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FORAGING BEHAVIOR, ECO-MORPHOLOGY, AND SYSTEMATICS OF SOME ANTSHRIKES (FORMICARIIDAE: *THAMNOMANES*)

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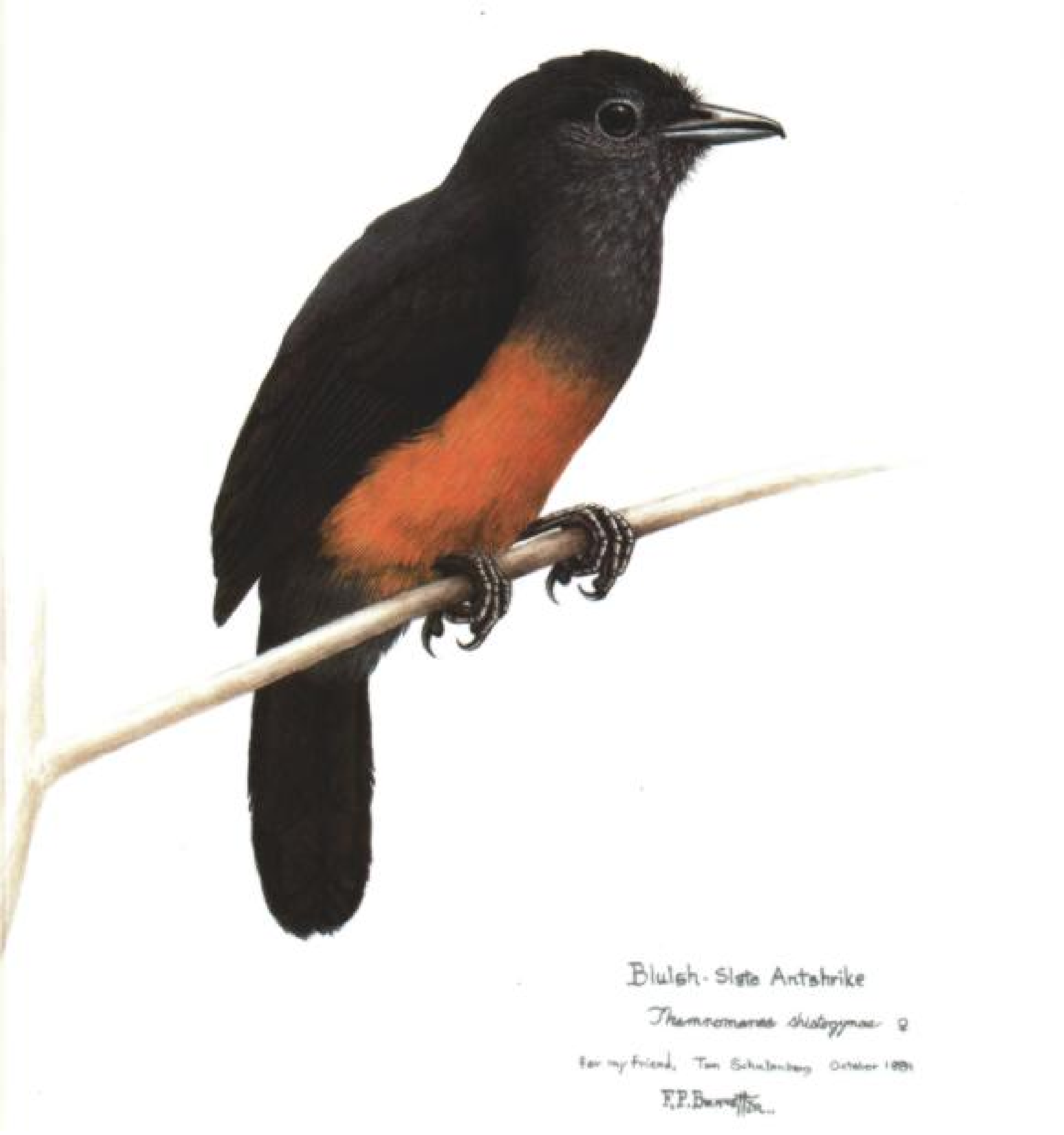
The external morphology of a bird is a reflection of two factors: phylogeny and adaptations to the environment. Traditionally birds have been classified by systematists on the basis of similarities in morphology, especially at lower taxonomic ranks. Ecologists frequently study the same morphological characters used by systematists (e.g., Hespenheide 1973, Karr and James 1975, Ricklefs and Cox 1977). When taxa are arranged on the basis of characters influenced by ecological adaptations, are the resulting classifications reflections of ecological similarity, phylogeny, or both?

The present study is an eco-morphological and systematic study of *Thamnomanes*, a genus of six species of tropical South American antshrikes (Formicariidae). The majority of the species of antshrikes (*Thamnophilus*, *Dysithamnus*, and related genera) are generalized perch-gleaning insectivores. Several species of *Thamnomanes*, however, have recently (Oniki and Willis 1972, Pearson 1975, Munn and Terborgh 1979, Wiley 1980) been recognized to have a specialized "fly-catching" foraging behavior, characterized by a distinctive upright posture (Frontispiece), a "sit-and-wait" foraging strategy, and long prey-capture sallies. These features of *Thamnomanes* foraging behavior are all more typical of families other than the Formicariidae (e.g., Tyrannidae, Bucconidae, Galbulidae). The foraging behavior of *Thamnomanes* appears to represent an evolutionary "experiment" in "fly-catching" behavior unique within the Formicariidae. The aim of this study is threefold: to obtain quantified information on the foraging behavior of *Thamnomanes* antshrikes; to determine what, if any, morphological adaptations accompany this divergent foraging behavior; and to use this information to reconsider the systematics of the genus.



Adult female Bluish-slate Antshrike. Gouache painting by F.P. Bennett, Jr.

