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A DISTINCTIVE NEW SPECIES OF TYRANT FLYCATCHER (PASSERIFORMES: TYRANNIDAE: *CNIPODECTES*) FROM SOUTHEASTERN PERU

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ABSTRACT.—We describe a distinctive new species of twistwing (Tyrannidae: *Cnipodectes*) from southeastern Peru. Despite extensive ornithological research in the region, this species has escaped notice, which suggests that it may be restricted to larger blocks of forest dominated by bamboo (*Guadua* spp.), a habitat poorly surveyed in Amazonia. Currently known from only a few sites in the departments of Madre de Dios and Cuzco, the species appears to be a *Guadua* specialist, though its life history is very poorly known. To date, the only other species of *Cnipodectes*, *C. subbrunneus* (Brownish Twistwing), is not known from most of southeastern Peru.

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Key words: Amazonia, *Cnipodectes superrufus*, *Guadua* bamboo specialization, new species, Peru, Rufous Twistwing, Tyrannidae.

Una Nueva Especie Distintiva del Género *Cnipodectes* (Passeriformes: Tyrannidae) del Sureste de Perú

RESUMEN.—Describimos una nueva especie del género *Cnipodectes* (Tyrannidae) de la región sureste de Perú. A pesar de las extensas investigaciones ornitológicas en la región, esta especie no ha sido reportada anteriormente, lo que sugiere que se encuentra restringida a grandes extensiones de bosque dominadas por bambú (*Guadua* spp.), un hábitat que ha sido escasamente muestreado en la Amazonía. Actualmente se le conoce solamente para pocos sitios en los departamentos de Madre de Dios y Cuzco. La nueva especie de *Cnipodectes* parecería ser una especie residente local y estar asociada a parches de bambú, aunque se conoce muy poco de su historia natural. Hasta la fecha, la única especie en el género era *C. subbrunneus*, la cual no ha sido reportada para el sureste de Perú.

ON 22 FEBRUARY 1990, G.P.S. netted a large rufous flycatcher in a patch of bamboo (*Guadua weberbaueri*) while making avifaunal surveys at Pakitza Vigilance Post within the Reserve

Zone of Parque Nacional Manu (hereafter "P. N. Manu"), department of Madre de Dios, Peru. At the time, without reference material available, the bird was photographed in hand, prepared as a dried skin, and left unidentified. The specimen was deposited at the Museo Nacional de Historia Natural de la Universidad San Marcos (hereafter "MUSM") under the name *Casiornis rufus* and published as such by G.P.S. (Servat 1996). The specimen remained

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unstudied until November 2002, when D.F.L. found it in the MUSM collection and realized that it was an undescribed species of tyrannid in the genus *Cnipodectes*. After reviewing the literature and making specimen comparisons, it is clear that this is the correct generic allocation (see below). The first natural-history information was obtained on 15 September 2003, when F.R.L. independently found and videotaped an individual in a stand of *Guadua* spp. near Cocha Cashu Biological Station in P. N. Manu. Amazingly, while we were writing the first draft of this paper in February 2004, T.V.H. reported the species from the lower Río Urubamba, department of Cuzco, while conducting survey work there with a team from Environmental Resource Management (ERM). There, he made the first tape recordings of the species' voice and made additional behavioral notes. The ERM team collected two additional specimens in February 2004 and another in June. Another specimen was collected by a team of biologists working the lower Río Urubamba in 1997 (Aucca 1998) and deposited in the collection of the Universidad San Antonio Abad in Cuzco (hereafter "MUSAAC"). That specimen was viewed and confirmed to be the same undescribed species of *Cnipodectes* by D.F.L. in June 2004. Finally, several observers armed with copies of T.V.H.'s recordings reported sightings at several sites in the department of Madre de Dios and even the department of Pando, Bolivia, between August and November 2004. At the time of this writing, these are the only confirmed records of this distinctive new species, which we describe here as

***Cnipodectes superrufus*, sp. nov.**
Rufous Twistwing
Alitorcido Rufo (Spanish)

Holotype.—MUSM 14023; adult male, netted at Puesta Vigilancia Pakitzá on the left (north) bank of Río Manu (approximately 11°56'S, 71°15'W) in the Zona Reservada del Parque Nacional Manu, elevation 350 m; 22 February 1990 by Grace P. Servat, field number 322.

Diagnosis.—A tyrannid assignable to genus *Cnipodectes* by a combination of relatively large size; broad, flat bill surrounded by well-developed rictal bristles; shaggy plumage texture overall; broad, squared tertials with pale inner and outer edges; and primaries twisted

in their orientation, with primaries 8–6 having a modified shaft structure on the underside and a raised ridge along the inner web (Zimmer 1939; Fig. 1). Further distinguished from all forms of *C. subbrunneus* by its richly saturated rufous plumage, larger size, and proportionately narrower bill.

