

A NEW SPECIES OF TODY-TYRANT (TYRANNIDAE: *POECILOTRICCUS*) FROM NORTHERN PERU

NED K. JOHNSON^{1,2,3} AND ROBERT E. JONES²

¹Department of Integrative Biology, University of California, Berkeley, California 94720, USA; and

²Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, USA

ABSTRACT.—We describe a new species of tody-tyrant of the genus *Poecilotriccus*, isolated in midelevation forests of the Cordillera de Colán and nearby mountains to the east in the northeastern Andes of Peru. The new species is allopatric from, and forms a probable superspecies with, the Rufous-crowned Tody-Tyrant (*P. ruficeps*), the nearest known populations of which inhabit the Cerro Chinguela of northern Peru. The geographic ranges of those sister taxa are divided by the North Peruvian Low, occupied by the Río Marañón, the major break in east-slope Andean forest between Venezuela and Bolivia. The new species and its allospecies, *P. ruficeps* are identical in color of the back and in lightness and hue of the crown, but are 100% separable in lightness, chroma, and hue of the belly; in color and pattern of the face; and in song. We infer that differences in vocalizations and facial markings would serve as premating reproductive isolating mechanisms should the two forms become sympatric. Received 5 January 2000, accepted 12 September 2000.

ON 15 AUGUST 1970, Johnson collected an apparently mated pair of a suspected undescribed species of *Poecilotriccus* in the northeastern Andes of Peru. Subsequent comparison of the pair of specimens with series representing all taxa of *P. ruficeps*, the obvious closest relative, in the American Museum of Natural History, New York City, confirmed their uniqueness.

In the 1970s, reluctance to name the new species on the basis of only two specimens led N. Johnson to shelve the description and to plan field work to seek additional material. Further collecting on our part proved unnecessary, however, because in 1974, 1976, 1978, and 1983, field parties from the Museum of Natural Sciences, Louisiana State University (LSUMZ) collected 18 additional specimens of the new taxon, bringing the total to 20. Aware of our two specimens, and with uncommon generosity and patience, LSUMZ authorities allowed our full access to their new material and deferred to us the authorship of the new species. The accumulation of additional specimens and gathering of tape recordings during the long delay has allowed a level of analysis in this description that otherwise would have been impossible. We propose to name this new flycatcher:

Poecilotriccus luluae sp. nov. Lulu's Tody-Tyrant

Holotype.—Museum of Vertebrate Zoology (MVZ), No. 161008, adult (but with cranium 50% pneumatized) male (testis 2 × 1 mm), Peru, Departamento Amazonas, 3.5 road mi (=5.63 km) SE Corosha, 6,900 ft (=2,104 m), 15 August 1970; collected by Ned K. Johnson.

Description of holotype and diagnosis.—Plumage color names and numbers are based on visual matching with the most similar swatches in Smithe (1975) and are therefore approximations.

Dorsally, *P. luluae* is identical to all subspecies of *P. ruficeps*: crown near Mahogany Red (132B), hind neck band Jet Black (89) anteriorly and Medium Neutral Gray (84) posteriorly; back and rump near Yellowish Olive-green (50); greater and middle secondary coverts narrowly tipped with Buff (24) or Buff Yellow (53); three inner secondaries (tertials) with Fuscous (21) inner webs and Straw Yellow (56) outer webs; and the remaining secondaries, primaries, and rectrices Fuscous with narrow edging of Yellowish Olive-green on outer webs.