STUDY SITES AND METHODS

Field observations of *Thamnomanes* were made at two study sites. Two species, Bluish-slate Antshrike (*Thamnomanes schistogynus*) [Frontispiece] and Dusky-throated Antshrike (*T. ardesiacus*), occur at the first study site, the Explorer's Inn (12°40'S, 69°15'W), elev. 260 m, Dept. Madre de Dios, Peru; only *T. schistogynus* occurs at the second site, on the Río Beni, about 20 km by river north of Puerto Linares (ca. 15°24'S, 67°33'W), elev. 600 m. Dept. La Paz, Bolivia. I was at the Explorer's Inn from 31 October–11 December 1979 and at the Río Beni site from 5 June–8 July 1981. Both study sites are tropical lowland forest (Subtropical Moist Forest Life Zone: Unzueta 1975; ONERN 1976). The forest at these sites has never been cleared, although both localities have experienced minor human disturbance. The canopy was tall at both localities: 30–40 m at the Explorer's Inn, and 30 m at the Río Beni. The forest was structurally similar at the two sites, although the Río Beni site had more treefalls, which are usually sites of dense vine tangles. These tangles are favored foraging sites for many perch-gleaning antbirds, including some with which *Thamnomanes* spp. regularly forage. The Río Beni site is also more hilly than the Explorer's Inn site, which has very little relief.

Data were gathered by locating a flock containing foraging *Thamnomanes* and following the flock as long as possible (on occasion up to 2 h). For comparison to *Thamnomanes*, I quantified the foraging behavior of two more typical antshrikes, Black-capped Antshrike (*Thamnophilus schistaceus*) and Plain Antvireo (*Dysithamnus mentalis*), at the Río Beni study site. I recorded the type of foraging motion, distance of all prey-capture flights, foraging substrate, and height above the ground for each foraging motion. Data were recorded continuously about a bird until I lost contact with it.

Morphological data were taken from museum study skins. The length of the wing (chord), tarsus, and culmen (from base), depth of the bill at the nostril, and the width of the bill at the gape and anterior edge of the nostril were measured with dial calipers to the nearest 0.1 mm. Body weight was recorded from the specimen label.

Most analyses were performed using a minimum of five specimens per species. Data were analyzed using two different statistical procedures, a Mann-Whitney *U*-test (two-tailed) on ratios of characters and an analysis of covariance (ANCOVA) on linear regressions between characters. The relative length of the wing and tarsus were assessed by comparing these parameters to the cube root of body weight (Amadon 1943). Adequate sample sizes for weight data were available for only three species of *Thamnomanes* (Cinereous Antshrike *T. caesius*, *T. schistogynus*, and *T. ardesiacus*), and 10 species of *Thamnophilus* and *D. mentalis*. The relative shape of the bill was assessed by comparing bill width to culmen length; because this analysis was not dependent upon weight data, more species of *Thamnomanes*, *Thamnophilus*, and *Dysithamnus* could be compared.

Samples from various localities were pooled because geographic variation in size was minor. I followed the taxonomy of Meyer de Schauensee (1970), with one exception. Central and South American populations of Slaty Antshrike (*T. punctatus*) were treated separately, as there is a significant size difference between the two populations in the specimens examined for this study (8 g difference in population means, with no overlap), and they may not be conspecific (Oniki 1975).

Wing tracings were made from antbirds collected at the Río Beni site. These were made by spreading the open wing flat onto a piece of paper, with the anterior edge in a straight line, and with the remiges evenly spread.

Foraging behavior.—A variety of terms, not always clearly defined, have been used to describe the prey-capture motions used by insectivirous birds. The terminology I use is based on that of Fitzpatrick (1980).

(1) Perch-glean—stationary prey is removed from a substrate while the bird is perched.

TABLE 1
PREY-CAPTURE MOTION, SALLY DISTANCE, AND PREY-CAPTURE SUBSTRATE OF FOUR SPECIES OF ANTSHRIKES

Prey-capture motion	*D. mentalis* N = 60	*T. schistaceus* N = 19	*T. ardesiacus* N = 38	*T. schistogynus* N = 84
Sally-glean	15 (25%)	14 (73.7%)	36 (94.7%)	76 (90.4%)
strike	11 (18.4%)	12 (63.2%)	22 (57.9%)	49 (58.3%)
hover-glean	4 (6.6%)	2 (10.5%)	14 (36.8%)	27 (32.1%)
Aerial-hawk	—	—	1 (2.6%)	7 (8.3%)
Perch-glean	45 (75%)	5 (26.3%)	1 (2.6%)	1 (1.2%)
Sally distance (m)	N = 15	N = 14	N = 25	N = 71
Mean	0.3	0.5	1.0	1.4
Range	0.2–0.3	0.2–1.0	0.1–4.6	0.1–4.6
Substrate	N = 58	N = 19	N = 27	N = 74
Air	—	—	1 (3.7%)	7 (9.4%)
Leaf	46 (79.4%)	18 (95%)	24 (88.9%)	56 (75.7%)
top surface	6 (10.3%)	—	3 (11.1%)	10 (13.5%)
bottom surface	26 (44.8%)	10 (53%)	11 (40.7%)	21 (28.4%)
surface ?	11 (19.0%)	8 (42%)	10 (37.1%)	24 (32.4%)
dead leaf	3 (5.2%)	—	—	1 (1.3%)
Branch	12 (20.6%)	1 (5%)	2 (7.4%)	11 (14.9%)
≤5 cm	12 (20.6%)	1 (5%)	1 (3.7%)	9 (12.2%)
>5 cm	—	—	1 (3.7%)	2 (2.7%)

(2) Sally-glean—stationary prey is removed from a substrate by a pursuit flight from a perch. Sally-gleans may be further divided into "hover-gleans" and "strikes." In a hover-glean, the bird performs a brief hover at the substrate as the prey is captured, whereas in a strike the capture is performed with a flight that carries the bird up to and away from the substrate in a single rapid movement.

(3) Aerial-hawk—flying prey is captured in the air by a pursuit flight from a stationary perch (sometimes referred to as "true flycatching").

