

- grey Shrike and the ecological implications of its impaling prey. M.S. thesis, Ben-Gurion Univ. of the Negev, Beer-Sheva, Israel.
- YOSEF, R. 1993. Influence of observation posts on territory size in Northern Shrikes. *Wilson Bull.* 105:180-183.
- YOSEF, R., W. A. MITCHELL, AND B. PINSHOW. 1991. The proximate costs and benefits of polygyny to male Northern Shrikes. *Wilson Bull.* 103:146-149.
- YOSEF, R., AND T. C. GRUBB, JR. 1992. Territory size influences nutritional condition in non-breeding Loggerhead Shrikes: A ptilochronology approach. *Conserv. Biol.* 6:447-449.
- YOSEF, R., AND T. C. GRUBB, JR. 1993. Effect of vegetation height on hunting behavior and diet of Loggerhead Shrikes. *Condor* 95:127-131.
- YOSEF, R., J. N. LAYNE, AND F. E. LOHRER. 1993. Trends in numbers of Loggerhead Shrikes on roadside censuses in peninsular Florida, 1974-1992. *Fla. Sci.* 57:28-33.

Received 9 November 1992, accepted 1 July 1993.

The Auk 111(2):469-475, 1994

Behavior, Vocalizations, and Possible Relationships of Four *Myrmotherula* Antwrens (Formicariidae) from Eastern Ecuador

BRET M. WHITNEY

Field Guides Incorporated, P.O. Box 160723, Austin, Texas 78716, USA

The genus *Myrmotherula*, as currently recognized (Sibley and Monroe 1990), comprises 31 species of small, insectivorous antbirds, many of which have restricted geographic distributions. *Myrmotherula* reaches its greatest diversity at approximately 400-m elevation near the base of the Andes in western Amazonia between about 2°N and 13°S latitude, where up to eight species have been observed foraging with a single mixed-species flock at at least one site (pers. obs.). There is, however, a rapid drop-off in the number of species of *Myrmotherula* occurring above about 600 m in the foothills of the Andes just a few kilometers to the west. Coincident with this reduction in the number of species is a change in species composition within the genus as "foothill" species replace lowland species. Furthermore, the foothill antwrens occupy an altitudinally compressed range, being virtually absent above about 1,300 m. Thus, it is not surprising that some of these birds are among the most poorly known members of *Myrmotherula* and, indeed, of the family Formicariidae.

In the next few years, as our taxonomy of birds is increasingly determined by evidence of genetic relatedness that comes from the laboratory, there should be a corresponding body of knowledge available on the behavior and vocalizations of birds that will allow a test of our ability to use data from both fields to predict evolutionary relationships (Hackett and Rosenberg 1990). Tissue samples are fast accumulating, and molecular-based phylogenies will be worked out, in many cases, before pertinent data from the field are gathered and assimilated. In this paper I provide standardized data on the behavior and vocalizations of four little-known *Myrmotherula* antwrens from

western Napo Province, Ecuador: *M. spodionota* (Foothill Antwren); *M. behni* (Plain-winged Antwren); *M. sunensis* (Rio Suno Antwren); and *M. schisticolor interior* (Slaty Antwren).

Methods.—All observations and tape recordings were made between 27 and 30 March 1990, and between 10 and 20 January 1991 on the lower slopes of Mt. Sumaco (ca. 0°33'S, 77°44'W), an isolated, forest-cloaked mountain rising out of the lowlands to 3,900 m some 30 km east of the Andes. I observed birds with Zeiss 10 × 40 binoculars. When I located a mixed-species foraging flock containing *Myrmotherula* species (always first detected by characteristic vocalizations of one or more flock members), I made representative tape recordings of as many different vocalizations as possible, and followed the birds for as long as possible (always at least 20 min, and for as long as 2.5 h), observing foraging and other behaviors, which I summarized verbally on cassette tape. All measurements given below (heights, distances, etc.) are estimates. Terminology for foraging behavior follows Remsen and Robinson (1990). Tape recordings were made using Nagra E, Nagra 4.2, and Sony TCM-5000 recorders, and Sennheiser MKH-416 and ME-80 shotgun microphones. All recordings have been or will be archived at the Library of Natural Sounds, Cornell University, Ithaca, New York. Sonograms were produced with "SoundEdit" of Farallon Computing, Inc., Emeryville, California, and "Canary" of the Bioacoustics Research Program at the Cornell Laboratory of Ornithology, Ithaca, New York.

