

BEHAVIORAL CHARACTERISTICS OF SERPOPHAGININE TYRANNIDS

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The tyrant flycatchers comprise a family with unusually broad ecological radiation, but most are birds for which we have as yet very little information about even gross behavior patterns, and for which phylogenetic relationships remain uncertain. One group is ecologically interesting because its species forage in ways at least superficially analogous to wood warblers, vireos, titmice, wagtails, and Old World reed warblers and grass warblers. In many cases the tyrannids even resemble these other groups in plumage characteristics. This group falls within Hellmayr's (1927) subfamilies Serpophaginae and Euscarthminae. Although I shall argue in subsequent papers that these two subfamilies should not be distinguished, a large number of species and genera are involved and it is convenient to use Hellmayr's classification as a framework for presenting information about their behavior. Most of his serpophaginine species form a coherent phylogenetic group even if they appear to be as closely related to some euscarthminine genera as they are to each other.

My studies began in 1959 and continued intermittently through 1969 when time was available from more intensive work with other tyrannid genera. The amount learned about the behavior of different species varies greatly, but some major patterns of display behavior (i.e., evolutionarily stylized signalling) and of behavioral aspects of ecology are now apparent. These permit reassessment of some relationships currently recognized (e.g., by Hellmayr 1927, Zimmer, MS, and de Schauensee 1966) at the generic level, and based in large part on characteristics available in museum skins. Because these characteristics (primarily bill and leg morphology and plumage pattern and coloration) relate to environmental parameters, knowledge of ecological behavior is pertinent to the interpretation of their systematic significance. Display characteristics add yet another dimension for comparison.

The material is presented below by taking each of Hellmayr's genera, briefly describing

the plumages and ranges of its species, seeking similarities and differences in general habitat preferences and foraging methods, then considering the vocal and visible displays. Displays are given capitalized names in accordance with established ethological procedure, and are described and compared in physical form and employment, emphasizing similarities and differences among displays that are *used* in similar ways (i.e., accompanied by comparable behavior patterns) by different species. Through what is now known about the employment of displays in tyrannid genera where whole repertoires have been much more thoroughly studied (e.g., *Tyrannus*, Smith 1966; *Sayornis*, Smith 1969b, 1970a, b; *Contopus*, *Myiozetetes*, *Pitangus*, and *Myiodynastes*, Smith, MS), it is possible to estimate what kinds of serpophaginine displays have been sampled. Further, studies of members of yet other Hellmayrian subfamilies such as the Euscarthminae (Smith, unpubl. data) and Fluvicolinae (Smith 1967, 1970c, 1971) permit the forms of these displays to be considered within a broader perspective.

All recording was done on Nagra III-B tape recorders. Through 1962, tape speed was 15 ips and an Electro-Voice 650 microphone was used with a 30-inch diameter parabolic reflector. Subsequently tape speed was reduced to 7.5 ips and a Sennheiser 404 cardioid microphone was used without a parabola. All physical analyses of recorded sounds were done on a Kay Electric 6061A Sona-Graph. Illustrations were traced from sonagrams, omitting only features clearly definable as noise or machine-induced artifacts. This technique does involve interpreting sonagrams and so introduces some error, but it is widely accepted by ethologists working extensively with bird vocalizations as preferable to the loss of resolution involved in reproducing photographs of sonagrams.

SERPOPHAGA

PLUMAGES AND GEOGRAPHICAL DISTRIBUTIONS

Hellmayr (1927) recognized the following species in *Serpophaga*: White-crested Tyrannulet (*S. subcristata*), White-bellied Tyrannulet

nulet (*S. munda*), River Tyrannulet (*S. hypoleuca*), Sooty Tyrannulet (*S. nigricans*), Torrent Tyrannulet (*S. cinerea*), and Plain Tyrannulet (*S. inornata*). Zimmer (MS) and de Schauensee (1966) removed the last of these, which lacks the white crown patch typical of the others, to the genus *Inezia* (see below), and added the Gray-crowned Tyrannulet (*S. griseiceps*) and Bananal Tyrannulet (*S. araguayae*), thus far known only from type localities. In addition, Zimmer placed *S. munda* in *S. subcristata*, feeling the latter to be locally variable in coloration. Most authors, however, have considered them specifically distinct and geographically overlapping, and, as they differ in coloration and in some vocalizations, I shall adhere provisionally to that view.

The White-crested Tyrannulet (*S. subcristata*) is the brightest, with an olive back, yellow belly, grayish chest, and white throat; the rear central feathers of the otherwise gray crown are black and slightly elongated, covering those with white bases that form a concealed crown patch. Wings and tail are olive-brown, with two pale yellowish wing bars and yellowish edgings to the flight feathers. *S. munda* is similar but gray on the back and white below. *S. hypoleuca* is relatively pale, very white below, and medium gray on the back, with a slight brownish tone, particularly on the wings and tail. *S. nigricans*, the largest species (about 25–30 per cent longer than *S. subcristata*), is sooty gray, slightly darker, and tending toward olive-brown on the back, wing bars, and wing edgings. Its remiges are dark brown, its tail black, and its crown is quite similar to that of *S. subcristata* except that the black feathers are less elongate; its undertail coverts are slightly olivish. *S. cinerea* is the most strikingly unusual species, being entirely gray, black, and white. Its black crown has a white concealed central patch, but no elongated feathers. Its throat is lightest and belly nearly as light, but its chest is gray and its back slightly darker, contrasting with the black of the wings, tail, and head. I have not examined *S. araguayae* but Zimmer (MS) remarks that it is “probably most nearly related to” *S. nigricans*. Similarly, *S. griseiceps* is like *Inezia inornata* in color (i.e., like *S. munda*, but without a white crown patch, see Berlioz 1959), and de Schauensee (1966) agrees that it belongs in *Serpophaga* because it has an exaspidean tarsus.

The genus is generally distributed throughout lowland tropical South America. *S. hypoleuca* is relatively equatorial, and *S. subcristata*, *S. munda*, and *S. nigricans* are largely in the southern tropics south to the central South

Temperate. *S. cinerea* is the exception, living primarily in the subtropical elevations of the Andes and southern mountains of Middle America from Costa Rica to northern Bolivia, and descending to the Pacific in central Perú. *S. griseiceps* is known only from Cochabamba, Bolivia, and *S. araguayae* only from Goias, Brazil.

FIELD SITES

Field studies were conducted as follows.

S. subcristata. At the Instituto Fitotécnico Santa Catalina, near the city of Buenos Aires, Argentina, 28 October–3 November 1962, a pair observed daily was engaged in pre-nesting activities. Another five individuals were each studied on several occasions as they foraged and moved about, apparently patrolling territories.

S. munda. Several single individuals and pairs were studied in Tucumán Province, Argentina, 13–17 November 1962, at two sites, a wooded stream valley (Quebrada de Lules near the city of Tucumán), and a dense thorn forest near La Cocha in the south of the province.

S. nigricans. Two adults were found with two fledglings on 21 December 1962 along the Rio Claro in the Serra do Mar of São Paulo State, Brazil, near the Boraceia field station.

S. cinerea. Individuals were observed from 26 to 28 March 1962 at and near a nest with eggs on the property of G. Lewis along the Río Chiriquí Viejo about 3 km below Cerro Punta, Panamá. Observations were made of two pairs with adjacent territories along the Río Guayllabamba near San Antonio, Ecuador, 14–17 June 1966. Different and separate pairs observed within 8 km of this site on 4 and 6 August 1959 were not then breeding, nor were two solitary individuals foraging along streams several kilometers north of Cumbaye, Ecuador, on 6 August 1959.

HABITATS AND FORAGING BEHAVIOR

Members of this genus use a considerable range of habitats. *C. subcristata* and *S. munda* are birds of forest, scrub, riverine woods, and thickets, although they use herbaceous vegetation in open sites adjacent to more woody growth and will nest as low as 1 m (e.g., Gibson 1918). Wetmore (1926) reports that during autumn in Mendoza Province, Argentina, migrating *S. munda* occur both in the low scrub of dry slopes and in “better watered sections in growths of weeds.” As the pampas have become relatively densely settled and plantations of trees have appeared, *S. subcristata* has become abundant in these new habitats.

The family of *S. nigricans* was by a fast flowing stream in open, second growth forest, and Hudson (1920), says they seldom occur far from such sites. Wetmore (1926), however, found the species in “lowland marshes where dense thickets of low willows and other water-loving shrubs stood in shallow water” in Uruguay. Gibson (1918) found it in the “rushes”

of a swamp and at other wet sites in Buenos Aires, Argentina, and Hussey (1916) found it by drainage ditches at La Plata, Argentina. Grant (1911) calls it a "woodland" bird but says that it nests near water. Thus, although it uses leafy vegetation, *S. nigricans* seems restricted to sites near water. *S. cinerea* is further restricted to fast mountain streams, which appear to be its principal source of food. It is largely independent of surrounding vegetation, which in cloud forests may meet over the stream in some parts of a territory, or in sub-arid country may be sparse. It occurs in few lowland areas, and is typical of the altitudinal vegetation zones usually called "subtropical" and even "temperate" (e.g., de Schauensee 1964, 1966). These altitudinal preferences may be determined by stream characteristics (see Skutch 1960).

S. subcristata and *S. munda* forage rapidly among twigs and leaves, gleaning and flight-gleaning like very active warblers rather than pursuing flying prey like most North American flycatchers. Although they search at all heights above about 0.5 m, I have found them most commonly in higher foliage levels (5–15 m, depending on vegetation type). *S. nigricans* and *S. cinerea* are also unusually active, but do more aerial flycatching. Further, both take prey from on or near the water surface. They flight-glean, *S. nigricans* from leaves and *S. cinerea* from the surfaces of rocks and cut banks, perching on roots, small plants, or outcroppings of the substrate and scanning nearby surfaces; *S. cinerea* is particularly attentive to wet soil by springs. A *S. cinerea* nearly always, but particularly if perched atop a bush, scans for flying prey within about 5 m. It will also alight on mud or sand bars or rocks and run and pause like a species of *Muscisaxicola* (terrestrial Andean tyrannids, see Smith 1971), stopping to peck at the ground and pick up prey. Occasionally I have seen one wade in very shallow water off a sand bar, or in water running over rocks in a rapids.

Because *S. cinerea* has such unusual foraging behavior for a tyrannid (it is, for instance, very unlike the larger Black Phoebes, *Sayornis nigricans*, which share its habitat in many areas), I have kept some records of prey captures at each field site. Of 72 instances (6 of which included multiple captures during repeated passes through insect swarms without alighting), 33 were by aerial pursuit of flying prey, 1 insect was chased and seized by a running bird. Eight prey were taken from the surface of streams by flying birds, 11 from river banks (mostly by flight-gleaning), 18 from soil by the run and peck method, and 1

was obtained under the surface of shallow water. This sample gives only a rough idea of the foraging methods, as there must be considerable variation among individuals and habitats and in different seasons.

Serpophaga thus appears to be an ecologically varied genus of rather specialized flycatchers, as the studied species are highly active and do considerable gleaning or flight-gleaning. Two obtain prey primarily from twigs and leaves, but two have become attached to habitats with open water. One of the latter has become virtually independent of vegetation for foraging and requires rapidly flowing streams.

VOCAL DISPLAYS AND THEIR EMPLOYMENT

Regularly Repeated Vocalization (RRV). Prolonged, more or less continuous, and regular bouts of calling that fit descriptive criteria for "song" have been recorded from some *Serpophaga subcristata* and *S. munda*. The most rapid averaged about one burst every 3 sec, was heard in the predawn twilight on two mornings from various individuals of *S. munda*, and was fully comparable with the patterned vocal bouts that have been called the Regularly Repeated Vocalization in many other tyrannid genera (e.g., *Tyrannus*, Smith 1966, and *Sayornis*, Smith 1969b, 1970a). Attempts to hear such performances from other species of *Serpophaga* were unsuccessful. However, both *S. subcristata* and *S. munda* performed singing very like the RRV (about one burst every 4 sec with occasional pauses and occasional breaks for long flights) at about sunrise and for roughly an hour thereafter as they moved rapidly about, apparently patrolling territories. In addition, two patrolling *S. subcristata* twice approached and used such bouts in countersinging duels with one another.

Repeated Vocalization (RV). The patterned RRV and RRV-like song bouts comprised several different vocalizations which were differently and separately employed both in bouts and as non-song vocalizations. In both *S. subcristata* and *S. munda* the predominant one was a brief trill, the RV (see fig. 1, line 1a, fig. 2, line 1), uttered from a perch with the head thrown back. RVs of both species are comprised of four to six (usually six) very brief chevrons. The first several of these are usually simple, while the last one to three have two peaks. In recorded samples of three individuals from each population the secondary peaks in RVs of *S. munda* tend to be more prominent than those of *S. subcristata*. A briefer, four-unit form recorded from *S. munda* in postdawn patrolling (fig. 2, line 1c) is com-

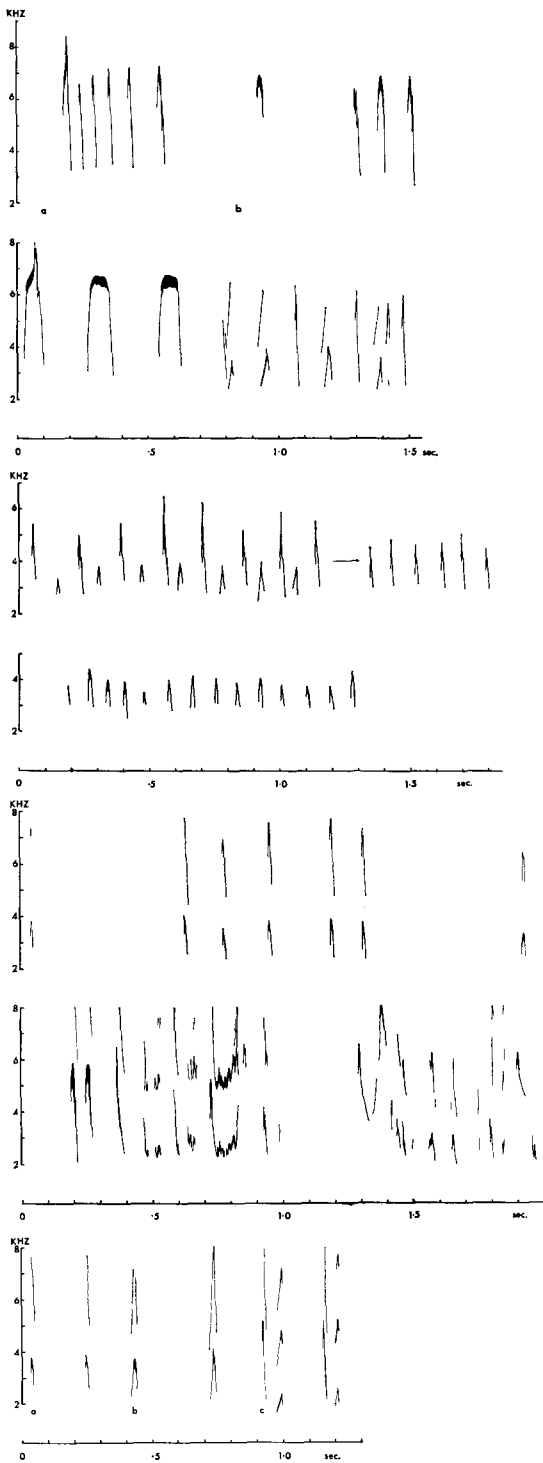


FIGURE 1. *Serpophaga subcristata*: (top to bottom) line 1 (a), Repeated Vocalization (RV) uttered by a patrolling individual; line 1 (b), Repeated Vocalization (RV) uttered in an agonistic situation; line 2, RV Variant, developing into Locomotory Hesitance Chatter (LHC), in an agonistic situation; line 3, LHC, long form, developing into simple ending with non-couplet elements (some elements are removed from the figure in section indicated by arrow); line 4, Chatter Vocalization (CV) used in Nest-Site-Showing (note that it is similar to but not identical with simple ul-

parable to a four-unit form (fig. 1, line 1b) recorded from an *S. subcristata* in mid-morning agonistic encounters with its apparent mate, while the predawn *S. munda* forms are very like the early postdawn patrolling and countersinging forms of *S. subcristata* (e.g., fig. 1, line 1a). Each individual varied the duration of RVs, but the recorded sample is too small to show whether other forms of variation differ in usage, or are typical of different individuals.