The foraging behavior of most antshrikes (*Thamnophilus*, *Dysithamnus*, and allies) is not well known. Antshrikes seem to be primarily generalized foliage-gleaning insectivores. As with other gleaning insectivores, e.g., wood-warblers (Parulini), prey is captured by perch-gleaning or by short sally-gleans (e.g., Oniki 1975, Jones 1977). Due to the paucity of careful field observers in the New World tropics and to the generally secretive nature of these birds, little is known about the relative frequency of perch-gleaning vs sally-gleaning, average sally distance, and substrate utilization.

RESULTS

Quantified data on the foraging behavior of *D. mentalis*, *T. schistaceus*, and two species of *Thamnomanes* are shown in Table 1. *Dysithamnus* *mentalis* is primarily a perch-gleaner, very short sally-gleaning accounting for only a quarter of all observed prey captures. *Thamnophilus schistaceus*, in contrast, is predominately a sally-gleaner that forages methodically in vine tangles, and often makes short sally-gleans to surrounding vegetation.

Although *T. schistaceus* is predominantly a sally-gleaner, it does not approach *Thamnomanes* in the degree of specialization for sally-gleaning. Three parameters of the foraging behavior of *Thamnomanes* reflect adaptations of this genus to sally-gleaning (Table 1): (1) the almost total absence of perch-gleaning; (2) the addition of aerial-hawking to the foraging repertoire; and (3) the longer sally in *Thamnomanes*. The sally distance data may be biased towards shorter, easier-to-observe sally-gleans, because the longer the sally, the greater the chance of losing sight of the bird before the moment of prey capture, and of being unable to distinguish a foraging flight from a flight to a new perch.

The foraging behavior of the two *Thamnomanes* studied may also differ from that of *T. schistaceus* in two additional parameters, foliage density of the foraging station and length of time spent searching for prey at each foraging station. *Thamnomanes* typically perch in relatively open sites in the forest understory, unlike *Thamnophilus*, which typically inhabit rather densely vegetated undergrowth. Fitzpatrick (1981) showed that median search time in tyrannid flycatchers is correlated with foraging strategy: perch-gleaning tyrannids spend less time at each foraging station than do sally-gleaning species. My impression is that a similar pattern could be found in antshrikes; quantification of these parameters is desirable.

Most sally-gleans by *Thamnomanes* are strikes, which are often explosively rapid. Hover-gleaning is also commonly used. The relative contribution of each prey capture technique to the overall foraging behavior of the two species of *Thamnomanes* observed is remarkably similar. The major difference between the two is the shorter mean sally distance of *T. ardesiacus* (1.0 m vs 1.4 m, $t = 1.94$, $P < 0.05$).

Other authors have also noted similarities in the foraging techniques of syntopic *T. ardesiacus* and *T. caesius* (Oniki and Willis 1972, Pearson 1975, Wiley 1980), and *T. ardesiacus* and *T. schistogynus* (Munn and Terborgh 1979). It is not clear how syntopic sally-gleaning antshrikes minimize potential interspecific competition. As *T. schistogynus* and *T. ardesiacus* differ in their mean sally distance, this may suggest that they are searching for prey at slightly different distances from their perches. Pearson (1977) showed that several species of antwrens (*Myrmotherula* spp., Warbling Antbird [*Hypocnemis cantator*]) differ in resource utilization patterns in vertical foraging height and foraging substrate. At the Explorer's Inn *T. ardesiacus* and *T. schistogynus* use similar substrates, primarily leaf surfaces. There was a difference in perching height ($t = 7.826$, $P < 0.001$)

between *T. ardesiacus* ($\bar{x}$ = 2.6 ± 1.4 m, range 0.3–10.7 m, N = 221) and *T. schistogynus* ($\bar{x}$ = 4.0 ± 2.4 m, range 0.3–12.2 m, N = 235). *Thamnomanes ardesiacus* has previously been noted to forage lower than *T. schistogynus* (Munn and Terborgh 1979) and *T. caesius* (Oniki and Willis 1972). Despite this vertical segregation, however, there is considerable overlap in foraging height between *T. ardesiacus* ($\bar{x}$ = 2.9 ± 1.1 m) and *T. schistogynus* ($\bar{x}$ = 5.1 ± 2.2 m) at the Explorer's Inn.

Thamnomanes schistogynus and *T. ardesiacus* regularly forage in mixed-species flocks with each other and with other species of antbirds (Munn and Terborgh 1979; pers. obs.); indeed, I have never seen a *Thamnomanes* that was not associated with other birds. As with other mixed-species assemblages of birds, the benefits to each species from flocking are not clear. Munn and Terborgh (1979) and Wiley (1980) suggested that *Thamnomanes* might derive a feeding advantage by flocking with other birds because other members of a flock might flush insects while foraging that a hawking *Thamnomanes* could capture. Wiley (1980) noted, however, that members of a flock are often spaced so far apart as to make this kind of feeding benefit uncommon. Neither Munn and Terborgh (1979) nor Wiley (1980) reported *Thamnomanes* catching insects flushed by another bird, nor did I observe this. If *Thamnomanes* did not attempt to capture in flight prey items that had been flushed by other birds, but waited until the prey had landed upon a substrate to attempt prey capture, feeding benefits derived from flocking would be difficult to detect by direct field observation. The following observations on the vertical foraging height of *T. schistogynus* suggest indirect evidence of such feeding advantages.

At the Explorer's Inn site, *T. schistogynus* typically foraged in forest understory. The average perching height of foraging *T. schistogynus* at this locality was 4.0 ± 2.4 m (N = 235), and the average height at which sally-gleans were performed was similar, 5.1 ± 2.2 m (N = 38). Although flocks containing *T. schistogynus* sometimes foraged below mixed-species canopy flocks of insectivorous birds, the antshrikes usually did not change their vertical foraging position in the presence of these flocks, i.e., they did not begin to perch higher to benefit from prey flushed by birds foraging above them.