Foothill Antwren (*M. spodionota*).—*Myrmotherula spodionota* (including the southern subspecies *sororia*) occurs from northeastern Ecuador south in a narrow

elevational band in the foothills of the eastern Andes to Depto. Junín, Peru. I encountered *spodionota* from 600 to 1,250 m; it was especially common between about 700 and 1,100 m. The upper elevational limit for the species previously has been reported as 1,100 m (Hilty and Brown 1986, Sibley and Monroe 1990). During a two-week survey in apparently suitable habitat between 1,000 and 1,300 m in Depto. San Martín, Peru, *spodionota* was not found (Parker and Parker 1982), which probably indicates that it is at least locally absent from this elevational range in northern Peru. Nothing has been published on the behavior or vocalizations of *spodionota*.

I observed the foraging behavior of 30 to 40 individuals and tape-recorded approximately 10 different birds. *Myrmotherula spodionota* was almost always observed foraging with mixed-species flocks of insectivores in the understory of undisturbed forest. All foraging took place between about 0.5 and 8 m above ground, most often between 1 and 4 m above ground. Within each mixed-species flock, *spodionota* occurred in male-female pairs or occasionally small groups of up to four individuals in which case three of the birds were usually in female/immature plumage, almost certainly representing a family group. A food-begging juvenile with two adults was observed on 28 March. This juvenile was also foraging independently, and was singing a good approximation of the adult's song. On two occasions I noted the presence of two birds in adult male plumage in a single flock. Whether this represented an advanced plumage state in an offspring or the presence of more than one adult male (and, thus, presumably more than one pair) in these flocks could not be determined, but I suspect the former. The only *spodionota* that I observed away from mixed-species flocks were a single adult male singing shortly before dawn, before formation of mixed-species flocks, and a probable family group of four that did not seem to be associated with any flock. While searching for food, the birds frequently flicked the tail up or down sharply through an irregular arc, and flicked the wings shallowly, especially after landing on a new perch.

Myrmotherula spodionota foraged almost exclusively at isolated dead leaves and dead-leaf clusters hanging or trapped above ground in the forest understory. On several occasions I noted *spodionota* probing in tufts of moss and in the shaggy, dead bark of understory vines. The birds approached a dead leaf or leaf cluster by flying in to land immediately beside it, or by hopping or hitching along limbs ("hitching" defined as a sideways movement of one foot followed immediately by other, producing short advances of less than about 2 cm [or the distance between the legs when perched normally]). Isolated dead leaves, especially smaller ones, were scanned for prey items by stretching the legs, and craning the neck in various positions. Foraging at a cluster of dead leaves or large, isolated dead leaves usually was initiated as the bird

hopped onto a leaf in the cluster or poked or grasped it with the bill. These actions probably serve to startle any hiding arthropods into making noise with even a slight movement, thus alerting the bird to the presence of a hidden prey item. The birds often spent several seconds, usually not more than about 1 min, rummaging audibly in clusters of dead leaves as they reached into curls and crevices. I noted that *spodionota* scanned live leaves as it hopped along limbs, but I saw only a couple of brief lunges (and no prey captures) in live foliage. By the definition of Remsen and Parker (1984), *spodionota* should be considered a dead-leaf foraging specialist.

All foraging attacks were near-perch maneuvers. Reaches were most common, but gleanings also were employed frequently, and I noted hang maneuvers on several occasions. If a large prey item was captured, the bird held it in the bill as it flew or hopped from the dead leaves to a nearby horizontal perch and there mashed the body in the bill and thrashed the head of the arthropod against the substrate forcefully and rapidly, sometimes for nearly 1 min. Prey items included a variety of arthropods ranging in size from small roaches, caterpillars, and adult moths to an orthopteran ("katydid") in excess of 5 cm in length. Large prey items required several minutes to subdue and swallow (legs and wings were sometimes removed), a delay that usually resulted in the other members of the mixed-species flock having moved off some distance. The only congeners I found in the same mixed-species flocks with *spodionota* were *M. longipennis* (Long-winged Antwren; which foraged at similar heights but primarily in live foliage), *M. behni* (which generally foraged higher and more in live foliage), and *M. menetriesii* (Gray Antwren; which foraged higher above ground and primarily in live foliage).

