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SPECIES LIMITS IN PALE-TIPPED TYRANNULETS (*INEZIA*: TYRANNIDAE)

KEVIN J. ZIMMER^{1,3,4} AND ANDREW WHITTAKER²

ABSTRACT.—New information on the vocalizations and behavior of populations of the Pale-tipped Tyrannulet (*Inezia subflava*), along with analysis of biometric and plumage characters, reveal that it actually consists of two species-level groups: a northern/Guianan group, the member taxa of which are weakly differentiated from one another; and a group whose distribution is primarily Amazonian, the member taxa of which are morphologically distinct but vocally and behaviorally similar to one another. The two groups differ from one another in several vocal, plumage, and biometric characters. Tape playback experiments suggest that the vocal differences alone present effective mechanisms for reproductive isolation between the two groups. Analysis of vocalizations further suggests a possible link between the Amazonian representatives of *Inezia subflava* and the Yellow Tyrannulet (*Capsiempis flaveola*). Received 10 May 1999, accepted 9 Sept. 1999.

The current taxonomic limits of many Neotropical birds were established by taxonomists who lacked field experience with the birds they were describing. Even the most basic information on vocal characters, behavior, or habitat preference was unknown, and thus, taxa were delimited entirely on the basis of similarities and differences in morphological characters. Consequently, scores of taxa were lumped into wide-ranging polytypic species based solely on shared similarities of plumage (Ridgway 1907, Hellmayr 1927). Modern taxonomists have access to a wealth of behavioral, ecological, vocal, and molecular data on Neotropical birds that was not available to workers just one generation ago. This should allow a more informed classification, and indeed, recent reevaluations of many wide-ranging taxa have resulted in the elevation of many subspecies to full species rank (Pierpont and Fitzpatrick 1983; Willis 1988, 1991; Prum 1994; Bierregaard et al. 1997; Krabbe and Schulenberg 1997; Isler et al. 1997, 1998; Zimmer 1997). Unfortunately, we are still far removed from having a working taxonomy that accurately reflects species-level biodiversity in the Neotropics. Much work remains to be done with respect to reevaluation of species limits in already described polytypic taxa (Prum 1994, Isler et al. 1998, Peterson 1998).

Until such work is completed, regional patterns and levels of endemism will continue to be misinterpreted or underestimated, with the result that unique reservoirs of biodiversity could be overlooked when critical conservation decisions are made.

We examine taxonomic limits in one such polytypic species, the Pale-tipped Tyrannulet (*Inezia subflava*). As currently recognized (Sibley and Monroe 1990), *Inezia subflava* ranges widely through the tropical lowlands of eastern Colombia, Venezuela, the Guianas, and Amazonian Brazil to Bolivia (Ridgely and Tudor 1994). Four subspecies were recognized by Traylor (1979): *I. s. subflava*, *I. s. caudata*, *I. s. intermedia*, and *I. s. obscura*.

While conducting avifaunal surveys in Amazonas and Roraima, Brazil, we discovered that local populations of Pale-tipped Tyrannulets differed markedly in their vocalizations from populations with which one or the other of us were intimately familiar. Subsequent analysis of specimens and tape recorded vocalizations, together with tape-playback experiments, revealed that *Inezia subflava* consists of two vocally and morphologically distinct species-level groups: a northern/Guianan group consisting of two weakly differentiated subspecies, and an Amazonian group consisting of two morphologically distinct yet vocally similar subspecies.

METHODS

K.J.Z. studied "Pale-tipped" Tyrannulets at various sites in edo. Cojedes, Venezuela (1987–1998) and edo. Amazonas, Venezuela (February–March 1998). Both authors also made numerous observations of these birds along the Rio Juma, Amazonas, Brazil (January

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1993 and 1995); along the Rio Branco near Boa Vista, Roraima, Brazil (November 1994); along the Rio Teles Pires, Mato Grosso, Brazil (September 1997 and 1998); and at multiple sites along the Rio Negro from Manaus to the Anavilhanas Archipelago, Amazonas, Brazil (1991–1998). All behavioral data were summarized verbally on tape in the field, and later transcribed. All measurements used in such data (distances, heights, etc.) are estimates. Mapped distributions (as they appear in this paper) are based on label data from specimens which K.J.Z. examined, and by more recent records documented with tape recordings. These localities, along with the type localities for each taxon, were entered into a geographic information system (Isler 1997) and mapped by M. Isler.

We assume that vocalizations of tyrannulets, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989; Kroodsma and Konishi 1991), and consequently provide potentially important characters for systematic study (Lanyon 1978, Willis 1992, Isler et al. 1997, Krabbe and Schulenberg 1997, Zimmer 1997). To analyze vocalizations we assembled recordings of each of the named subspecies of *Inezia subflava*. Locations and recordists for all recordings examined are listed in the Appendix. For comparison, vocalizations were categorized as loudsongs, duet songs, duets, or calls. Loudsongs were consistently patterned multinote vocalizations (Isler et al. 1997) given by an individual bird, seemingly in the context of territorial advertisement. Duet songs were sex-specific multinote vocalizations typically given as part of a duet, but frequently delivered independently as an alternate song type to the loudsong. Duets involved simultaneous delivery of duet songs by both members of a pair. Vocalizations characterized as calls were usually of low amplitude and/or structurally simple (usually involving repetition of identical notes) and were most often given in the context of contact vocalizations between mates. Exceptions are noted in the Results. Our tape recordings were made with Sony TCM-5000 recorders and Sennheiser MKH-70, ME-66, and ME-80 microphones. Spectrograms used in illustrations were made by P. Isler on a Power Macintosh 7500 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York), Canvas graphics software (version 5.0.3, Deneba Software, Miami, Florida), and a Hewlett Packard Laserjet 6MP printer.

Playback experiments were conducted to determine the reactions of tyrannulets of a given population to vocalizations of another population. In each case, an individual or pair of tyrannulets was first presented with 5–10 tape recordings of one of the other taxa, given at about 15-second intervals. If there was no response, the tyrannulets were then presented with 5–10 tape recordings of their own vocalization type. This was done to account for potential seasonal influences by resolving the question of whether birds that were unresponsive in the first trials were discriminating between the different vocalizations or were generally non-territorial during the trial period and therefore un-

responsive to playback of any kind. Failure to account for seasonal differences in responsiveness has been cited as a potential design weakness in other playback experiments (Kroodsma 1986). Responses to playback were characterized as strong, weak, or none. A strong response involved immediate and repeated vocalizations (from previously non-vocalizing birds) as well as approach toward the sound source. A weak response involved single or unsustained vocalizations (from previously non-vocalizing birds) without approach. The none category includes instances in which birds remained silent and did not approach the sound source, as well as instances in which already vocalizing birds neither changed the delivery or pace of their vocalizations nor approached the sound source.

To identify morphological differences, K.J.Z. examined representative specimens of *I. s. subflava* ($n = 31$), *I. s. caudata* ($n = 33$), *I. s. intermedia* ($n = 8$), and *I. s. obscura* ($n = 8$). These specimens are housed at the American Museum of Natural History, New York (AMNH); Carnegie Museum, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Peabody Museum of Natural History, Yale University (YPM); and the Los Angeles County Museum of Natural History, Los Angeles (LACM). A list of the specimens examined is provided in Appendix 2. A wing rule with a perpendicular stop at zero was used to measure flattened wing chord (wing) and tail length (tail), and dial calipers were used to measure tarsus length (tarsus), culmen length from the anterior end of the nares to the tip (culmen), bill depth at the anterior end of the nares (bill depth), and bill width at the anterior end of the nares (bill width). All measurements made with calipers were made to the nearest 0.1 mm; those taken with the wing rule were made to the nearest 0.5 mm. Measurement terminology conforms with that used by Pyle and coworkers (1987).

