OBSERVATIONS ON THE SYSTEMATICS, BEHAVIOR, AND VOCALIZATIONS OF "THAMNOMANES" OCCIDENTALIS (FORMICARIIDAE)

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ABSTRACT.—In January 1991 I rediscovered "Thamnomanes" occidentalis in eastern Ecuador, following a period of more than 50 years without a record. I review its controversial taxonomic history and, based upon observations of its behavior and vocalizations, suggest that occidentalis be reinstated in the genus Dysithamnus. Received 1 April 1991, accepted 10 January 1992.

THAMNOMANES OCCIDENTALIS, the Western Antshrike, has a confused taxonomic history at both the specific and generic levels. It is known from only two small areas on opposite sides of the northern Andes. These two populations currently are regarded as conspecific, but generic affinities remain obscure. Known from but nine specimens, *T. occidentalis* has not been recorded for more than 50 years, and there is no account of it in life.

In part due to taxonomic confusion that stems from the earliest descriptions of its two subspecies, the literature summarizing the distribution and elevational range of *T. occidentalis* (Hilty and Brown 1986, Ortiz et al. 1990) is inaccurate with regard to the Ecuadorian subspecies *punctitectus*. I provide the first information on the behavior and vocalizations of *T. occidentalis*, which allows a reassessment of the generic alignment of this elusive antbird of the subtropical forests of the northern Andes.

SUMMARY OF RECORDS AND DISTRIBUTION

Nominate occidentalis is known only from the Department of Cauca, Colombia, on the west slope of the Western Andes in the vicinity of Munchique. There are four specimens: one male from the type locality "Cocal, 4000 feet" in the American Museum of Natural History (AMNH; R. Sloss, pers. comm.); one female from "Rio Munchique, El Tambo, 3000 feet" in the Academy of Natural Sciences (M. Robbins, pers. comm.); and one male and one specimen with sex unknown from "La Costa, 1100–1200 m" in the Swedish Museum of Natural History (Gyldenstolpe 1941).

The subspecies *punctitectus* is known from five specimens taken within a small area of Napo Province, Ecuador: two males and one female from the type locality "Oyacachi, abajo, Chaco (Ecuador)" in the AMNH (R. Sloss, pers. comm.); one male from "Sumaco Abajo (Ecuador)" in the AMNH (Chapman 1926; R. Sloss, pers. comm.); and one male "reportedly from Baeza" in the British Museum (T. Schulenberg, pers. comm.). The localities "San Jose, Sarayacu, Zamora" listed for punctitectus by Hilty and Brown (1986) apparently are in error, as I am not able to find any specimens or reference in the literature to substantiate them. Hilty and Brown (1986) stated the elevational range of punctitectus as 500-1,000 m, but based upon my field experience and the published elevational data for all known localities of collection (Chapman 1926, Paynter and Traylor 1977), I believe that all records are from above at least 1,500 m. Most of the type locality and much of the suitable habitat within the small known range of this subspecies, with the notable exceptions of Mt. Sumaco and portions of Huacamayo Ridge, have been deforested (pers. observ.).

TAXONOMIC HISTORY

In June of 1911, while on an ornithological expedition of the American Museum of Natural History in Colombia, W. B. Richardson collected a single male specimen of an antbird of unknown identity near Cocal, Department of Cauca, on the west slope of the Andes. Chapman sent this specimen to C. E. Hellmayr for identification and, on the authority of Hellmayr, described it as a subspecies of *Thamnophilus aethiops* (White-shouldered Antshrike), naming it occidentalis (Chapman 1923). Less than a year after the publication of his description of occidentalis, Chapman received three specimens of an apparently new species of antbird collected by the Olalla brothers below Oyacachi, Prov-

ince of Napo, on the east slope of the Andes in Ecuador. He described these as a new species, naming it Dysithamnus punctitectus and diagnosing it as resembling D. leucostictus leucostictus (=D. plumbeus leucostictus, Plumbeous Antvireo) of the subtropical zone of eastern Ecuador and eastern Colombia (Chapman 1924). In 1933 Zimmer, examining the genus Thamnophilus in the course of his study of Peruvian birds, recognized that T. aethiops occidentalis and D. punctitectus were almost identical, and removed the former from Thamnophilus, placing both in Dysithamnus. He noted like Chapman a close resemblance between occidentalis and D. l. leucostictus (Zimmer 1933). In concordance with the laws of zoological nomenclature, occidentalis became the specific epithet for the two subspecies. This classification was followed by Peters (1951).