Description of the holotype.—Feathering of crown and auricular areas are between Mahogany Red and Auburn (capitalized colors from Ridgway 1912) with the centers of the elongated "crest" feathers Raw Umber. Loral area with feather bases Ochraceous-Salmon, tips more rufescent; rictal bristles tipped blackish. Back feathers a rich Mahogany becoming

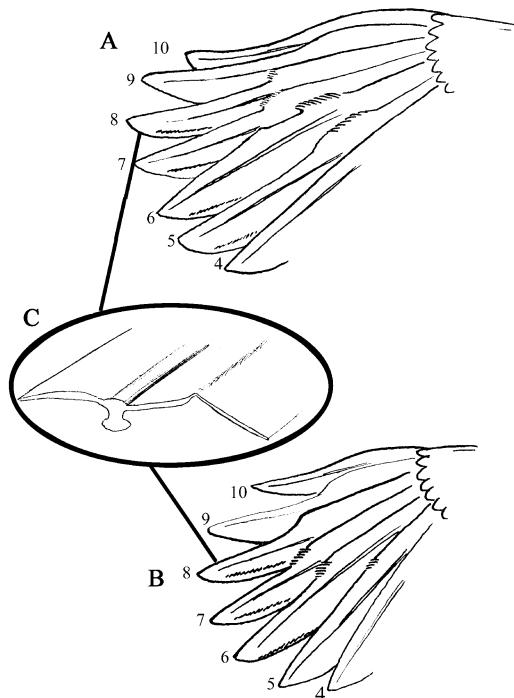


FIG. 1. Primary formulae of adult male (A) *Cnipodectes superrufus* and (B) *C. subbrunneus*. Numbers refer to primary number. Notice particularly the pattern of emargination of the leading edges of the outer primaries and the dark stripe near the trailing edges of primaries 8, 7, 6, and (in *C. superrufus* only) 5. (C) Cross-section of primary 8 of both species, showing the thickened, inverted T-shaped shaft and the raised portion on the trailing vane that corresponds to the dark stripe. Partly adapted from Zimmer (1939). Drawing by Daniel F. Lane.

intermediate between Mahogany and Burnt Sienna on the rump and uppertail coverts. The chin and upper throat have feather bases Zinc Orange with tips more like Sanford's Brown. There is a broad, ill-defined pectoral band that is between Burnt Sienna and Sanford's Brown. The belly and flanks are between Sanford's Brown and Xanthine Orange, with the vent and undertail coverts a richer color between Burnt Sienna and Sanford's Brown. The uppertail coloration is Chestnut Brown on the inner webs and basal outer web of each rectrix. The edge of the outer web, which has a decomposed texture, is a richer color between Mahogany Red and Burnt Sienna. The undertail is a drabber Prout's Brown, with the very inner edge of each rectrix Argus Brown. The secondary wing covert feathers (including greater, median, and lesser coverts) are Raw Umber with discrete edging of Mahogany Red. The leading edge of the primary coverts and underwing lining are Xanthine Orange. The primary coverts are Bone Brown. The primaries have the basal shaft area Bone Brown with the outer portions Olive Brown becoming very pale on the basal inner primary webs. The secondaries are Olive Brown, with the very outer edge Sudan Brown. The tertials have the interiors Prout's Brown with a broad inner edge Tawny and an outer edge between Brussels Brown and Auburn Brown. The undersides of the remiges fade to pale Vinaceous-Fawn by the basal inner edge. Soft part colors in life: irides bright red; maxilla brown with tomia appearing paler; mandible pink; tarsi and toes gray.

Wing feather modification.—Peculiar modifications of certain primary feathers are worthy of mention and are very reminiscent of those noted by Zimmer (1939) for *C. subbrunneus* (Fig. 1). The twisted orientation of the leading edge of the wing is immediately obvious and very like that noted for *C. subbrunneus* (Zimmer 1939). Primary 10 has a strongly curved leading edge. Primaries 9 through 5 have noticeable emarginations, least exaggerated on primary 9. There is a "bulge" of slightly decomposed barbs on primaries 8, 7, 6, and 5 more basal than the emarginations. These are similar to decomposed barbs on primaries 7, 6, and 5 of *C. subbrunneus*. In addition to the unique primary modifications, both species of *Cnipodectes* share a darkened, longitudinally raised "ridge" that is a narrowing of the vane of the inner webs of

primaries 8, 7, and 6 (and 5 in *C. superrufus*). The shaft structure of these primaries also has the same T-shaped cross-section noted by Zimmer (1939) for *C. subbrunneus*. Although the evidence is not conclusive, some or all of these feather modifications may be involved in the production of mechanical sound (see below).

Measurements of the holotype.—Wing chord, 111.9 mm; tail length, 99.6 mm; bill length (from posterior edge of nares to tip of maxilla), 11.1 mm; bill width (at nares), 6.5 mm; tarsus length (from tibiatarsus–tarsometatarsus joint to ventral base of halux), 20.9 mm; mass, 35 g; testis, 4 × 2.5 mm (Table 1). Additional label data: some fat present in the furcula, light molt on the breast, and 50% skull ossification.