P. luluae and *P. ruficeps* differ in (a) color and pattern of the breastband, which is Yellowish Olive-green faintly streaked with Yellow Ocher (123C) in *P. luluae* and pencilled black or Yellowish Olive-green on a Sulphur Yellow (157) background in all forms of *P. ruficeps*; (b) color of the

³ E-mail: neddo@socrates.berkeley.edu

lower breast and belly, which ranges from near Orange Yellow (18) to near Yellow Ocher in *P. luluae* and is Sulfur Yellow in all subspecies of *P. ruficeps*; and (c) color and pattern of the throat and sides of the head. In *P. luluae* the entire superciliary, supraloral region, lores, auriculars, suborbital region, and mid-throat are Mahogany Red (132B); the mid-forehead at the base of the bill is also Mahogany Red, sometimes with a trace of Jet Black and a white band crosses the lower throat. *P. ruficeps* is highly variable in the aforementioned features, depending upon the subspecies (N. Johnson unpubl. data): the posterior superciliary ranges from Cinnamon Rufous (40) with a trace of Jet Black to a wide Jet Black mark; the anterior superciliary and supraloral region vary from Cinnamon Rufous with or without a trace of Jet Black to Cream Color (54) with a trace of Jet Black; the lores range from Cinnamon Rufous with or without a trace of Jet Black to Jet Black with a trace of Buff Yellow; the mid-forehead at the base of the bill varies from Cinnamon Rufous with or without a trace of Jet Black to entirely Jet Black; the auriculars and suborbital region range from Cinnamon Rufous through Buff Yellow to Cream Color; the malar region varies from Cinnamon Rufous through mixtures of Cinnamon Rufous or Cream Color with speckles or blotches of Jet Black to a large, continuous Jet Black mark; the mid-throat ranges from Cinnamon Rufous through Buff Yellow or Cream Color to white; and the pale band across the lower throat varies from a modest white band through a broad white band with a tinge of Cream Color to a broad white band. Maxilla and mandible black (16 specimens). Tarsi and feet gray-flesh (two specimens), light gray (two), gray (six), pinkish gray (three), or blue-gray (one). Irides brown (one), dark brown (one), red-brown (one), purple-brown (one), café (three), or maroon (five). See cover for a portrait of the holotype. Hornbuckle (1999) published, without description, a color photo of a live hand-held bird.

Distribution.—Known from four localities between 6,000–7,216 ft (= 1,829–2,200 m) elevation in the Cordillera de Colán and areas to the east in the Eastern Andes, Department Amazonas, Peru (Fig. 1). For precise localities see list of specimens examined, below.

Measurements of holotype.—Chord of unflattened wing 48.2 mm, tail length 32.5 mm (in

molt), bill length from nostril 7.9 mm, bill width 3.8 mm, bill depth 2.9 mm, length of tarsus plus length of middle toe 26.2 mm, body mass 7.6 g. Colorimetric readings in L*C*h° color space: crown lightness 32.88%, chroma 28.63%, hue 53.9°; back lightness 28.49%, chroma 14.9%, hue 95.7°, belly lightness 63.84%, chroma 51.88%, hue 87.3°.

Etymology.—The new species is named in honor of the late Lulu May Von Hagen in recognition of her generous and dedicated support of research in avian genetics.

Specimens examined.—Peru: Amazonas: 3.5 road mi (= 5.63 km) southeast Corosha, 6,900 ft (= 2,104 m), one male (MVZ 161008 [holotype]), one female (MVZ 161009 [paratype]); ~33 km by road northeast Ingenio, 6,000 ft (= 1,829 m), on road to Laguna Pomacoches, two males (LSUMZ 78779, 82081), one male? (LSUMZ 78781), 1 female (LSUMZ 78780); ~20 trail km east of La Peca (=La Peca Nueva), 6,500 ft (= 1,982 m), Cordillera de Colán, two males (LSUMZ 88425, 88426), five females (LSUMZ 88422, 88423, 88424, 88428, 88429) one sex? (LSUMZ 88427); ~30 km by road E of Florida, 2,200 m, on road to Rioja, five males (LSUMZ 117242, 117244, 117245, 117246, 117247), one female (LSUMZ 117243). Davis (1986) describes habitats and species composition of the avifauna found at the latter locality by a field party from the Louisiana State University Museum of Zoology from 26 November to 9 December 1983.

QUANTITATIVE COMPARISONS OF *P. LULUAE* AND *P. RUFICEPS PERUVIANUS*

We assessed seven characters of size and nine of color in *P. luluae* and *P. r. peruvianus*, the geographically closest representative of *P. ruficeps*. A thorough comparison of size, color and facial pattern of *P. luluae* with all populations of *P. ruficeps* will be presented in a companion paper (Johnson 2001) that focusses on geographic variation and a systematic revision of the latter species.

