leaf (but the spider circled the leaf and was captured by a nearby *Gymnopithys rufigula*). Records in other regions were similar: 17 pecks at the ground, 1 run-peck, 4 leaf tosses, and 3 pecks at a low log. Pecking birds lower the tail to the horizontal. Leaf tossing is either by a sidewise swipe of the beak or by peck-tossing.

Since *colma* generally wandered ahead of the competing antbirds over ants, it seldom disputed with them. *F. analis* displaced two *colma* at Nappi Creek, and a small *Percnostola rufifrons* supplanted one *colma* at Manaus. There an unusually pugnacious *colma* supplanted 3 *Pithys albifrons* one day (walking around the perch of one *albifrons* and leaping at it with a "snap" of the beak) and displaced a *Conopophaga aurita*.

One color-banded male (weight 46.2 g, cloacal temperature 41.5°C; a female weighed 48.3 g and was 43.0°C) at Reserva Ducke followed ant swarms over a wide area, on both sides of the entrance road and its forestry plantations, from 4 Feb to 11 July 1974. Never seen with a female, he was probably a wandering immature. Once an unbanded male gave several loud chips and ran after him a few m. When a male and female followed ants, they generally wandered separately. Several independent young birds, with brown areas on their faces or with dark forecrowns, followed ants at Manaus. At Santo Amaro (Bahia), 22-25 Nov 1974, a grown young male with pale gape angles and with a dusky forehead gave faint *peip* notes constantly as it followed a male about. A nest 0.7 m up in a hollow snag there had two white eggs 26 Nov 1974.

3. *Formicarius nigricapillus* (Black-headed Antthrush), which normally wanders away from ants in wet foothill forests west of the Andes, followed one *Eciton burchelli* raid at El Tigre, Chocó, Colombia, 1 Mar 1952. It pecked one prey from the ground and tossed leaves once, pounding its tail as it walked about, like related *Formicarius* and *Myrmeciza* species. To sing a ghostly rising trill of 30-40 notes (*te-e-e...* etc. at 8 notes/sec) every 10 sec, it lowered the tail and stretched the neck upward, the throat puffing out and the beak opening for the song itself. The song is like that of *F. colma*, not like that of *analís*. There is blue skin behind and below the eye, so that the head is not completely black.

4. *Chamaeza campanisona* (Short-tailed Antthrush) normally walks far from ants in lower montane woodlands around the edges of the Amazon basin, but stayed near *Labidus praedator* 25 Jan 1973 in scrubland on the Turiamo Road, north slope of Rancho Grande National Park, Aragua, Venezuela. It froze near the ground several minutes at the cough of a wren (*Thryothorus rufalbus*), then gave a *kwert* "chip" and walked off. The "song" in Venezuela, Colombia (Paraíso 800 m, Caquetá) and to 800 m el. in southern Brazil is a ghostly, descending and accelerating low trill (*hoo, hoo, hoo, hoo-hoo-hoo-ho-o-o-o-o-o-o-o*) that ends in a series of *whoomp* sneezes. Gochfeld & Tudor (1978) record it following ants at 1350 m at Rancho Grande.

5. *Chamaeza ruficauda* (Rufous-tailed Antthrush) normally walks far from ants in upper montane forests around the edges of the Amazon basin, but stayed 30 min at an *Eciton burchelli* raid 18 Dec 1974 at 1500 m, Serra de Caparaó, Minas Gerais, Brazil. It tossed a leaf as it walked about. The song at Caparaó and in Venezuela was a long series of *hoo* notes, but another song in more common in southern Brazil: a rapid, ghostly short trill that rises in pitch. A series of brief *kwert* "rolls" are also given in southern Brazil. At Rancho Grande, 1400 m, Venezuela, *ruficauda* gave loud *whit wheet* "chips", lengthened at times to a *whert wheet eet eet you-you-you-you-you* "roll". This species, the preceding species, and upper Amazonian *C. nobilis* cock their tails upward and "pound" them to the horizontal at each step as they walk, much like *Formicarius*.

6. *Pittasoma michleri* (Black-crowned Antpitta) bounded up to 1 m at each jump on the ground and low perches around an *Eciton burchelli* raid at the Limbo Hunt Camp, near Gamboa, Panama, 4 July 1969. It supplanted one *Phaenostictus mcleannani*. West of the Andes, few species of antbirds follow ants, perhaps allowing the two antpittas of the present genus to become the only antpittas that are regular ant followers. Karr (1971) gives more information on the present species.