Perch height was not recorded at the Río Beni study site. At this location, however, *T. schistogynus* regularly left the undergrowth to forage in the lower part of the forest canopy with mixed-species flocks containing such birds as *Tangara* spp., Yellow-crested Tanager (*Tachyphonus rufiventer*), and White-winged Shrike-Tanager (*Lanio versicolor*). This shift in vertical foraging position is reflected in the mean height (9.0 ± 6.1 m, N = 26) at which sally-gleans were performed at the Río Beni, almost twice the mean height at the Explorer's Inn. The reasons for this vertical shift are not clear. It is possible that at the Río Beni, *T. schistogynus* actually was joining canopy flocks to capture insects flushed by other flocking species.

ECO-MORPHOLOGY

I examined four morphological characters thought to be directly related to prey capture: wing, tarsus, bill, and rictal bristles.

Wing.—Most passerine birds, and all formicariids, share a single basic wing design, the elliptical wing. This design provides maneuverability and high lift efficiently at low to moderate speeds (Savile 1957).

Several groups of highly aerial feeders, including some passerines (Hirundinidae, Artamidae), have independently evolved long, narrow, pointed wings. This wing design produces a moderately high aspect ratio (wing span^2/wing area). Fitzpatrick (1978) demonstrated that within the Tyrannidae, relative wing length and aspect ratio varied in accordance with foraging behavior. Relatively longer wings and higher aspect ratios were found in species such as aerial hawkers that made longer pursuit flights for their prey. Consequently, I predicted *Thamnomanes* would have longer wings, with higher aspect ratio, than perch-gleaning antshrikes.

The relative length of the wing (wing length/cube root of body weight) is greater in *Thamnomanes* than in *Thamnophilus* (Fig. 1A; $P < 0.002$, Mann-Whitney U-test). Wing lengths of *Thamnophilus* and *Thamnomanes* are also significantly different after the effect of size is reduced ($P < 0.001$, ANCOVA).

To test the hypothesis that the long wings of *Thamnomanes* are correlated with an increase in aspect ratio in sally-gleaning antshrikes, aspect ratios were calculated for 25 species of antbirds (including *T. schistogynus*) from the Río Beni study site (Fig. 2). *Thamnomanes* does not have an appreciably higher aspect ratio than *D. mentalis*, the three species of *Thamnophilus* or most other antbirds whose wings were examined. The highest aspect ratios were found primarily in some antbirds feeding on or near the ground (i.e., Banded Antbird [*Dichrozona cincta*], Scale-backed Antbird [*Hylophylax poecilonota*], Hairy-crested Antbird [*Rhegmatorhina melanosticta*], and Black-faced Antthrush [*Formicarius analis*]).

The wings of *T. schistogynus*, despite their greater length, have essentially the same shape as the wings of the perch-gleaning *Thamnophilus*

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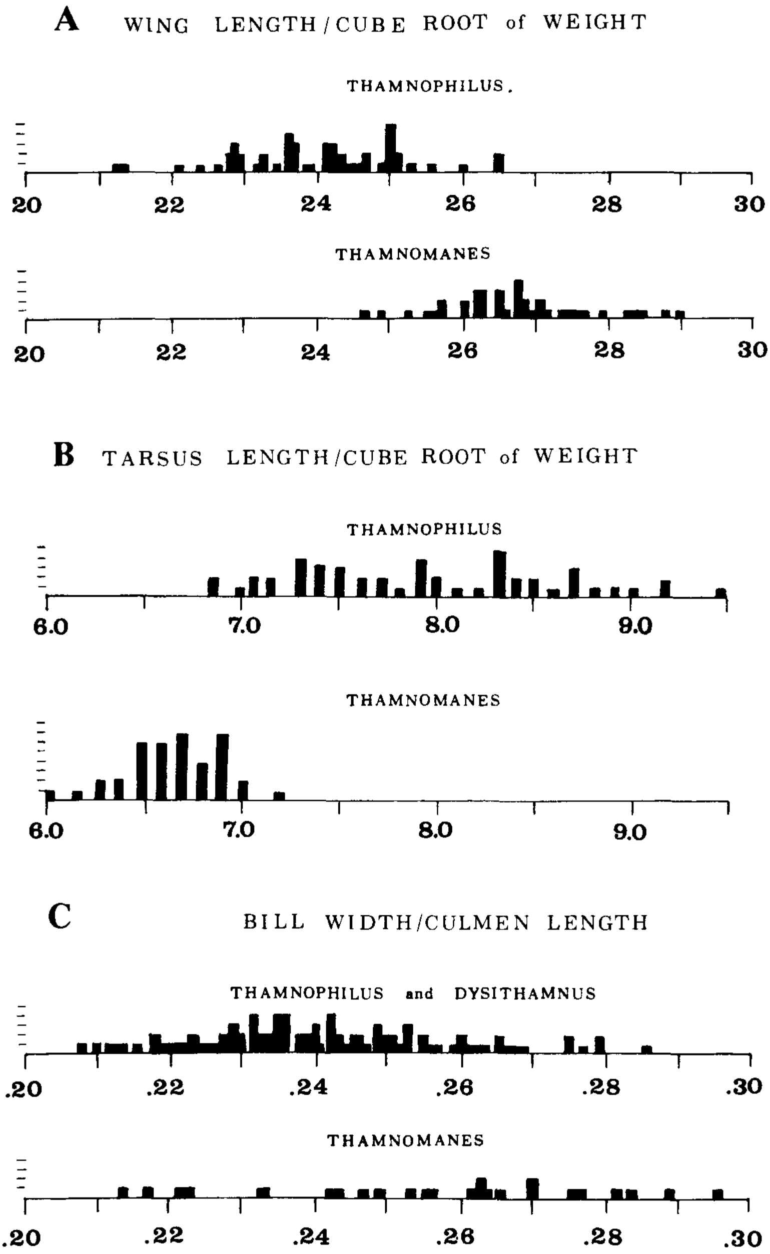
FIG. 1. Comparative morphology of antshrikes, expressed as ratios of: (A) wing length to cube root of body weight in 10 species of *Thamnophilus* and three species of *Thamnomanes*; (B) tarsus length to cube root of body weight in 10 species of *Thamnophilus* and three species



of *Thamnomanes*; and (C) bill width at the nares to culmen length in 14 species of *Thamnophilus*, five species of *Dysithamnus* and five species of *Thamnomanes*.