While foraging, *spodionota* was generally quiet except for soft, but sharp, single-note contact calls given by members of a pair or family group. My approach to a mixed-species flock containing *spodionota* usually stimulated at least one bird to deliver an alarm vocalization consisting of a rapid series of high, thin notes lasting about 1 s (Fig. 1A). A distinctive vocalization in which the notes are at about 3.5 kHz and delivered much more slowly and with a raspy quality, was also given occasionally, mostly after tape playback. This vocalization is often employed in agonistic situations, such as flock-territory defense (K. Rosenberg pers. comm., M. and P. Isler pers. comm.; Fig. 1B). During January to March, *spodionota* did not sing often except in the early morning (mostly prior to the formation of mixed-species foraging flocks) or following tape playback. The song is a rapid series of 15 to 20 notes at about 5.5 kHz that is loudest in the middle and trails off as it drops slightly in frequency toward the end, the whole lasting approximately 1.0 to 1.5 s (Fig. 1C). In eastern Ecuador, at least, both sexes of *spodionota* have a dark-brown iris.

Plain-winged Antwren (*M. behni*).—*Myrmotherula behni* is poorly known throughout its range, which forms a fragmented arc around the northwestern border of Amazonia. It occurs in: the Pantepui region of southern Guyana, southern Venezuela, and extreme northwestern Brazil; the Sierra de Macarena of eastern Colombia; and the Sumaco region of eastern Ecuador, where first recorded by D. Norton in the early 1960s (R. Ridgely pers. comm.). Nothing has been published on the behavior or vocalizations of *M. behni* except for the brief statement by Snyder (1966:178) that it occurs in "forests and clearings, fairly low in trees and undergrowth," and her description of the voice as "a medium high trill, 'kyerrrrrrr.'"

I found *behni* to be fairly common (15 to 20 individuals observed) between about 780 and 1,100 m, most common at about 1,000 m. My highest record was 1,200 m, although I conducted observations in continuous, mostly undisturbed forest up to 1,750 m. The observed elevational spread is well below that reported by Hilty and Brown (1986:395; 1,300 to 1,800 m) and Meyer de Schauensee and Phelps (1978:210; 1,000 to 1,800 m) for Colombia and Venezuela, respectively. Although it is possible that I missed all birds above 1,200 m or that localized conditions were suboptimal for *behni* above that elevation, it is perhaps more likely that *behni* occurs at somewhat lower elevations in the Sumaco region of Ecuador than in other known areas of its distribution.

Myrmotherula behni foraged exclusively with mixed-species flocks in the understory and midstory of undisturbed forest. They seemed to be partial to damp ravines. Although bamboo (*Guadua* sp.) was common in some of the areas in which I found *behni*, the birds did not seem to prefer to forage in bamboo more than in other vegetation. I observed *behni* foraging from 1 to 10 m above ground. In areas of the forest having dense (interlocking plants) understory, *behni* foraged primarily in the lower part of its foraging range. Where the understory was open, the birds foraged more in the 4- to 10-m range. When in the understory (less than about 3 m above ground), *behni* foraged more often in dead leaves than when foraging in the mid-story, probably because of the higher density of suspended dead leaves at lower levels in the forest. I do not believe that *behni* sought dead-leaf substrates over other substrates, although this was difficult to ascertain. I observed *behni* foraging at dead leaves about half of the time, which would categorize it as a "regular user" of dead leaves as a foraging substrate by the definition of Remsen and Parker (1984). However, *behni* rarely manipulated dead leaves (by tapping, probing, or rummaging), which suggests a low level of specialization in dead-leaf foraging (Rosenberg 1993).

Searches of dead and live foliage were concentrated at the periphery of trees, where single or small clusters of dead leaves had become trapped in twigs and live foliage. The birds hopped or hitched along limbs