7. *Pittasoma rufopileatum* (Rufous-crowned Antpitta) bounded 0.4 m at a jump on the ground and on low perches, at 0-60° with the horizontal, around 2 *Eciton burchelli* raids at El Tigre, Chocó, Colombia, 1-2 Mar 1962. It waited spraddle-legged, looking about, at each stop. Foraging records were 1 sally to the ground, one peck at the ground, and one peck at a leaf 0.6 m up. Aggressive, it supplanted a *Phaenostictus mcleannani* in a try for prey, a *Myrmeciza immaculata* trying for prey, and a *Gymnophis bicolor* waiting nearby. Clouds of mosquitoes hovered around it and me. It flicked its wings out several times when it saw me nearby, then bounded off. I have seen *Grallaria varia* (Variegated Antpitta) bounding similarly around the rear of an *Eciton burchelli* swarm at Reserva Ducke, Brazil, and even eating one prey; but the series of hollow low owl-like whistles of this species normally are heard near small forest ravines far from ants. Likewise, I have seen *Hylopezus perspicillatus* (Streak-chested Antpitta) repeatedly fluffing out its belly feathers, hopping rapidly from one root to another, or giving faint *kwirr* "buzzes" and some songs near ant raids on Barro Colorado Island, Panama; but it seems to ignore ants and ant-following birds. *Grallaria dignissima* (Ochre-striped Antpitta) at Andoas, Peru and probable *G. eludens* (Elusive Antpitta) at Benjamin Constant, Brazil (heard only, 17 Apr 1966) also called their mournful tinamoulike *go, joe* "songs" (*dignissima* attracted by a whistled imitation also gave nasal *hoot, hee-ont* songs and *ruzz ruzz ruzz* faint "buzzes") in dense or swampy parts of the floodplain forest interior and never went near ants. Most other antpittas are montane, dependent on relatively dense understory either for protection or for food density, and live above the normal elevations for army ants.

8. *Conopophaga aurita* (Chestnut-belted Gnateater) briefly visited 35 ant raids, Colombia (Mitú 2) and Ecuador (Yaapi 1, Putuimi 1) to Brazil (Itapucurá 1; Diamantina 2; Reserva Ducke 28, including 2 raids studied by Douglas Wechsler). Single birds were at all raids except for 2 birds at an *Eciton rapax* raid at Mitú and at 8 of the Reserva Ducke raids. All raids were of *Eciton burchelli* except for the single *rapax* raid.

C. aurita normally moves quietly near the forest floor in moderately open undergrowth around treefalls and logs, and does not pause long near ants. At Reserva Ducke, individuals near ants perched crosswise very low 10-7-3-4-2-1-0-1-0-0 records 0 - 1.0 m up, by 0.1 m intervals; 5 more records just over 1 m up) on horizontal to vertical perches (13-3-2-0-10 records, 0°-100° above the horizontal, by 20° intervals), of various diameters (6-5-6-0-1-1-1 records 0-7 cm diameter, by 1-cm intervals; 2 large perches), including large logs. Flitting the wing tips at intervals, *aurita* watches for a few seconds to a minute and tries for prey or moves on. Prey attempts near ants included 8 sallies and 4 pecks at the ground, plus single short sallies to air, trunk, or leaf and 2 pecks at trunks. At Putuimi, one moved as high as 6 m up and sallied like a flycatcher to leaves or vines, but most records in other areas were of birds sallying for ground prey. One at Reserva Ducke, 8 Feb 1974, fluffed out the body and head and spread its wings and tail (once dragging one leg) as it gave *kiff* "sneezes" and *cough* "coughs" in a distraction display. 12-13 July 1973, a grown young gave *ti-i-i* tinny "chitters" and faint *wee we we we weed* descending "peepsongs" as it followed a female low near ants. One at ants pecked when they attacked its toes, and once a *Formicarius colma* displaced an *aurita*, which displaced a *Hylophylax poecilinota* once; but *aurita* should follow ants much more often and persistently.