General linear models were used to investigate gender corrected differences between the four subspecies for each of the six characters measured. Residual diagnostics indicated no violations of the general linear model assumptions of error normality and constant variance. Bonferonni multiple comparisons (two-tailed t -test) with a family error rate of 5% were used to compare pairwise subspecies differences for each variable. Bonferonni intervals (Sokal and Rohlf 1995) ensure that the probability of falsely identifying a difference between subspecies when one does not exist remains at most 5% even though multiple comparisons are being made. Intervals that do not contain zero indicate a significant difference among the pair of subspecies. Statistical analyses (ANOVA procedure and Bonferonni multicom procedure) were performed using S-Plus version 4.5 for Windows.

RESULTS

Distribution.—The type localities of the various subspecies of *Inezia subflava*, along

show affinities for wooded areas in the vicinity of water. *Inezia s. intermedia* is particularly common in the seasonally flooded llanos region of Venezuela, where it inhabits the understory and mid-levels of humid gallery forest, as well as lighter deciduous woodland and scrub (K.J.Z., pers. obs.). Similar habitats are occupied in Colombia (Hilty and Brown 1986). *Inezia s. caudata* is found primarily in várzea forest along the Orinoco and various tributaries in Venezuela (Meyer de Schauensee and Phelps 1978; S. Hilty, pers. comm.), but is apparently mostly restricted to mangroves in the Guianan portion of its range (Ridgely and Tudor 1994). *Inezia s. obscura* and *I. s. subflava* are found primarily in the shrubby, water-edge vegetation along forest-bordered rivers, streams, and lakes (K.J.Z. and A.W., pers. obs.). Both forms are locally common in the shrubby borders of seasonally flooded black-water forests (igapó). On river islands in the Rio Negro, nominate birds frequently occupy the thickets bordering central lagoons (K.J.Z. and A.W., pers. obs.).

Behavior.—Little has been recorded of the behavior of Pale-tipped Tyrannulets. In general, all forms occupy the lower to mid-levels of the forest strata, and are usually encountered singly or in pairs independent of mixed-species flocks (Hilty and Brown 1986; K.J.Z. and A.W., pers. obs.). They perch-glean a variety of arthropods from mostly live foliage, while moving with their tail partially cocked (Hilty and Brown 1986; Ridgely and Tudor 1994; K.J.Z. and A.W., pers. obs.). In the Venezuelan llanos, *I. s. intermedia* shows a greater tendency to forage within 2 m of the ground and frequently drops to the ground to glean arthropods from the tops of leaf litter (K.J.Z., pers. obs.). This behavior may be accentuated during the pronounced dry season when most of the trees have dropped all or most of their leaves. At least in this region, *I. s. intermedia* is commonly associated with mixed-species flocks of woodcreepers, Rusty-backed Spinetails (*Cranioleuca vulpina*), other tyrant-flycatchers, and greenlets (K.J.Z., pers. obs.).

Plumage.—The four subspecies of Pale-tipped Tyrannulet are so similar in plumage characters that silent birds could defy identification in the field. In direct comparison, specimens are readily separable into two

groups based on ventral coloration. *Inezia s. caudata* and *I. s. intermedia* are tinged buffy or ochraceous on the throat and breast, contrasting with a whitish chin and a clearer yellow belly and vent. This ochraceous coloring is strongest in *I. s. caudata*, whereas *I. s. intermedia* has a paler throat and less ochraceous on the breast. Both *I. s. subflava* and *I. s. obscura* lack any buffy or ochraceous tones to the underparts, are more saturated with yellow on the chin and throat, and are flammulated olivaceous on the sides of the breast. *Inezia s. obscura* is strongly washed olivaceous across the center of the breast, making the throat appear contrastingly brighter yellow, whereas the median underparts of *I. s. subflava* are yellow from the chin down. *Inezia s. caudata* and *I. s. intermedia* have slight contrast between the grayish crown and the olive-brown back, whereas *I. s. subflava* and *I. s. obscura* are more uniformly olivaceous above. All forms have the wings and tail dusky, with two whitish wingbars, pale edges to the outer vanes of the rectrices, and the rectrices tipped pale buffy-white. Field work suggests that there may be consistent differences in iris color, with *I. s. intermedia* having conspicuously pale (whitish or yellowish-white) irides, whereas those of *I. s. subflava* and *I. s. obscura* are brownish. We have not been able to ascertain the eye color of *I. s. caudata*.

Size.—Subspecies of *Inezia subflava* differed significantly from one another in mean measurements of several characters (Tables 1, 2; Fig. 2). Significant between-taxa differences were found in measurements of culmen ($F_{3,74} = 40.4$, $P < 0.001$), bill depth ($F_{3,74} = 12.0$, $P < 0.001$), bill width ($F_{3,74} = 12.2$, $P < 0.001$), wing chord ($F_{3,74} = 6.0$, $P < 0.001$), and tarsus ($F_{3,74} = 16.9$, $P < 0.001$). *Inezia s. caudata* and *I. s. intermedia* differed from one another only in culmen length ($t = 2.96$, $df = 74$, $P < 0.005$) and bill width ($t = 2.78$, $df = 74$, $P < 0.01$). *Inezia s. caudata* and *I. s. obscura* differed in culmen length ($t = -8.93$, $df = 74$, $P < 0.001$), bill depth ($t = -4.45$, $df = 74$, $P < 0.001$), bill width ($t = -4.16$, $df = 74$, $P < 0.001$), and tarsus length ($t = 4.88$, $df = 74$, $P < 0.001$). Nominate *I. s. subflava* and *I. s. caudata* differed in culmen length ($t = -4.12$, $df = 74$, $P < 0.001$) and tarsus length ($t = 5.89$, $df = 74$, $P < 0.001$). *Inezia s. intermedia* and *I. s. subflava* differed

TABLE 1. Means (\pm SD) and ranges of selected measurements (mm) of the four subspecies of Pale-tipped Tyrannulet (*Inezia subflava*). Significance: * = $P < 0.001$; ** = $P < 0.0001$. Values of F and P (= probability of a greater value of F) derived from Analysis of Variance (ANOVA). Asterisks following a character indicate significant differences between two or more of the subspecies, after correcting for potential sex differences within taxa.

Characters	<i>caudata</i> $n = 33$	<i>intermedia</i> $n = 8$	<i>subflava</i> $n = 31$	<i>obscura</i> $n = 8$	F
Culmen**	6.3 \pm 0.3 5.5–7.0	6.0 \pm 0.3 5.6–6.3	6.6 \pm 0.3 6.2–7.3	7.4 \pm 0.3 7.0–8.0	40.4
Bill depth**	3.1 \pm 0.2 2.5–3.5	2.9 \pm 0.2 2.5–3.1	3.1 \pm 0.2 2.6–3.5	3.5 \pm 0.1 3.3–3.6	12.0
Bill width**	3.6 \pm 0.3 3.0–4.3	3.3 \pm 0.3 2.7–3.8	3.5 \pm 0.3 2.9–4.4	4.1 \pm 0.2 3.7–4.4	12.2
Wing chord*	49.5 \pm 2.2 45–53.5	50.4 \pm 2.0 48–52.5	48.2 \pm 1.5 46–51	50.3 \pm 1.9 48–53	6.0
Tail	50.0 \pm 2.6 44–54	51.2 \pm 1.6 49–53	49.0 \pm 2.4 44–53	50.6 \pm 1.9 48–53.5	2.6
Tarsus**	16.5 \pm 0.9 14.2–18.3	16.3 \pm 0.8 15.1–17.3	15.3 \pm 0.6 14.4–16.6	15.0 \pm 0.5 14.2–15.8	16.9

in culmen length ($t = -5.52$, $df = 74$, $P < 0.001$), bill depth ($t = -2.84$, $df = 74$, $P < 0.01$), wing chord ($t = 2.71$, $df = 74$, $P < 0.01$), and tarsus length ($t = 3.08$, $df = 74$, $P < 0.01$). *Inezia s. intermedia* and *I. s. obscura* differed in culmen length ($t = -9.29$, $df = 74$, $P < 0.001$), bill depth ($t = -5.83$, $df = 74$, $P < 0.001$), bill width ($t = -5.39$, $df = 74$, $P < 0.001$), and tarsus length ($t = 3.32$, $df = 74$, $P < 0.01$). Nominate *I. s. subflava* and *I. s. obscura* differed in culmen length ($t = 6.26$, $df = 74$, $P < 0.001$), bill depth ($t = 4.02$, $df = 74$, $P < 0.001$), bill width ($t = 4.79$, $df = 74$, $P < 0.001$), and wing chord ($t = 2.77$, $df = 74$, $P < 0.01$). The two southern subspecies (*I. s. subflava* and *I. s. obscura*) were larger billed and shorter legged than the

two northern subspecies (*I. s. intermedia* and *I. s. caudata*). *Inezia s. obscura* was the largest billed and shortest legged of the four taxa, whereas *I. s. intermedia* was the smallest billed and longest winged.