Paratypes.—In addition to the holotype, there are four additional specimens of *C. superrufus*. Two were netted on the Río Pavoreni close to Kirigueti and prepared by T. Valqui H. A female (MUSM 26447), collected 23 February 2004: 26.3 g; no fat; molt on the two innermost primaries; ovary, 7 × 3 mm; ova minute; oviduct <1 mm wide, straight; no bursa; stomach contained insects (contents preserved); skull 50% ossified; iris red; legs pinkish-brown with gray wash; maxilla fleshy dark brown; mandible pink with dark venation. A male (MUSM 26448), collected 25 February 2004: 40.5 g; no molt; no fat; testes 10 × 5 mm; no bursa; stomach contained insects (contents preserved); skull 100% ossified; iris red; legs pinkish-brown washed with gray; maxilla blackish-brown; mandible pink with black veination. While being handled prior to collection, the male exhibited a raised crest, whereas the female did not, which suggests that this is a sexually dimorphic plumage character.

Members of the ERM team netted the fourth specimen in June 2004 at Nuevo Mundo, but we have no further information about this individual. Finally, a fifth specimen was netted at Las Malvinas, department of Cuzco, prepared by C. Auca C., and deposited at MUSAAC. This specimen is labeled on its tag as "*Attila boliviensis*." This record, we presume, was published by Auca (1998), identified therein as "*Attila boliviensis*" in table 1 and as "*Attila cinnamomeus*" in table 2. The specimen is a male (no institutional or personal catalogue numbers are available), collected 21 September 1997: 29.5 g; little fat; molt on body; left testis, 6.5 × 3.5 mm, right testis, 4 × 2.5 mm; skull 70% ossified; iris white or pale cream (it is not clear whether this was recorded

TABLE 1. Mean measurements (mm) of male (M) and female (F) twistwings^a.

Sex	Wing chord	Tail	Culmen length	Culmen width	Tarsus
M (2) ^b	111.9, 112.9 ^c	99.0, 99.6	<i>Cniodectes superrufus</i> 11.1, 11.5	6.5, 7.4	20.9, 21.9
F (1)	87.3	83.0	11.7	7.1	21.4
			<i>C. sub. subbrunneus</i>		
M (2)	93.5, 95.9	79.7, 83.6	10.7, 11.6	7.5, 7.7	19.4, 19.5
F (3)	64.3, 72.1, 79.5	55.2, 65.7, 72.0	9.8, 10.0, 10.7	7.0, 7.0, 7.6	16.8, 17.0, 17.6
			<i>C. sub. panamensis</i>		
M (3)	90.9, 92.3 ^d	79.3, 86.0, 88.9	11.0, 11.6, 12.0	7.3, 7.7, 7.8	19.2, 20.3, 21.6
F (4)	71.2, 71.7, 73.1, 74.0	61.5, 64.0, 66.3, 66.3	10.9, 11.1, 11.4, 11.9	7.0, 7.8, 7.9, 8.2	15.1, 16.3, 17.3, 17.9
			<i>C. sub. minor</i>		
M (12)	88.4 ± 3.8 (83.5–93.9) ^e	77.1 ± 3.3 (73.2–82.2)	10.3 ± 0.7 (9.3–11.4)	7.2 ± 0.3 (6.9–8.0)	17.7 ± 1.6 (15.5–21.8)
F (12)	72.0 ± 1.5 (69.1–75.7)	63.0 ± 1.9 (60.6–67.5)	9.9 ± 0.4 (9.2–10.5)	7.0 ± 0.4 (6.4–7.6)	16.3 ± 0.8 (14.7–17.7)

^aSee text for localities and specimen numbers.^bSample size in parentheses.^cFor samples where $n < 5$, raw measurements are provided.^dWing chord measurement of one individual was excluded because of primary molt.^eMean ± SD; range in parentheses.

in life or after death, when the color may have faded); maxilla gray with yellow base; mandible yellowish-pink; legs pale bluish-gray. Inspection of the specimen showed that it did not have the modified primaries we noted on the other two male specimens. Thus, we suspect that it represents a first basic male plumage.