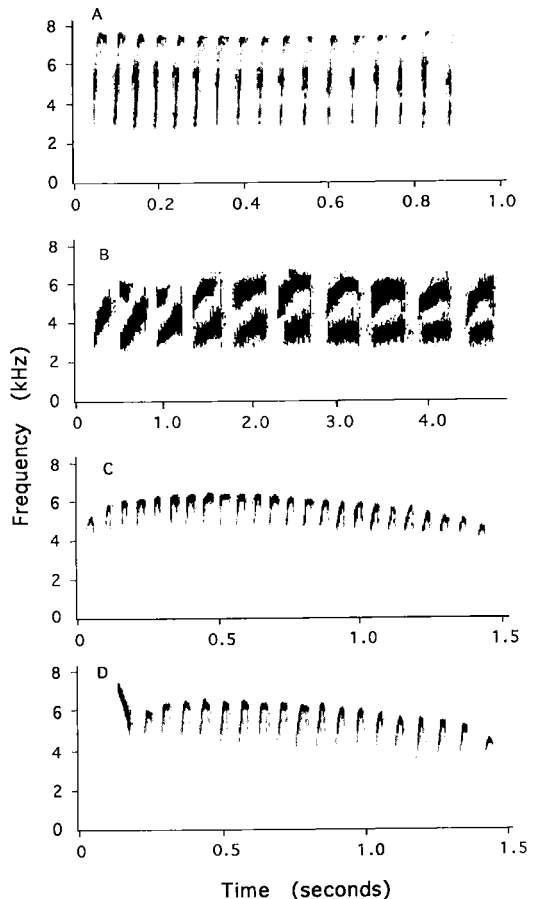


Fig. 1. (A) High-pitched scold and (B) raspy "alternate song" given in agonistic context of *Myrmotherula spodiota* (recorded on Mt. Sumaco, western Napo Prov., Ecuador). Songs of (C) *M. spodiota* (recorded on Mt. Sumaco, western Napo Prov., Ecuador) and (D) *M. ornata* (recorded at Serra dos Carajas, central Pará, Brazil; song shared by both rufous-backed and gray-backed populations). These vocalizations, with little interspecific variation, are shared by all members of checker-throated group (as defined by Hackett and Rosenberg [1990], but excluding *M. gularis*).

and upon reaching the end of the limb, peered at the underside of the leaves, or hung sideways or upside-down at the tips of leaves, sometimes clinging to the leaf margins with the feet, and sometimes maintaining a hang for several seconds as they craned the neck to scan surrounding foliage. In general, *behni* foraged actively and acrobatically, reaching and gleaning arthropod prey, most of which were too small and consumed too quickly for me to see clearly. The birds also performed short flutter chases, and sometimes seemed to be inspecting foliage by fluttering close to