Vocalizations.—We assembled 96 separate recordings containing more than 600 individual songs, duets, or calls. Analysis of vocalizations reveals that the four taxa separate into two distinct groups. The loudsong of *I. s. intermedia* (Fig. 3A, B) is a short series of notes in which the first 1–2 notes are louder and slightly separated from the rest (*cheep chee-deleet*). It is often preceded by several irregularly spaced single-note *pip* or *kep* calls (second song in Fig. 3A). This is the most frequently heard vocalization from *I. s. inter-*

TABLE 2. Results of Bonferroni multiple comparisons of five biometric variables (culmen, bill depth, bill width, wing chord and tarsus length) between the four subspecies of Pale-tipped Tyrannulet (*Inezia subflava*). A sixth variable (tail length) showed no significant differences in any of the comparisons, and is excluded from this table. Codes for the taxa are as follows: caud = *I. s. caudata*; inter = *I. s. intermedia*; obsc = *I. s. obscura*; and subfl = *I. s. subflava*. Degrees of freedom for all t -values = 74. Differences between taxa are considered significant only when $P < 0.0083$, to achieve a Bonferroni family error rate of 0.05.

	Culmen		Bill depth		Bill width		Wing		Tarsus	
	t	P	t	P	t	P	t	P	t	P
caud-inter	2.96	0.004	2.48	ns	2.78	0.007	-1.01	>0.05	0.62	>0.05
caud-obsc	-8.93	<0.001	-4.45	<0.001	-4.16	<0.001	-1.01	>0.05	4.88	<0.001
caud-subfl	-4.12	<0.001	-0.58	>0.05	1.13	>0.05	1.62	>0.05	5.89	<0.001
inter-obsc	-9.29	<0.001	-5.38	<0.001	-5.39	<0.001	-0.01	>0.05	3.32	0.001
inter-subfl	-5.52	<0.001	-2.84	0.006	-2.05	>0.05	2.71	0.008	3.08	0.003
obsc-subfl	6.26	<0.001	4.02	<0.001	4.79	<0.001	2.77	0.007	-1.18	>0.05

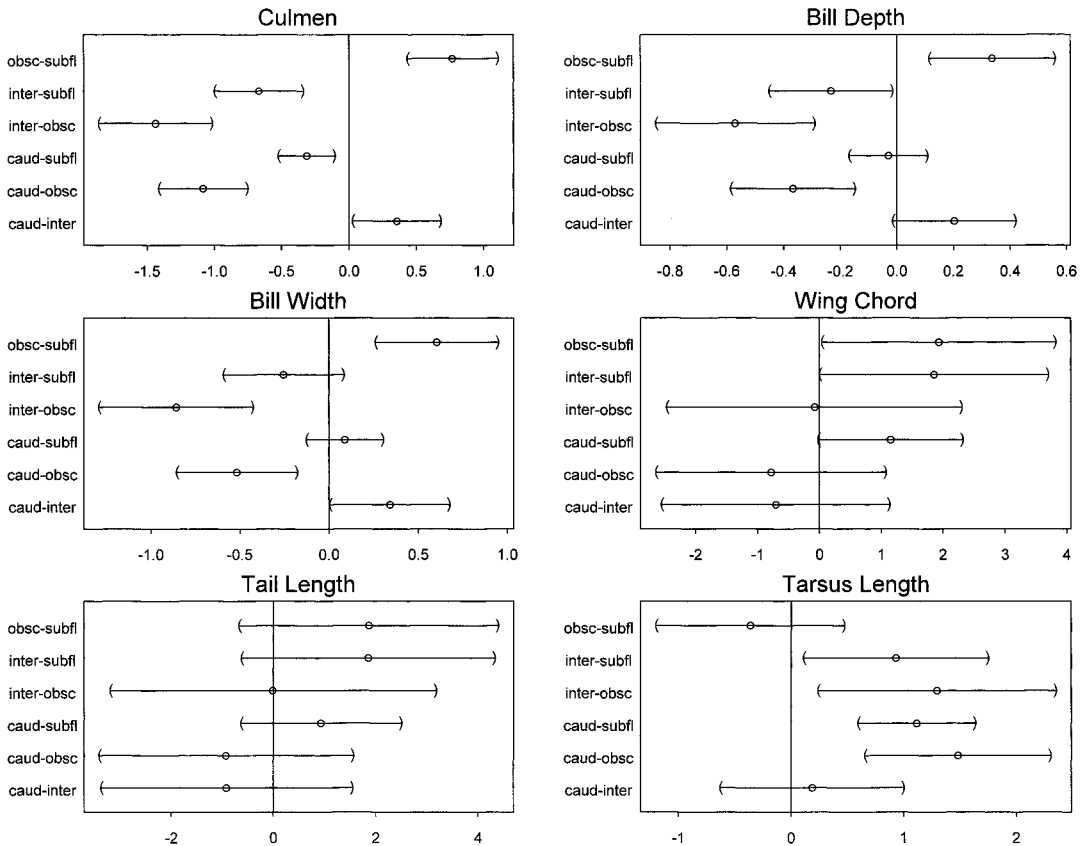


FIG. 2. Graphical display of Bonferonni multiple comparisons of six biometric variables (culmen, bill depth, bill width, wing chord, tail length, and tarsus length) between the four subspecies of Pale-tipped Tyrannulet (*Inezia subflava*; two-tailed t -test, $df = 74$). Test values are found in Table 2. Codes for the taxa are as follows: obsc = *I. s. obscura*, subfl = *I. s. subflava*, inter = *I. s. intermedia*, and caud = *I. s. caudata*. Intervals that do not contain zero indicate a significant difference among the pair of subspecies being compared.

media and is given throughout the day (K.J.Z., pers. obs.). The loudsong of *I. s. caudata* (Fig. 3C) is similar in pattern, number of notes, frequency range, and shape of some of the individual notes. The similarities between loudsongs of the two taxa are even more pronounced to the human ear than the spectrograms would suggest. *Inezia s. intermedia* has an alternate song (Fig. 3D) that is a loud, descending series of about 8–15 evenly spaced notes (*chee, cheep cheep cheep cheep chew chew*), in which the first note is slightly separated from the rest. A version of this song is given by both sexes during duets (Fig. 3E). The pattern, number of notes, and pitch of these respective male and female duet songs are similar, although they differ in tonal quality and inflection. One or two loud notes from

one member of the pair is often the synchronizing cue for the partner to join in. Duet songs may be delivered in an antiphonal manner such that the notes of the male's song alternate with those of the female, or they may be delivered in nearly perfect synchrony. These songs are frequently given by a single bird outside of a duet context, particularly in response to tape playback of the loudsong. Our small sample of *I. s. caudata* vocalizations does not include duets or alternative songs. The dawn song (Fig. 3F) of *I. s. intermedia* is similar to its loudsong, but is faster and repeated at about 1 s intervals for several minutes. Two additional types of calls are regularly given by *I. s. intermedia*. The first is a loud *chew* note that may be given singly (Fig. 3G) or in a series of 5–15 well-spaced (1 note/