In 1966, Meyer de Schauensee removed four species—ardesiacus, saturninus, plumbeus, and occidentalis—from Dysithamnus, placing them together with caesius and schistogynus in Thamnomanes. He considered ardesiacus to belong in Thamnomanes based upon unpublished observations by E. O. Willis of similarities in foraging behavior between ardesiacus and caesius, and considered the other three species concurrently admitted to Thamnomanes to be related to ardesiacus based upon similarities in morphology and general appearance (Meyer de Schauensee 1966:275). In a later publication (Meyer de Schauensee 1970), he followed this arrangement.

Schulenberg (1983) recommended that occidentalis and plumbeus be removed from Thamnomanes, suggesting that the latter be placed in Dysithamnus, and that based upon bill structure occidentalis was a Thamnophilus. He pointed out the occidentalis was originally described in that genus. Zimmer's (1933) basis for removing occidentalis from Thamnophilus 50 years earlier, however, was also based upon the bill structure (albeit different characters than those measured by Schulenberg) together with plumage differences. The checklist of Hilty and Brown (1986) and most current ones, including Ortiz et al. (1990), followed Meyer de Schauensee (1966, 1970) in placing occidentalis in Thamnomanes. Hilty and Brown (1986) stated that "Its true taxonomic placement (sallying Thamnomanes or gleaning Dysithamnus) is unknown," apparently discounting the possibility of Thamnophilus being the appropriate genus.

Most recently, Sibley and Monroe (1990:383)

assigned occidentalis to Dysithamnus, stating that in so doing they have followed Hilty and Brown (1986) rather than Schulenberg (1983), who they cited as treating occidentalis in Thamnomanes. This is an incorrect citation of both Hilty and Brown (1986) and Schulenberg (1983). The taxonomy of Sibley and Monroe (1990:383) is not based upon biochemical or other evidence and, unfortunately, adds further confusion to an already complicated taxonomic question.

BEHAVIOR AND VOCALIZATIONS

In January 1991, I located Thamnomanes occidentalis punctitectus on the lower slopes of Mt. Sumaco (approximately 0°33'S, 77°44'W), Province of Napo, Ecuador. This area is approximately 40 km by road west northwest of the village of Loreto, and approximately 13 km north of the main road connecting Tena/Baeza with Loreto and Coca. I observed the habitat preference, various behaviors, and vocalizations of several different individuals of both sexes. Observations and recordings were carried out with 10 × 40 binoculars, a Sony TCM-5000 tape recorder, a Nagra 4.2 tape recorder, and a Sennheiser MKH-416 microphone. All tape recordings cited in this paper have been or will be archived at the Library of Natural Sounds, Cornell University, Ithaca, New York.

Along an essentially continuous forest transect from 400 to 1,750 m, I found no T. occidentalis lower than approximately 1,675 m; the upper elevational limit was not determined, although birds were encountered up to 1,750 m. All birds I observed were along a rather narrow ridge cloaked in primary subtropical forest. Within this general habitat, however, I found T. occidentalis only in situations where greaterthan-average amounts of sunlight penetrated the mature forest canopy, creating locally dense vegetative growth in the understory. Such areas usually represented treefalls, landslides, or other "light gaps." Depending on the age and successional state of those light gaps in which I found T. occidentalis, the height of vegetation in them ranged from about 2 to 10 m, and was often dominated by woody plants and herbaceous growth with trunks and stems less than about 2 cm in diameter at their bases. The layer of vegetation covering the forest floor in these light gaps was composed of patchy growth of small herbaceous plants and ferns over a dense, uniformly distributed leaf litter. Bamboo was a

conspicuous element in some of these areas, but I did not observe *T. occidentalis* foraging in bamboo for any extended period, although I did see them moving through and foraging coincidentally in bamboo understory. My limited observations do not suggest that *T. occidentalis punctitectus* is a "bamboo specialist."