RVs are not wholly restricted to song bouts. An RV was the only call heard following a chase that terminated a long, silent territorial encounter of two *S. subcristata*.

RV Variant. Individuals of *S. munda* periodically introduced an RV Variant (fig. 2, line 2) into predawn singing. It clearly resembles an RV Variant that was recorded once (fig. 1, line 2) from *S. subcristata*, in a mid-morning encounter between mates. In the latter, the RV Variant changed without intergradation into a Locomotory Hesitance Chatter (LHC; q.v.). No comparable shift was recorded in *S. munda*, but possibly the RV Variant in both species is in some ways intermediate between the RV and the LHC. It is relatively prolonged for an RV, and each of its units is prolonged, as is the first unit of a LHC, at least in *S. munda*.

S. cinerea has a single unit vocalization (see fig. 3, line 1) described as "chite" by Skutch (1960). I have recorded Chite most often from birds foraging alone or with their mates, and who called it either while alighting (instead of a Chite-Churr Series, see below), or a second or two later, or while perched. It was perhaps most commonly uttered when one foraged alone near its territorial boundary (i.e., apparently patrolling). It was used by individuals proceeding in short flights outward to their boundaries, there to counter call with a neighbor, although counter calling itself never comprised single Chite vocalizations. In addition, Skutch (1960) reports a "single note" repeated at dawn, "over and over" from a rock in a river. This corresponds to circa-dawn "singing" behavior of the other species, with Chite used in place of their elaborate combinations of RVs, RV Variants, and chatters. On

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mate portion of long LHC); line 5, five Brief Units (BU) in a series, preceded and followed by single BUs; line 6, complex combination of BUs and other calls, based on a noisy recording; line 7 (a) and (b), different forms of two-note calls that appear to be closely related to some of the longer chatters, perhaps to the ultimate portions of prolonged, two-part LHC; line 7 (c), a similar call, but based on a couplet structure clearly related to the initial portions of LHC.

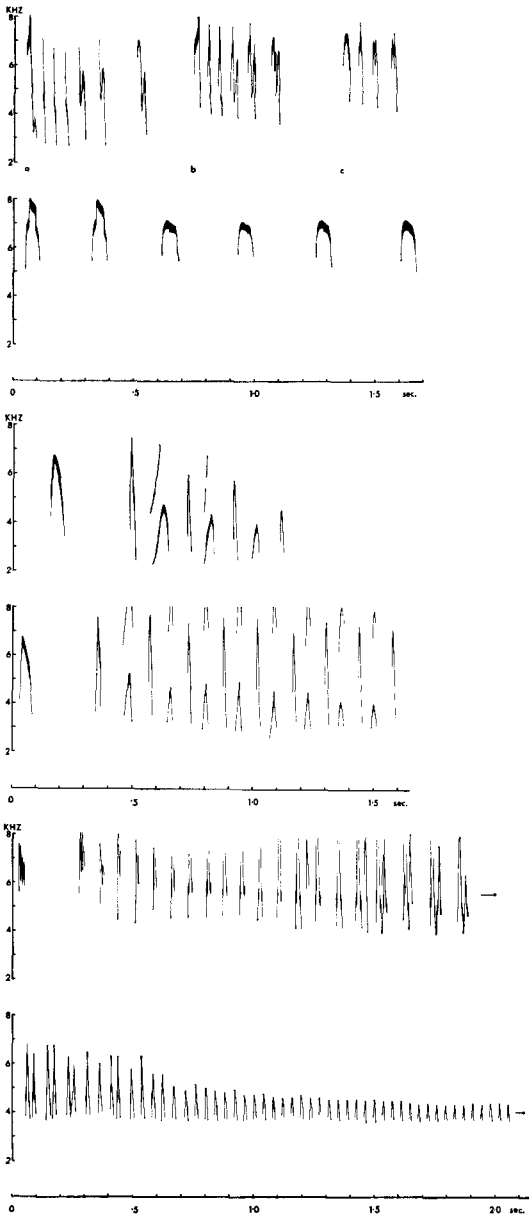


FIGURE 2. *Serpophaga munda*: (top to bottom) line 1 (a), Repeated Vocalization (RV) from continuous Regularly Repeated Vocalization (RRV) calling; line 1 (b), a similar RV from a different individual; line 1 (c), RV from postdawn usage; line 2, RV Variant from predawn RRV calling; line 3, Brief Chatter (BC) from session of predawn RRV calling; line 4, Locomotory Hesitation Chatter (LHC) from postdawn singing, probably during patrolling; lines 5 and 6, Long Chatter; the arrows indicate that some elements have been omitted from the figure.

the whole, Chite is more comparable to the RV Variants than the RVs of the other species.

Chatters. Interspersed among the usually more abundant RVs in the song bouts of *S. subcristata* and *S. munda* are one or more of the following four forms of chatters.

(1) In the very rapid predawn RRV bouts

of *S. munda*, the chatter is very stylized, with minor variations after the first three units (sampled from two individuals; see fig. 2, line 3). These "Brief Chatters" (BC) comprised 20 per cent or less of the vocalizations in the bouts, and were the only chatter based on couplets these species used while remaining still on a perch (as is done when uttering most RVs).

The BC of *S. cinerea* is similar in form, although lacking couplets, and its usage corresponds at least in part to that of the BC of *S. munda*. For example, one individual used several BCs in rapid sequence (see fig. 3, lines 4, 5) in countercalling with a neighbor using Chite-Churr Series (see below). Another instance in which a BC was uttered by a bird foraging alone (perhaps patrolling) suggests more the LHC usages of the other species. This BC was also used in greetings, usually by a perched bird as its mate alighted nearby (fig. 3, line 2), a situation for which I have no comparable observations of the other species.

(2) The couplet form of the BC of *S. munda* relates it to the more prolonged and variable Locomotory Hesitation Chatter (LHC) of that species and *S. subcristata* (fig. 1, line 3, and fig. 2, line 4). These very similar LHCs are abundant in patrolling, and typically occur just as the displaying bird is alighting from a flight. More than half the flights in maximally vocal patrolling of *S. subcristata* ended with LHCs. As LHCs do not correlate with other movements, such as turning on a perch, it appears that some conflict between locomotory tendencies and other, opposing tendencies underlies their usage. That LHCs have also been recorded during a few flights of at least *S. subcristata* lends support, since in all such flights the bird veered and faltered, giving much indication of hesitation.

Samples of over 10 min each were taken during maximally vocal patrolling by two different individuals of *S. subcristata*. Each averaged about eight RVs to each LHC, and all LHCs came in flight or on alighting, whereas only 7-8 per cent of the RVs came on alighting, and none in flight. In one case an *S. munda* used many more LHCs than RVs while almost never remaining more than 2 sec on a perch; when it remained for several seconds, it did use RVs.

LHCs were also recorded from the *S. subcristata* pair during apparently agonistic encounters when they may have had a "greeting" function. This pair was in dense vegetation and hard to follow, but at least once the LHCs came as they began to approach the site where

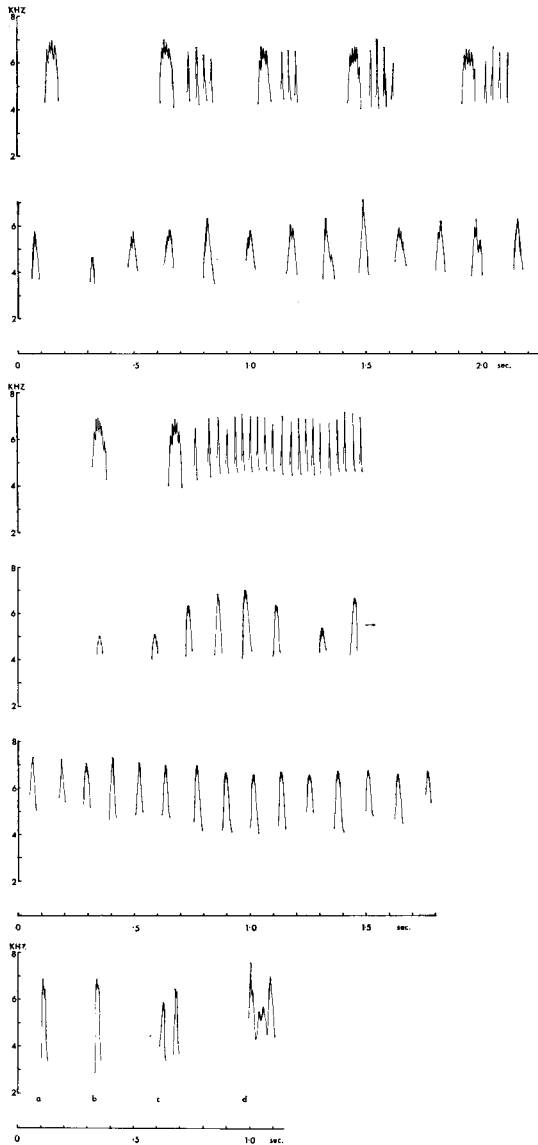


FIGURE 3. *Serpophaga cinerea*: (top to bottom) line 1, Chite Churr series used in patrolling in Ecuador (Often one additional Chite precedes such a series by about 1 sec. The Chite units uttered singly do not differ in form from those in the series.); line 2, greeting reply to the Chite Churr series of a mate (this example, from Panamá, has the most complex units I've found); line 3, Chite Churr uttered by bird patrolling alone near its territorial boundary in Ecuador (the Churr is unusually prolonged; the subsequent three Chite Churrs were all of the usual length; see line 1 above); line 4, one of several Brief Chatters (BCs) used in rapid sequence during a boundary encounter, while calling against an individual that was using less frequent Chite Churr series (Ecuador); line 5, unusually long chatter in the set in which the BC of line 4 occurred (compared with line 2).

Serpophaga nigricans (calls recorded from a family group): line 6 (a) and (b), loud, single, "teek" calls, perhaps the species' Brief Unit (BU); line 6 (c), an example of the fainter couplet vocalizations; line 6 (d), the one more complex vocalization, recorded after a begging fledgling approached an adult.

they performed the Nest-Site-Showing display (q.v.); they always approached it together and once there did not use LHCs. Hudson (1920) said that mates will sing a "little confused song" together, perhaps a description of greeting with a vocalization such as the LHC.

S. cinerea has a call that in form (fig. 3, line 1) and usage appears to combine RV Variant and LHC. This can be termed the Chite-Churr Series, basing the names on descriptions by Skutch (1960).

Chite-Churr Series have been most commonly recorded as a bird alighted during apparent boundary patrolling, usually preceded by one or two Chites (RV Variants) in the last second or so of flight. Also, one individual uttered such series in countercalling with a neighbor using BCs. They are thus similar in usage to the LHCs of *S. subcristata* and *S. munda*. However, during patrolling they are also used, with occasional Chites, from a perch, not nearly as often as on alighting, but too often to support a clearly defined locomotory message.

The second most common usage of the Chite-Churr Series was as a greeting uttered by an individual alighting near its mate. Although heard frequently, only six samples were sufficiently well recorded to determine unambiguously the overlapping vocalizations used by each individual. In each case (two from Panamá and four from Ecuador) the mate replied with a BC (see fig. 3, line 2). The alighting Panamanian birds used Chite-Churr in combination starting their series, then repeated several Churrs before terminating with a Chite-Churr. Ecuadorean birds employed Chite-Churr in combination throughout the series. In addition, one good recording was obtained of one Panamanian bird alighting alone near the nest, slightly nervous in my presence. It again omitted many of the Chite units. As this pair was not seen in any apparently aggressive behavior, the fewer Chites may have reflected a lowered probability of aggression.

No calls comparable to RVs or chatters were recorded from *S. nigricans*. Hudson (1920) appears to describe greetings between mates, however, in which the birds "utter a series of trills and hurried sharp notes in concert."

(3) One *S. subcristata* did Nest-Site-Showing display on several occasions while its mate watched. During the display at least one uttered Simple Chatters (SC, fig. 1, line 4) of quite variable length. This shared with all chatters a tendency for the members of a series to fluctuate sinusoidally in peak frequency, but comprised simple chevron elements not

grouped into couplets, and not identical with the usual terminal forms of prolonged LHCs. It appears to be a display of distinct and limited usage.

S. cinerea may also have an SC, as Skutch (1960) reports one female "twittered" as she settled on her eggs in the presence of her mate, which was perched near the nest and tail pumping.

(4) Although no forms closely comparable with the long two-parted LHCs of *S. subcristata* were recorded from *S. munda*, one very prolonged and somewhat comparable chatter was obtained. This Long Chatter (fig. 2, lines 5, 6) was recorded from an otherwise silent bird foraging near a singing individual thought to be its mate. The chatter began like nothing recorded from the other species, but quickly developed into couplets of very brief chevron elements and then changed gradually into a simpler, SC-like terminal portion. The apparent mate uttered an RV during it; this may have been the singing together of mates mentioned by Hudson (1920) and Wetmore (1926). Functionally, it could resemble duetting (see Hooker and Hooker 1969) or greetings (see Smith 1966), or both.

Brief Units (BUs), and Brief Unit Combinations. The pair of pre-nesting *S. subcristata* had several apparently agonistic encounters in the treetops not far from their display site. These fast-paced events could not be followed in detail because of the foliage. All were characterized by abundant single chevron units (fig. 1, line 7a), pairs of these (fig. 1, line 7b), or pairs of couplets (fig. 1, line 7c), and by less abundant brief series of similar units (fig. 1, line 5) when activity was highest. When the birds appeared to be chasing, more varied series (e.g., fig. 1, line 6) sometimes were recorded in which some units were joined by portions of rapid frequency-modulation, and in which others, usually initial units, made them appear RV-like. All other forms of BU looked primarily like chatters.