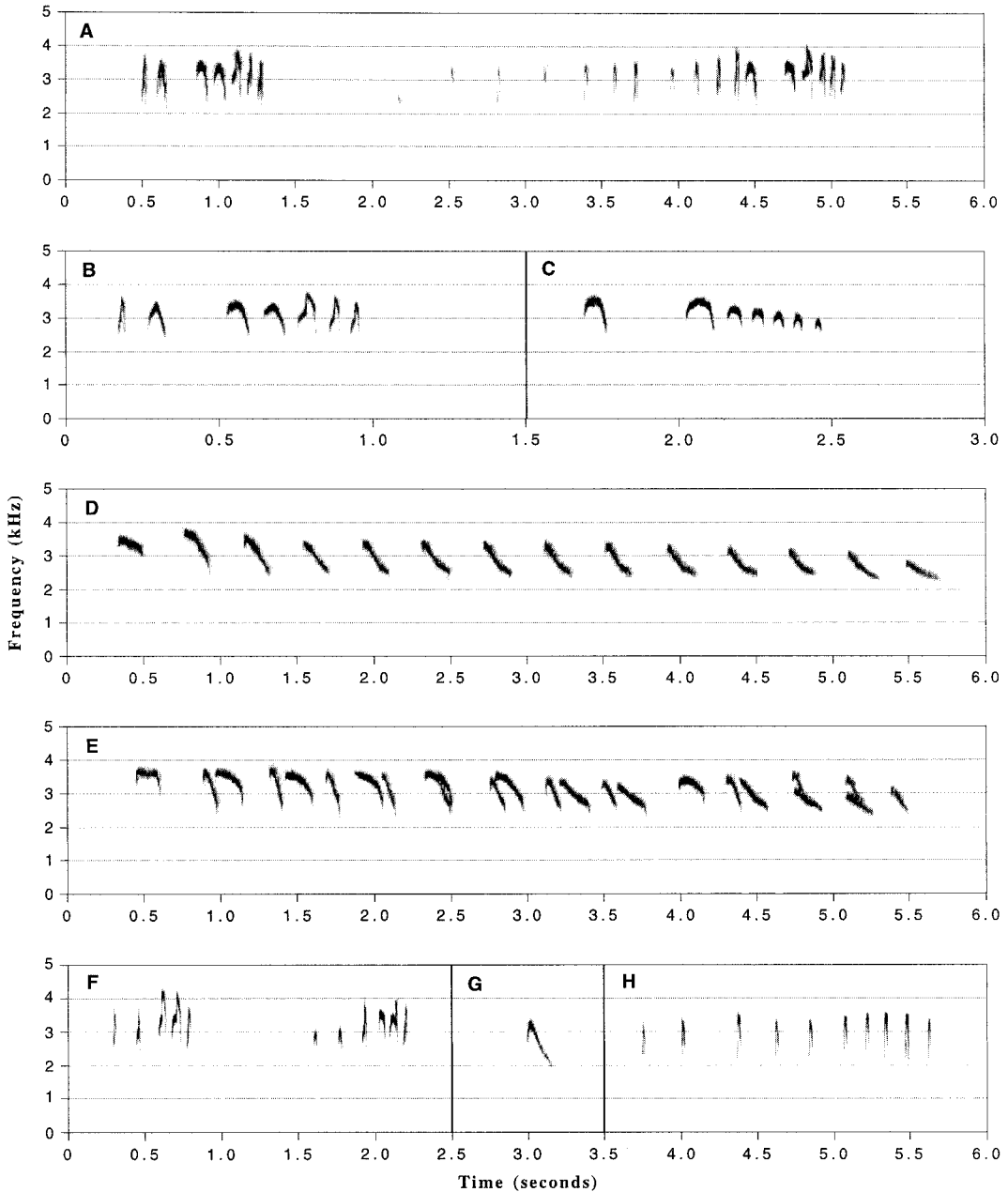


FIG. 3. Types of vocalizations of *Inezia subflava intermedia* and *I. s. caudata*: (A) two loudsongs of *I. s. intermedia* from edo. Cojedes, Venezuela (K. J. Zimmer recording); (B) first song of 3A magnified 200% on the time axis; (C) loudsong of *I. s. caudata* (same scale as 3B) from Suriname (M. and P. Isler recording, LNS #26586); (D) alternate or duet call of *I. s. intermedia* from edo. Cojedes, Venezuela (T. A. Parker recording, LNS #45560); (E) duet of *I. s. intermedia* from edo. Cojedes, Venezuela (T. A. Parker recording, LNS #45560); (F) dawn song of *I. s. intermedia* from edo. Guarico, Venezuela (P. Schwartz recording, LNS #66629); (G) pew call of *I. s. intermedia* from edo. Cojedes, Venezuela (K. J. Zimmer recording); (H) pit call of *I. s. intermedia* from edo. Cojedes, Venezuela (K. J. Zimmer recording).

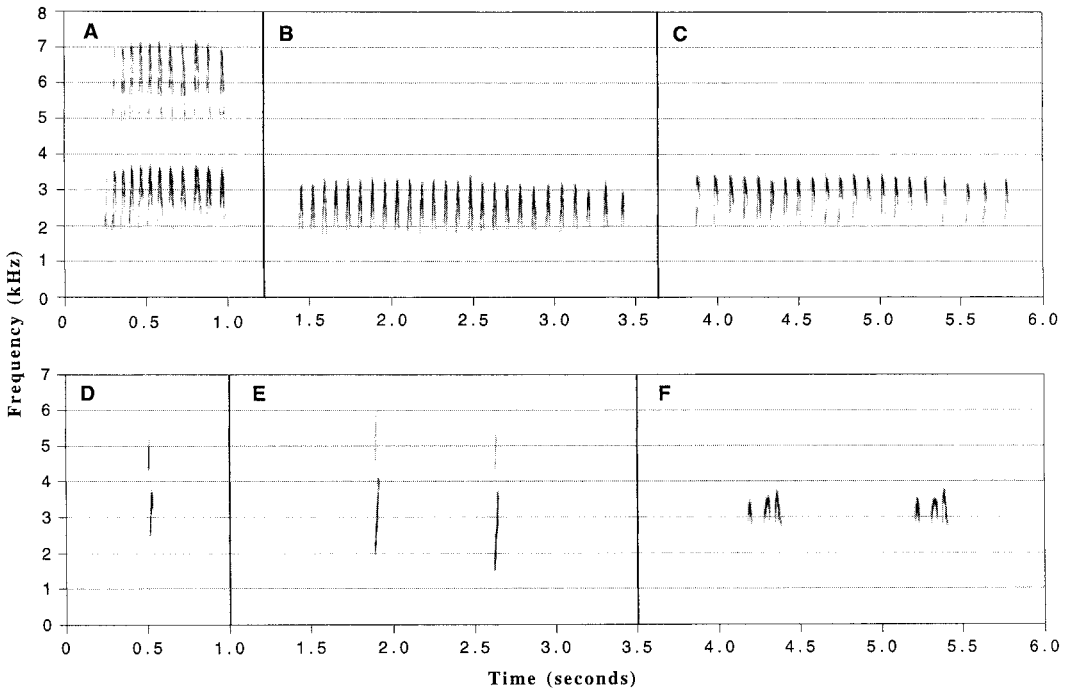


FIG. 4. Types of vocalizations of *Inezia subflava*: (A) loudsong of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil (B. M. Whitney recording); (B) loudsong of *I. s. subflava* from Alta Floresta, Mato Grosso, Brazil (B. M. Whitney recording); (C) rattle of *I. s. intermedia* in response to tape playback, from edo. Cojedes, Venezuela (K. J. Zimmer recording); (D) *pik* call of *I. s. subflava* from Rio Juma, Amazonas, Brazil (K. J. Zimmer recording); (E) *pik* calls of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil (B. M. Whitney recording); and (F) *teedlee* calls of *I. s. obscura* from edo. Amazonas, Venezuela (K. J. Zimmer recording).