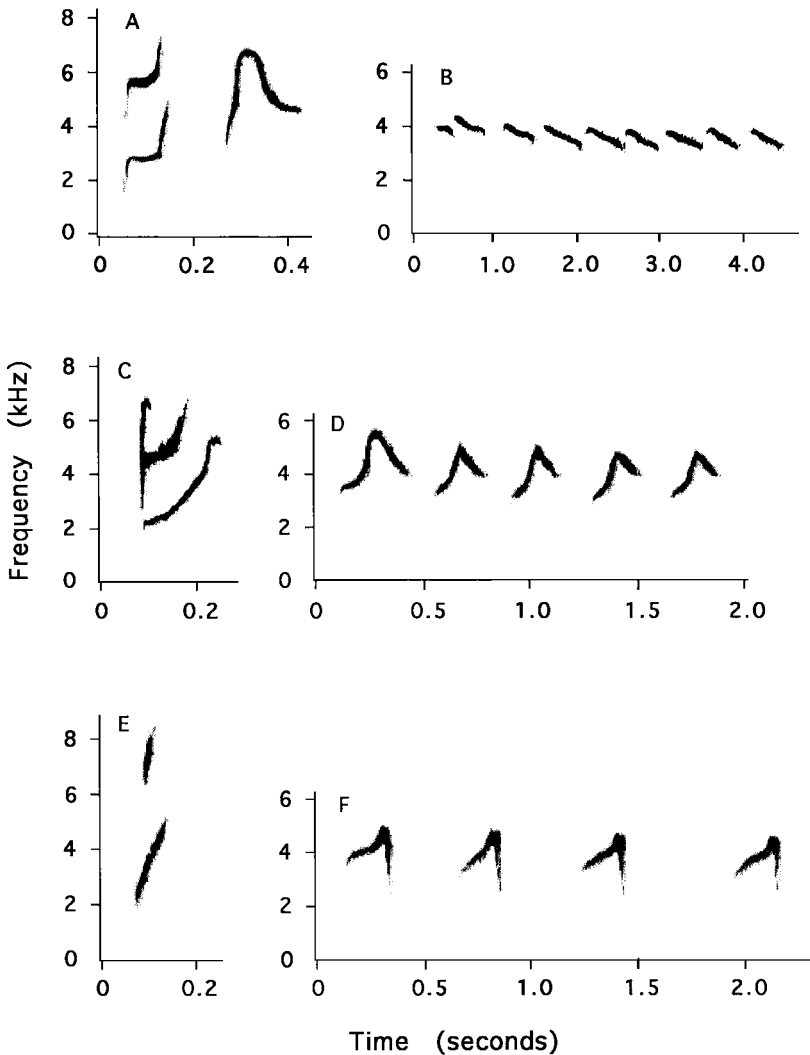


Fig. 2. Some calls and songs of *Myrmotherula* antwrens recorded on Mt. Sumaco, western Napo Prov., Ecuador, presented for interspecific comparison. *Myrmotherula behni*: (A) "dyink!" or "deenk!" call (left), which seems to function as an alarm or heightened-awareness note, and "kleek" or "wheet" call (right), which seems to function as a general contact note. (B) One song. Few songs were heard, so it was not possible to determine if this is a typical song. *Myrmotherula sunensis*: (C) "sueét" or "tueét" call, which seems to be a general contact note. (D) One song. First note sounds slightly more bisyllabic and is slightly higher in frequency than subsequent notes; number of notes variable from two to five. *Myrmotherula schisticolor interior*: (E) "pseeeyt" call, which seems to function as a general contact note. (F) One song. Last note is usually given after a fractionally longer interval than those between other note pairs. Song is much like that of *sunensis*, but differs in being "sharper" in quality owing to louder notes and sudden syringeal closure at high end of individual notes. There also is a somewhat longer interval between notes; number of notes variable from two to four (fewer than 10 songs heard from two individuals).

it. The birds almost constantly flicked their wings and tails shallowly while foraging, more emphatically in response to tape playback. Congeners observed in the same mixed-species flocks with *behni* were *M. spo-*

dionota, *M. erythrura* (Rufous-tailed Antwren; once, foraging almost exclusively in dead leaves and more in the interior of vine tangles), *M. axillaris* (White-flanked Antwren; once, foraging more in live foliage

and less at the periphery of trees), *M. longipennis* (twice, foraging in live foliage while *behni* foraged mostly in dead leaves), and *M. menetriesii* (generally foraging higher above ground).

Upon my initial approach toward a mixed-species flock, *behni* sometimes gave a single-noted call, which I believe functions as an alarm note or heightened awareness call. I have transcribed it as "dyink!" or "deenk!" (Fig. 2A, left side). The most common vocalization of *behni*, however, was a rather loud "kleek" or "wheet" that members of a pair seemed to use for keeping in contact, especially when flying from perch to perch (Fig. 2A, right side). This vocalization was also given frequently in response to tape playback of any vocalization of *behni*. I did not hear *behni* give anything similar to the call described above by Snyder (1966). I heard the song of *behni* on only one occasion in several hours of observation. An adult male delivered two or three quiet songs from a horizontal perch about 5 m above ground after playback of both calls described above. The song is a series of five to nine clear, very slightly descending, evenly spaced whistled notes at 3.5 to 4.0 kHz lasting 4 to 5 s (Fig. 2B).

Rio Suno Antwren (*M. sunensis*)—*Myrmotherula sunensis* probably has the most restricted distribution of any *Myrmotherula* occurring in western Amazonia. It is known from one locality in southeastern Colombia, a cluster of localities in western Napo Province, Ecuador, and two localities in northern and central Peru, all of which lie in a narrow elevational band between about 250 and 500 m along the eastern base of the Andes. Additionally, Stotz (1990) reported a single male specimen from the middle Rio Juruá in western Amazonian Brazil, which he distinguished from the morphologically very similar *M. iheringi* (Ihering's Antwren) by its "gray underwing coverts, instead of pure white." Apart from the equivocal statement of Hilty and Brown (1986) that its behavior is "apparently much like Long-winged Antwren," *sunensis* is virtually unknown in life.

I observed two pairs of *sunensis* foraging with mixed-species flocks in the understory of old second-growth terra firme rainforest (possibly flooded on occasion) at approximately 400 m. This forest was regenerating from essentially clear-cut condition, but had remained undisturbed for long enough to attain an average canopy height of about 20 m, and was directly connected to essentially undisturbed forest on the lower slopes of Mt. Sumaco. Scattered through the canopy were numerous light gaps choked with vine tangles in which the canopy height was lower than about 8 m. Dense patches of *Guadua* sp. bamboo were present, and another type of bamboo was more generally distributed throughout. Despite the abundance of bamboo, *sunensis* rarely foraged in it, and actually seemed to prefer other types of vegetation. The understory was generally dense and viny with abundant *Heliconia* spp., and suspended dead leaves were abun-

dant below about 5 m. Several exceptionally diverse mixed-species flocks of insectivores were encountered in this old second growth, including one flock in which the following species of *Myrmotherula* were observed foraging over a period of about 2.5 h: *brachyura* (Pygmy Antwren), *hauxwelli*, *ornata*, *erythrura*, *axillaris*, *longipennis*, *sunensis*, and *menetriesii*. The first two species are not inveterate members of mixed-species foraging flocks (the others are; pers. obs.), but were definitely moving with this flock, which contained no fewer than 42 bird species observed foraging for arthropods.