Methods.—The following size measurements were taken: wing length, as the chord of the unflattened wing from the bend of the wing to the tip of the longest primary; tail length, the distance from the basal point between the insertions of the central pair of rectrices (1–1) to the tip of the longest rectrix; bill length, the dis-

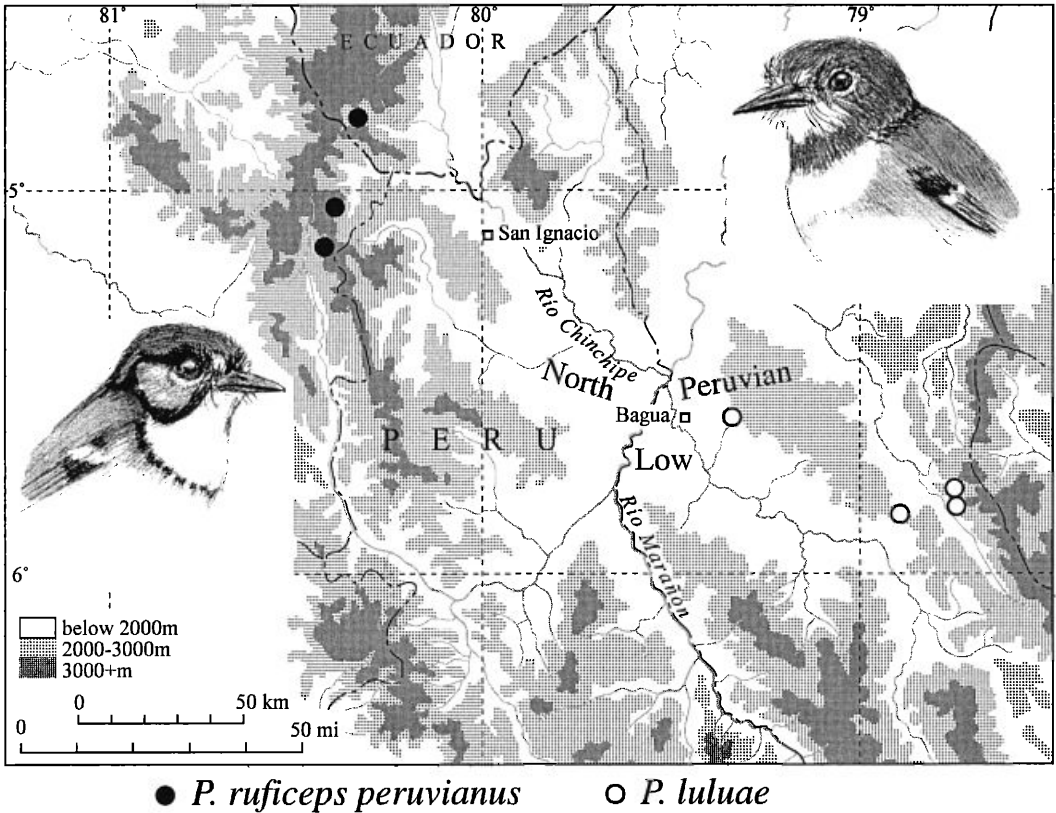


FIG. 1. Map of extreme southern Ecuador and adjacent northwestern Peru showing known specimen localities of *Poecilatriccus ruficeps peruvianus* (dots) and *Poecilatriccus luluae* (circles). The distribution of three additional subspecies of *P. ruficeps* continues northward along the Andes through Ecuador, Colombia, and western Venezuela. Sketches show *P. ruficeps peruvianus* at left and *P. luluae* at right.

tance from the anterior edge of the nostril to the tip of the upper mandible; bill width, the distance from one tomium to the other where a plane drawn at right angles to the bill passes through the anterior margin of the nostril; bill depth, the distance from the ridge of the culmen to the lower edges of the rami taken on the same plane as bill width; length of tarsus, distance from the midpoint of the posterior surface juncture of the tibia and the metatarsus to the anterior lower edge of the scute opposite the insertion of the proximal part of the base of the hind toe; length of middle toe without claw, distance taken as the diagonal of the middle toe from the anterior edge of the undivided scute opposite the insertion of the proximal part of the base of the hind toe to the tip of the toe pad on the ventral surface of the toe.