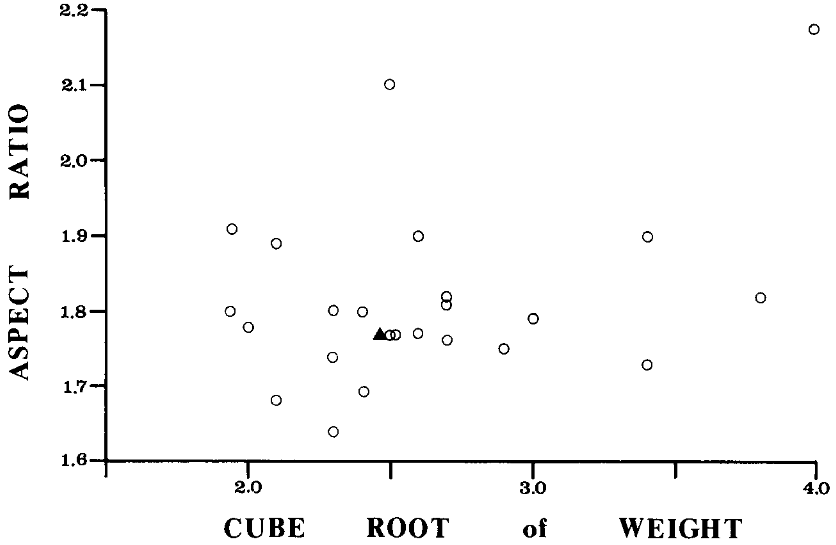


FIG. 2. Cube root of mean body weight by mean aspect ratio for 25 species of antbirds. The closed triangle represents *T. schistogynus.*

and *Dysithamnus.* Wing shape in *Thamnomanes* is probably a compromise between several competing factors. Long wings are favored for sustained flights and for hover-gleaning (Norberg 1979). Wing length is limited however by the somewhat closed vegetation in which *Thamnomanes* forage. Broad, rounded wings are found in many birds that repeatedly make sudden take-offs, as foraging *Thamnomanes* do (Savile 1957). Rounded wings have "slots" at the wing tip, which further increase lift (Savile 1957). Fitzpatrick (1978) found that rounded, slotted wings are typical of many understory sally-gleaning tyrannids.

The relatively greater wing length in *Thamnomanes* is also reflected in relative increase in wing area. Wing area in birds is correlated with weight (Greenewalt 1962). Nonetheless *T. schistogynus* has a relatively large wing area, resulting in low wing-loading (Fig. 3). Lower wing-loading facilitates hovering (Partridge 1976, Norberg 1979), and *T. schistogynus* regularly hover-gleans.

Tarsus.—The length of the tarsus in antshrikes may be affected by at least two aspects of foraging behavior. Longer tarsi may be favored among active perch-gleaning insectivores if it effectively increases the birds' "stretch-and-pick" distance. Longer tarsi may also be selected for in insectivores that scan close, dense vegetation, regardless of prey-capture

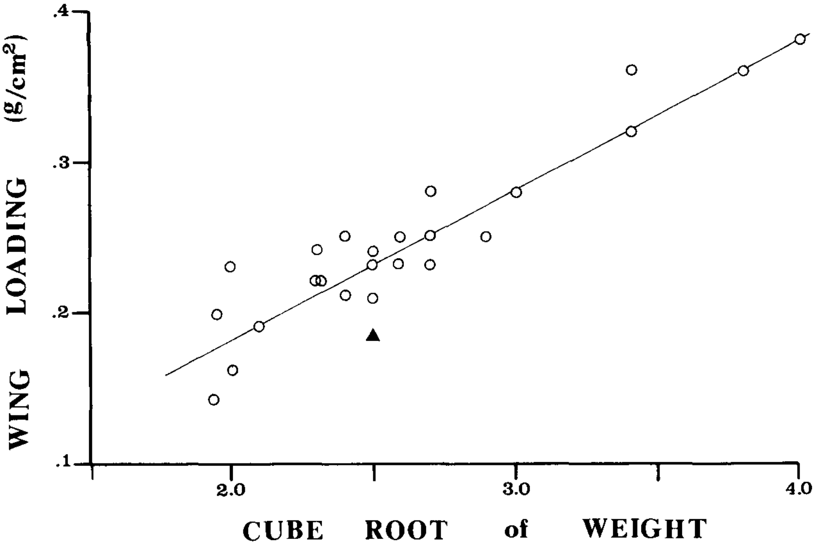


FIG. 3. Cube root of mean body weight by mean wing loading values for 25 species of antbirds. The closed triangle represents *T. schistogynus.*

technique. In this situation longer tarsi allow the bird to bob vertically, and search more substrates from the same perch (see Fitzpatrick 1978: fig. 12, p. 51). Among insectivorous birds such as aerial hawkers that remain for relatively long periods of time at one perch, however, shorter tarsi should be favored, as the birds center of gravity is closer to the perch, enhancing balance at the expense of maneuverability. This advantage would be expected to be important to *Thamnomanes,* which typically sit with a characteristic upright posture, close to the perch, much like many hawking tyrannids.