Distribution.—In addition to the type locality, *C. superrufus* has been encountered at six other

sites, two of which will be published elsewhere (see below). In Figure 2, the following localities are plotted, all from Peru: department of Madre de Dios: Playa Bonita, ~7 km north of Cocha Cashu Biological Station, ~370 m elevation, 11°54'S, 71°18'W; department of Cuzco: Nuevo Mundo on the lower Río Urubamba (elevation unknown) 11°32'S, 73°08'W; close to the community of Kirigueti on the Río

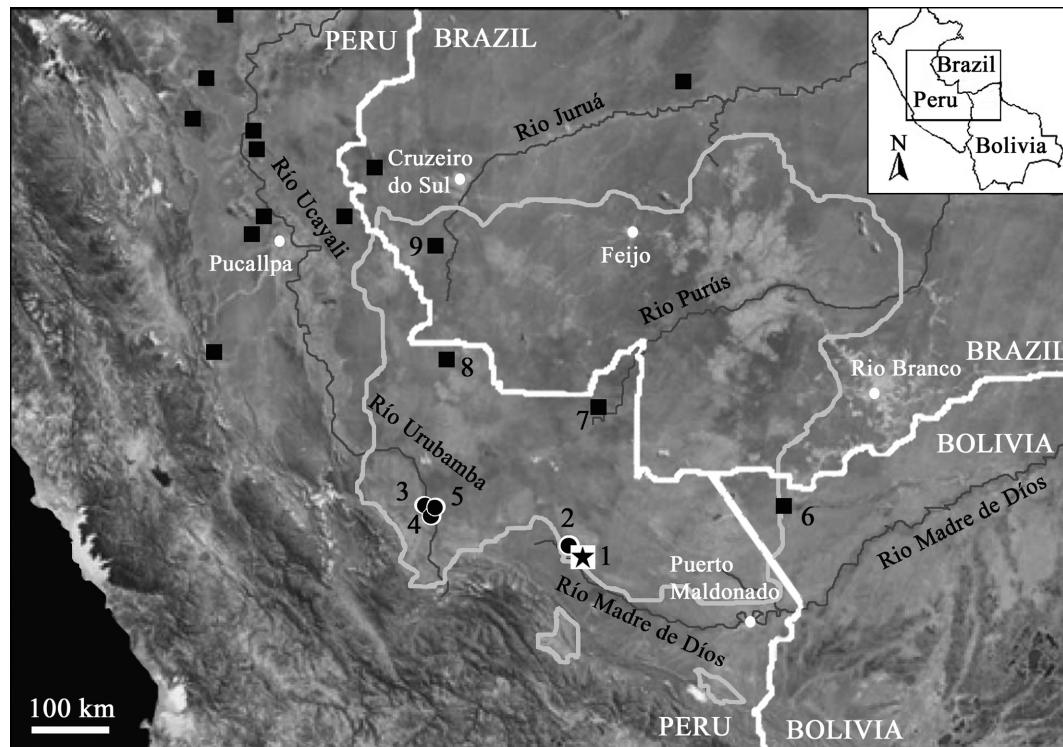


FIG. 2. A satellite image showing distribution of *Cnipedectes* twistwings and approximate extent of bamboo-dominated (*Guadua* spp.) forests in southwestern Amazonia. The star indicates the type locality of *C. superrufus*, circles indicate other sites from which we report the species, and solid squares indicate sites from which *C. subbrunneus* is known (Gyldenstolpe 1945, Traylor 1979; LSUMZ and MUSM specimens; K. Balta A. and B. M. Whitney pers. comm.). Bamboo-dominated forest is outlined by a gray border. Dense patches of *Guadua*, apparently “groundtruthed” as blooming patches, show up as paler regions, particularly noticeable northwest of the Brazilian city of Rio Branco and also near the Río Urubamba in southern Peru. *Cnipedectes* localities within the bamboo-dominated forest: (1) PERU: department of Madre de Dios; Pakitza (type locality of *C. superrufus*). (2) PERU: department of Madre de Dios; Playa Bonita. (3) PERU: department of Cuzco; Nuevo Mundo. (4) PERU: department of Cuzco; Kirigueti. (5) PERU: department of Cuzco; Las Malvinas. (6) BOLIVIA: department of Pando; Mucden (Parker and Remsen 1987). (7) PERU: department of Ucayali; Balta (O'Neill 1974, 2003). (8) PERU: dept. Ucayali; Río Beu (K. Balta A. pers. comm.). (9) BRAZIL: Acre; Riozinho das Minas (B. M. Whitney pers. comm.). Map adapted from Leite Pitman et al. (2003); vegetation interpretation based on Silman et al. (2003) and additional information from B. Nelson and M. Silman (pers. comm.).

Pavoreni, a tributary of the Río Urubamba, ~380 m elevation, 11°38'S, 73°07'W; and Las Malvinas, ~360 m elevation, 11°54'S, 72°57'W (Aucca 1998). We expect that the species will be encountered elsewhere in stands of *Guadua* in southeastern Peru and northwestern Bolivia, and perhaps into southwestern Amazonian Brazil (see below).