No similar vocalizations were recorded from *S. munda*, although Wetmore (1926) says that in the autumn foraging individuals often utter a "low tseet." Skutch (1960) mentions hearing "many slight, sharp notes" with "much darting back and forth" in a dispute among *S. cinerea* over a territorial boundary.

In the *S. nigricans* family the most commonly used calls of both adults and fledglings were rather loud, single "teek" units. On careful examination of sonagrams (e.g., fig. 3, line 6a and b), most show a very slight tendency to have a second peak close after the first, but all are very brief. This is likely what Hudson

(1920) described as a "loud, complaining chuck" uttered "perpetually" during foraging by this species. Less common were fainter, variable couplets (e.g., fig. 3, line 6c) with usually a slightly lower peak frequency than the single "teek" units, uttered primarily when several calls were given in close proximity. Couplets may have been uttered mostly by the fledglings. In addition, a more complex vocalization was recorded once (fig. 3, line 6d) after a fledgling approached an adult with harsh begging calls. It resembles some calls recorded in the *S. subcristata* encounters (compare with example in fig. 1, line 6).

Begging Calls. The only young seen were *S. nigricans* fledglings. These begged from the accompanying adults with bursts of faint, harsh calls that did not record well over the background noise of the stream. Sonagrams reveal little of the detailed structure of the begging calls other than that they peaked at about the same frequency as the "teek" units, with their energy concentrated in two bands at about 2.5 to 3.7 kHz, and about 5 to just over 7 kHz. Their harshness apparently results from rapid frequency-modulation. Duration of the bursts ranged from about 0.1 to 0.3 sec.

NON-VOCAL DISPLAYS

Revealed Crown Patch (RCP). Although all four species studied have a central white crown patch, I saw it used in display behavior only by *S. subcristata*. It occurred in agonistic disputes, but abundantly only in a prolonged territorial encounter (see below). The crown feathers were parted laterally and slightly elevated at the back, making the otherwise concealed white feathers visible (much as they appear in many species of *Elaenia*). In an Ecuadorean pair of *S. cinerea*, white was occasionally glimpsed at the rear of the crown as they foraged, but without orientations or restriction to socially defined situations that would suggest use as a display. Skutch (1960), who has studied this species extensively, makes no mention of the white patch. The foraging pair of *S. nigricans* had the white persistently exposed but also did not appear to use it as a display. Hudson (1920) says that two foraging individuals of *S. nigricans* will meet with "crests erect" but mentions nothing about the white patch.

Crouch. This display is known only from a silent, territorial dispute between two *S. subcristata* in which both frequently postured near one another for many minutes, with much sidling and pivoting and many short flights. One consistently faced more directly toward his opponent. The latter more consistently

made little flights away, and was the only one to flee more than 10 m (twice, chased the second time). Both, however, used an identical pose, squatting on their tarsi, ruffling their back but not their rump feathers, using frequent RCP, and Wing and Tail Flicking. Except in not pointing their bills downward, their posture closely resembled Crouching in the distantly related genus *Tyrannus* (Smith 1966; see figs. 3:1b and 4:6b).

Wing and Tail Flicking. The two Crouching *S. subcristata* repeatedly flicked their drooped wing tips rapidly upward through a small arc, and flipped their tails up over their backs while fanning them open. A similar tail motion has been seen in greetings of the Panamanian pair of *S. cinerea*, but with what is probably a different wing display. The latter fluttered rather than flicked their drooped wing tips. Forms and usages suggest the difference between the Wing Flutter and Wing Flick displays of *Tyrannus* (Smith 1966). *S. cinerea* also flicks its tail, but downward, with each "churr" of a Chite-Churr Series. Hudson (1920) briefly describes what may be greetings between foraging mates of *S. nigricans* in which they call together while "flirting their wings and tails."

Both *S. cinerea* and *S. nigricans* use conspicuous tail movements while foraging, a type of behavior common to many species of stream-side birds and in most instances not ritualized into display behavior, although in use it at times intergrades with displaying. Both species frequently pump their tails: a short downward stroke followed by a large, conspicuous upstroke, the tail then usually returning to its resting position. Sometimes it remained cocked over the back, with occasional small forward flicks. If an *S. cinerea* perched on a mud bank, it often omitted the initial brief downstroke. The manner of tail fanning differed: *S. cinerea* partially opened the tail on the downstroke, kept it open until near the end of the upstroke, then closed it, whereas *S. nigricans* usually began to half-fan the tail as it started the upstroke. *S. nigricans* also sometimes left the tail fanned after pumping it, especially if it then began to move about in a bush. These minor differences may reflect differences in the species' modes of foraging, since *S. cinerea* commonly tail pumps during pauses while running, something *S. nigricans* is not known to do, although it will perch on the ground (Wetmore 1926). Otherwise both species tail pump immediately after alighting from some flights, or while perched anywhere.

Nest-Site-Showing (N-S-S). Many tyrannids have a display, used primarily before and in

the early stages of nest-building, in which one or both mates squats in either a suitable nest site or in the nest and makes nest-forming movements, usually uttering the homologue of an SC. The pair of *S. subcristata* was seen several times to visit a particular crotch on a limb. One bird would precede its mate, pause and look at the crotch, then squat in it with nest-forming movements, sometimes subsequently beginning the SC. Its mate approached very close and watched each time, once actually stepping on the back of the performer, although without attempting to copulate.

Wing Whirr. Two brief (less than 0.1 sec, and just over 0.2 sec) bursts of white noise elements were produced in flight by one *S. subcristata* during an agonistic encounter. These sounded like, and were probably comparable to, Wing Whirring in other tyrannids, which is usually produced by a bird while pursuing another.

INEZIA

One tyrannid, the Plain Tyrannulet, looks so much like *Serpophaga munda* and *S. subcristata* that specimens are best distinguished not by plumage but by tarsal characteristics (Zimmer 1955:1-2). It lacks a white crown patch, Zimmer having found at most only "a suggestion of obscure shaft marks without noticeable elongation of the feathers," but he also noted that some *S. subcristata* have just a trace of a crown patch. He called the species *Inezia inornata*, since members of *Serpophaga* have the exaspidean tarsus considered to be the usual tyrannid form, while this species and others assigned to *Inezia* have a taxaspidean tarsus. He considered such tarsal differences to be "certainly of generic value," but did not say why. Hellmayr (1927), on the other hand, had long since concluded that the taxonomic value of tarsal scutellation has been "unduly overestimated," particularly since form varies among different individuals of the same species. Indeed, it is difficult to think of a priori reasons why this should be a magically decisive taxonomic characteristic, and we lack much understanding of functional differences among the various tarsal patterns. Many tyrannids (see footnotes in Hellmayr 1927; de Schauensee 1966) have been left in limbo because of odd tarsi; it has even been suggested that these *Inezia* species might be cotingids. Yet in view of the great similarities to arboreal *Serpophaga* species, the three species of *Inezia* probably belong in the genus *Serpophaga*, where their lack of crown patches and their tarsal differences perhaps mark them as a species group.

The most different from *Serpophaga* species is the Plain-tipped Tyrannulet, *I. subflava*, which has a graduated, white-tipped tail reminiscent of *Stigmatura*. The Slender-billed Tyrannulet, *I. tenuirostris*, however, bridges between *I. subflava* and *I. inornata* in both color and bill shape. Interestingly, the recently described *S. griseiceps* (Berlioz 1959), known only from the type locality, is very like *I. inornata* in plumage, but has an exaspidean tarsus.

The three species inhabit lowland forest or scrub, the group ranging from northern Colombia and Venezuela to northwestern Argentina and northern Paraguay. *I. inornata* may be the most typically forest-dwelling, *I. tenuirostris* inhabits xerophytic scrub, and *I. subflava* ranges through forests, forest edge, wooded savanna, and mangroves (Haverschmidt 1955; de Schauensee 1964; Snyder 1966). Wetmore's (1926) description of the foraging of *I. inornata* makes it sound like *Serpophaga subcristata*, and he described its "low trill" very much as he described trills heard from the latter species.

I found *I. subflava*, the most extreme species in form, on 12, 13, and 15 March 1963 in the Botanic Garden of Georgetown, Guyana. On the first date two pairs met along what must have been a territorial boundary; two individuals repeatedly faced, fought, and chased, while the other two remained agitated on opposite edges of the dispute. All four were usually close together and moving in rapid, erratic darts in the foliage, so that observation was difficult. Afterward I followed a male apparently patrolling away from the disputed region, while his mate foraged in loose association and twice met and greeted with him. Similar foraging of this pair was seen the next day, and on the final day one individual was located in the predawn twilight. The birds always remained hard to see in second growth trees, but detailed tape recordings were obtained.

DISPLAYS

Repeated Vocalization (RVs) and related forms. The recordings of these from the patrolling bird are shown in figure 4, line 1a. The broad, second element was sometimes omitted or replaced by an element like the one preceding it; the very brief third element was often (see fig. 4, line 1b) developed into a descending element with rapid frequency modulation, particularly during encounters. RVs, usually variants of the last form, often came as "answers" to a mate calling some meters distant or in greetings, and occurred in each recorded aggressive encounter. In these situations, RVs

were most abundant very near times of actual fighting, and once an individual uttered one as he launched an attack. They also occurred in most brief chases following fights.

A shortened version (fig. 4, line 2c) resembling the three-part *Stigmatura* vocalization in fig. 11, line 2e) occurred in greetings, in apparent "duetting" by the foraging pair (i.e., behavior in which one would call and the other answer), and in some territorial encounters. A two-element derivative (fig. 4, line 2d) was also used in duets as an answer to either a basic RV or to the three-element form. Two-element forms with various degrees of frequency-modulation occurred in the disputes.

In the predawn singing heard on 15 March the RV was employed in the regular, very stylized type of performance known as Regularly Repeated Vocalization in other species.

Various chatter-type vocalizations. One, very like the six-element Brief Chatter of *Stigmatura budytoides* (fig. 4, line 3a, compare with fig. 11, line 2d), was recorded twice in patrolling, and shorter versions of usually four elements immediately followed territorial fights.

All other chatters had much broader chevron-shaped elements with fewer harmonics. Rapid forms with four to six elements were abundant in and after fights (fig. 4, line 3b and line 5a) while longer variants occurred, perhaps from the observing mates, in the brief intervals between some fights. One rapid form in a greeting changed abruptly into an RV (see fig. 4, line 6, note how it resembles the RV Variant joined to an LHC of *Serpophaga subcristata* in fig. 1, line 2). These chatters of *I. subflava* and the so-called RV Variants in other species are closely related, but because of the great intergrading among the displays in each species' repertoire, the exact homologies are as yet unclear.

Chatters of similarly broad but less rapidly uttered elements were recorded from one bird in the patrolling pair, usually when not calling in close temporal association to its mate. Two were simple series of six chevron-shaped elements; a third (fig. 4, line 4) prefixed such a set with three slightly more elaborate elements. They probably intergraded with the longer forms heard between fights. Note their resemblance to the Brief Chatter of *Serpophaga cinerea*.

Brief Units (BUs). These were recorded as single calls or couplets, and sometimes replaced the last described chatters (which may be no more than stylized series of BUs). A single BU was uttered by a bird as it attacked its opponent with Bill Snaps (fig. 4, line 5). Others,

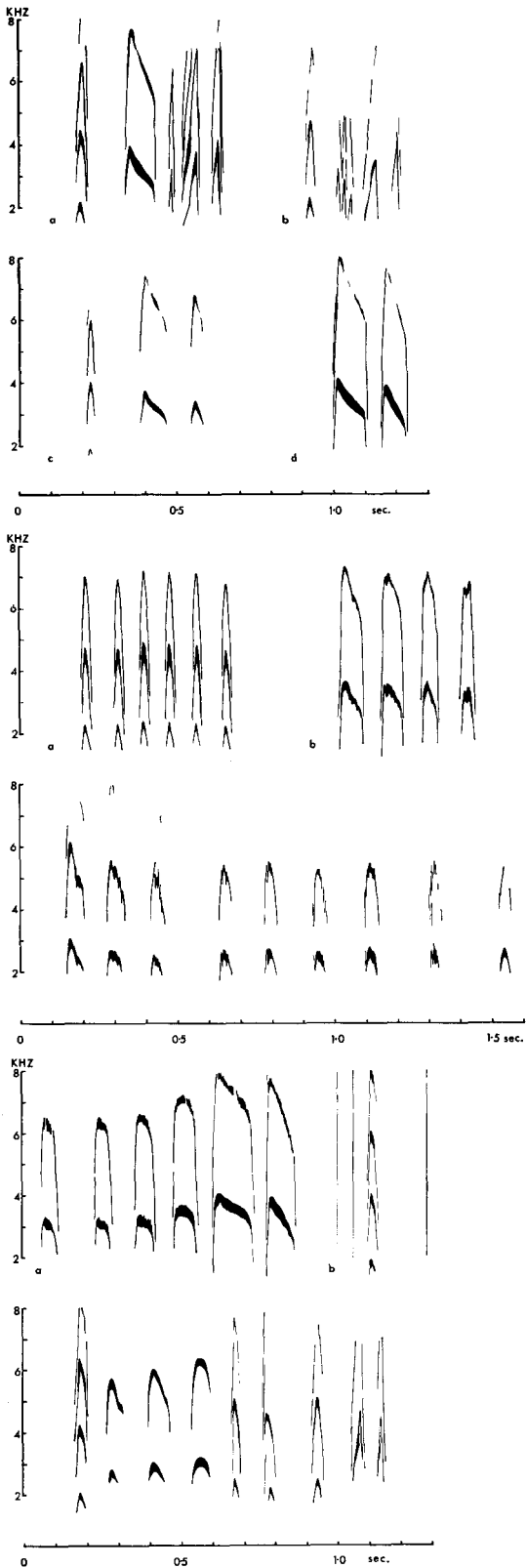


FIGURE 4. *Inezia subflava*: (top to bottom) line 1 (a), basic Repeated Vocalization (RV) form; line 1 (b), RV form in which the third element descends in frequency while showing rapid frequency modulation; line 2 (c), shortened RV from a greeting (com-

and couplets, were recorded in close temporal proximity to fighting and in chases.

Bill Snapping. This non-vocal display by attacking birds is widespread among tyrannids. During the same territorial disputes the antagonists would grapple, and between times often adopted a Crouch posture, wings drooping and their long tails slightly cocked, a display posture also widespread in tyrannids and of little taxonomic help.

In summary, nothing about the vocal displays suggests that this species should be removed to the Cotingidae in spite of its tarsal scutellation (see remark by de Schauensee 1966:378). In fact, the vocalizations indicate very close relationship to members of *Serpophaga*, *Mecocerculus*, and *Stigmatura*. These vocal characteristics (at least to the extent that we understand them now) cannot be used to distinguish among these genera, and are consistent with the above suggestion that the three species now in *Inezia* be included in the genus *Serpophaga*.

ANAIRETES

PLUMAGES AND GEOGRAPHICAL DISTRIBUTIONS

The species of *Anairetes* have been called "tit-like tyrants" (Goodall et al. 1957) or "tit-tyrants" (de Schauensee 1966), in part because of their very active mode of foraging, but largely because of their small size and conspicuous crests. To one familiar with North American tyrannids, they do not immediately suggest their phylogenetic affinities when encountered in the field.