Within mixed-species flocks, *M. sunensis* foraged in male-female pairs (one pair per flock), ranging from 1 to 7 m above ground, most often between about 2.5 and 5 m. The birds foraged rather lethargically, performing gleans and reaches in a deliberate manner without hanging, sallying, fluttering, or other acrobatic moves. They hopped and hitched along horizontal and diagonal limbs, sometimes clinging momentarily to vertical stems and vines as they progressed toward the ends of limbs. *Myrmotherula sunensis* foraged in both live foliage and at isolated, often small, dead leaves by stopping immediately beside the substrate then stretching the legs and craning the neck and bending over to scan various surfaces for prey items. *Myrmotherula sunensis* did not hop directly onto dead leaves and usually did not poke or probe them with the bill. The birds did not rummage in dead leaf clusters, but did occasionally inspect clusters from the periphery. If a prey item was found, the bird rapidly snapped it up and quickly swallowed it, sometimes after mashing it in the bill and beating it on a limb for a few seconds. A majority of my foraging observations of *sunensis* were at dead leaves (ca. 40 foraging moves observed), which would categorize it as a dead-leaf-foraging specialist under the definition of Remsen and Parker (1984). Rosenberg (1990) defined a specialist, however, as a species that manipulates the substrate physically with the bill or feet, offering further clarification in stating that "non-specialists visually inspected dead leaves but rarely disturbed the leaves to facilitate prey detection." Based upon my rather limited observations, I would classify *sunensis* as a nonspecialist, regular user of dead-leaf foraging substrates. Both members of a pair foraged in the same manner, usually keeping within about 5 m of each other. They flicked the tail irregularly and shallowly, and seemed to flick the wings somewhat less often than do most species of *Myrmotherula*.

Myrmotherula sunensis was generally quiet while foraging, but occasionally members of a pair called actively to each other with single-noted, rising "sueét" or "tueét" calls that were often delivered in pairs (Fig. 2C), and quieter calls on a lower frequency that were usually given in a short series of three or four notes, especially when moving quickly or flying between perches. These calls were also given in response to tape playback of these vocalizations or the song. None

of the calls of *sunensis* that I heard were obviously given in the manner of an alarm or scold. One of the male *sunensis* that I observed was singing occasionally while it foraged with a mixed-species flock about 2.5 h after dawn. The song is short and simple, consisting of two to five (usually three or four) evenly spaced notes at about 5 kHz that rapidly rise through about 1 kHz. The first note is about 0.5 kHz higher in frequency, and is slightly more drawn out (more bisyllabic) than the rest. A five-note song is about 1.75 s long (Fig. 2D). I have transcribed it as, "suweee-swee-swee-swee-swee." A female also sang this song one time. In the absence of tape playback, *sunensis* delivered songs quietly and at irregular intervals, often going for several minutes without singing, then singing several songs a few seconds apart.

Slaty Antwren (*M. schisticolor interior*).—Although *schisticolor* is among the most widely distributed members of *Myrmotherula* (occurring from southern Mexico to Depto. Cuzco, Peru), its foraging behavior and most of its vocalizations remain poorly known. The subspecies *M. s. interior* is sympatric with *sunensis* throughout the range of that species, but the two do not overlap altitudinally (*schisticolor* does not seem to occur below about 1,000 m on the east slope of the Andes, and is rare that low; pers. obs.). Like *sunensis*, *schisticolor interior* forages with mixed-species flocks in the understory of forest, ranging from near the ground to as high as about 12 m, most often between about 2 and 6 m above ground. *Myrmotherula schisticolor* also appears to be a generalist forager and a "regular-user" of dead-leaf foraging substrates. It is somewhat more acrobatic than *sunensis*, performing more rapid motions as it reaches, gleans, and hangs in live and dead foliage. On Mt. Sumaco, most mixed-species flocks containing *schisticolor* contained no other species of *Myrmotherula*, but often seemed to have two pairs of *schisticolor*, or at least two adult males and two or three female-plumaged birds.