Relative tarsus length (tarsus length/cube root of body weight) is less in *Thamnomanes* (*T. caesius, T. schistogynus,* and *T. ardesiacus*) than in *Thamnophilus* (Fig. 1b; $P < 0.002$, Mann-Whitney U-test). Tarsus lengths of *Thamnophilus* and *Thamnomanes* are also significantly different after the effect of size is removed ($P < 0.025$, ANCOVA). The two analyses indicate that these sally-gleaning *Thamnomanes* have relatively shorter tarsi than do the predominately perch-gleaning *Thamnophilus.*

Bill.—A broad, flat bill is often found in species that capture much of their food on the wing (Keast 1972). Such bills typify entire families of highly aerial feeders, e.g., Apodidae and Hirundinidae. The functional importance of this bill type can be gauged by noting that it frequently appears in species that habitually hover-glean or hawk, even though closely-related perch-gleaning species have a more typical narrow bill (e.g., *Setophaga* in the Parulini; Bennett 1980).

Relative bill width in antshrikes was determined for 14 species of *Thamnophilus*, five species of *Dysithamnus*, and five species of *Thamnomanes* (data not available for Western Antshrike [*T. occidentalis*]). The relative width of the gape (width of gape/culmen length) is not significantly different between *Thamnomanes* and a pooled sample of *Thamnophilus* and *Dysithamnus*. Bill shape nonetheless varies among antshrikes. The relative width of the bill (bill width at the nares/culmen length) is not significantly different between *Thamnophilus* and *Dysithamnus*; therefore, these two genera were pooled to compare to *Thamnomanes*. Relative bill width (bill width at the nares/culmen length) is greater in *Thamnomanes* than in *Thamnophilus* and *Dysithamnus* (Fig. 1c; $P < 0.05$, Mann-Whitney *U*-test; $P < 0.001$, ANCOVA).

As Fig. 1c shows, however, there is overlap between *Thamnomanes* and *Thamnophilus* plus *Dysithamnus* with regard to relative bill width. This overlap is due both to a narrow-billed *Thamnomanes* (Plumbeous Antshrike [*T. plumbeus*]: mean bill width ratio = 0.236, N = 20) and to several wide-billed *Dysithamnus* (Spot-crowned Antvireo [*D. puncticeps*]: mean bill width ratio = 0.254, N = 20; Streak-crowned Antvireo [*D. striaticeps*]: mean bill width ratio = 0.275, N = 20). *Thamnomanes plumbeus* in Venezuela forages by perch-gleaning or sallying in low mixed-species flocks in forest understory, much like *D. mentalis* (P. Schwartz and E. Willis, pers. comm. Willis). *Dysithamnus puncticeps* is reported to regularly hover-glean (Greenberg and Gradwohl 1980), and *D. striaticeps*, which is closely related (Cory and Hellmayr 1924) may do the same. Bill shape in insectivorous birds, however, may be influenced not only by the manner in which the prey is caught, but also by the nature of the prey itself (e.g., Greenberg 1981). A full understanding of the significance of bill shape variation in antshrikes will require more complete information of both the foraging behavior and prey of these birds.

Bristles.—Semibristles, a feather-type intermediate in structure between bristles and contour feathers (Lucas and Stettenheim 1972), are found on the face and gular region in all species of *Thamnophilus*, *Dysithamnus*, and *Thamnomanes*. In addition to semibristles, two species of *Thamnomanes*, *T. caesius*, and *T. schistogynus*, have feathers approaching the bristle grade in which the rachis clearly extends beyond the distal barbs (Fig. 4). These bristles are distributed on the lores, along the edge of the maxilla, and on the gular region. The bristles of *T. schistogynus* and *T. caesius* are often well developed and resemble the rictal bristles of tyrant flycatchers, although the rachis is less stiffened and the distal barbs

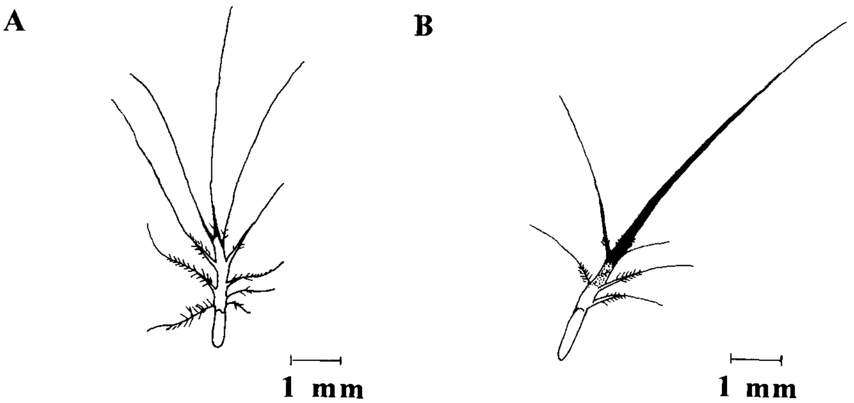


FIG. 4. Facial feathers of *Thamnomanes*: (A) rictal semibristle of *T. ardesiacus*; (B) loral bristle of *T. schistogynus*. Note the absence of distal barbs and the prominence of the rachis over the proximal barbs in the bristle of *T. schistogynus*.

are more fully developed. The remaining species of *Thamnomanes* (*T. ardesiacus*, Saturnine Antshrike [*T. saturninus*], *T. plumbeus*, and *T. occidentalis*) lack bristles, although semibristles are distributed in the same facial areas that contain bristles in *T. caesius* and *T. schistogynus*.

The function of rictal bristles has never been clear (Stettenheim 1973). They are often found in hawking or sally-gleaning birds such as tyrannids, and, thus, it has been suggested that they aid in prey capture by increasing the effective surface area of the bill, a claim that has never been substantiated. Furthermore, some birds that feed extensively on the wing, including such highly-specialized aerial feeders as the Apodidae and Hirundinidae, lack well-developed rictal bristles. Conover and Miller (1980) presented experimental evidence that the rictal bristles do not aid in food capture, but may help to protect the eyes. In this case, development of rictal bristles would still be selected for in sallying or hawking birds. Prey size might affect the development of rictal bristles, however, as birds feeding on relatively small or soft-bodied insects may not subject their eyes to as much danger as would birds feeding on larger insects.