The most widespread, the Tufted Tit-tyrant (*A. parulus*), ranges down the Andes from Colombia into Tierra del Fuego. Its several recognized subspecies are basically gray or brownish gray above, and pale to very pale yellowish below with moderate to heavy black streaking on the head, throat, chest, and flanks. The iris is white and there are white marks in the face and white crown feathers, plus elon-

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pare with three-part *Stigmatura budytoides* greeting vocalization in fig. 11e); line 2 (d), two-element form that appears to be a derivative of that just shown; line 3 (a), chatter recorded during patrolling (compare with BC of *Stigmatura budytoides* in fig. 11d); line 3 (b), rapid chatter recorded in a fight sequence; line 4, less rapid chatter from a patrolling bird; line 5 (a), rapid chatter recorded in a fight sequence; line 5 (b), Brief Unit (BU) with Bill Snaps (the vertical lines of "white noise") by an attacking bird; line 6, rapid chatter changing into an RV during a greeting (compare with fig. 1, line 2c, for *Serpophaga subcristata*).

gate, narrow, black feathers that form a conspicuous, forward-curving crest.

The Pied-crested Tit-tyrant (*A. reguloides*) ranges through the Andes from northern to southern Perú, barely reaching northern Chile at Arica. It is similar to *A. parulus*, but boldly black and white, with a more conspicuously white crown set off by a black face and throat. The black facial characteristics and lack of yellowish below are also found in the San Juan Fernández Tit-tyrant (*A. fernandezianus*), an endemic of Masatierra in the Juan Fernández Islands off Chile, that otherwise resembles a large *A. parulus*.

The Yellow-bellied Tit-tyrant (*A. flavirostris*) ranges from central western Perú to northern Chile, and on the other side of the Andes from south-central Perú through Bolivia and well into Argentina (de Schauensee 1966). Like *A. reguloides*, it is more heavily streaked with black below than is *A. parulus*, but except for its face and throat it is not basically a black and white bird. Its back is brownish or olive-brown, and it is buffy below with a white chest. Its crown resembles that of some subspecies of *A. parulus*. The base of its mandible is yellow, and the iris is dark.

Although easily distinguished from one another in the field, all these *Anairetes* species share a number of plumage characteristics (such as the black streaks below, and elongate, recurved, black crown feathers) that immediately distinguish them from any plumage patterns found in *Serpophaga*. A fifth species, *A. alpinus*, with a very restricted range in the Peruvian and Bolivian Andes, differs, but is not more like *Serpophaga*. Large and charcoal gray, it has a black and white crown, but the elongate feathers are not recurved, and it is not streaked with black below; the underside is plain with a central patch of pale yellow. It will be discussed further with the genus *Uromyias*.

FIELD SITES

A. parulus was studied in Ecuador on 4 and 5 August 1959, 4 February 1962, and 10–16 June 1966. All sites were within 50 km of Quito, ranging from the arid country to the north near San Antonio, south to the paramo in the pass of Machachi by Volcán Cotopaxi. *A. parulus* was also studied in Chile at intervals between 22 October and 19 December 1961 and between 12 September and 11 October 1962. Most sites were in central Chile, in one area on Cerro Manquehue close to Santiago, and in four main areas along the coast from El Tabo north to Zapallar (villages north of Valparaíso). Occasional observations were made elsewhere in this general region, and once to the south in Temuco. Both *A. flavirostris* and *A. reguloides* were studied much less intensively, and only along the valley of the Río Rimac above Lima, Perú, in both cases on 25 January, and 28–30 August 1962.

HABITATS AND FORAGING BEHAVIOR

Members of the genus all inhabit densely brushy or forested Andean regions (except *A. fernandezianus*, which is insular) in "temperate" vegetation, i.e., the vegetation of the South Temperate southern Andes and their foothills, or vegetation at relatively high altitudes in the tropics. *A. parulus* prefers relatively dense vegetation where this is available, as may *A. reguloides*. In Perú I found the latter only within steep-sided quebradas where fairly dark green bushes about 3–7 m tall were densely leaved and densely grouped. In the same immediate areas, *A. flavirostris* was primarily above the narrower parts of the quebradas where bushes (mostly *Schinus molle*) of similar stature were more scattered, and had lighter green, relatively fine, compound pinnate leaves. That is, the browner species was in the more open, arid, lighter colored habitat, and the black and white species in the denser, darker, habitat. Drs. Hans Wilhelm and Maria Koeppke tell me that in Perú *A. flavirostris* generally occurs in more open country than does *A. reguloides*, although in many places both are in the same general vicinity. Along the Río Negro in Argentina, Wetmore (1926) found *A. flavirostris* apparently restricted to sparse bushy vegetation of dry hillsides, whereas *A. parulus* penetrated denser riparian stands. These observations tend to indicate that *A. flavirostris* is a species of more arid country than either *A. parulus* or *A. reguloides*. From Carriker's description (1933) *A. alpinus* may inhabit very dense, high altitude woodlots.

A. parulus, *A. reguloides*, and *A. flavirostris* forage similarly, alternating frequent short flights with brief pauses in which they peer jerkily about, holding their wing tips drooped, occasionally tail-flicking, and often pivoting on their perches. Prey is plucked from the plants or occasionally pursued in the air. They may remain near the ends of flowering branches, or dodge rapidly in and out of the bushes. They appear to be almost constantly in motion, more so than most other gleaning tyrannids. Commonly, perhaps more commonly than most parulids, they flight glean by hovering in front of a leaf to pluck prey which is usually first spotted from a nearby perch. Only rarely have I seen one swing acrobatically on a twig like a parid.

VOCAL DISPLAYS OF *A. PARULUS*

Repeated Vocalization (RV) and related displays. A brief "chuh-lik" (fig. 5, line 1) comprises a very faint introductory element

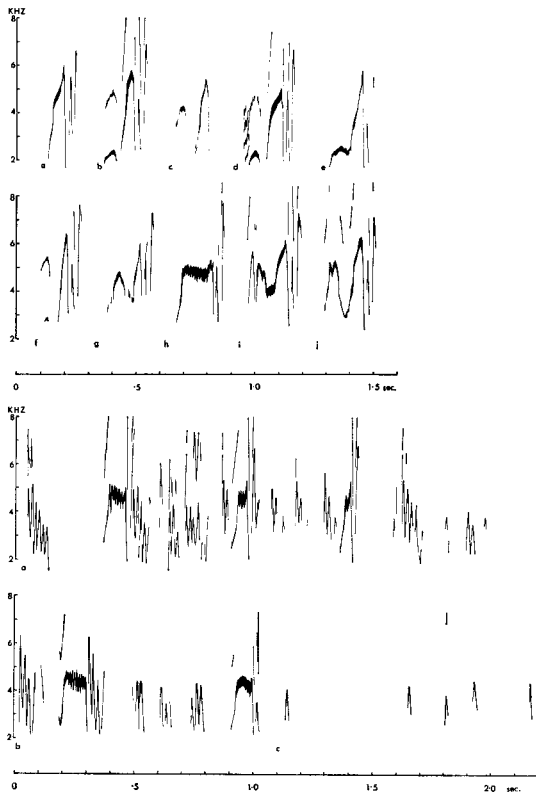


FIGURE 5. *Anairetes parulus*: (top to bottom) line 1 (a) through (f), various examples of Repeated Vocalizations (RVs), recorded from different individuals; line 2 (g) through (j), RV Variants from early post-dawn calling, showing different development of the introductory element; line 3 (a), mixed vocalization, beginning with one Multiply-peaked Vocalization (MV), then an RV Variant grading into the first of a series of MVs, another RV Variant preceding a Multiply-peaked Chatter (MC), another RV Variant, an MV, and an MV-MC termination; line 4 (b), another mixed vocalization with an MV followed by an RV Variant-MV, three MV-MC units, and an RV Variant; line 4 (c), a burst of single Brief Units (BUs).

followed by a prominent chevron (in form very like the first RV element of *Serpophaga subcristata* or *S. munda*) and then usually by two very narrow chevrons. Except for the faint introduction, the whole vocalization is obviously similar to a contraction of the RV forms of the *Serpophaga* species.

Several variant forms (RV Variants, fig. 5, line 2) have the introductory element as loud as the remainder and variously developed into elements that often resemble the RV Variants of *Serpophaga* species.

Particularly in the predawn twilight, this call is often repeated in rapid and regular series that per se constitute a display corresponding to the Regularly Repeated Vocalizations (RRVs) of many other tyrannid genera.

The maximal rate of repetition is about one call per second, but this is not usually sustained and maximum rates are commonly about 45 calls per minute. *A. parulus* usually begins very late in the predawn chorus, in central Chile often 30 min after the first species of the morning.

Bouts of RRV sometimes continue after dawn or occur at any time of day, especially under a heavy overcast. These bouts are brief and often less regular. When regular, the rate of repetition is often only about one-third of that of predawn bouts. Like RRV bouts, intermittent RVs are usually uttered by birds on "stations" who remain perched; they sometimes preen. When a bird is more active and perhaps "patrolling" its territory, the RV is largely replaced by the Brief Chatter (BC).

Most RV Variants are known only from the irregular terminations of predawn RRV bouts and early postdawn station calling when RV is sporadic. One, at present categorized here on the basis of form (see fig. 5, lines 3a and 4b; note that it is most like the "chite" of *Serpophaga cinerea*), comes primarily in exchanges thought to be greetings, and in challenges. In challenges it is typically given in the pauses between fights, often when nearly evenly matched opponents, separated by 1-10 m or more, are disputing a well-marked boundary. Then bursts in which this RV Variant is prominent are used primarily by one individual, often just *before* he flies to attack. (In attack he switches immediately to Multiply-peaked Vocalizations, MVs.) Sometimes, as one uses RV Variants, the other individual uses MVs and there is no attack; the birds may gradually drift apart, one uttering occasional bursts of RV Variants. The latter bird also uses more Brief Units (BUs) and fewer MVs than his opponent, although most RV Variants are in strings with MVs and similar calls (see below). In a different form of "challenge," I have sometimes been scolded with RV Variants by a bird near its nest.

In all situations in which this variant is used the communicator appears at least momentarily restrained (by any of a variety of conflicting motivations) from attacking immediately.

Multiply-peaked Vocalization (MV). This is a harsh, rapidly frequency-modulated "turrr," the modulations becoming less pronounced as peak frequencies sweep downward; it is shown with other calls in figure 5, lines 3a and 4b. Of several MVs uttered by one individual in rapid succession, all but the first are usually much shortened and grade in form toward (not necessarily into) the Multiply-peaked Chatter (MC, see fig. 7, line 4).

MVs are most abundant in territorial challenges as two opponents approach to within as little as 1 m of each other and pivot on their perches. Usually one faces fairly directly toward the other at least part of the time, and then attacks. As this aggressor flies toward his opponent, he repeats loud MVs rapidly. Both birds use them as they fight, and usually as one begins to chase the other. A chase is often followed by more posturing and challenging, the less aggressive bird tending to intersperse more BUs among his MVs than the attacker, or to call less; in bursts of 3-5 MVs he may replace the middle ones with several single BUs or couplets of BUs. In general, MVs typify portions of a territorial encounter that are more aggressive than those in which RV Variants are employed.

After one long set of such disputes I recorded a bird patrolling alone with MVs and bursts of MVs, but they are uncommon in patrolling.

Usually when I investigated a nest the pair would approach, the individual approaching me more closely uttering MVs singly or in bursts. It would not visit the nest; a bird visiting the nest in my presence would use an RV Variant instead.

In some in-pair greetings one bird would utter a string of Brief Units while its mate gave MVs embedded in a MC, each often developing from the terminal element of an RV Variant.

Brief Units (BUs). BUs are simple chevrons, uttered singly (fig. 5, line 4c) or in couplets that may be joined or slightly separate (fig. 6, line 3). The single units in particular are sometimes used alone, but most BUs are in loose strings or in more coherent series resembling slow chatters and intergrading with at least MCs and Simple Chatters (SCs).

BUs occur in a very large range of agonistic situations, suggesting that they may encode not only "attack" and "escape" messages, but also some indication that various other, unspecified, behavioral tendencies may be interfering with either of these (i.e., they may encode what Smith 1969a called the "general set" message). For instance, a bird scolding me near its nest would always use BUs, along with either RV Variants or MVs in different cases. When a bird approached its mate and they greeted, one usually used primarily BUs. (Often this was the female, while her mate used RV Variants and other vocalizations in a highly variable, rapid sequence.) In territorial disputes both opponents almost always used BUs, the less aggressive one relatively more than his opponent, but both primarily in the less active phases after fights or chases. Some

BUs were interpolated among MVs in a burst during challenging at close quarters. Occasionally a patrolling male uttered some BUs, particularly if also using Brief Chatters, but BUs were not common in patrolling unless social encounters were recurring fairly frequently.

Chatters. Many vocalizations of *A. parulus* comprise primarily repeated simple or modified chevron elements, usually fluctuating sinusoidally in peak frequencies. Several displays employ this basic form, but they intergrade and it is not yet fully clear which should be recognized as distinctive.

(1) A Brief Chatter (BC) is a dry sounding trill or chatter, not very prolonged, but longer than an RV. Its most common Chilean form (fig. 6, line 1a) terminates in abrupt-sounding elements similar to those closing an RV. Figure 6, line 1b, shows one of the shortest recorded; it lacks the typical terminal elements and was uttered on alighting by a bird leaving a territorial dispute. Several variants are reasonably common, all sharing features with RV Variants. That in figure 6, line 2c, apparently has the BC form interrupted by an RV Variant, and in addition resembles an expansion of the call in figure 5, line 2i. Those in figure 6, line 2d and e, are similar, but with the second half of the chatter greatly contracted.

The standard BC has "song"-like uses, such as replacing the RV during active patrolling or whenever a solitary communicator is flying about (e.g., it is often used by foraging males). BCs are sometimes used in countercalling, and by two males approaching one another at a boundary, but I have never heard them during boundary disputes. During one unrecorded case of late evening twilight patrolling at Temuco, Chile, a bird using primarily BC apparently alternated it with something more like an RV several times.

All the variant BCs recorded in Chile were by birds with nestlings or fledglings, acting "nervous" in my presence and uttering occasional BUs. Those in figure 6, line 2d and e, were uttered by a bird hesitantly approaching its nest with food. Note the relationship to the RV Variants that are also employed in these situations.