The most frequently heard contact call of *schisticolor interior* was probably transcribed by Eisenmann (in Peterson and Chalif 1973) as "pseeeyt" (Fig. 2E). The song of *schisticolor interior* (only one bird recorded) is a series of two to four notes at about 4 kHz that rise rapidly through about 1 kHz and end with an abrupt syringeal closure (Fig. 2F). It may be much like the song of nominate *schisticolor* as Skutch (1969:210), who provided the only description of the species' song, transcribed it: "t'weet t'weet t'weet, t'weet weet weet weet weet, in very low soft tones." The best-known vocalization of *schisticolor* is a nasal, descending "nyeeah" (Peterson and Chalif 1973) or "yyeeet" (Hilty and Brown 1986). This vocalization may be an alarm or heightened-awareness call, given by one or more individuals as soon as any threat, such as the appearance of an observer, is detected. The extent to which it is given in the absence of disturbance needs further investigation.

Possible relationships.—*Myrmotherula spodiota* ap-

pears to be a dead-leaf foraging specialist, like all other *Myrmotherula* species having a "checked" throat (Remsen and Parker 1984, Gradwohl and Greenberg 1984, Rosenberg 1993) with the exception (pers. obs.) of *M. gularis* (Star-throated Antwren), which is isolated in the Atlantic Forest of southeastern Brazil, and seems closer to *M. guttata* (Rufous-bellied Antwren) and *M. hauxwelli* (contra the suspicion of Remsen and Parker 1984). The song of *spodiota* clearly allies it to the other checker-throated members of the genus, and the closely related (Hackett and Rosenberg 1990) *M. ornata* (pers. obs.; compare Fig. 1C and 1D). The high-pitched scold of *spodiota* (Fig. 1A) is typical of all true checker-throated antwrens. The raspy vocalization given by *spodiota* in an agonistic context (Fig. 1B) has been characterized as "apparently a unique type of alternative song in this [checker-throated] group" (K. Rosenberg pers. comm.), although it is not known whether all of the members of the group give it. Most of the vocalizations (especially the songs) of the checker-throated group are audibly and structurally distinct from those of all other species of *Myrmotherula* (pers. obs.), and the close vocal similarity found within the group supports the finding of Hackett and Rosenberg (1990) that the checker-throated group (including *M. ornata*) forms a clade.

In the allozyme study of Hackett and Rosenberg (1990), *M. behni* (sample from Cerro de la Neblina, Venezuela) and *M. grisea* (Ashy Antwren) of the Bolivian foothills clustered with *M. schisticolor* (sample of nominate, trans-Andean subspecies from Darién, Panama). Such a relationship would be hard to predict from nonmolecular evidence, given the different vocalizations and very different plumages of *behni* and *schisticolor*. A close relationship of *behni* to the other all-gray, plain-winged taxa, *grisea* and *M. unicolor* (Unicolored Antwren of Atlantic Forest of Brazil) is suggested, however, by available morphological, behavioral, and vocal evidence (pers. obs.) *Myrmotherula behni* includes at least three geographically isolated populations, and three subspecies, although two of the subspecies are in Pantepui and the Ecuadorian population is not subspecifically named. In light of apparent differences in the morphology, elevational spreads, and calls of some of these isolates, I suspect that *behni* might include more than one species-level taxon. Tape recordings of songs and calls and additional tissue samples of all of the populations of *behni* (and similar material from other species) are needed to clarify its taxonomic relationships.

Myrmotherula sunensis bears a striking morphological resemblance to *iheringi*. The two also forage in a similar, lethargic manner, often inspecting small, isolated dead leaves trapped in live vegetation. In southwestern Amazonia, at least, *iheringi* seems to be largely restricted to bamboo thickets (pers. obs., K. Rosenberg pers. comm.); the extent to which *sunensis* might be tied to bamboo needs further investigation. Songs of

sunensis and *iheringi* are quite different in structure, frequency, rate of delivery, and overall duration (pers. obs.). That these two otherwise closely similar species should have very different songs finds parallel, with in *Myrmotherula*, in *brachyura* and *sclateri* (Sclater's Antwren), which Hackett and Rosenberg (1990) found to be quite closely related genetically.