1.5–2 s) notes. This call is frequently given by birds responding to playback. The most common call is an abbreviated *pit* note, which may be given singly, or, more commonly, in an irregularly spaced series of several notes (Fig. 3H). These *pit* calls are typically given as contact notes between mates or family members, and often serve as a prelude to duets.

What we consider the loudsong of both *I. s. obscura* and *I. s. subflava* is a dry rattle on one pitch, formed by a series of closely spaced, identical notes, delivered at about 2–3.5 kHz and lasting 0.5–2.0 s (Fig. 4A, B). These rattles are given at regular intervals throughout the day by individual birds in the absence of playback. The only similar vocalization that we have ever heard from *I. s. intermedia* or *I. s. caudata* was a single sputtering rattle given by a highly agitated *I. s. intermedia* in response to playback (Fig. 4C).

This represented a single occurrence in over 400 field hours with *I. s. intermedia* and no similar vocalization is present on any of the tape recordings from other recordists in our inventory. Thus, we believe that rattles are rarely used components of the vocal repertoires of those forms.

Both *I. s. subflava* and *I. s. obscura* routinely give abrupt *pik* notes (Fig. 4D, E) that are analogous to the *pit* calls of *I. s. intermedia* (Fig. 3H), but which are higher pitched. These calls are typically given as contact calls between mates. K.J.Z. has recorded a somewhat musical *teedlee* call (Fig. 4F) from *I. s. obscura*. This call seems to be given rarely, and we are uncertain of the context. We have not recorded a similar call from *I. s. subflava*.

Both sexes of *I. s. obscura* and *I. s. subflava* have an alternate song that is most frequently given as part of a duet. What we believe to be the male duet song in both forms is an

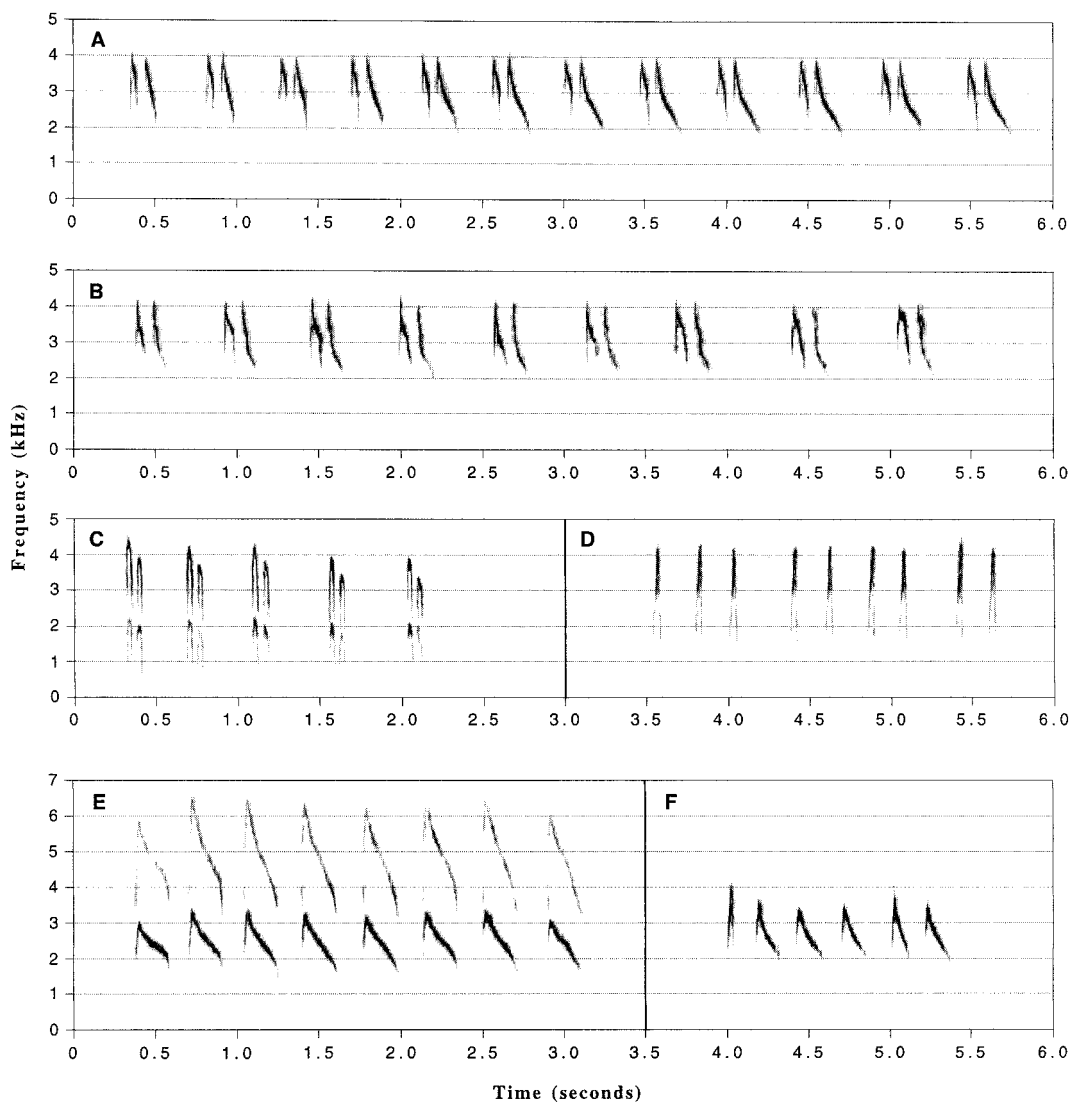


FIG. 5. Types of vocalizations of *Inezia subflava obscura* and *I. s. subflava*: (A) *pee-chew* duet songs (presumed male) of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil (B. M. Whitney recording); (B) *pee-chew* duet songs (presumed male) of *I. s. obscura* from edo. Amazonas, Venezuela (K. J. Zimmer recording); (C) *kutup* duet songs (presumed female) from edo. Amazonas, Venezuela (K. J. Zimmer recording); (D) *kip* calls of *I. s. subflava* from depto. Santa Cruz, Bolivia (S. L. Hilty recording); (E) response calls of *I. s. subflava* from Amazonas, Brazil (A. Whittaker recording); and (F) response calls of *I. s. obscura* from edo. Amazonas, Venezuela (K. J. Zimmer recording).

explosive series of evenly pitched *pee-chew* couplets, delivered at about 2/s (Fig. 5A, B). What we believe to be the female duet song in both forms is a lower amplitude series of bisyllabic *kutup* or trisyllabic *kutterup* calls, delivered slightly faster (Fig. 5C). Because these tyrannulets are sexually monomorphic,

it was not possible (in the absence of hand-sexed, color-marked birds) to assign a particular vocalization to one sex with absolute certainty. However, birds of both forms which gave the louder *pee-chew* series were also consistently the first members of a pair to respond aggressively to tape playback. These

pee-chew songs were more frequently delivered independent of a duet. Within duets by mated pairs, one individual consistently gave the *pee-chew* series, whereas the other individual consistently gave the *kutup* or *kutterup* song. Thus, we assume that the different types of alternate songs are specific to one sex or the other. The louder amplitude of the *pee-chew* songs, along with their greater frequency of occurrence outside of duets, and the more aggressive territorial response of individuals which gave them point to these being male songs.

Duets of *I. s. subflava* (Fig. 6A–C) and *I. s. obscura* (Fig. 6D, E) were similar to one another, but differed markedly from those of *I. s. intermedia* (Fig. 3E). One or more *pik* notes delivered by each member of a pair was most often the synchronizing cue for one of the birds (usually the one giving the *pee-chew* calls, and thus, the presumed male) to begin its duet song, with the mate immediately chiming in with its duet song. The male and female duet songs were then delivered simultaneously, creating a jumbled, rollicking effect that was distinctly different from the measured, penetrating duets of *I. s. intermedia*. Less frequently, one member of a pair would give 5–10 emphatic *kip* notes (Fig. 5D) to initiate a duet (Fig. 6C). Duets varied in length and pace between and within pairs. Pairs that were particularly agitated by playback frequently sang at a faster pace and gave more prolonged duets.