Coloration of specimens was assessed with a Minolta CR-300 Colorimeter using the $L^*C^*h^*$

color space (Minolta Company 1994), where "L" (value [=brightness]) is percentage lightness on a scale of 0 for black to 100 for white, "C" (chroma [= "purity"]) is percentage saturation on a scale of 0 for white to 100 for pure color; and "h" (=hue) is expressed in degrees of a circle, starting with red (0°), continuing through yellow (90°), green (180°), blue (270°), and completing the circle at red (360°). Measurements were taken from the center of the crown, dorsum, and belly. To reduce measurement error, this instrument takes three readings and computes an average.

Size.—Male *P. luluae* have significantly (t -test, $P < 0.05$) longer wings and deeper bills than those of *P. ruficeps peruvianus*. In contrast, in length of tail and bill, width of bill, length of tarsus plus length of middle toe, and in body mass, the two species are similar if not identical ($P > 0.05$) (Table 1). Sexes of *P. luluae* are slightly

TABLE 1. Summary statistics for seven size characters of two taxa of *Poecilatriccus*.

Character	Taxon	Males			Females		
		<i>n</i>	X	SD	<i>n</i>	X	SD
Wing length (mm)	<i>P. luluae</i>	10	48.4	1.36	8	47.2	0.81
	<i>P. r. peruvianus</i>	3	47.2	0.51	1	44.8	
Tail length (mm)	<i>P. luluae</i>	9	38.8	1.12	7	36.7	1.89
	<i>P. r. peruvianus</i>	3	37.4	0.86	1	37.4	
Bill length (mm)	<i>P. luluae</i>	10	7.06	0.46	8	6.9	0.35
	<i>P. r. peruvianus</i>	3	7.0	0.0	1	6.9	
Bill width (mm)	<i>P. luluae</i>	9	3.77	0.16	7	3.91	0.13
	<i>P. r. peruvianus</i>	3	3.80	0.10	1	3.5	
Bill depth (mm)	<i>P. luluae</i>	9	2.99	0.14	4	2.75	
	<i>P. r. peruvianus</i>	3	2.70	0.10	1	2.60	
Tarsus + middle toe (mm)	<i>P. luluae</i>	8	26.4	1.02	8	25.6	1.06
	<i>P. r. peruvianus</i>	3	25.6	0.74	1	26.0	
Body mass (g)	<i>P. luluae</i>	10	7.27	0.49	7	7.21	0.61
	<i>P. r. peruvianus</i>	3	7.0	0.50	1	7.0	

TABLE 2. Summary statistics (mean plus standard deviation) for nine color characters^a of two taxa of *Poecilatriccus*.

Character	<i>P. r.</i>	
	<i>P. luluae</i> (<i>n</i> = 20)	<i>peruvianus</i> (<i>n</i> = 4)
Lightness of crown (%) ^b	31.1 (2.20)	29.1 (1.79)* _c
Chroma of crown (%)	26.9 (2.32)	24.5 (0.92)**
Hue of crown (°)	51.4 (2.04)	51.1 (1.30)*
Lightness of back (%)	32.4 (2.02)	32.4 (0.68)*
Chroma of back (%)	23.9 (2.85)	24.8 (1.17)*
Hue of back (°)	96.2 (1.09)	96.7 (0.72)*
Lightness of belly (%)	62.3 (2.81)	72.9 (1.47)***
Chroma of belly (%)	47.4 (5.69)	60.7 (6.51)***
Hue of belly (°)	87.2 (2.58)	96.8 (2.74)***

^a The sexes were not significantly different in any of the nine color characters (Two-tailed *t*-test, $P > 0.05$) and were therefore combined in this analysis.