In each of two Ecuadorean events (at Quito and at the Machachi pass by Cotopaxi), two foraging individuals countercalled with each other. Each was accompanied by one or more silent individuals. Once the calls were all similar (fig. 8, line 1a and b), resembling the basic Chilean BC form but with multi-peaked, more complex elements. Each individual appeared

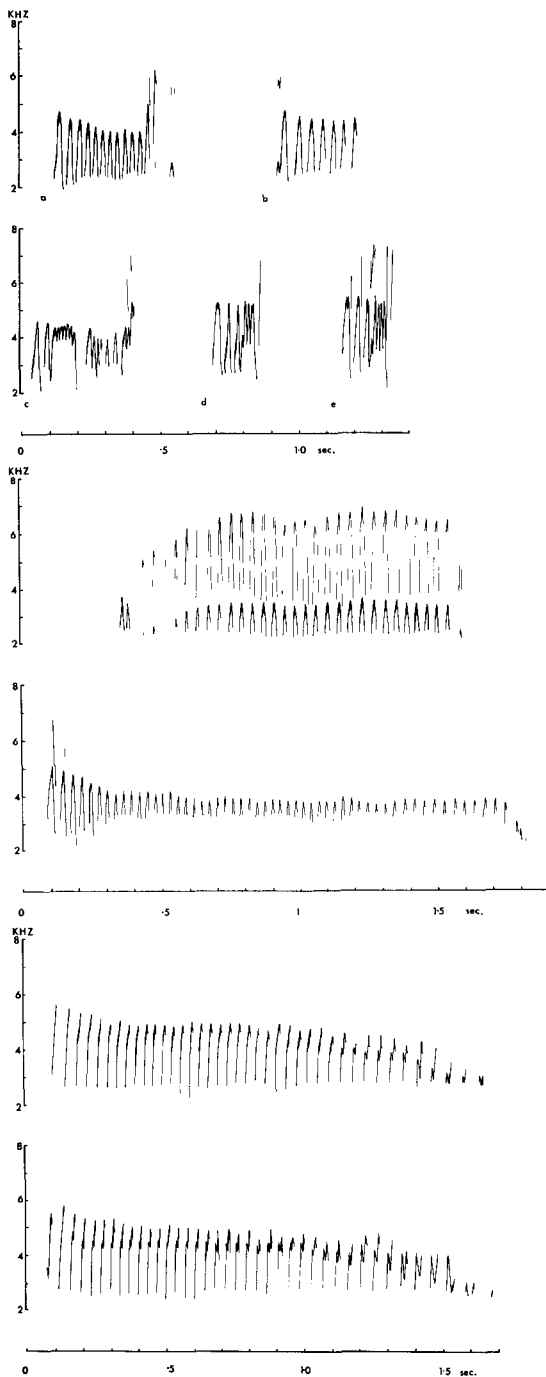


FIGURE 6. *Anairetes parulus*, Chatters: (top to bottom) line 1 (a), most common Chilean form of Brief Chatter (BC); line 1 (b), shortest standard BC recorded in Chile, lacking the typical terminal elements; line 2 (c) Chilean BC interrupted by RV Variant; line 2 (d) and (e), brief Chilean BC-RV Variant intermediates; line 3, relatively brief example of Simple Chatter (SC), the first two elements of which are a couplet of BUs (a similar couplet was uttered somewhat over a second before the illustrated call); line 4, longer form of SC (the second harmonic was not prominent in this instance) with a relatively higher frequency initial portion (in both examples note the sinusoidal fluctuations in peak frequencies); line 5, an

to adhere to one form, consistently different from the other individual in detailed structure. Both, however, varied the length and the use of the high-frequency elements. (One is illustrated with and one without the special termination.)

(2) The Simple Chatter (SC) is a series of simple chevron elements, very like the BC but usually much more prolonged, without the abrupt, specialized termination (fig. 6, lines 3 and 4). Very prolonged SCs may change part-way through to elements peaking consistently at lower frequencies, as in many LHC of *Serpophaga* species. Yet even the initial elements of Chilean SCs usually peak lower than those of BCs and Two-phased Chatters (TCs, see below). Several SCs recorded from one individual in Ecuador began as high as TCs, got higher, and then diminished in frequency very abruptly in their last four elements. Further, the first three-quarters of their chevron elements had prominent shoulders on the ascending arms.

SCs are used primarily by mates, calling and answering as they forage separately in dense bushes or separately make hesitant mobbing approaches to an observer near their nest. I have heard females utter an SC on flying from incubation to forage in the general vicinity of their mates, and have recorded similar greeting-like situations as one bird flew toward its unseen mate. Occasionally when mates are close together, one gives an SC as it or its mate flies farther away. Finally, when a male patrols, uttering occasional BCs, his mate may forage in the same part of the territory and answer each BC with an SC.

In August 1959, SCs were used among the members of small non-breeding flocks (perhaps family groups) as they foraged.

The form of the SC and its use primarily within the pair suggest the Chatter Vocalizations of many other tyrannids (e.g., *Serpophaga subcristata*; *Tyrannus* species, Smith 1966; *Sayornis* species, Smith 1969b, 1970a; *Muscisaxicola* species, Smith 1970b; *Contopus* species, Smith, MS; and species of *Myiozetetes* and related genera, Smith, MS). As those CVs are employed in nest-oriented situations, it is unfortunate that no such events were witnessed in *A. parulus*.

(3) Two-phased Chatter (TC) is among the most prolonged of chatters. These begin

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example of Two-phased Chatter (TC) in which the secondary peak on the ascending arm shifts to a relatively low frequency; line 6, an example of TC in which this secondary peak becomes the higher peak.

with simple chevrons or chevrons with slightly modified ascending arms (see fig. 6, lines 5 and 6) that peak at frequencies about 1.5 times as high as the initial chevrons of an SC. Peak frequencies typically vary slightly sinusoidally and, as they diminish through the series, the modified ascending arm develops a secondary peak that shifts to a lower frequency (fig. 6, line 5) or becomes as high as or higher than the main peak (fig. 6, line 6). During the shift, the two peaks become more distinct, so that the series ends with elements resembling coupled chevrons. Although different in detail, the combination of simple and essentially coupled chevrons in one long chatter is strikingly similar to that of the LHCs of *Serpophaga* species.

TCs were recorded from Ecuadorean and Chilean birds, although not commonly, in countercalling between what appeared to be patrolling neighbors. One was recorded from a bird that had just left a territorial dispute and was returning to his mate. Irregularly spaced, prolonged TCs were used during the pre-dawn chorus on 17 June 1966 by an Ecuadorean bird that did not utter an RRV bout. One other Ecuadorean individual (4 February 1962) uttered TCs while hesitantly approaching to within a meter of me, retreating and approaching again several times as I investigated some bushes.

The TC is employed more like the BC than the SC. This is borne out by its form: the relatively high-peaked initial elements, and the terminal couplet typical of a BC, which may be a modification of a bi-peaked TC element.

(4) Multiply-peaked Chatters (MCs) are quite variable assortments of chevrons, most joined in couplets, triplets, or even larger trains (fig. 7, lines 1 and 2). Each MC appears to be a series of reduced and fragmented MVs, often with interpolated BUs. One form (fig. 7, line 3) derives from the initial portions of MVs and omits most components of the descending frequency sweep, substituting a terminal ascending chevron arm resembling the termination of an RV or BC; it sounds relatively high-pitched, and can be confused in the field with MCs that incorporate RV Variants.

MCs were recorded in Chile several times in close, tense challenges, replacing MVs in fights and the initial portions of chases. Such MCs usually in turn became looser in structure and gave way to strings of BUs. MCs did not occur in the challenging phases per se, but correlated with aggressive flight (however, see final paragraph of this section).

Brief MCs, or mixtures of MCs and RV Variants, sometimes followed MVs as a bird scolded

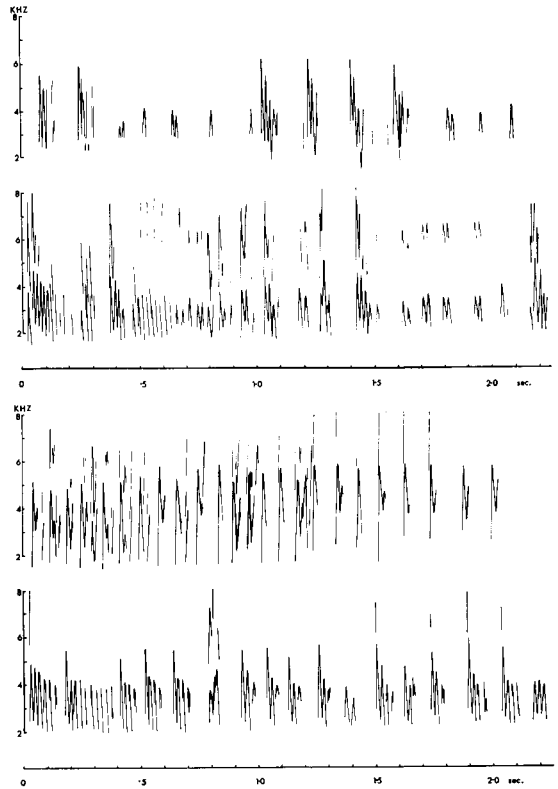


FIGURE 7. *Anairetes parulus*, Multiply-peaked Chatter (MC): (top to bottom) line 1, a relatively fragmented, chevron-element form of MC; line 2, a more complex form of MC (both examples show the relation of this chatter to the Multiply-peaked Vocalization, MV); line 3, an extreme form of MC, omitting most of the descending frequency sweep of the MVs; line 4, an example of MC in which the types of relationship to the component MVs are somewhat clearer.

me near its nest; these gave way shortly to BU strings.

MCs also mixed with RV Variants and BUs in greetings, as a bird (usually the male, when known) flew to near its mate. Such MCs sometimes derive directly from an MV, and are usually interpolated into brief strings of RV Variants (e.g., fig. 5, line 3a and 4b); they may also be replaced by BU couplets. MCs with high-pitched portions were uttered in some solitary patrolling, usually when alone in or shortly before flying to the area of a recent boundary dispute. These seem strongly dependent upon a state of flight hesitancy, as do MVs and RV Variants uttered just before attacking or just before alighting (a relatively rare usage, and not involved with attacks). In unrecorded cases I may not always have distinguished between high-pitched MC forms and strings incorporating RV Variants, so it can be said only that one or both correlated with evidence of locomotory hesitancy.

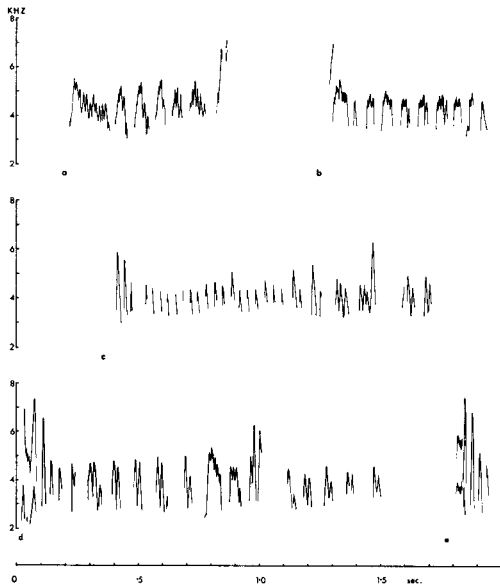


FIGURE 8. *Anairetes parulus*, Ecuadorian examples: (top to bottom) line 1 (a) and (b), calls resembling Chilean Brief Chatters (BCs), uttered by two counter-calling individuals near Quito; line 2 (c) and line 3 (d), calls resembling Chilean Multiply-peaked Chatters (MCs), employed in a different counter-calling event near Machachi; line 3 (e) Repeated Vocalization Variant-Multiply-peaked Vocalization element, interpolated into an MC in the event near Machachi.

In an Ecuadorean event involving counter-calling individuals with silent companions (mentioned above under BC) long chatters were used that were very like the variable Chilean MCs (fig. 8, lines 2c and 3d). In particular, they often appeared to derive from an MV and pass into a series that might become simply a string of (usually couplet) BUs. Often, though, the series had a distinctive termination that was either clearly the BC form described above, or was even more contracted and perhaps an RV Variant. In addition, these series sometimes began with an apparent MV prefixed by a relatively faint element like that beginning a standard RV, or such combinations were simply interpolated in couplet BU series (as was that shown in fig. 8, line 3e). The principal differences in form between these Ecuadorean calls and those recorded in Chile lie less in the structure of the MCs than in the form of elements in the BCs, and in the more open form of the MVs initiating the chatters.

VOCAL DISPLAYS OF *A. REGULOIDES*

The only type of vocalization recorded from *A. reguloides* in Perú was a quick series of whistles (fig. 9, line 1a) sounding much like

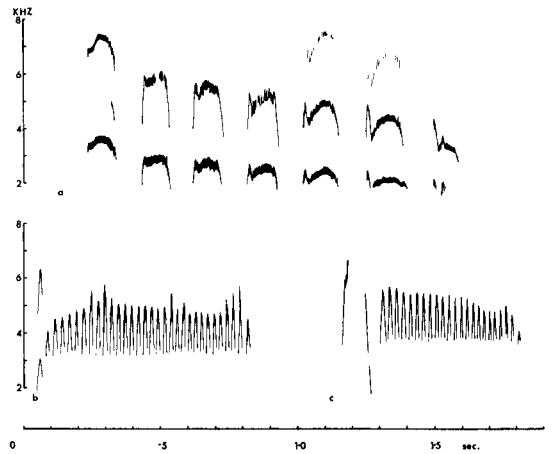


FIGURE 9. *Anairetes reguloides* and *A. flavirostris*: (top to bottom) line 1 (a), an example of the series of whistles recorded from a foraging *A. reguloides* in Perú; line 2 (b) and (c), examples of the Simple Chatter (SC) recorded from individuals of *A. flavirostris* foraging in groups in Perú.

a call of the local *Camptostoma obsoletum*. The two tyrannids are together in the same habitat, and possibly they have converged in the form of this call. I have heard only two calls from other *Anairetes* species that sounded like it: a series of BUs used once in Chile by a patrolling *A. parulus* that had just uttered a BC, and the unusual Ecuadorean BCs, just described. The form of the vocalization does suggest a modified BC, and what is known about its usage agrees: the birds were alone and foraging, largely silently.

VOCAL DISPLAYS OF *A. FLAVIROSTRIS*

Usually two or three individuals of this species were found together, and when two got close to one another, one usually uttered a brief SC (fig. 9, line 2b and c; note how similar this is to the corresponding SC of *A. parulus*). Other vocalizations heard occasionally from individuals foraging alone sounded like "cleep" or "cleep cleep," louder and clearer than the BUs or RVs of *A. parulus* with which they may correspond. Once a brief series occurred in this usage: "cleep cleep cleo cleep." In Figure 9, line 2c, the unit introducing the SC is similar to a simplified RV of *A. parulus*.

Wetmore (1926) reports that males in the Río Negro region of Argentina who were "practically in breeding condition . . . were singing constantly, a low buzzing, squeaky effort, barely audible above the wind . . . *seet zwee-ee seeta seeta seeta*." In form and usage this may be like the call just described for *A. reguloides*.