An additional vocalization given by both *I. s. subflava* and *I. s. obscura* is a loud series of five or more *chew* notes delivered at about 3 notes/s and usually preceded by a differentiated first note (as in *pee chew chew chew chew chew*; Fig. 5E, F). We call this the response call because it was typically given only in response to tape playback. Birds of both sexes gave this call. These calls were similar in quality to the *chew* call of *I. s. intermedia*, but were always given in a series and much faster.

In both their rollicking, jumbled duets and their rattled loudsongs, *I. s. subflava* and *I. s. obscura* are far more similar vocally to the Yellow Tyrannulet (*Capsiempis flaveola*; Fig. 7) than either is to *I. s. intermedia* or *I. s. caudata*.

Playback experiments.—K.J.Z. conducted

playback experiments in edo. Cojedes, Venezuela in February 1995, 1997, and 1998; in edo. Amazonas, Venezuela in February 1998; and in Mato Grosso, Brazil in September 1998. In the 1995 and 1997 trials, individuals or pairs of *I. s. intermedia* were presented with tape recordings of *I. s. subflava* from the Rio Juma (a west-bank tributary of the Rio Madeira, south of the Amazon), Amazonas, Brazil. There was no response to these recordings from any of the 28 pairs or individuals tested. When presented with recordings of *I. s. intermedia*, tyrannulets in all 28 territories responded strongly. In 1998, individuals or pairs of *I. s. intermedia* from 15 territories were presented with recordings of *I. s. obscura* from São Gabriel da Cachoeira, Amazonas, Brazil. None of the 15 pairs responded. When presented with recordings of their own vocal type, all birds responded strongly.

In the other February 1998 trials, individuals or pairs of *I. s. obscura* at three different sites in edo. Amazonas, Venezuela (Yapacana National Park, San Fernando de Atabapo, and Puerto Ayacucho) were presented with a recording of *I. s. subflava* from the Rio Juma, Amazonas, Brazil. Tyrannulets from each of the 11 territories we sampled responded strongly to tape playbacks of nominate birds. In September 1998, a pair of *I. s. subflava* near Alta Floresta, Mato Grosso, Brazil was first presented with tape of *I. s. caudata* from Suriname. The birds did not respond to these playbacks. We then switched to a tape of *I. s. obscura* from edo. Amazonas, Venezuela and the birds responded with an immediate approach and duet.

DISCUSSION

Analysis of vocal characters links *I. s. subflava* with *I. s. obscura*. The two forms have similar loudsongs, male and female duet songs, duets, and calls. Based on current sample sizes of tape recorded vocalizations, we are unable to diagnosably differentiate vocalizations of the two subspecies. *Inezia s. intermedia* differs markedly from the *subflava-obscura* group in its loudsong, male and female duet songs, duets and some calls. Neither our inventory of tape recordings nor our limited field experience with *I. s. caudata* allows a comparison of duet songs or duets of that form with any of the other subspecies. How-

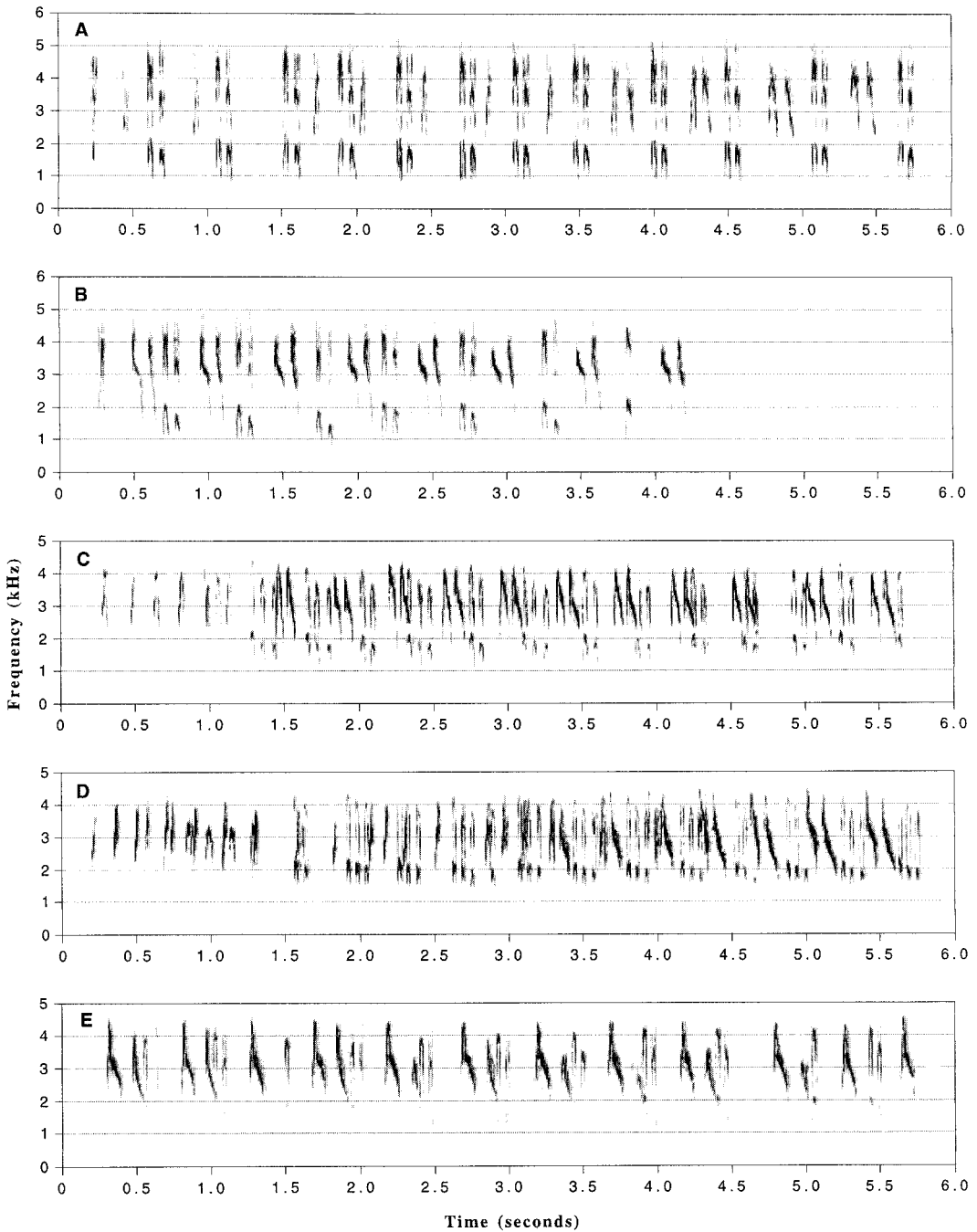


FIG. 6. Duets of *Inezia subflava subflava* and *I. s. obscura*: (A) *I. s. subflava* from Ziggylandia, Amazonas, Brazil (A. Whittaker recording); (B) *I. s. subflava* from depto. Santa Cruz, Bolivia (S. L. Hilty recording); (C) *I. s. subflava* from Alta Floresta, Mato Grosso, Brazil (B. M. Whitney recording); (D) *I. s. obscura* from Yapacana National Park, edo. Amazonas, Venezuela (K. J. Zimmer recording); and (E) *I. s. obscura* from Pto. Ayacucho, edo. Amazonas, Venezuela (K. J. Zimmer recording).