^b The color swatches in Smithe (1975) have been widely used in recent years for plumage descriptions because this reference is readily available and permits easy comparisons. Smithe names enable those without training in reflectance colorimetry to assess quickly the approximate colors involved. However, we caution that the Smithe names provide only relatively crude color descriptions. Not only is there an insufficient selection of published swatches available (Pratt and O'Neill 1976), substantial individual variation in human color perception (Ender 1990, Mollon 1995) renders subjective most such comparisons. That point is illustrated by comparing color-reflectance measurements of the swatches themselves, whose colors approximate those of specific areas of plumage: Mahogany Red (crown of both species): L, 44.97%; C, 35.49%; h°, 37.8; Yellowish Olive-green (back of both species): L, 49.48%; C, 37.57%; h°, 98.7; Orange Yellow (L, 79.99%; C, 8; h°, 79.2) and Yellow Ocher (L, 73.20%; C, 46.97%; h°, 77.6) (belly of *P. luluae*) and Sulphur Yellow (not Sulphur Yellow, a distinctly different color in Smithe, 1975) (L, 89.74%; C, 59.56%; h°, 99.1) (belly of *P. ruficeps*). The agreement is weak at best between those swatch colorimetric values and the plumage colorimetric values shown in the table above. Clearly, quantitative colorimetry is preferable for objective descriptions of plumage variation when reliable instruments are available and the areas to be measured are sufficiently large.

^c Two-tailed *t*-test for unequal sample sizes, where degrees of freedom = $n_1 + n_2 - 2$; * $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$.

dimorphic, with males having longer wings and tail ($P < 0.05$) and deeper bill ($P < 0.01$) than females. Small samples of female *P. r. peruvianus* precluded statistical comparison of size features between it and *P. luluae* and the examination of sexual dimorphism in that form.

Color.—Males and females of *P. luluae* were identical in all nine parameters of color. Inter-specific comparisons, however, revealed that *P. luluae* and *P. ruficeps peruvianus* were indistinguishable in lightness, chroma, and hue of crown; and lightness, chroma, and hue of back; but 100% separable in lightness, chroma, and hue of belly (Table 2). Unfortunately, the complicated colors and patterns of the face and breastband or neckplate that distinguish the two species are too small in extent on study skins to allow the use of quantitative colorimetry. Thus, those features were compared among all taxa of the two species with a qualitative method of scoring in Johnson (2001).

Voice.—The pair collected by Johnson in 1970 was silent. However, Tristan J. Davis (pers. comm.) took careful field notes on voice of the new taxon:

Calls consisted of an emphatic 'chick!' with a piercing quality heard throughout the day from both males and females (sexed by specimens). Song (?) consisted of a short trill with a sort of harsh quality, 'prrrrrt,' usually preceded by a 'chick' note as described above. All singing specimens collected were males. Songs were most often heard in early mornings before 1000 h or briefly after 1600–1630 h. When singing they held their bodies and tail in a very horizontal position, and the tail vibrated slightly during the 'prrrrrt.'