Within this microhabitat, which was fairly common along the ridge, I encountered T. occidentalis as solitary individuals or in solitary mated pairs. At least in January, the birds were quiet, secretive, and generally difficult to detect and observe. I located most of them with playback of a recording of the scold of the first adult male I found. After an initial response ranging from aggressive, vocal approach to one of quiet, but interested approach, the birds soon settled into an undisturbed foraging routine. The foraging behavior of five different individuals was observed. Two individuals that I managed to keep in sight for about 20 min each performed a foraging move of some sort about once every 30 s, although they peered about constantly on the lookout for a prey item. While foraging, the birds moved from perch to perch through the understory in short jumps and flights, occasionally longer flights, usually staying on a perch for less than about 15 s, often considerably less. On occasions when an individual maintained a perch for several seconds or longer, such as when preening or apparently just resting, an upright posture recalling that of Thamnomanes antshrikes was adopted. They perched both on horizontal twigs and branches, and on vertical trunks and stems of understory plants. These general movements were accompanied almost constantly by short, rapid flicks of the wings, and to a lesser extent, the tail. In no context did I observe T. occidentalis perform any sort of the regular tail-pumping motion characteristic of several species of Thamnophilus and other thamnophiline antbirds (pers. observ.).

Both sexes foraged by perch-gleaning arthropod prey directly from leaves and twigs, always within 2 m of the ground, usually within 1 m of the ground, and occasionally by flipping leaves while standing directly on the ground. I watched one male as it rummaged audibly for nearly 30 s in a dead-leaf cluster caught in the fork of a sapling about 2 m above ground; I was not able to tell whether it captured any prey items during this search. This was the only instance of specific dead-leaf searching that I noted. Sally-gleaning also was commonly em-

ployed in foraging. Such moves were usually less than 2 m in range, laterally or slightly upward directed, and varied in execution from rapid and graceful scooping motions to rather clumsy lunges. The prey items captured that I was able to see well were a couple of small caterpillars, a small adult moth, a katydid or mantid about 2 cm in length, and a whitish cricket about 4 cm long obtained from the undersurface of a leaf by hanging acrobatically.

I did not observe *T. occidentalis* with mixed-species understory flocks, although such flocks were common in the area. It would not be surprising to discover that *T. occidentalis* occasionally joins mixed-species flocks passing through its territory, much as does *Thamnophilus aethiops*, for instance (pers. observ.). Apparently, *T. o. punctitectus* does not characteristically forage with mixed-species flocks unless, perhaps, it displays a significant temporal or seasonal shift in its foraging strategy.

Some other behaviors were noted following tape playback. Once a male approached in several short rapid flights to stop about 4 m away from me at eye level. It assumed an exaggeratedly erect posture and held its wings out from the body slightly so as to dramatically expose the white lesser primary coverts; the feathers of the head and neck were erected in an apparently agonistic display. This attitude was maintained for only a few seconds. Hilty and Brown (1986) described male T. occidentalis (referring to the nominate race?) as having a "concealed white interscapular patch"; I was not able to see this feature on any of the punctitectus I observed. On another occasion after tape playback, a male T. occidentalis approached from low in the undergrowth, then gradually climbed upward to a height of about 7 m, where it sat quietly for about a minute. A slight movement from me sent the bird darting vertically into the undergrowth, where it disappeared.

Only one interaction between a pair of *T. occidentalis* was observed. The male of a pair that had recently responded to tape playback flew a distance of about 10 m to rejoin the female, landing immediately beside her from which position the two gave several quiet "reassurance" calls sounding like muffled "barks" and a short, quiet trill, the whole episode lasting about 2 s. They then resumed foraging independently, soon wandering out of direct line-of-sight without further vocalizations of any kind.