Notwithstanding the observed similarities to *iheringi*, *sunensis* appears to be most similar overall to *schisticolor* in plumage, behavior, and structure and quality of the contact note and especially the song. In the type description of *sunensis*, Chapman (1925) discussed this relationship based upon observed similarities in plumage, and subsequent taxonomic lists have invariably placed the two close together. Comparison of the songs of *sunensis* and *schisticolor interior* (Fig. 2D and 2F, respectively) reveals a close similarity, although the song of *schisticolor interior* is generally louder and sounds "sharper" in quality owing to the sudden cut-off at the high end of the individual notes. The songs of *schisticolor interior* and *sunensis* are much more similar to each other than either is to the song of any other species in the genus (pers. obs.). The "sueét" contact call of *sunensis* is much like the common, apparently analogous "pseyeyt" call of *schisticolor* (compare Fig. 2C and 2E). I would not be surprised to learn, eventually, that similar basic contact calls are shared by many species of *Myrmotherula* (and perhaps some other thamnophilines). I did not hear any vocalization of *sunensis* that I thought was analogous to the distinctive, nasal "nyeeah" (Peterson and Chalif 1973) of *schisticolor*.

Like *behni*, *schisticolor* includes three named subspecies (with the name *interior* assigned to populations both north and south of the Rio Marañon in northern Peru), which are probably geographically isolated by either low-elevation gaps or intervening dry forests despite the range map shown for *schisticolor* in Hilty and Brown (1986). Elucidation of both the intra- and intergeneric relationships of *schisticolor* will benefit greatly from further fieldwork, especially more recordings of songs.

Because of close similarity of the adult male plumages, *sunensis*, *schisticolor*, and *longipennis* traditionally have been placed together in systematic lists. In the allozyme analysis of *Myrmotherula* presented by Hackett and Rosenberg (1990), however, *schisticolor* and *longipennis* did not cluster together (*sunensis* was not available for study). Although their plumages are quite similar (but with different distribution of white on tips of wing coverts), the separate clustering of *schisticolor* and *longipennis* is supported by vocal differences at least (pers. obs.). Whether molecular analysis eventually confirms the antwren relationships suggested above or not, the behavioral and vocal data presented here may be helpful in arriving at a well-corroborated phylogeny for *Myrmotherula* and the family Formicariidae.

Acknowledgments.—I thank Morton and Phyllis Is-

ler, Theodore A. Parker III, J. V. Remsen, Jr., and especially Kenneth V. Rosenberg for their helpful comments on the manuscript.

LITERATURE CITED

- CHAPMAN, F. M. 1925. Descriptions of one new genus and of species of birds from Peru and Ecuador. *Am. Mus. Novit.* 205:1-11.
- GRADWOHL, J., AND R. GREENBERG. 1984. Search behavior of the Checker-throated Antwren foraging in aerial leaf-litter. *Behav. Ecol. Sociobiol.* 15: 281-285.
- HACKETT, S. J., AND K. V. ROSENBERG. 1990. Comparison of phenotypic and genetic differentiation in South American antwrens (Formicariidae). *Auk* 107:473-489.
- HILTY, S. L., AND W. L. BROWN. 1986. A guide to the birds of Colombia. Princeton Univ. Press, Princeton, New Jersey.
- MEYER DE SCHAUENSEE, R., AND W. H. PHELPS, JR. 1978. A guide to the birds of Venezuela. Princeton Univ. Press, Princeton, New Jersey.
- PARKER, T. A., III, AND S. A. PARKER. 1982. Behavioural and distributional notes on some unusual birds of a lower montane cloud forest in Peru. *Bull. Br. Ornithol. Club.* 198:63-70.
- PETERSON, R. T., AND E. L. CHALIF. 1973. A field guide to Mexican birds. Houghton Mifflin Co., Boston, Massachusetts.
- REMSEN, J. V., JR., AND T. A. PARKER III. 1984. Arboreal dead-leaf-searching birds of the Neotropics. *Condor* 86:36-41.
- REMSEN, J. V., JR., AND S. K. ROBINSON. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Pages 144-160 in *Avian foraging: Theory, methodology, and applications* (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). *Stud. Avian Biol.* 13.
- ROSENBERG, K. V. 1990. Dead-leaf foraging specialization in tropical forest birds. Ph.D. dissertation, Louisiana State Univ., Baton Rouge.
- ROSENBERG, K. V. 1993. Diet selection in Amazonian antwrens: Consequences of substrate specialization. *Auk* 110:361-375.
- SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, Connecticut.
- SKUTCH, A. F. 1969. Life histories of Central American birds, vol. III. Cooper Ornithol. Soc., Pacific Coast Avifauna 35.
- SNYDER, D. E. 1966. The birds of Guyana. Peabody Museum, Salem, Massachusetts.
- STOTZ, D. 1990. Corrections and additions to the Brazilian avifauna. *Condor* 92:1078-1079.

Received 23 December 1992, accepted 2 July 1993.