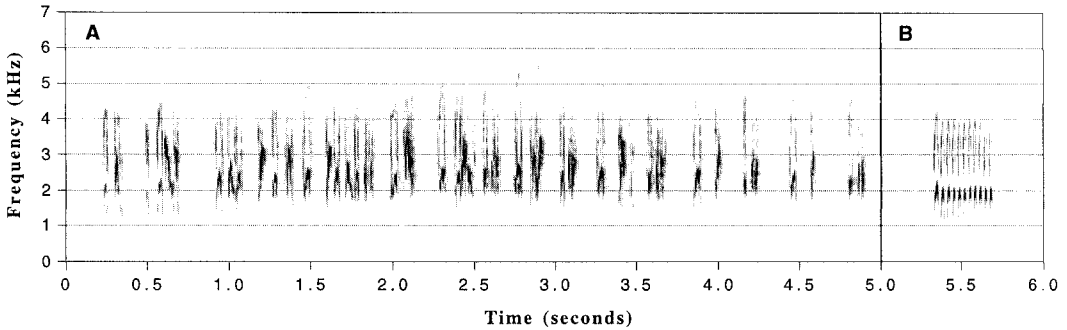


FIG. 7. Vocalizations of Yellow Tyrannulet (*Capsiempis flaveola*) from Pto. Ayacucho, edo. Amazonas, Venezuela: (A) duet; (B) loudsong (K. J. Zimmer recordings).

ever, *I. s. caudata* is similar to *I. s. intermedia* in both its loudsongs and *pit* calls, and is therefore strongly differentiated from the *subflava-obscura* group. We expect that further work will reveal that *I. s. caudata* has duet songs and duets similar to those of *I. s. intermedia*.

Pairings of taxa based on vocal differences are supported by the results of tape playback experiments. Although we were unable to conduct all possible pairwise tests, the ones performed were unequivocal. *Inezia s. intermedia* did not react to playback of either *I. s. subflava* or *I. s. obscura* in any of the 43 trials conducted. Pairs of *I. s. obscura* responded strongly to playback of nominate *I. s. subflava* vocalizations in each of 11 trials. The lone pair of *I. s. subflava* tested did not respond to playback of *I. s. caudata*, but responded strongly to vocalizations of *I. s. obscura*. These trials demonstrate that *I. s. obscura* and *I. s. subflava* recognize and respond strongly to one another's voices, whereas *I. s. intermedia* responds to neither. The lack of response of nominate *I. s. subflava* to playback of *I. s. caudata* songs suggests that *I. s. subflava* would be similarly unresponsive to playback of the nearly identical sounding *I. s. intermedia*.

Morphological differences within the complex correspond to the divisions suggested by vocal characters. *Inezia s. intermedia* and *I. s. caudata* are weakly differentiated from one another. Of six mensural characters we examined, the two forms differed only in culmen length and bill width. Both forms differed from *I. s. obscura* by four characters (culmen length, bill depth, bill width, and tarsus

length) and from *I. s. subflava* by culmen length and tarsus length (*I. s. intermedia* further differed from nominate *I. s. subflava* by bill depth and wing chord.). Despite the pronounced vocal similarities between them, *I. s. subflava* and *I. s. obscura* were as biometrically different from one another as either was from *I. s. intermedia* or *I. s. caudata*.

Differences in plumage characters, although subtle, also correspond with the vocal differences. *Inezia s. intermedia* and *I. s. caudata* are distinguished from the other two subspecies in having a buffy or ochraceous wash to the breast, a whiter chin, and a somewhat grayer crown. *Inezia s. subflava* and *I. s. obscura* are united by their brighter yellow throat and breast (with no buffy or ochraceous tones), olivaceous sides of the breast, and more uniformly olivaceous upperparts. This agrees with Hellmayr (1927:389), who stated that *I. s. subflava* "closely resembles the better known *I. s. caudata* from Venezuela and Guiana, but differs principally by more olivaceous (less brownish) upper parts, without any grayish suffusion on forehead; more yellowish sides of the head; less white on chin, and deeper yellow under parts, without buffy tinge on throat and foreneck."

In plumage, as in biometrics, *I. s. intermedia* and *I. s. caudata* are only weakly differentiated. Hellmayr (1927:390) described *I. s. intermedia* as "very similar to *I. s. caudata*, but slightly more olivaceous above; wing bands more whitish; under parts brighter as well as more uniform yellow, with the buffy tinge on the chest barely suggested." He also noted that upperpart coloration in *I. s. caudata* was "rather variable", that "the amount of

buffy suffusion below is also subject to considerable variation”, and that some specimens from Venezuela “closely approach the western race *intermedia* by having very little buffy on the foreneck.” Our examination of specimens did not suggest any consistent plumage differences between the two forms except for a paler chin in *I. s. intermedia* and a buffier breast in *I. s. caudata*.

Differences in iris color could prove to be the most obvious morphological character separating the two groups. Iris color as we have observed it in the field is whitish or pale yellowish for *I. s. intermedia* and brownish for *I. s. subflava* and *I. s. obscura*. This agrees with Ridgely and Tudor (1994:470), who state that iris color “seems consistently yellow in n. Colombia and n. Venezuela, dark in s. Venezuela and the Guianas.” This statement suggests that *I. s. caudata* (the Guianan form) is dark-eyed, which, if correct, would be the most conspicuous morphological character separating that form from *I. s. intermedia*. Ridgely and Tudor (1994) also raise the possibility that observed variation in eye color is age related, with younger birds having dark eyes. This seems unlikely given that we have noted territorial pairs of *I. s. obscura* and *I. s. subflava* with brownish eyes, although this does not preclude the possibility that juveniles of *I. s. intermedia* are also dark-eyed. We need confirmation that perceived differences in iris color are consistent for all members of each form.

The vocal similarities between “Pale-tipped Tyrannulets” of the *subflava-obscura* group and *Capsiempis* are intriguing. Like *I. s. subflava* and *I. s. obscura*, *Capsiempis* is a small, foliage-gleaning tyrannid that occupies shrubby forest borders and second-growth (often lightgaps within forest), as well as open várzea and bamboo (Hilty and Brown 1986; Ridgely and Tudor 1994; K.J.Z. and A.W., pers. obs.). *Capsiempis* is currently considered a monotypic genus whose affinities have been debated. Traylor (1977) subsumed it with *Phylloscartes*, whereas Lanyon (1984) argued that on the basis of nasal septum and syringeal morphology it was closer to *Phaeomyias*. The monophyly of *Inezia* has also been debated (Lanyon 1988), spurred largely by heterogeneity of external morphology in the group. Both genera are considered part of the Tyr-

annidae subfamily Elaeniinae. To our knowledge, vocal characters have not been given weight in the debates regarding either the monophyly of *Inezia* or the relationships of *Capsiempis*, but perhaps they should. Vocal similarities between *Capsiempis* and *I. s. subflava* and *I. s. obscura* are stronger than between any of the other species currently placed in *Inezia* (K.J.Z. and A.W., pers. obs.).

More field work is needed to ascertain the location and nature of possible contact zones between *I. s. subflava* and *I. s. obscura* in the middle Rio Negro drainage; between either of those forms and *I. s. caudata* along the lower Rio Branco; between *I. s. obscura* and *I. s. caudata* in edo. Apure and edo. Amazonas, Venezuela; and between *I. s. intermedia* and *I. s. caudata* along the north bank of the middle and lower Orinoco. In particular, more field work with *I. s. caudata* is needed to clarify the extent of vocal differentiation from *I. s. intermedia*, as well as the question of possible differences in iris color.