M. Anderson, P. Hosner, and D. Lebbin (pers. comm.) encountered *C. superrufus* in northeastern department of Madre de Dios, and J. Tobias (pers. comm.) has reported the species just within the border of department of Pando, Bolivia. These records of *C. superrufus* will be published with details elsewhere by Tobias et al. Finally, B. M. Whitney and J. Rowlett recorded vocalizations that probably belong to the species but were not confirmed visually, near Manu Lodge (12°06'S, 71°06'W, 340 m) also in P. N. Manu, department of Madre de Dios, a site on the Río Manu upstream from the type locality. *Cnipodectes subbrunneus* is known from as close as Balta on the Río Curanja, department of Ucayali (O'Neill 1974, 2003), and Mucden, near Cobija, department of Pando, Bolivia (Parker and Remsen 1987; Fig. 2). Two other sites for *C. subbrunneus* within the area of bamboo-dominated forest include a locality near the ríos Beu and Juruá, department of Ucayali (09°30'S, 072°43'W; K. Balta A. pers. comm.) and Riozinho das Minas in western Acre state, Brazil (08°34'S, 72°53'W; B. M. Whitney pers. comm.; Fig. 2).

Etymology.—The specific epithet *superrufus* refers to the most striking feature of this new species, its rich rufous coloration—a color that, though commonly exhibited by other members of the Tyrannidae, is rarely so uniform or so deeply saturated. The prefix *super* underscores the degree of saturation, but alternatively can be interpreted as drawing attention to the large size of the species as compared with *Cnipodectes subbrunneus*, the only other species of this genus. We also refer to the rufous color in the English and Spanish common names for the bird.

Specimens examined.—Specimens in the collections of Louisiana State University Museum of Natural Science (LSUMZ), the American Museum of Natural History (AMNH), and MUSM were inspected and measured (unless otherwise noted) for this study. Whereas D.F.L. was able to view and confirm the identity of the MUSAAC *C. superrufus* specimen, it was not available for measurements, nor was the specimen collected

by the ERM group in June 2004. Furthermore, the specimen of *C. subbrunneus minor* from Balta, department of Ucayali, Peru (LSUMZ 52269), is a first basic male, and therefore not comparable to adult male specimens in wing or tail length. Unpublished distribution records for *C. subbrunneus* shown in Figure 2 are documented by specimens from Campamento El Fuerte Cerros de Orellana, department of Loreto, Peru (MUSM 12115); Calientillo (Contamana), department of Loreto, Peru (MUSM 7557); and Hacienda Flor, Río Pachitea, near Pte Victoria, department of Pasco, Peru (MUSM 3356), though these specimens were not measured. The specimens mentioned in this paragraph are not among those presented in Table 1.

C. superrufus: Peru: department of Madre de Dios; Pakitza (MUSM 14023; holotype). Department of Cuzco; Kirigueti (MUSM 26447, MUSM 26448).

C. subbrunneus subbrunneus: Ecuador: province of Manabí; Río de Oro (AMNH 120020). Province of Esmeraldas; Esmeraldas City (AMNH 118759, 118761). Province of Chimborazo; Chimbo (AMNH 173426). Province of El Oro; La Chonta (AMNH 171780).

C. subbrunneus panamensis: Panama: province of Colón; 17 km by road northwest of Gamboa, Río Agua Salud (LSUMZ 163630, 163631), Achiote Road at Quebrada Trenticinco, ~2 km west of Gatún-Escobal road (LSUMZ 164195). Province of Darién; Caná, eastern slope of Cerro Pirre (LSUMZ 108464, 108465, 108466, 108467).

C. subbrunneus minor: Ecuador: province of Napo; Limoncocha (LSUMZ 83466). Peru: department of Loreto; 1 km north of Río Napo, 157 km by river north-northeast of Iquitos (LSUMZ 110702, 110705, 110706, 110707, 110709), 1.5 km south of Libertad, south bank of Río Napo, 80 km north of Iquitos (LSUMZ 110699, 110700), lower Río Napo region, east bank of Río Yanayacu, ~90 km north of Iquitos (LSUMZ 115936, 115938, 115939, 115940), Quebrada Orán, ~5 km north of Río Amazonas, 85 km northeast of Iquitos (LSUMZ 120171), southern Río Amazonas, 85 km northeast of Iquitos (LSUMZ 115941, 115942, 115944, 115945), northeast bank of upper Río Cushabatay, 84 km west-northwest of Contamana (LSUMZ 161862), 86 km southeast of Juanjui on eastern bank of upper Río Puya (LSUMZ 170968). Department of Ucayali; Yarinacocha (LSUMZ 42802), western bank of Río Shesha, ~65 km east-northeast of Pucallpa

(LSUMZ 156658). Bolivia: department of Pando; province of Nicolás Suarez, 12 km by road south of Cobija, 8 km west on road to Mucden (LSUMZ 133495, 133497, 133500).