NON-VOCAL DISPLAYS

Raised Crest (RC). In all *Anairetes* species the black crest feathers that curl upward and forward are almost always conspicuous. These elongated feathers often blow about in the wind, and thus must be somewhat unreliable as devices signalling changeable information. The shorter crown feathers may be more reliable. In all three species I have seen individuals raise their crests when I have approached them. In *A. parulus*, birds have also raised their crests on approaching me near their nests, or on going to their nests while I stood nearby. In addition, both participants in disputes over territorial boundaries use RC, the more aggressive individual raising its crest more often, and higher. Its crest is usually higher than its opponent's just before it launches an attack, and remains high just afterward. The one nearly vertical crest I saw in such a dispute was provided by an attacker after routing his opponent. In apparently evenly matched bluffing, however, both individuals may raise their crests equally high.

The only *A. parulus* I saw conspicuously flatten its crest then fled from an opponent. The crest thus seems to be raised or flattened in agonistic situations, and the degree of elevation indicates the degree to which a tendency to approach or remain on site is ascendant over a tendency to escape. Although in many circumstances a bird with its crest raised is likely to attack, crest raising may correlate with factors in addition to probability of attack, as birds going to feed their nestlings in my presence often showed no signs of mobbing me.

Crouch. These "tit-tyrants" are all very active creatures, frequently seen in essentially horizontal poses with legs extended as they peer about briefly before rushing to another perch. This stance is probably not a display. I have, however, seen an *A. parulus* crouch with legs bent and crest flattened just before fleeing from a territorial opponent, a posture perhaps homologous with the Crouch known in a similar situation in *Serpophaga subcristata*.

Wing and Tail Flicking. As do most other active tyrannids, *Anairetes* species may flick the wings upright over the back and flick the tail upward and forward. Both movements sometimes occur as balancing or intention movements in vigorous activity of all kinds. In particular, during foraging, a bird may flick its tail and sometimes its wings on alighting, and flick either occasionally while peering about from each perch. Whether or not this is a prey-flushing specialization has not been investigated. But both wings and tail are com-

monly flicked in a more exaggerated fashion during agonistic events. The wings are then flicked more than is the tail, and sometimes reach very high over the back, making their pale linings especially conspicuous. The tail seems unspecialized for conspicuousness, and is not fanned open during flicking. Nonetheless, it is sometimes carried so far forward that it briefly achieves a cocked position.

Wing Whirr. I have heard *A. parulus* in two situations produce rapid bursts of a snapping, rattling sound with its wings, while flying from bush to bush as I stood near a nest, and during territorial boundary disputes. These distinctive flights undulated as the tail was pumped and the birds made bursts of rapid wing strokes.

UROMYIAS

Hellmayr (1927:378) split *Anairetes* because of two species, the Agile Tit-tyrant (*agilis*) and the Unstreaked Tit-tyrant (*agraphia*), with relatively short, wide bills, more developed rictal bristles, the elongate apical crest feathers not decurved, and longer and strongly graduated tails, more like the tail of *Stigmatura*. Recognizing that they were "nearly related" to *Anairetes*, he nonetheless assigned them to the new genus *Uromyias*, a decision followed by subsequent workers. However, the then unknown Ash-breasted Tit-tyrant *A. alpinus* (described by Carriker 1933, originally in a monotypic genus, *Yanacea*), is in part intermediate between them and the other *Anairetes* species; in particular, its dull coloration and near absence of streaking suggest *U. agraphia*. Its "habits" (presumably its general appearance during foraging) were said to be typical of *Anairetes*.

Like *Anairetes*, both *U. agilis* and *U. agraphia* inhabit semiforested or forested regions of the Andes; the latter is known only from its type locality in southeastern Perú. *U. agilis* looks very much like an obscurely marked and brownish *A. parulus* with a conspicuously longer, graduated tail. It is difficult to see why it should be considered generically distinct from *Anairetes*, especially when the closely related genus *Serpophaga* is admitted to include the markedly different ecological adaptations of *S. cinerea* and *S. subcristata*. The main *Uromyias* feature is the tail, and it probably indicates foraging specializations similar to those of *Stigmatura* (a more gnat-catcher-like rather than warbler-like mode of foraging; see below). *Stigmatura* and *Anairetes* appear reasonably closely related, but the *Uromyias* species are distinctly more like the latter than the former. Their relationship is

much better shown by retiring Hellmayr's genus and replacing them in *Anairetes*.

MECOCERCULUS

The six *Mecocerculus* species inhabit mountain forests and scrub from Venezuela and Colombia down the Andes to northwestern Argentina. The largest, the White-throated Tyrannulet (*M. leucophrys*), is brown above with white or buffy wing markings, a white throat, gray breast, and pale yellow abdomen; it has a white superciliary and a dark line through the eye. The others are similar in pattern, but olive-brown to olive-green on the back with gray crowns and usually pale throats and chests, with whitish or yellowish markings on their dark wings (ochraceous in the Rufous-winged Tyrannulet, *M. calopterus*, and the Sulphur-bellied Tyrannulet, *M. minor*). Only *M. minor* is richly colored, but in the basic yellow below, olive-green above hues of most of its congeners.

I observed the White-banded Tyrannulet, (*M. leucophrys*) on 12 and 13 June, and *M. strictoperus* on 12 June 1966 northwest of Quito, Ecuador, along and near the "old" (more northern) road from Quito to Santo Domingo de los Colorados. The higher site (13 June) was on the slopes of Cerro Atacaso about 1 km S of the pass at the interface between brushy and grassy paramo; the other (12 June), in partially cut cloud forest about 4 km W of the pass. *M. leucophrys* was thus found in both semi-open cloud forest with twisted trees about 6–15 m tall and hung with many epiphytes, and in dense brushy paramo with bushes up to about 5 m tall. Wetmore (1926) has found it in "groves and low thickets . . . scattered over the open slopes . . . above the heavy rain forest" in Argentina.

In the cloud forest, one member of each species was in a mixed-species flock including primarily tanagers and coerebids; they did not come close to one another. Both foraged slightly more actively than vireos, but with very vireo-like techniques. Their foraging behavior thus resembles that of *Serpophaga subcristata* and *S. munda* but, in keeping with their larger size, each is somewhat more sedate than the more warbler-like little *Serpophaga* species. Similarly, while the latter species do much wing and tail flicking, the two *Mecocerculus* did none.

The *M. leucophrys* on 13 June was found at 06:30 singing rapidly and with considerable regularity from the top of a dense bush in a brushy quebrada. He was probably completing his circa-dawn performance of a RRV, and

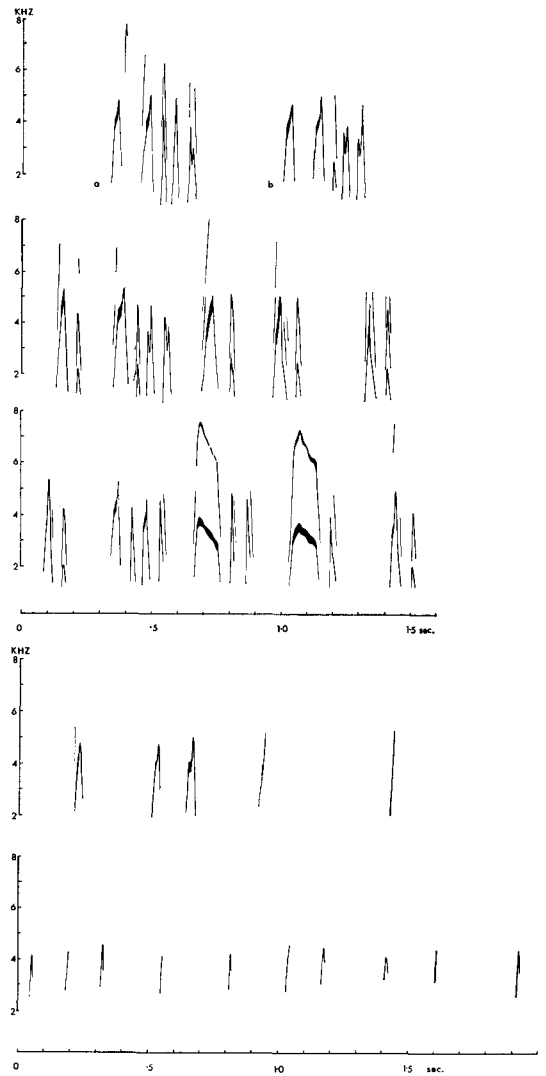


FIGURE 10. *Mecocerculus leucophrys*, (top to bottom) vocalizations from the circa-dawn song bout recorded on 13 June 1966: line 1 (a) and (b), two examples of Repeated Vocalization (RV); line 2, an example of the vocalization provisionally designated Brief Chatter-Repeated Vocalization (the vocalization begins with an RV portion which is not shown in the illustration); line 3, terminal portion (a more standard BC-RV portion preceded that which is shown) of a modified BC-RV that appears to "degenerate" into a series of simplified RVs; line 4, burst of Brief Units (BUs) recorded from two individuals in flight at the termination of an RRV bout of 13 June 1966; line 5, burst of BUs uttered by a perched foraging individual on 12 June 1966.

stopped with a relatively irregular final minute just 4 min after I began tape recording. Two basic units were repeated, both of which probably occur in other usages and are displays in themselves. To emphasize their similarities with apparently homologous vocalizations these may be called the RV (fig. 10, line 1a

and b) and the BC-RV (fig. 10, line 2). The latter may correspond to the BC of other genera, but those recorded began with and incorporated RV units, not unlike some of the BC Variants of *Anairetes parulus*.

As recording began, the RRV consisted of RVs alternating with the longer BC-RV. Alternation was not quite perfect (not unusual in the RRVs of most tyrannid species) and it became less so. In the final minute there were four single RVs and nine BC-RVs; again, such shifts from nearly 1:1 ratios of the components of RRVs as singing draws to a close each morning are common in other species. Counting the RVs as units, and each complex BC-RV as a unit, the rates per minute were: 17, 14, 15, and 13.

After the first minute, some BC-RV units showed variable modifications that made them somewhat more like continuous series of simplified RVs (fig. 10, line 3). Most of these variations developed as extensions to "standard" BC-RV units. (Note how the modified components shown in the illustration strongly resemble components of the Chite-Churr vocalization of *Serpophaga cinerea*.) In addition, there was one variation in an RV: an extra element was prefixed. Although a small change, it made the call more like the RV Variant vocalizations of *Serpophaga munda* and *S. subcristata*, further indicating the relatedness of these calls.

Vocalizations corresponding to the BUs of *Serpophaga* and *Anairetes* were also recorded from this and the other individual of *M. leucophrys*. The first flew immediately on completing its RRV, vocalizing (fig. 10, line 4) in flight. The other was fairly frequently vocal while foraging, uttering isolated, single units or occasional diffuse strings of units at variable intervals, and some more rapid bursts in flight. Most of these vocalizations were essentially the ascending arms and peaks of simple chevrons (fig. 10, line 5), indicating that those of the other individual may have been to some degree intermediate to the component elements of RVs or BC-RVs.

The use of these BUs is comparable with that of their homologues in *Serpophaga* and *Anairetes*. Note in figure 10, line 5, that the series show sinusoidal fluctuation in the peak frequencies of component BUs, like the SCs of *Serpophaga* species. Those SCs are more compact and have different employment, but are similarly related in form to the strings of BUs in the same repertoires. This may suggest that *Mecocerculus leucophrys* has an SC. In any event, all known vocalizations of *M. leucophrys* are remarkably similar to their

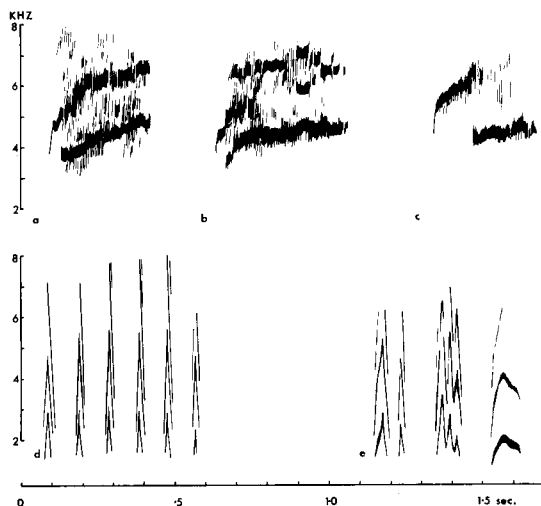


FIGURE 11. *Mecocerculus strictoperus* and *Stigmatura budytoides*: (top to bottom) line 1 (a), (b), and (c), examples of the variable "shreeeee" vocalization of the foraging individual of *M. strictoperus*, 12 June 1966; line 2 (d), rapidly repeated Brief Chatter (BC) from a greeting or duet performance of *S. budytoides*, 16 November 1962; line 2 (e), the more complex vocalization of *S. budytoides* uttered by the apparent mate in this same event.

apparent homologues in *Serpophaga* species and, in some cases, in *Anairetes parulus*, suggesting very close relationship among these genera.

The only type of call heard and recorded from another species of *Mecocerculus*, the individual of *M. strictoperus*, fails to aid this comparison, however. It was a distinctive, rather variable "shreeeee," usually having two prominent harmonics and an initial rise in frequency (fig. 11, line 1a, b, and e) that is readily audible. The sorts of variation in the 10 examples analyzed with the Sona-Graph resemble those that many fledgling flycatchers produce in similar-looking begging calls: emphasis shifts abruptly and irregularly from one harmonic to another, the sound is somewhat "noisy" (i.e., the harmonics are not clearly defined and many short vertical lines appear), and the note varies irregularly from being continuous to discontinuous. The last sort of variation, however, also occurs in some similarly prolonged calls of tyrannids in instances in which these are uttered in flight or on alighting (e.g., the IPV of *Sayornis saya*, Smith 1970b). Although the last example shown is an extreme, the amount of sequential variation strongly suggests that the recorded bird might have been an immature. It was not, however, closely associating with any other bird, and was the only individual of its species in the mixed flock.

Most of the recorded and unrecorded calls were uttered on or very shortly after alighting from flights. This is typical of what I have often called "locomotory hesitance" vocalizations, but not of begging calls. Possibly the call is some sort of special adaptation to mixed-species flocking, since it does not clearly fit any known tyrannid categories. It provides only limited but intriguing systematic clues at present (see below: *Xenopsaris*).

STIGMATURA

The one or two species of this genus are very distinctive looking tyrannids. (It is not yet clear that the Lesser Wagtail-tyrant, *S. napensis*, is specifically different from the Greater Wagtail-tyrant, *S. budytoides*.) They have a long, graduated tail, not unlike gnatcatchers or some furnariids. They are yellowish below and grayish olive-green above, with a yellow superciliary and a dark eyeline, wings and tail; the tail has conspicuous white or light outer margins, and medial and terminal spots. Representatives of the genus range through lowland South America from the Amazon Valley south to central Argentina.

I studied *S. budytoides* briefly on 16 and 17 November 1962 near La Cocha in southern Tucumán province, Argentina, in dense thorn forest partially opened by selective cutting and some cattle grazing. In early December I also saw it in similar habitats (*monte* and *monte chaqueño*) in the provinces of Salta and Jujuy; this is apparently typical of its habitat in Argentina (see Olrog 1959). The birds were foraging in pairs, apparently on territories. They acted unlike any other tyrannids I have seen but did closely resemble gnatcatchers (*Poliophtila* spp.) as they hopped quickly from twig to twig, gracefully flicking their tails (see below). As do other serpophaginines, they moved very rapidly. Most of their time was spent in the outer twigs of mid to upper branches of the larger (5–7 m) thorn trees, apparently gleaning.