SYSTEMATICS

The genus *Thamnomanes* was described by Cabanis (1847) for a new species of antshrike, *T. caesius*. Historically *Thamnomanes* contained only *caesius* and its allospecies, *T. schistogynus*. Meyer de Schauensee (1966) admitted to *Thamnomanes* four additional species, *ardesiacus*, *saturninus*, *plumbeus*, and *occidentalis* (all previously considered to be *Dysithamnus*).

Meyer de Schauensee considered *ardesiacus* to be a *Thamnomanes* on the basis of unpublished observations by E. O. Willis of similarities in foraging behavior between *ardesiacus* and *caesius*; the other three species were believed to be related to *ardesiacus*, and were also transferred to *Thamnomanes*. Two questions arise from this change in taxonomy: do the behavioral similarities between *ardesiacus* and *caesius* support congeneric status? Are *ardesiacus, saturninus, plumbeus,* and *occidentalis* more closely related to *caesius* than to other antshrikes?

The foraging behavior of *caesius, schistogynus,* and *ardesiacus* is associated with some subtle morphological differences distinguishing these species from other antshrikes. These similarities in foraging behavior and morphology may reflect common ancestry, or may have resulted from the independent development of a similar foraging technique. Antshrikes on the whole are very similar structurally. Their differences in morphology may be related to subtle differences in foraging technique. This relationship makes it difficult or impossible to correctly reconstruct phylogenetic history from standard morphological data.

These three species also share a common plumage pattern in each sex (except for the unique female plumage of *T. schistogynus*). These plumage patterns are quite simple, however, and differ from most *Thamnophilus* and all *Dysithamnus* by the lack of wing-bars, tail-spots, crown pattern, or other distinctive features, and not by the common possession of a unique plumage pattern. A few *Thamnophilus* (e.g., Uniform Antshrike [*T. unicolor*] and Mouse-colored Antshrike [*T. murinus*] also have similar, simple plumage, thus, this character cannot be relied upon to unite *caesius, schistogynus,* and *ardesiacus*.

The species *ardesiacus* thus shares with members of *Thamnomanes* a specialized foraging behavior and morphology. These similarities are difficult to interpret as evidence of phylogenetic relationship. There is no evidence, however, that *ardesiacus* is more closely related to any species in *Thamnophilus, Dysithamnus,* or any other genus of antbird. Therefore, I recommend following Meyer de Schauensee (1966, 1970) in treating *ardesiacus* as species of *Thamnomanes* and hypothesize that the specializations for sally-gleaning exhibited by *caesius, schistogynus,* and *ardesiacus* evolved only once. The taxon *saturninus* was for some time thought to be a subspecies of *ardesiacus* (see Cory and Hellmayr 1924, Zimmer 1932). The two taxa have very similar plumages, are largely parapatric and resemble each other morphologically (below), all of which suggest a close relationship between these two forms. The behavior and voice of *saturninus* is also similar to that of *ardesiacus* (E. Willis, pers. comm.).

Hellmayr (*in* Cory and Hellmayr 1924) believed *plumbeus* to be related to *ardesiacus* on the basis of similarities in "proportions," "shape of the

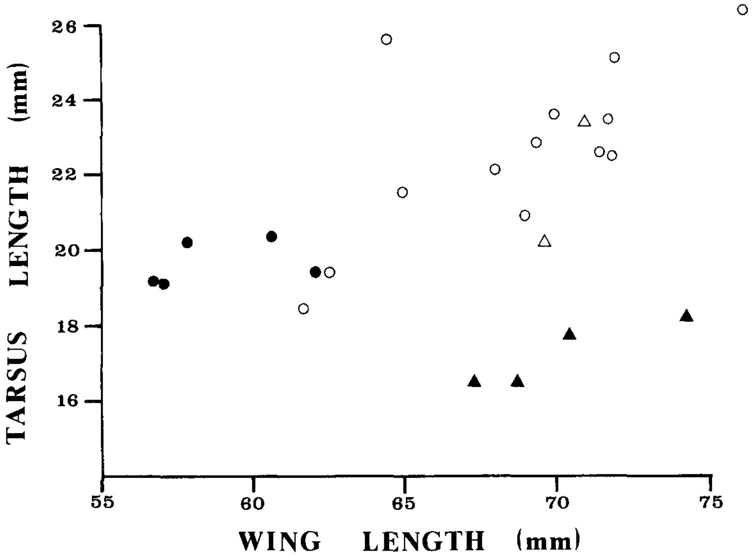


FIG. 5. Species means of wing length by tarsus length in *Thamnophilus* (open circles), *Dysithamnus* (closed circles), and *Thamnomanes* (triangles). The closed triangles represent four species of sally-gleaning antshrikes (*T. caesius*, *T. schistogynus*, *T. ardesiacus*, and *T. saturninus*).

bill," and male plumage. The shape of the bill of *plumbeus*, at least in terms of relative width, is actually not similar to that of *ardesiacus*; rather the bill of *plumbeus* is significantly narrower than is the bill of *ardesiacus* ($P < 0.002$, Mann-Whitney U-test). The bill of *plumbeus* more closely resembles the narrow bill shape predominant in *Thamnophilus* and *Dysithamnus* than it does the relatively broad bills of *caesius*, *schistogynus*, *ardesiacus* and *saturninus*. Hellmayr did not indicate what "proportions" he considered to be similar between *plumbeus* and *ardesiacus*. Weights for *plumbeus* are not available, and so the morphology of parts of the body cannot be considered individually. If two structures of the body, wing length and tarsus length, are compared simultaneously, however, one can compare at least some of the "proportions" of *plumbeus* and *ardesiacus*.

Wing length and tarsus length in antshrikes are compared in Fig. 5. There is a general positive correlation between the two characters. Two groups stand out from the general pattern. The first is composed of a single species, Rufous-capped Antshrike (*T. ruficapillus*), which has relatively long legs and short wings. This combination suggests that *ruficapillus* may be particularly adept at "stretch-and-pick" perch-gleaning. Another group, also separated from most antshrikes, is composed of several antshrikes with long wings and short tarsi. This group is composed of the sally-gleaning *caesius*, *schistogynus*, and *ardesiacus*, and also *saturninus*, strengthening the hypothesis of morphological similarity (and presumed relationship) between *saturninus* and other species of *Thamnomanes*.