REMARKS

Ecology and behavior.—In all the authors' encounters with *C. superrufus*, the individuals perched 1–3 m off the ground and sallied for arthropods, changing perches with each foraging maneuver. T.V.H. estimated a foraging maneuver about every 30 s as the bird progressed along a 30-m-wide bamboo corridor between two pastures. F.R.L. noticed that the species performs a lethargic wing-raising behavior, similar to that reported for *C. subbrunneus* (Hilty and Brown 1986, Ridgely and Tudor 1994, Ridgely and Greenfield 2001b, Fitzpatrick et al. 2004). This wing movement was repeated frequently with at least eight wing-raising motions in <10 min. Other tyrannids are known to perform wing-raising motions, including members of *Leptopogon*, *Phylloscartes*, *Phyllomyias*, *Mionectes*, and *Myiopagis*, but these species tend to do so more rapidly than either species of *Cnemidocetes* (Hilty and Brown 1986, Ridgely and Tudor 1994, Ridgely and Greenfield 2001b, Fitzpatrick et al. 2004; D. F. Lane pers. obs.). The purpose of this behavior is not clear. Both F.R.L. and T.V.H. observed *C. superrufus* in the vicinity of under-story mixed-species foraging flocks, but in neither case did the species appear to join the flock and move with it actively. The species also seems difficult to locate; after first encountering individuals, both Lambert and Valqui were unable to relocate individuals on subsequent visits to the same site, even with the use of playback.

In all our encounters, *C. superrufus* was found in conjunction with *Guadua* bamboo. The type locality features extensive patches of *G. weberbaueri*; the type specimen was netted in a sparse thicket near the edge of the Río Manu. At Playa Bonita, F.R.L. encountered the bird in the understory of dense, mature (actively flowering) bamboo on the floodplain between a small (10-m-wide) river and a terrace of *terra firme* forest. At Nuevo Mundo, T.V.H. found *C. superrufus* in the open understory of tall, mature (not flowering) stands of bamboo. At Kirigueti, T.V.H. and ERM captured the male paratype in similar habitat to that at Nuevo Mundo. The female paratype was captured in a more

mixed patch of about 50% bamboo and 50% non-bamboo vegetation with a denser structure. The MUSAAC specimen was netted at the border (?) of "bamboo forest and secondary forest." The only reports not pertaining to birds in bamboo-dominated habitat are the two voice encounters at Manu Lodge in the years 1991 and 2000, neither of which could be verified by sight (B. M. Whitney and J. L. Rowlett pers. comm.). Here, the habitat was reported to be in river-edge thicket vegetation with no bamboo growth visible. The individual(s) involved in the Manu Lodge reports was present at the same site nine years apart, which suggests that the site may offer acceptable habitat for the species, but it may be noteworthy that the locality is on the north bank of the Río Manu near large patches of *Guadua*.

Bamboo specialization.—On the basis of the habitat present at all sites where the species has been confirmed by sight or specimen, we believe that *C. superrufus* can be labeled a *Guadua* specialist (*sensu* Kratter 1997). If the Manu Lodge records were also of *C. superrufus*, this hypothesis is not necessarily refuted, because other "bamboo specialists" also occur marginally in other habitats (Kratter 1997, Aleixo et al. 2000). The patches of *Guadua* at the Pakitza and Playa Bonita sites have bloomed and died, or are dying at the time of this writing (G. P. Servat pers. obs.). Whether *C. superrufus* will remain at these sites for the long term in the absence of bamboo is a topic to study; other bamboo-specialist bird species are known to abandon dying patches (Kratter 1997). However, H. Lloyd (pers. comm.) found the species in a remnant patch of bamboo amid floodplain forest at Pakitza in August 2004, which suggests that the species can persist even in dying bamboo patches. It may be that the Manu Lodge records were of a bird maintaining its territory at a site where the bamboo had died and not yet regenerated.

Voice and other sounds.—On 20 February 2004 at Nuevo Mundo, T.V.H. recorded vocalizations of a presumed male *C. superrufus*, including both unsolicited and after playback. The unsolicited voice was a series of squeaky, rising *quec* or *cueet* notes evenly spaced at a rate of 5 notes s⁻¹. Both in unsolicited vocalizing bouts and after playback, the number of notes and the fundamental frequency of the vocalization varied (Fig. 3A). The overall effect of the voice is similar to a common vocalization of Sulfur-bellied Tyrant-