They were usually silent, but occasionally when close together, mates would appear to greet. Examples were tape recorded from two pairs. Each individual repeated its call 7–13 times in synchrony with the other. For one individual in each pair, the call was a simple BC of six or seven chevron elements (fig. 11, line 2d; there were as few as four or five elements in BCs at the beginning and end of a bout), much as one *Serpophaga cinerea* would use in greeting its mate. The mate's call also comprised six basically chevron-shaped elements, and was nearly of the same total duration. The elements, however, were grouped into three subsets (fig. 11, line 2e) of two,

three (nearly reduced to two by one individual), and one elements, respectively. Each subset is different, but the ascending arm of each first chevron element has a very slight shoulder, while the other elements in subsets one and two (there are none in the third) are simple chevrons. This detail is not insignificant, even if it contributes little to the sound of the vocalization: the same shoulder occurs on modified chevron elements in other genera. Certain general features of this vocalization also recur and may indicate phylogenetic relationships. For example, the RVs of *Serpophaga subcristata* and *S. munda* usually comprise six chevron elements, of which the first is modified to show this shoulder well, and the last differs fairly radically from the intervening ones. RVs of *Mecocerculus leucophrys* are similar, and a three-part RV form of *Inezia subflava* resembles this *Stigmatura* RV in many ways (see above). Thus the form and usage of the two described vocalizations strongly support the current systematic position of the genus *Stigmatura*.

Each individual repeatedly flips its wings and tail upward and forward during the "greeting" vocalizations. The one using BCs apparently does this once per BC, but its mate, using the more complex vocalization, does more rapid flipping. This species also makes considerable non-display use of its specialized tail, flicking it slowly up over the back in gnatcatcher fashion on alighting or during hops from twig to twig, and often carrying it above the horizontal. Somewhat analogous use of the tail during foraging is found in the two ecologically distinctive members of *Serpophaga*: *S. cinerea* and *S. nigricans*.

As a pair forages, each often marks its flights by tail pumping and a low pitched Wing Whirr. If the latter is a display, then it has likely diverged from the agonistic employment of Wing Whirring in other genera. Perhaps it helps mates to associate when visual contact is difficult or intermittent. Their "greetings," in fact, are sometimes comparable to the "duetting" of various species in which mates associate while foraging in dense vegetation (see Hooker and Hooker 1969).

TACHURIS

The single species, the Many-colored Rush-tyrant or "Siete Colores," (*T. rubrigastra*), is the most brilliant and distinctively colored of all tyrannids. The general plumage pattern is not unusual for a serpophaginine: a dark face, white throat and superciliary, a partially concealed crown patch, a greenish back and yellow underparts; the dark wings and tail are

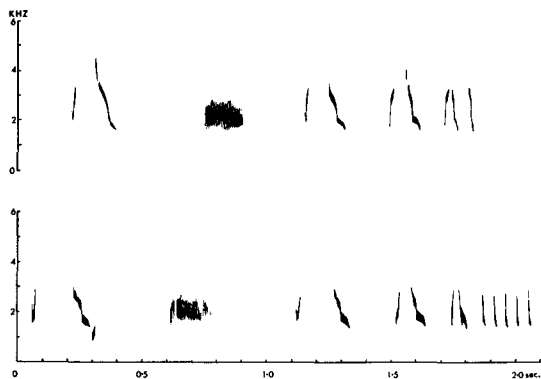


FIGURE 12. *Tachuris rubrigastra*: lines 1 and 2, two examples of Repeated Vocalization (RV) recorded from different individuals.

conspicuously marked with white, but even the tail pattern is more conservative than that of *Stigmatura*. Only the incomplete, dark chest band is a distinctive innovation in pattern. But the brightness of the yellow and green is unusual, the deep blue in the face and rose in the crown patch and undertail coverts are novel. Immatures are more conservatively buffier where adults are yellow or white, and lack the rose and blue.

The species ranges along western South America from northern Perú to south-central Chile, and east of the Andes from southeastern Perú, Bolivia, Paraguay, and southern Brazil to southern Argentina. It inhabits *Typha* and *Scirpus* marshes, primarily in the wetter parts where the plants grow tall out of standing water. In large marshes the birds often cluster; what Wetmore (1926) described as "little scattered colonies . . . many extensive areas of suitable growth not inhabited by them." The birds remain at their sites even as seasonal changes in water level and height of the vegetation alter their habitat. During migration, they are apparently more eclectic, and Hussey (1916) reports finding them even in flower beds.

I studied this species at intervals between 2 and 12 November 1961, in the Quilicura *Typha* marshes near Santiago, Chile, and 20 November–21 December 1961, and on 10 and 11 September 1962, in *Scirpus* marshes of a large fresh-water pond by the coast just south of El Tabo (Santiago Province), Chile. They were always difficult to observe in the vegetation, and difficult to follow with tape-recording equipment; most observations were of foraging individuals, engaged in little social behavior. They foraged actively, moving rapidly from point to point, usually perching on the nearly vertical vegetation, where their unusually long legs enable nearly horizontal postures. They also in-

vestigated both the bases of plants and the water surface between plants from which they sometimes flight-glean prey. When mud is exposed, they occasionally run on it briefly (also observed by Wetmore 1926). But much, perhaps most, of their foraging is by short pursuits of flying insect prey in the mid to upper levels of the vegetation.

The only vocalization heard commonly is a "song" used like the RV of other genera. Bouts of RV are uttered occasionally by one individual of a pair (presumably the male) from various points in a territory, and occasionally in counteringing with a neighbor. In its simplest form, the RV sounds like "pwee-oo pwenh pwee-oo pwee-oo pwee-oo -t-t-t-t-t." The "pwenh" (see fig. 12, lines 1 and 2) has a nasal quality unlike any component of any other RV yet recorded in the subfamily. Although the last "pwee-oo" of an RV, plus the dry terminal trill is roughly comparable to an RV of *Serpophaga subcristata*, or the whole vocalization to an RV Variant, or to an RV Variant-BC combination of *Anairetes parulus*, these similarities are not close and could be superficial.

One individual repeated a "pweechk" instead of "pwee-oo;" this was likely derived from the final "pwee-oo" unit and the start of the dry trill of a more standard RV. Not infrequently individuals repeated only a single "pwee-oo" or "pweechk" instead of the full RV.

Most *T. rubrigastra* did not begin calling until after sunrise; only one individual performed in the predawn twilight, and his bout of calling was not rapid or regular so there may not be a stylized RRV in this species. RV heard in the evening twilight was never rapid.

Occasionally a bird would utter RVs while watching me from a distance as I investigated a nest, although most nest owners watched silently. It was slightly more common for a bird to begin an RV bout shortly after I left a nest. One pair, however, began calling occasional "pwee-oo-chk" units as I searched for their nest, and were calling fairly rapidly when I found the half-built structure.

No other vocalizations were tape-recorded, but one bird repeated a faint, low-pitched "tut" at intervals of 1 or 2 sec as I investigated its nest. Occasionally similar calls were heard from unseen birds as I waded through a marsh. Both individuals uttered rapid and slightly variable series of "pwuh" units throughout the one territorial encounter seen in some detail. These usages suggest that the single calls and series are comparable to the BUs of other serpophaginine genera.

T. rubrigastra may have unusually well-

developed non-vocal displays. Birds were extremely fluffed or ruffled in two situations: a male repeatedly approaching and making little flights around his unreceptive mate, and both individuals in the territorial encounter, throughout the period in which they were within about 1 m of one another. They kept pivoting and shifting repeatedly, and one made several short chases of the other. The brilliant crown patch was employed once by an adult that turned toward an approaching, begging fledgling, spread its crown feathers, and raised the rose patch about half-way to vertical while lunging forward. The fledgling immediately fled. The display is comparable to the Raised Revealed Crown Patch display of other tyrannid genera (e.g., *Tyrannus*, Smith 1966).

Some activities are enhanced by making white feathers more visible. When vocalizing, for instance, the white throat bulges conspicuously with each call, and so pulses with the string of units in an RV. The male who repeatedly approached his unreceptive mate had his tail fully fanned with all of its white markings very prominent. In addition, during the several little flights he made within about 0.2 m around her, the white in his tail and flashing in his wing was very noticeable. The wings, meanwhile, made a loud whirring, a Wing Whirr display perhaps comparable to that of *Stigmatura budytoides*. Although this was the only situation in which I saw a tail fully fanned, mates I watched foraging near each other both kept their tails fanned, one slightly open and one about half open.

During most foraging the wing tips are drooped and the short tail is carried slightly cocked. Fairly frequently, both wings and tail are very quickly flicked. This is not exaggerated, but it makes prominent the white in the upper wing coverts and outer tail feathers. When mates have been seen foraging near one another, the rate of such flicking movements has been relatively high. Whether these are better classed as intention movements or visible displays, they are comparable to similar movements in *Serpophaga* species.

XENOPSARIS

On 16 November 1962 I found a male White-naped *Xenopsaris*, *X. albinucha*, foraging in a 7-m tall, semi-isolated tree in thorn forest thinned by cutting and grazing in southern Tucumán Province near La Cocha, Argentina. The species ranges from Venezuela south to north-central Argentina in lowland dry forests (e.g., Wetmore 1926:294; Friedmann and Smith 1950:509). Wetmore described the one male he found as watching "alertly for insects from

a low perch at the border of a thicket of vinal." Mine was moving and gleaning prey within its tree and in actions and general appearance reminded me of a *Pachyramphus*. Every few seconds it called a "shreee," ascending in pitch like the one known call of *Mecocerculus strictoperus*. (This was not tape-recorded.)

There is no common agreement on the systematic position of this monotypic genus. It has often been placed in the Serpophaginae because its plumage pattern superficially resembles that of *Serpophaga cinerea*: white below, with a gray back and a black crown (dark brown in the female) and dark brown wings and tail. There are white wing markings and a white loreal spot. But, while *S. cinerea* may be thought of as having converged with the plumage features of some Old World streamside species (e.g., some motacillids), *Xenopsaris* is an arboreal bird. Its plumage is similar to another tyrannid (*Sirystes sibilator*) and various cotingids that are also arboreal, such as species of *Tityra*, *Platypsaris*, and particularly *Pachyramphus*. The other main systematic position to which it is often assigned is close to the last two genera. Friedmann and Smith (1950) say its "lack of rictal bristles and the scutellation of the tarsus are cotingine." The question of just what is a cotingid is thus pertinent, although it would be premature (with respect to data on behavior) to go far into it. But one principal characteristic used to define and distinguish the Tyrannidae and Cotingidae has been tarsal scutellation, and its use has become partly circular. Further, recognition of tarsal forms has at times been rather casual, obscuring the considerable variation of which Hellmayr (1927) complained. Ridgway, for instance, too often described a species as having "typical exaspidean" scutellation (then assigned it to the Tyrannidae, compounding the idea that the usual tyrannid form is exaspidean) in cases for which, on closer examination, subsequent workers such as Zimmer felt he had made a gross oversimplification.

No known vocal displays of *Pachyramphus* and *Tityra* species (Smith, unpubl. data) suggest obvious similarities to the one known call of *X. albinucha*, although various species of *Platypsaris* have a descending-ascending call (e.g., "tuhREE" in *P. minor*) that is vaguely similar. Yet the one recorded call of *Mecocerculus strictoperus* may be very similar. Further, the members of the aforementioned cotingid genera nest either in cavities (*Tityra*) or build bulky, domed nests. The one nest attributed to *X. albinucha* that I have examined (no. 36431 in the Buenos Aires Mus. de

Ciencias Nat., collected by J. A. Pereyra) is a compact open cup of fine, dry grasses, similar to most serpophaginine nests. Foraging behavior does not yet help us assign the species. While it is relatively staid for an arboreal serpophaginine (and thus very like *Pachyramphus cinnamomeus* in foraging behavior), the trend from the small, warbler-like *Serpophaga subcristata* to the larger, vireo-like *Mecocerculus leucophrys* suggests that the relatively large *X. albinucha* could be expected to forage in this manner. Finally, it is also not clear how to treat the plumage pattern. For the habitat it seems more cotingid than serpophaginine, but the plumages of the sexes are very similar (typical of serpophagines), whereas in *Pachyramphus* and *Platypsaris* species having black and white males, the females are brown or gray, and much plainer. Perhaps *X. albinucha* has converged with the cotingid plumage pattern through "social mimicry" (see Moynihan 1968). In any event, the one vocalization and the nest form tip the scales very slightly in favor of leaving *Xenopsaris* in the Serpophaginae until we know more about it.

COLORHAMPHUS

It is uncertain whether the apparently uncommon Patagonian Tyrant, *C. parvirostris*, is a serpophaginine related to *Mecocerculus*, or a fluvicolinine related to *Ochthoeca*. Its brown and gray plumage resembles some species of both, although the chestnut in the wing suggests the latter. Its nest (Zotta 1939) is basically an open cup placed in a bush, and does not yet help us make a distinction. According to Wetmore (1926), it forages by aerial flycatching, perhaps more like *Ochthoeca* than like most serpophagines, but his observations made under only one set of ecological conditions may not permit generalization. Goodall et al. (1957) seem to suggest that it is a gleaner, saying that it spends its time in treetop foliage and flies only at long intervals. Tape-recordings of at least part of its vocal repertoire would be very helpful, as there are many differences among the forms of vocalizations in the two subfamilies. (For vocalizations of *Ochthoeca* species and other fluvicolinines, see Smith 1971.) The one described vocalization, a shrill and "rather sad whistle" (Goodall et al. 1957) like a descending "peeoo" (J. D. Goodall, pers. comm.), does suggest a call of *Ochthoeca* species.

COMPARISON OF THE GENERA

Many features of individual species have been compared as an aid to description. Now the general trends will be delineated and the main

exceptions discussed and similarities and dissimilarities evaluated for their usefulness in making decisions about phylogenetic relationships.

ECOLOGICAL CHARACTERISTICS

As currently constituted, the Serpophaginae comprise an assemblage of small to moderate-sized arboreal tyrannids, primarily specialized for active gleaning of invertebrate prey. The smaller, lowland species of *Serpophaga* forage much like active, arboreal, wood warblers. The similar-looking species usually assigned to the genus *Inezia* have comparable habitat preferences and are probably closely similar in foraging behavior. Similarly, *Anairetes* species are small, very active, and very warbler- or kinglet-like, and forage by gleaning in brushy habitats in the mountains or in the South Temperate lowlands. Although they occasionally swing on branches like titmice, the general parid-like impression they produce derives more from their crests than from their foraging behavior. Foraging of the larger and longer-tailed species usually placed in *Uromyias* has not been described, but anatomical considerations suggest that they are probably like both the *Anairetes* species and the lowland genus *Stigmatura*. The latter is noteworthy primarily for its long tail, and forages actively in a similar but at least superficially more gnatcatcher-like fashion.