I tape recorded several different vocalizations

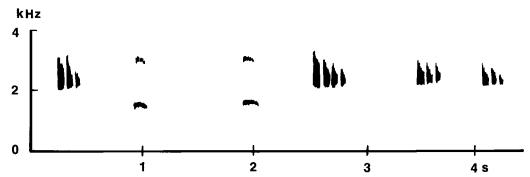


Fig. 1. Unsolicited scolds and calls of *Dysithamnus occidentalis punctitectus*. A series of "JEER-deer-dur" scolds with clear whistled calls interspersed. The scold is a highly distinctive vocalization.

of T. occidentalis. The most commonly heard of these was a low-pitched (about 2.5 kHz), throaty scold of 2 to 4 (most often 3) rapid-burst syllables repeated at a rate of about 1/s for continuous periods ranging from a few seconds to more than 3 min (Fig. 1). I have transcribed it as "JEER-deer-dur" and "JEER-deer-dur-dr," with the first syllable loudest and the subsequent syllables becoming progressively quieter. The first syllable is occasionally varied to a more whistled sound, like "ooEE-deer-dur." These highly distinctive vocalizations were heard in a natural (unsolicited) context and in response to tape playback. I interpreted them as scolds, based upon the birds' behavior of directing attention toward me while delivering the vocalization and the fact that the birds stopped vocalizing if I retreated.

Another vocalization is a short, low, clear, uninflected whistled note that has a complaining quality (sometimes doubled with the second slightly lower-pitched than the first) occasionally interspersed within a series of the scolds described above (Fig. 1). Another whistled note of similar quality, repeated at a more regular interval, has a downward inflection (Fig. 2A). I have transcribed it as "peeur." I recorded one vocalization from a female *T. occidentalis*: a short, very quiet, slightly burry whistled note much like the uninflected whistled note of the male shown in Figure 1.

The only vocalization I heard that may be an element of the song of *T. occidentalis* was a series of four low, whistled notes delivered so closely together as to sound like a stutter, the first three of which being essentially identical with the fourth slightly louder, rising in pitch, and much more drawn out (Fig. 3). This "song" was de-

livered six times and quietly, in the manner of a subsong, by a single male following tape playback of the scold. I have transcribed it as "dudu-du-duAYY."

DISCUSSION

Without respect to height above ground, the generalized foraging behaviors observed for T. occidentalis are typical of many species of Thamnophilus and of all species of Dysithamnus (pers. observ.). They are, however, quite unlike the flycatching behavior of all members of Thamnomanes (Schulenberg 1983; pers. observ.). That T. occidentalis apparently does not forage with mixed-species flocks finds parallel in some species of Thamnophilus, but is unlike most species of Dysithamnus (pers. observ.). Among all species of Dysithamnus, nominate plumbeus appears to me to be the most similar behaviorally to T. occidentalis, as pairs frequently forage apart from mixed-species flocks, keeping near the ground in dense undergrowth of forest and adjacent second-growth (pers. observ.; also R. Ridgely, pers. comm.). All species of Thamnomanes, except for brief early morning and late afternoon periods when mixed-species flocks are inactive, invariably forage with mixed-species flocks (Munn and Terborgh 1979; pers. observ.). In its habit of rapidly and consistently flicking the wings while foraging, T. occidentalis appears to me to be more typical of Dysithamnus than of either Thamnophilus or Thamnomanes.

On Mt. Sumaco, Thamnomanes occidentalis was sympatric with Dysithamnus plumbeus leucostictus. These two are quite similar in both morphology and plumage, as remarked by Chapman (1924, 1926) and especially by Zimmer

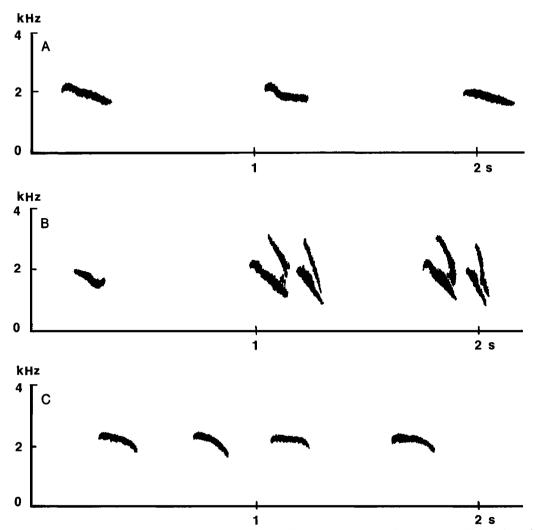


Fig. 2. (A) Unsolicited series of whistled "peeur" calls of Dysithamnus occidentalis punctitectus. (B) Unsolicited "peeur" call of D. plumbeus leucostictus followed by two similar bisyllabic calls with harmonic components. (C) Unsolicited series of whistled "peeur" calls of D. mentalis napensis. All recorded on Mt. Sumaco.