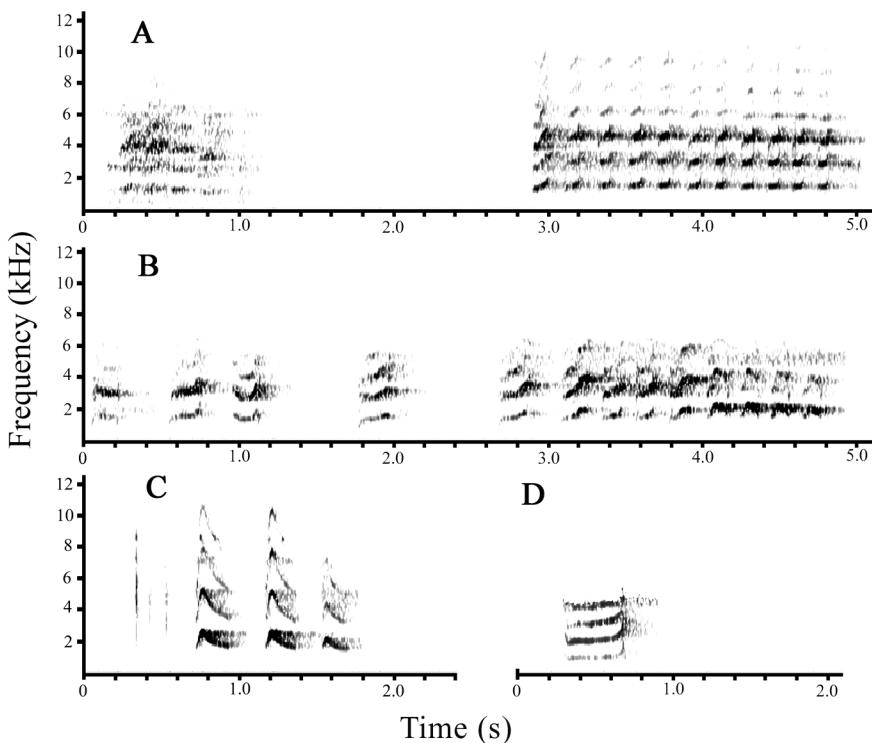


FIG. 3. Spectrograms of vocalizations of *Cnipodectes superrufus* and *C. subbrunneus*. (A) *C. superrufus*: presumed agitated calls; response to playback. 23 February 2004, Peru: department of Cuzco; Kirigueti (T. Valqui H.). (B) *C. subbrunneus*: agitated calls; response to playback. 11 April 1994, Ecuador; province of Napo; Maxus Road (N. Krabbe from Krabbe and Nilsson 2003). (C) *C. subbrunneus*: song; response to playback. 1 April 2003, Peru: department of Loreto; Río Yavarí (D. F. Lane). (D) *C. subbrunneus*: call; unsolicited. 1 April 2003, Peru: department of Loreto; Río Yavarí (D. F. Lane).

Manakin (*Neopelma sulphureiventer*). Shortly after playback, the same individual gave a series of notes at a rate of ~ 8 notes s^{-1} . This vocalization closely resembles one of *C. subbrunneus* recorded, in agitated response to playback, by N. Krabbe while the bird performed aggressive approaches toward the recordist (Krabbe and Nilsson 2003; N. Krabbe pers. comm.; Fig. 3B). The vocalization recorded by T.V.H. after playback was also given in conjunction with aggressive approaches. These vocalizations are not stereotyped as is typical of most tyrannid songs, but rather seem to vary in pace and intensity in relation to the emotional state of the bird. Thus, we conclude that the *C. superrufus* vocalization recorded by T.V.H. is not a song but rather a call given when agitated. The vocalizations recorded near Manu Lodge by Whitney and Rowlett sound very like those on T.V.H.'s recording. However, in response to playback,

the Manu Lodge bird(s) quickened the pace of its vocalizations even more than the bird at Kirigueti.

The song of *C. subbrunneus* (Fig. 3C) is a stereotyped series of loud, descending whistled notes, sometimes preceded by sharp ticking sounds (Fig. 3C). These ticking sounds appear to be made either by bill snaps or vocally, or by a combination of both, but do not involve the wings (D. F. Lane pers. obs.). Another call of *C. subbrunneus*, commonly given in an unsolicited manner, is a long, mewing 'cueet' (Fig. 3D) given singly or in a very loose series. We expect that, with more field experience, *C. superrufus* will be found producing vocalizations similar to the song and "unsolicited" call of *C. subbrunneus*.

Mechanical noises have been noted in both species of *Cnipodectes*. Hilty and Brown (1986: 483) note that *C. subbrunneus* "can produce a very audible *pr'r'r'r'r'r'* in flight with wings."

This description is similar to mechanical sounds T.V.H. witnessed, performed by *C. superrufus* at Kirigueti. In response to playback, Valqui observed the bird approaching aggressively, making an accelerating and decelerating buzzing noise, while flying ~4 m off the ground. Although it was not clear what the source of the sound was (and it was not tape recorded), it seems likely that it was mechanical and produced by the wings (see above).

Systematics and biogeography.—The relationships of the genus *Cnipodectes* within the Tyrannidae need clarification. On the basis of morphological characters, Traylor (1979) and Traylor and Fitzpatrick (1980) placed the genus in the “flatbill assemblage” along with genera such as *Tolmomyias*, *Rhynchocyclus*, *Platyrinchus*, and *Ramphotrigon*. Subsequently, Lanyon (1985) removed *Ramphotrigon* from this group, a decision followed by most recent authors (e.g., Ridgely and Tudor 1994, Fitzpatrick et al. 2004). Parker and Remsen (1987:103) noted that *Cnipodectes* shares several behavioral characters with the *Neopelma* and *Tyranneutes* “tyrant-manakins” and labeled it a “very atypical tyrannid.” Judging from the distinctiveness of the morphology and vocalizations of the members of the genus, we are inclined to agree. Future research using molecular techniques to evaluate the hypothesized relationships of the genus should help answer this vexing question.