Convergence with gnatcatchers in foraging behavior is not surprising in this group. Even the parulid-like species of *Serpophaga* occasionally flick their tails rapidly into a cocked position, a habit that has led Hussey (1916), Friedmann (1927), and Wetmore (1926) to compare *S. subcristata*, *S. nigricans*, and *A. flavirostris*, respectively, to gnatcatchers. I have seen *Anairetes parulus* and *Inezia subflava* do the same thing, but agree with most observers that these smaller species appear warbler-like when foraging, whereas the much more frequent graceful cocking of the long tail of *Stigmatura budytoides* is distinctive.

A trend may exist for larger serpophaginine species to forage less actively, more like vireos. The two *Mecocerculus* species observed did so. The relatively large *Xenopsaris albinucha* appears less active and rather *Pachyramphus*-like in foraging.

There are two divergent sorts of foraging and habitat preference. At least two species of *Serpophaga* are specialized with respect to streamside habitats. The more extreme *S. cinerea* has become considerably terrestrial, although even *S. nigricans* shows some tendency in this direction. *Tachuris rubrigastra*

inhabits rush and cat-tail marshes. Like *S. cinerea* it spends some time running on the ground, and is also relatively likely to pursue aerial prey; but both *S. cinerea* and *T. rubrigastra* actively glean and flight-glean like other members of the assemblage.

Plumage, anatomical characteristics, and particularly the existence of essentially intermediate adaptations in *S. nigricans* link *S. cinerea* to other members of its genus. *T. rubrigastra* has no such obvious bonds, particularly as its coloration is unique in several respects. But its plumage pattern and gross anatomy are consistent with the general characteristics of the other genera. Species ecologically more comparable to *Tachuris* are at present artificially segregated in the subfamily Euscarthminae, and will be discussed in subsequent papers (Smith, MS).

While *Tachuris* is brightly colored, most species in this group are not. Many differences in plumage among species within each genus appear to be cryptic adaptations to their different habitats.

DISPLAY BEHAVIOR

Comparisons with other tyrannids. Judging from the display repertoires of *Anairetes parulus* and the better known *Serpophaga* species, each has at least eight adult vocal displays (when better known the Brief Unit category, at least, may be divisible) and about six non-vocal displays. Such a repertoire size is comparable to that in other tyrannid genera such as *Tyrannus* and *Sayornis*. Further, the ways in which the displays are used fit very well with what is known of other tyrannids. There are, for instance, some displays used like "song" in more or less continuous bouts of predawn or later station calling, in patrolling, and in countersinging with territorial neighbors: e.g., RRV, RV, RV Variants, BC, and the *Serpophaga subcristata* LHC in part of its usage. Other vocalizations are used by mates in greeting (the Long Chatter of *S. munda*, the LHC of *S. subcristata*, in part the Chite-Churr series and BC of *S. cinerea*, the SC and MC of *A. parulus*, and calls of both *I. subflava* and *S. budytoides*) or in a stylized nest site oriented performance (Nest-Site-Showing with Simple Chatter), while yet others occur primarily in agonistic encounters (the Brief Units of *S. subcristata* and *A. parulus*). Also as for other tyrannids, such a gross categorization of modes of use must be qualified by such variables as the amount of locomotory activity. For instance, the proportion of LHCs to RVs increases as a "singing" *S. subcristata* or *S. munda* becomes more active, and the precise

mode of employment of *S. subcristata* LHCs and *Mecocerculus strictoperus* "shreeeee" calls that usually coincide with the act of alighting closely resembles that of displays encoding locomotory and other conflicting messages in other tyrannids.

Approximately the same range and kinds of behavioral events appear to be covered by the displays of at least *Serpophaga* species and *A. parulus* as have been found to be covered by displays of other tyrannid genera. Yet the forms of the displays are distinctive, and the display repertoires would not easily be mistaken for most of those known from genera outside the Serpophaginae. It is particularly striking that sonagrams show most vocalizations either as chevrons (the BU) or concatenations of chevrons and modified chevrons, the latter in distinctive sets.

At least the best known species, *A. parulus*, offers an unusually good opportunity for the study of encoding, although this is somewhat lessened by the interference offered to continuous observation by the dense vegetation of the species' habitats. It has several distinctive but intergrading vocalizations built up of complex combinations of series of basically similar components. The amount of variation found in the usage of vocal displays by individuals, among the individuals of a local population, and among populations in Chile and Ecuador suggests that the species can provide a very useful source for comparative study. The range of employment of each kind of variation in form should be investigated, and compensatory shifts in usage among the vocal displays in the repertoires of different populations would be especially worth seeking.

Comparisons among the serpophagines. A detailed basis for comparison within the group is provided by those vocal displays used in ways closely comparable to oscine "song." In the Repeated Vocalizations of *Anairetes parulus*, *Serpophaga subcristata*, *S. munda*, and *Mecocerculus leucophrys* the same components are combined in complex but extremely similar ways. Each RV begins with a relatively broad chevron with a "shoulder" (see illustrations) on its ascending arm; in *A. parulus* this is preceded by a relatively faint chevron that makes the RV in this case more like an RV Variant. Next come two or more very narrow, simple chevrons whose successive peak frequencies ascend. In all but *A. parulus* these are followed by one or more two-peaked chevrons, in which the first peak is usually the higher. The two peaks are only just distinguishable in *S. subcristata*. In addition, the basic RV form

of *Inezia subflava* uses very similar components in a just slightly different way.

The song-like displays generally include Brief Chatters, employed instead of RV when the communicators are more active, and having some of the same structural characteristics as RVs. In Chilean *A. parulus*, the BC is little more than a distinctively prolonged RV form; Ecuadorean samples of apparently the same display are more complex, but differ primarily in having prolonged and multi-peaked components. In *S. munda* we find a distinctive coupling of elements in the chatter, but a structure easily derivable from that of the Chilean *A. parulus* BC. Comparable coupling appears in the homologue or near-homologue in *M. leucophrys*, a call also incorporating RVs and provisionally designated a BC-RV. Finally, in duet-like exchanges recorded from pairs of *Stigmatura budytoides*, one individual uses a very simple chatter comprising only about six simple chevrons (very like the BC of *Inezia subflava*) while the other uses a much more complex form (see detailed description above) comprising RV or BC type components in a sequence similar to an RV form of *I. subflava*, and to some RV forms of the other genera.

The known BCs vary in the calling of each individual and differ more among the species and genera than do the known RVs, but still indicate very close relationships. When compared with published descriptions of the vocalizations of tyrannids of other subfamilies, they form an obviously distinctive set. Further, the relatively specialized song-like vocalizations of *Tachuris rubrigastra* could easily belong to this set.

Other vocalizations are as yet less helpful in determining phylogenetic relationships, although with only a few more data this should change. Many species, for instance, utter simple BUs (in at least *Serpophaga*, *Inezia*, *Anairetes*, *Mecocerculus*, and probably *Tachuris*) singly, or in loose series resembling the SCs that may also be widespread. But the form of BUs and SCs is so simple that even their widespread occurrence provides only limited phylogenetic clues. Too little is known yet about the more complex chatter vocalizations to trace relationships, although the fact that several types of chatter are present in the repertoires of species of both *Serpophaga* and *Anairetes* again probably indicates phylogenetic relationship. But the Multiply-peaked Chatters (and Multiply-peaked Vocalization) used by *A. parulus* in strongly agonistic events do not have easily identified homologues in *Serpophaga* species, apparently relating primarily to the BUs of both genera.

Vocal display behavior is more helpful for systematic comparisons within the group than are the known non-vocal displays. The latter show no obvious trends, and some (e.g., Wing and Tail Flicking, Crouching, Bill Snapping) are very conservative. There may be specializations in non-vocal display, perhaps primarily in *Tachuris rubrigastra*, which may depend more on this mode than do most of the others. This is suggested by the observed non-vocal displays such as the male's flights around his mate, by the unusual plumage adaptations, many of which are probably "badges" (in the sense of Smith, in press) used in communication, and by the quietness of the species in dense populations at the height of its breeding season. If *Tachuris* has evolved relatively great dependence on visual communication, it may be due to the characteristic vegetation it inhabits; to be close enough to see one another easily, birds may have to be so close that the carrying power of vocalizations (one of their prime advantages) may be irrelevant. Similar reasoning might suggest that *S. cinerea* should have developed more dependence on non-vocal displays in its very noisy environment, but this is not known to be the case.

It is interesting that species exceptional in their foraging behavior also appear to be exceptional in their displays: *S. cinerea*, *T. rubrigastra*, and perhaps *X. albinucha*. The first two, however, show at least superficial similarities with the display characteristics that are widespread in the group, and neither is sufficiently different to be easily excluded. The case for inclusion of *X. albinucha* is tenuously based on a single vocalization apparently similar to a vocalization in *M. strictoperus*, but is not unreasonable in the light of other characteristics. Only the monotypic genus *Colorhamphus* appears to be misplaced in this subfamily, but the evidence is extremely scanty.

The extent of differences to be expected among the displays of congeners in the group can as yet be only roughly estimated from that known in *Serpophaga*. The relatively terrestrial, stream-adapted *S. cinerea* is much more different in display form from the more arboreal *S. subcristata* than is the similarly arboreal *S. munda*. But the comparison is difficult to evaluate, in part because it is not yet certain that *S. subcristata* and *S. munda* are specifically distinct, despite a geographical overlap and obvious differences in plumage coloration and vocalizations. It would be most useful at this point to have information on the River Tyrannulet, *S. hypoleuca*, which, because of its riverside habitat (Phelps and Phelps 1963) and plumage characteristics,

might be expected to be somewhat intermediate between the extremes that have been described.

Finally, comparisons would be facilitated by data (very time-consuming to obtain) on the whole display repertoires of at least several species. Because conditions of observations were not matched for all species (e.g., *A. parulus* was often found in higher population densities than was any *Serpophaga* species, but was not observed through the early nest-building phase of breeding behavior), the differences in their vocal repertoires are likely to be somewhat less than are indicated by present data.

SERPOPHAGININE AFFINITIES

On the basis of the extant behavioral and non-behavioral information, the genera *Serpophaga* (including *Inezia*), *Anairetes* (including *Uromyias*), *Mecocerculus*, and *Stigmatura* appear to form a closely coherent group. *Tachuris*, probably, and *Xenopsaris*, possibly, belong with them. But *Tachuris* may have closer relatives in Hellmayr's subfamily Euscarthminae, and other euscarthminine-serpophaginine relationships are likely on the basis of general plumage and anatomical similarities (e.g., *Pogonotriccus* to *Mecocerculus*, and *Phylloscartes* to *Serpophaga*, to choose only two), as well as widespread ecological similarities. It is by no means clear that two subfamilies can be recognized, but a full discussion can await behavioral analyses of genera now in the Euscarthminae (Smith, MS).

Hellmayr did not state why he recognized two subfamilies here, but did remark that he expected his subfamilies to be criticized as new information became available. Von Ihering (1904) proposed that the structure and placement of the nest (essentially behavioral characteristics) provide good means with which to separate these and other genera into two subfamilies. He felt that one group built open, cup-shaped nests, while the second built hanging, "purse-shaped" nests with side entrances. He recognized as intermediate the bulky nest of *Camptostoma obsoletum* (not in either of Hellmayr's subfamilies) and the more cup-like, partially domed nest reported for *Phylloscartes ventralis*. The former he called "pear-shaped . . . but not suspended from the top of a twig but fixed at different points on the branches," a description fitting the nest of *C. imberbe*, then unknown to him.

The existence of these intermediates somewhat weakens von Ihering's arguments about the significance of the characteristics. More importantly, at least some aspects of such in-

termediacy are within the flexibility of individuals within a species. This apparently applies more to the means of attaching a nest than to whether or not it is domed. Most of the cup-shaped nests are on upright stems or in upright crotches, and are attached only to one or two sturdy supports. Even *Tachuris rubrigastra*, however, which usually attaches its nest to a single upright *Scirpus* stalk, has been found to fix it to several flowering stalks of *Typha* (pers. observ.). More importantly, *Anairetes parulus* often nests, not in crotches, but among several twigs coming from convergent stems. These twigs may be upright (pers. observ.) or even pendant (in the introduced *Salix babylonica*, Valenzuela 1962). Another species that sometimes fixes its nest to a number of independent twigs, instead of saddling it on a larger stem or placing it in a crotch, is *Stigmatura budytoides* (nest no. 1435, Inst. Miguel Lillo, Tucumán, Argentina).

Von Ihering's distinction of two main nest forms with different means of attachment remains of potential interest in delineating generic relationships. However, it does not seem likely to imply a sufficiently large evolutionary step to permit us to distinguish subfamilies. (With respect to the distinction between domed and cup-shaped nests, in a different part of the Tyrannidae the closely related species *Pitangus sulphuratus* and *P. lictor* build domed and cup-shaped nests, respectively, with occasional intermediates; see Smith 1962.) As with tarsal scutellation, nest form and attachment cannot be assumed a priori to be a sufficient means, taken alone, for discriminating between higher taxonomic categories. Undoubtedly these are useful characters, but in combination with other characters, and at different levels in different cases.

CONCLUSIONS

The tyrannid subfamily Serpophaginae, as recognized by Hellmayr (1927), comprises nine genera. The birds are mostly very active, gleaning insectivores of low forest and second growth. The smaller species appear comparable to very active wood warblers, kinglets, or gnatcatchers, and at least some larger species are less active and more like vireos or even some cotingids such as *Pachyramphus*. Two independent specializations to foraging in habitats dominated by water are seen, one to streamsides (in part of the genus *Serpophaga*) and one to marshes (the monotypic genus *Tachuris*). These species have converged in such ways as apparently increasing their amount of aerial pursuit of prey, and adopting partially terrestrial habits.

Such detailed similarities have been found in aspects of the display behavior of members of four genera, *Serpophaga* (including *Inezia*), *Anairetes*, *Stigmatura*, and *Mecocerculus*, that these are felt to be very closely related. In addition, no good reasons can be found for continuing to recognize a fifth genus, for which no behavioral studies have been made: *Uromyias*, comprising two slightly *Stigmatura*-like species that are otherwise clearly members of *Anairetes*. Of the remaining three genera, *Tachuris* is specialized in almost every sort of characteristic, but in most is comparable to the genera already mentioned. Consideration of its taxonomic position brings up the likelihood that the division between the subfamilies Serpophaginae and Euscarthminae is artificial, and other genera support this contention. *Xenopsaris* is poorly known, but on the balance of present information more likely to be a serpophaginine than a "cotingid." *Colorhamphus*, also poorly known, seems on the other hand more likely to be a fluvicolinine than a serpophaginine.

The habitats of most species of this assemblage interfere with easy and continuous observation of the birds, making them less than ideal subjects for behavioral studies. Nonetheless, their apparent convergences in foraging behavior with members of other avian families suggest that they can provide useful comparative tests of concepts derived from the study of behavioral ecology. And their use of complexly formed vocalizations based on series of often fairly simple components makes them attractive subjects for studies of encoding in display repertoires. It will be worthwhile to seek special field situations in which members of different species of this group can be more thoroughly studied.

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