(1933). Even with close comparison in the field, they appeared to me to be essentially the same size, notwithstanding that *T. occidentalis* is described as "much larger than *leucostictus*" (Chapman 1924). Adult males of the two species, which are strikingly similar in plumage, are readily distinguished with attention to some details. *Thamnomanes occidentalis* is a blackish bird (slightly darker dorsally than ventrally), lacking the black-throated, gray-bellied effect of *D. p. leucostictus*, and it does not show any suggestion of pale streaking on the lower belly as is often the case in *leucostictus*; the white dots on the wing coverts appear rounder and with

more contrast on occidentalis than on leucostictus. The female plumages appeared to me to be quite distinctive, but Zimmer (1933) was impressed with similarities here as well, stating that "much more must be known of both species before any further association should be attempted." Although I found these species virtually side-byside in the forest, their foraging strategies were so markedly different, with D. p. leucostictus rarely encountered away from mixed-species flocks and foraging more inside the forest and higher above ground on average, that I doubt that they come into direct contact very often.

The simple "peeur" call of T. occidentalis (Fig.



Fig. 3. Songlike vocalization of *Dysithamnus occidentalis punctitectus* given after playback of scold and calls in Figure 1. This vocalization delivered consistently (six times) but quietly (in the manner of a subsong) by a male.

2A) is very similar to calls of several species of *Dysithamnus*. As a type, this call is characteristic of *Dysithamnus* (although it may not be given by all species) and may function as a contact note between members of a pair or family group (pers. observ.). I am unaware of any members of *Thamnophilus* or *Thamnomanes* that regularly give this call. A comparison of the "peeur" calls of the sympatric *T. occidentalis* (Fig. 2A), *D. p. leucostictus* (Fig. 2B), and *D. mentalis napensis* (Fig. 2C) reveals the close similarity in this call among these three species.

Conclusions

Thamnomanes occidentalis, with regard to its morphology, generalized foraging behavior, and vocalizations is unlike any other member of the genus and should be removed from Thamnomanes, as suggested by Schulenberg (1983). However, a more difficult question remains to be answered: Is occidentalis a Thamnophilus antshrike, a Dysithamnus antvireo, or something else? The only known behavioral trait of occidentalis that may be of significance on the generic level is its habit of rapidly and almost constantly flicking the wings while foraging and in response to tape playback, which I believe to be typical of *Dysithamnus* and relatively rare or lacking among the members of Thamnophilus. Concerning morphology, Schulenberg (1983) stated that such characters as overall size and measurements of the bill cannot be relied upon as evidence of common phylogenetic history in the genera Thamnophilus and Dysithamnus, although his figure 6 shows a significant difference in length and depth of culmen between the two, with occidentalis placed among the Thamnophilus. This notwithstanding, close similarity in the "peeur" call between occidentalis and several members of Dysithamnus and the close similarities between occidentalis and D. plumbeus in overall size, size and shape of the bill, plumage, and foraging behavior suggest that occidentalis indeed belongs in Dysithamnus. As Schulenberg (1983) also placed emphasis upon vocal similarities in supporting the supposed relationship of several members of Dysithamnus, I recommend that occidentalis be reinstated in the genus Dysithamnus. Further elucidation of the relationships of nominate occidentalis and punctitectus, both to each other and to other presumably related species, must await the rediscovery of occidentalis and a thorough biochemical analysis.

The English name of Western Antshrike, introduced by Meyer de Schauensee (1964), should be considered obsolete. Hilty and Brown (1986) incorrectly stated that Meyer de Schauensee (1964) named occidentalis "Western Antvireo," a name that was applied by Sibley and Monroe (1990) in their attempt to follow Hilty and Brown (1986). Given that this antvireo is no more "western" in its distribution than several others (being, in fact, just as "eastern" as it is "western"), a more descriptive name such as Bicolored Antvireo, reflecting the dorsoventrally twotoned plumage of both sexes, would be more appropriate.

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