9. *Conopophaga melanops* (Black-cheeked Gnateater) followed 6 *Eciton burchelli* raids (3 with 2 birds) at Fazenda Três Pancadas, Ituberá, Bahia and 1 such raid at Fazenda Barreiro Rico, Anhembi, São Paulo, Brazil. A pair at Ituberá stayed for 222 min in one case, though normally this species wanders low through forests far from ants. Over ants at Ituberá, *melanops* perched low to high in the understory (14-6-2-0-2-1 records 0-6 m up, by 1-m intervals), on perches of various angles (6-2-2-3-4 records 0° to 100° above horizontal, by 20° intervals) and diameters (1-6-2-1-2-3 records 0-6 cm diameter, and 1 more record to 10 cm). It sallied to the ground (4), air (1), a leaf (1), liana (1) and pecked prey off a trunk (1). One moth captured in the air was taken off a spider web. I noted *a-a-ah* "chitters", like beak snapping, *shriek* or *zwieieest* "sneezes", and flitting the wing tips, but birds are not usually wary.

10. *Conopophaga lineata* (Rufous Gnateater) followed 12 raids in upland southern Brazil, 1 at Jacupiranga State Park, São Paulo, and 1 at Barreiro Rico being of *Labidus praedator* and the others being *Eciton burchelli* raids on the Serra de Caparaó 1300 m (1) and at Barreiro Rico (9 raids, one with 2 birds). Like gnateaters generally, it tends to stay near treefalls and dense zones or logs as the raids move. Sallies to the ground (3) and to a liana 0.7 m up were much like foraging attempts away from ants (Willis, Oniki & W. Silva in prep.). It normally wanders near the ground or to 10 m up, far from ants.

11. Related species: Hilty (1974) records ground-foraging *Scytalopus femoralis* (Rhinocryptidae) following ants in montane Colombia.

DISCUSSION

Anthrushes of the genera *Formicarius* and *Chameza* could easily follow ants regularly, except when ants move into dense tangles, and it is not clear why anthrushes are not good followers. The most likely problem is that they are susceptible to predation themselves, being walkers and poor fliers that could be easy prey for hawks or cats attracted by numerous ant-following birds. It was rare for more than one anthrush to follow a given ant raid, even though anthrushes form pairs (Skutch, 1969).

Danger of predation may be the reason why antpittas and gnateaters seldom become ant followers, or rather specialization to hop or walk after prey may interfere with flying ability necessary to avoid predators and hence cause such birds to avoid any predator-attractive bird groups. Gnateaters and antpittas almost never follow mixed bird flocks, and typically paired indivi-

duals wander separately. Inability to fly rapidly may also put such ground birds at a disadvantage in competition with low-flying antbirds.

Antthrushes pound the tail downward, and for this reason seem related to the genus *Myrmeciza* rather than to the tail-flicking antbirds (*Phaenostictus*, *Myrmornis*) with which antthrushes are usually placed. It is not likely that antpittas are related to antthrushes, and the nearest relatives of antpittas are therefore not evident. Gnateaters seem similar to *Grallaricula antpittas*, and perhaps are related to them.

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REFERENCES

- Buffon, G. L. L., 1841. *The book of birds*, ed. M. Achille Comte, transl. Benjamin Clarke. London, 292 pp.
- Gochfeld, M. & G. Tudor, 1978. Ant-following birds in South American subtropical forests. *Wilson Bull.* 90: 139-141.
- Hilty, S. L., 1974. Notes on birds at swarms of army ants in the highlands of Colombia. *Ibidem* 86: 479-481.
- Johnson, R. A., 1954. The behavior of birds attending army ant raids on Barro Colorado Island, Panama Canal Zone. *Proc. Linn. Soc. N. Y.* 63-65: 41-70.
- Karr, J. R., 1971. Ecological, behavioral, and distributional notes on some central Panama birds. *Condor* 73: 107-111.
- Oniki, Y., 1972. Studies of the guild of ant-following birds at Belém, Brazil. *Acta Amazonica* 2: 59-79.
- Oniki, Y. & E. O. Willis, 1972. Studies of ant-following birds north of the eastern Amazon. *Ibidem* 2: 127-151.
- Skutch, A. F., 1969. Life histories of Central American birds, III. *Pacific Coast Avifauna* 35: 1-580.
- Willis, E., 1960. A study of the foraging behavior of two species of ant-tanagers. *Auk* 77: 150-170.
- Willis, E. O. & Y. Oniki, 1978. Birds and army ants. *Ann. Rev. Ecol. Syst.* 9: 243-263.