The remaining species currently assigned to *Thamnomanes*, *T. plumbeus* and *T. occidentalis*, fit the general antshrike pattern of intermediate wings and tarsi, suggesting that they lack the morphological adaptations for sally-gleaning. There is no reason on the basis of "proportions" to consider either of these two species to be related to members of *Thamnomanes*. The only remaining character that would unite these species in *Thamnomanes* is plumage pattern. Zimmer (1933) noted a resemblance in the male plumage between *plumbeus* and *occidentalis*, and suggested that they were congeneric. Zimmer (1933) did not mention *ardesiacus* in his discussion, although earlier Hellmayr (*in* Cory and Hellmayr 1924) had considered *plumbeus* and *ardesiacus* to be related because of similar male plumages. All three taxa (*ardesiacus*, *plumbeus*, and *occidentalis*) have dark gray or blackish male plumages; *plumbeus* and *occidentalis* differ from *ardesiacus* by having white tips to the wing coverts. Black and gray are common colors for male antshrikes, including *Thamnophilus* and *Dysithamnus*, many of which also have white-spotted wing coverts. Although the male plumage of *T. plumbeus leucostictus* resembles the male plumage of *ardesiacus* in the common possession of a blackish throat, the male plumage of other populations of *plumbeus* shows as much or more resemblance to some *Thamnophilus*, e.g., *murinus*, as they do to *ardesiacus*. As no unique plumage pattern is shared by *plumbeus*, *occidentalis* and *ardesiacus*, this character again fails to provide evidence that *ardesiacus* is related to the other two species, and I suggest that *plumbeus* and *occidentalis* be removed from *Thamnomanes*.

The question then becomes, what are the affinities of *plumbeus* and *occidentalis*? Empirically, the species of *Dysithamnus* are separated from *Thamnophilus* by their smaller size and slimmer (less deep) bill (Fig. 6). Neither character can be relied upon as evidence of common phylogenetic history. Nonetheless, vocal similarities among several species of *Dysithamnus* (*mentalis*, *striaticeps*, and *puncticeps* [Slud 1964]; *mentalis* and the Spot-breasted Antvireo [*D. stictothorax*], T. A. Parker, pers. comm.]) support the hypothesis that these species are related. When bill structure of *plumbeus* and *occidentalis* is compared to other antshrikes, *occidentalis* falls into the *Thamnophilus* group. This is not surprising, as *occidentalis* was originally described as a *Thamnophilus* (Chapman 1923). The dimensions of the bill suggest that *plumbeus* is a *Dysithamnus*, although *plum-*

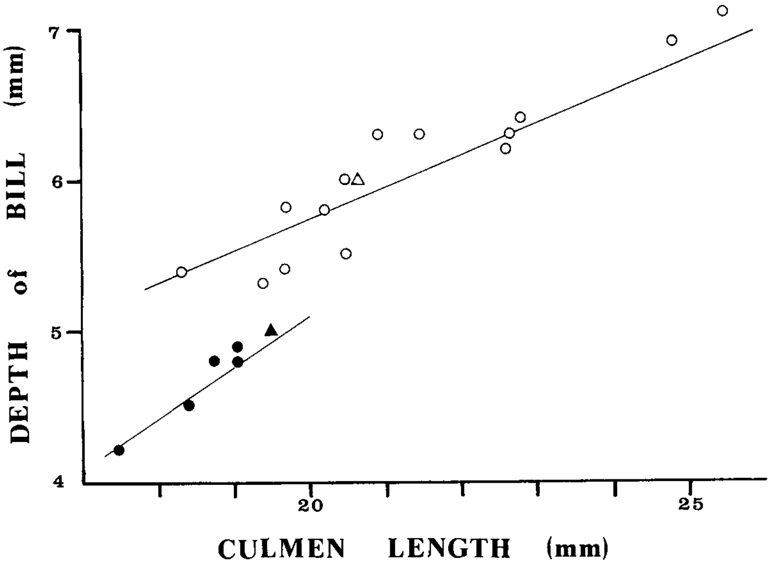


FIG. 6. Species means of culmen length by depth of bill at the nostrils in *Thamnophilus* (open circles) and *Dysithamnus* (closed circles). The regressions are significantly different ($P < 0.001$, ANCOVA). The species *occidentalis* and *plumbeus* are represented by open and closed triangles, respectively.

beus is larger than all other *Dysithamnus* and is approaching a size and morphology intermediate between *Dysithamnus* and *Thamnophilus*.

SUMMARY

Most antshrikes (Formicariidae: *Thamnophilus*, *Dysithamnus*, and allies) are generalized perch-gleaning insectivores. Several species of the South American antshrike genus *Thamnomanes*, however, are characterized by a foraging behavior that appears to be unique within the family. These *Thamnomanes* are sally-gleaning insectivores that utilize a "sit-and-wait" foraging strategy accompanied by long prey-capture sallies. Quantitative data on some aspects of this foraging behavior are presented for two species of *Thamnomanes* studied in the field in Peru and Bolivia.

The morphology of *Thamnomanes* is predicted to show specializations reflecting their sally-gleaning behavior: sally-gleaning antshrikes are predicted to have relatively longer wings, shorter tarsi, and wider bills than perch-gleaning antshrikes. These predictions are tested using museum specimens, and the morphology of *Thamnomanes* is shown to fit the predictions.

The systematics of *Thamnomanes* is re-evaluated with special consideration given to foraging behavior and accompanying morphological specializations. The genus *Thamnomanes* is recommended to contain four species known or inferred to be sally-gleaners. Two species

currently classified in *Thamnomanes*, *T. plumbeus*, and *T. occidentalis*, are believed on the basis of morphology to be perch-gleaners, and are removed from the genus.

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