TAXONOMIC CONCLUSIONS

Inezia subflava subflava and *I. s. obscura* differ substantially from *I. s. intermedia* and *I. s. caudata* in multiple vocal and morphological characters. The magnitude of these differences is more than sufficient to support the recognition of the two groups as separate species under any of the widely accepted species concepts (McKittrick and Zink 1988). Because the two groups of taxa are allopatrically distributed, the most difficult species concept to satisfy is the biological species concept. A primary challenge in applying the biological species concept to allopatrically distributed taxa is the need to judge whether or not the taxa are sufficiently differentiated as to prevent extensive hybridization in the event of secondary contact. Carefully designed playback experiments can provide convincing evidence of whether vocal differentiation confirmed by spectrographic analysis is a sufficient barrier to interbreeding. In the *Inezia subflava* complex tape playback experiments suggest that the vocal differences alone present effective mechanisms for reproductive isolation between the two groups. Thus, we propose that the complex consists of two polytypic biological species as follows:

Inezia subflava Sclater and Salvin—Amazonian *Inezia*

I. s. subflava Sclater and Salvin

I. s. obscura Zimmer

Inezia caudata Salvin—Pale-tipped *Inezia*

I. c. caudata Salvin

I. c. intermedia Cory

The two forms of *I. subflava* are united by vocal characters, but are well differentiated on the basis of plumage and biometrics. The two forms of *I. caudata* appear to be weakly differentiated. The existence of morphologically intermediate specimens from the vicinity of the Río Orinoco suggests that *I. c. caudata* and *I. c. intermedia* intergrade in central Venezuela, and that morphological variation between the two forms could be clinal. In the absence of more complete vocal data for *I. c. caudata*, we will continue to recognize *I. c. intermedia* as a distinct taxon.

We advocate a return to the use of “*Inezia*” in the English names of these birds. Such usage will serve to distinguish this small genus (four species now recognized) from the myriads of other “tyrannulets.” With respect to modifiers, we suggest the application of “Amazonian *Inezia*” to *I. subflava*, which is the only species in the genus with an essentially Amazonian distribution. “Pale-tipped *Inezia*” offers a link with the former name of Pale-tipped Tyrannulet, and we feel that it should be applied to the two forms of *I. caudata*, which are the most familiar members of the complex to most biologists and birders.

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Special thanks are due M. and P. Isler for lending their time and talents in producing the map and spectrograms (respectively) for this paper. K. Garrett and the staff at LACM were of inestimable help in coordinating specimen loans from various institutions, as well as logistical support for the senior author’s frequent museum visits. T. Schulenberg was always available with helpful advice, and also provided access to several key references. Thanks are also due J. V. Remsen and S. Cardiff (LSUMZ); T. Schulenberg, D. Willard, and S. Hackett (FMNH); K. Parkes and R. K. Panza (CM); G. Barrowclough and R. Sloss (AMNH); and F. C. Sibley (YPM) for arranging specimen loans from their respective institutions. G. Budney, A. Priori, and the rest of the staff at the Library of Natural Sounds, Cornell Laboratory of Ornithology were of great help in providing access to the LNS collection of recordings. S. Hilty and B. Whitney generously provided additional tape recordings to add to our inven-

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- edo. Guarico (P. Schwartz 6); Hato la Trinidad, edo. Guarico (P. Schwartz 2); Hato Masaquaral, edo. Guarico (P. Schwartz 1); Pie de Cuesta, edo. Lara (P. Schwartz 1); Cañada el Gordo, edo. Zulia (P. Schwartz 1).
- Inezia s. caudata*.—BRAZIL: Boa Vista, Roraima (K. J. Zimmer 1). SURINAME: 8 km east of Meerzorg (T. H. Davis 2, M. and P. Isler 1).
- Inezia s. obscura*.—BRAZIL: São Gabriel da Cachoeira, Amazonas (B. M. Whitney 3). VENEZUELA: Pto. Ayacucho, edo. Amazonas (K. J. Zimmer 2); Picua, south bank of the Río Ventuari, Yapacana National Park, Amazonas (K. J. Zimmer 3); Caño Chiguire, north bank of the Río Ventuari, Yapacana National Park, Amazonas (K. J. Zimmer 21).
- Inezia s. subflava*.—BOLIVIA: depto. Santa Cruz (S. L. Hilty 2). BRAZIL: Alta Floresta, Mato Grosso (B. M. Whitney 1); Amazon Lodge, Rio Juma, Amazonas (A. Whittaker 1, K. J. Zimmer 1); lower Rio Negro, Amazonas (A. Whittaker 2); Ziggylândia, west bank lower Rio Negro, Amazonas (A. Whittaker 2).
- Inezia s. subflava/obscura*.—BRAZIL: 35 km west of Barcelos, Amazonas (A. Whittaker 2).

APPENDIX 2

List of localities and lending institutions for specimens examined. All specimens were from one of the following institutions: American Museum of Natural History, New York (AMNH); Carnegie Museum, Pittsburgh, Pennsylvania (CM); Field Museum of Natural History, Chicago, Illinois (FMNH); Los Angeles County Museum, Los Angeles, California (LACM); Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana (LSUMZ); and the Yale Peabody Museum of Natural History, New Haven, Connecticut (YPM).

Inezia s. intermedia (6 males, 2 females).—COLOMBIA: Cartagena, Bolívar (CM, 2 males); Fundación, Magdalena (CM, 1 male); Dibulla, La Guajira (CM, 1 female); Arroyo de Arenas, La Guajira (CM, 1 male). VENEZUELA: Sabana de Mendoza, Trujillo (CM, 2 males); Ocumare de la Costa, Aragua (FMNH, 1 female).

Inezia s. caudata (19 males, 11 females, 3 sex unknown).—BRAZIL: Ilha São Bento do Surrão, Roraima (FMNH, 1 female); mouth of Rio Mucajai, Roraima (LACM, 4 males, 2 females, 1 sex unknown); Flexal, Roraima (AMNH, 1 female). FRENCH GUIANA: Mana (CM, 2 males, 1 female; YPM, 3 males, 2 females). SURINAME: Leonsberg (AMNH, 1 male; LACM, 2 males; YPM, 1 sex unknown); Paramaribo (AMNH, 1 male; LACM, 1 male). VENEZUELA: Barrancas, Monagas (AMNH, 1 male); Altagracia, Bolívar (AMNH, 2 males, 1 female); Caicara, Bolívar (AMNH, 1 male, 1 female, 1 sex unknown); Ciudad Bolívar, Bolívar (AMNH, 1 male, 1 female); San Félix, Bolívar (CM, 1 female).

Inezia s. obscura (3 males, 3 females, 2 sex unknown).—BRAZIL: São Gabriel da Cachoeira, Amazonas (AMNH, 1 female); Tabocal, Amazonas (AMNH, 1 male); Camanaus, Amazonas (AMNH, 2

APPENDIX 1

Recording locations and recordists. Numbers following each name represent the number of recordings from the recordist at each site.

Inezia s. intermedia.—VENEZUELA: Hato Piñero, edo. Cojedes (T. A. Parker 1, K. J. Zimmer 36); Hato El Milagro, edo. Cojedes (P. Schwartz 4); Hato Corozal, edo. Barinas (P. Schwartz 1); Hato Flores Morades,

sex unknown). VENEZUELA: Esmeralda, Amazonas (AMNH, 2 males, 2 females).

Inezia s. subflava (17 males, 13 females, 1 sex unknown).—BOLIVIA: depto. Beni (AMNH, 1 female); Rio Paucerne, depto. Santa Cruz (LSUMZ, 1 sex unknown). BRAZIL: Borba, Amazonas (AMNH, 1 male, 1 female); Mirapinima, Amazonas (AMNH, 1 male, 2 females); Rio Tapajós, Pará (AMNH, 3 males, 3 fe-

males); Mirituba, Pará (YPM, 1 male; CM, 1 male); Rio Iriri, Pará (AMNH, 1 female); Vila Braga, Pará (CM, 1 female); Ilha das Poças, Pará (AMNH, 1 male); Bela Vista, Pará (CM, 1 male); São Raimundo, Pará (LACM, 1 male); Aveiro, Pará (CM, 1 male); Rio Xingu, Pará (AMNH, 1 male); Hupiranga, Pará (LSUMZ, 1 male); north bank Rio Amazon, site unknown (AMNH, 4 males, 4 females).