Given that *Cnipodectes superrufus* shares many morphological characters with *C. subbrunneus*, including the “shaggy” plumage texture and unique modifications of the primaries diagnostic of the genus (Zimmer 1939), we have no doubt that the new species is correctly assigned to *Cnipodectes*. This relationship is further reinforced by the shared sexual size-dimorphism (see Table 1), a trait that appears to be restricted to this genus within the Tyrannidae, as well as the sluggish wing-lifting behavior.

The distinctive coloration and morphometrics are our basis for treating *C. superrufus* as a species-level taxon with respect to *C. subbrunneus*. We believe that these characters uphold species status under any species concept. In addition, with so little known about the status and distribution of *C. superrufus*, we are reluctant to suggest that it and *C. subbrunneus* even be treated as a superspecies. Compared to *C. superrufus*, *C. subbrunneus* is a relatively widespread species, with two trans-Andean and one

cis-Andean subspecies. The two forms west of the Andes include *panamensis*, which occurs from central Panama (Ridgely and Gwynne 1989) to the Chocó forests of the northern Pacific slope of Colombia, and the nominate *subbrunneus* on the Pacific slope of Ecuador (Ridgely and Greenfield 2001a). Subspecies *minor* occurs east of the Andes from central Colombia and the west bank of the Rio Negro in Brazil south to Ucayali department in Peru, Pando department in Bolivia, and the lower Rio Madeira in Brazil (Hilty and Brown 1986, Parker and Remsen 1987, Ridgely and Tudor 1994, Borges et al. 2001, Ridgely and Greenfield 2001a, B. M. Whitney pers. comm.). These three subspecies differ primarily in measurements and minor differences in plumage color (Zimmer 1939), and there seems to be little, if any, geographical variation in song (Krabbe and Nilsson 2003, B. M. Whitney pers. comm., D. F. Lane pers. obs.). No taxon within *C. subbrunneus* exhibits overall plumage coloration of such saturated rufous as *C. superrufus*. *Cnipodectes subbrunneus* is found in relatively low densities in transitional and *terra firme* forest with dense patches of understory and is best detected by voice or netting (D. F. Lane pers. obs.). In Pando, Bolivia, it is known to occur in *Guadua* bamboo stands (Parker and Remsen 1987). J. Tobias’s record (pers. comm.) of *C. superrufus* from bamboo stands nearby suggests that the two species may occur syntopically in the region. Interestingly, the thamnophilid genus *Cymbilaimus* parallels *Cnipodectes* in having a widespread, “generalist” species (Fasciated Antshrike [*Cymbilaimus lineatus*]) and a sister species restricted to southwestern Amazonia (Bamboo Antshrike [*C. sanctaemariae*]), the latter a *Guadua* specialist. These antshrikes occur sympatrically, but they partition habitats where they co-occur (Pierpont and Fitzpatrick 1983). Other genera (e.g., *Celeus*, *Monasa*, *Synallaxis*, *Cercomacra*, *Lophotriccus*, *Hemitriccus*, and *Ramphotrigon*) also exhibit this pattern, but it is less clear that sister taxa are involved.

Potential distribution and conservation status.—Satellite imagery suggests that there are immense blocks of *Guadua*-dominated *terra firme* forest in southwestern Amazonian Brazil, southeastern Peru, and northwesternmost Bolivia (Del Bon Espírito-Santo et al. 2003, Silman et al. 2003; Fig. 2). Remarkably, exceptionally little ornithological work has been conducted in these areas, probably because of

their distance from large, navigable rivers. We predict that future ornithological field work in these *Guadua*-dominated upland forests will result in more records of *C. superrufus*, and may even find it to be a common species.

The presence of *C. superrufus* at Pakitza and Playa Bonita, in river-edge *Guadua* thickets that appear to be peripheral to the larger blocks of *terra firme* bamboo, may be the result of source-sink population dynamics, with these two sites acting as sinks. Perhaps, unlike most other *Guadua* specialists, *C. superrufus* may be more restricted to larger blocks of bamboo habitat. If this is true, it explains the species' apparent absence from the better-known *Guadua* sites: small, outlying patches along the ríos Madre de Díos and Tambopata. A similar Peruvian distribution pattern is known for Long-crested Pygmy-Tyrant (*Lophotriccus euphantes*), and it too may be affected by such a source-sink phenomenon (B. Walker pers. comm.). Until more field work is conducted to test our hypotheses about the habitat requirements of *C. superrufus* and its potential distribution, we are hesitant to make any suggestions regarding its conservation status. However, we will point out that Pakitza and Playa Bonita are within the Manu Biosphere Zone and, therefore, receive protection. Presumably, there is a healthy population within this protected zone.

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