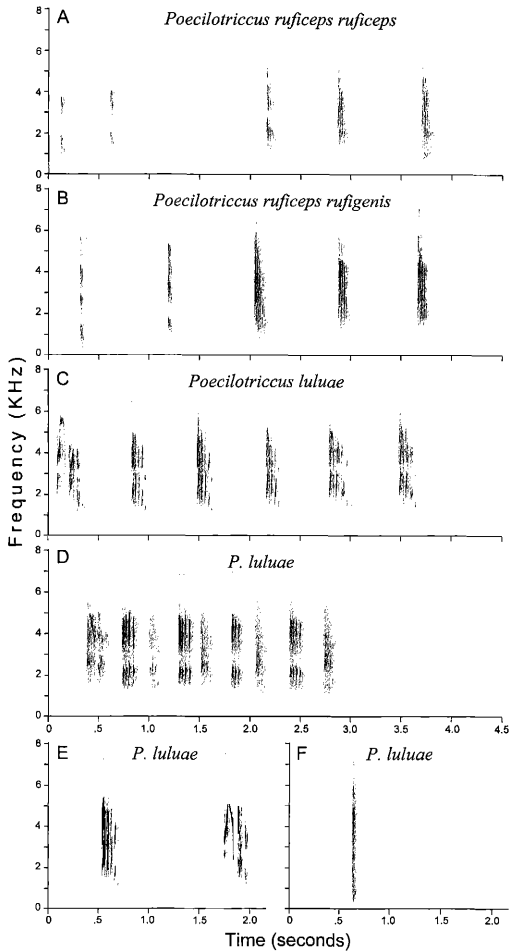


FIG. 2. Audiospectrograms of two calls and three song syllables of (A) *Poecilatriccus ruficeps ruficeps*, near the southern limit of its known range at Loja-Zamora Road, 2,135 m, Prov. Zamora-Chinchi, Ecuador (Library of Natural Sounds cut 55778, Cornell Laboratory of Ornithology), recorded by P. Donahue on 23 April 1990; (B) two calls and three song syllables of *Poecilatriccus ruficeps rufigenis*, 6 km north Mindo 5,300 ft (= 1,616 m), west Andes, Pichincha, Ecuador (Library of Natural Sounds cut 47307, Cornell Laboratory of Ornithology), recorded by B. Whitney on 10 March 1990; and (C–F) *Poecilatriccus luluae*, recorded a few kilometers east of Florida de Pomachochas, Depto. Amazonas, Peru on 25 August 1989 by Bret M. Whitney (personal collection). In (C), an introductory song syllable is followed by five syllables of a different type. In (D), three syllable types are shown followed by different, alternating types in a suspected duet; the first syllable in (D) is the same type as the first in (C); they differ only in quality of recording. In (E), the syllables are reversed, with the first syllable being similar to syllables 2–5 in (C) and the second syllable being the same as the first two

Furthermore, Bret M. Whitney tape recorded vocalizations from a presumed male and a duetting pair of the new species on 25–26 August 1989, at a few miles east of Florida de Pomachochas, 6,600 ft elevation (= 2,012 m), Amazonas, Peru. Representative audiospectrograms of the voices of those birds are shown in Figure 2C–F where at least three song syllable types and a single kind of call note are evident.

In the only published description of the voice of *P. ruficeps* known to us, Hilty and Brown (1986) state that in the latter species (subspecies unspecified) the call is a "short, pebbly stutter, *patreer-pit*, last note sometimes omitted, or several stutters given in succession..." Through the courtesy of the Laboratory of Natural Sounds, Laboratory of Ornithology, Cornell University, single examples of tape recordings of the voices of *P. ruficeps ruficeps* and *P. ruficeps rufigenis* were analyzed (Fig. 2A, B). Note the great similarity of the song syllables between the two geographically adjacent subspecies of *P. ruficeps*. Furthermore, only a single syllable type is represented in the latter species in contrast to three types in *P. luluae*. When compared with song syllables of *P. luluae*, those of *P. ruficeps* are briefer and apparently less complicated internally. Aurally, the differences in song between the two species are clearly evident. Call notes, in contrast, seem very similar if not identical from the limited material at hand.

Although differences between the two species are obvious in the limited samples of recordings analyzed here, larger samples will be necessary for a thorough, quantitative appraisal of their vocal repertoires.

REMARKS

Ecological notes.—The holotype and its mate were taken in undergrowth of residual subtropical forest. Annotations on specimen tags state that other specimens were taken in forest undergrowth, shrubby second-growth, groundstrata in cloud forest, bosque de bambú, tope-do, and "netted in tall second-growth" (at an

←
syllables in (C) and (D). (F) illustrates a call note of *P. luluae* that is assumed to be homologous to the introductory pair of call notes shown in (A) and (B) for *P. r. ruficeps* and *P. r. rufigenis*, respectively.

unspecified level above the ground). More specific notes on ecology were provided by Tristan J. Davis (pers. comm.), who found the species to be fairly common at ~30 km by road east of Florida (de Pomachochas) on the road to Rioja, Dpto. Amazonas, at 2,200 m, between 26 November and 9 December 1983 (Davis 1986) and collected six specimens:

Poecilotriccus was consistently encountered in pairs foraging in forest edge bamboo. Occasionally they would be encountered within the forest, usually in or near some bamboo. They usually remained in the mid-story at the edge about 4 to 10 m up. Only once (on 1 December at 0820 h) was a solitary individual seen. This bird was silent (unlike the majority of the birds encountered) and was only 2 m up and was not foraging. It was only 10 m from a calling pair in the same area. Foraging motions of the species consisted almost exclusively of upward-directed sally-gleans (mostly short sallies of <0.5 m) to the undersurface of live leaves. Other foraging movements were sally-gleans to the undersurface of small branches/bamboo stalks, aerial sallies of <0.5 m and perch gleanings from the surface of moss covered branches. The only food item I was able to see very clearly was some sort of small (~0.5 cm) hymenopteran that it kept beating against a branch before eating it. At no time were they ever seen to accompany any mixed species flocks in the area, although they did seem to occasionally 'associate' with them if they passed directly through their territory. One individual not collected was carrying nesting material on 5 December in an area where a pair was seen throughout the 2 week period. No nest was located although there was undoubtedly one in the vicinity. Most of the edge habitat where we located them most frequently was created by the heavy logging that was taking place in the area.

Hornbuckle (1999) summarized the preferred habitat as roadside second-growth shrubbery and bamboo but with occurrence also in bamboo thickets within undisturbed forest.

Geographic isolation and endemism.—The Cordillera Colán and the unnamed range of the Eastern Andes of Peru immediately to the east ("Afluente-Abra Patricia," Graves et al. 1983), the two areas of occurrence for the tody-tyrant described here, have also been regions for the discovery in recent decades of other avian novelties, for example, the Long-whiskered Owlet, *Xenoglaux lowreyi* (O'Neill and Graves 1977); Ochre-fronted Antpitta, *Grallaricula ochraceifrons* (Graves et al. 1983); Cinnamon-breasted Tody-Tyrant, *Hemitriccus cinnamomeipectus* (Fitzpatrick and O'Neill 1979); and Bar-winged Wood-Wren, *Henicorhina leucoptera* (Fitzpatrick

et al. 1977). The biogeographic role of the arid Rio Marañón valley and North Peruvian Low (Vuilleumier 1968) in dividing the distributions of at least 18 allospecies pairs of forest birds, in addition to *P. ruficeps* and *P. luluae*, is discussed at length by Parker et al. (1985).

The significance of vocal differences.—A large body of research in recent decades supports the view that bird songs function in species discrimination and mate attraction (Payne 1986, Catchpole and Slater 1995). Voice in New World tyrannid flycatchers in particular has been identified as a rich source of evolutionary and taxonomic information because of its species specificity and consequent role in reproductive isolation (Kroodsma et al. 1996). Moreover, because songs and calls are innate in suboscines such as tyrannids, and intraspecific variability is vastly reduced over that seen in species of oscine birds with learned songs (Kroodsma 1996), even the limited information on calls and songs provided here can shed important light on species limits of close relatives such as *P. luluae* and *P. ruficeps*.

Species concept and taxonomic conclusion.—In suggesting guidelines for the publication of descriptions of new species, LeCroy and Vuilleumier (1992) proposed that, besides the actual description, "desirable additional information that may be the necessary basis upon which to judge the validity of the new species [should include] voice recordings, blood samples, tissue samples, anatomical specimens, notes on behaviour, ecology, etc." Further, they advise that the species concept being followed needs to be explained when the newly described species is allopatric with its nearest congener. We agree with LeCroy and Vuilleumier's position.

We follow the Comprehensive Biologic Species Concept, recently articulated by Johnson et al. (1999), in which a species is

a system of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilization system through time and space, represent an independent evolutionary trajectory, and demonstrate essential but not necessarily complete reproductive isolation from other such systems.

Obviously, as *P. luluae* is allopatric with its closest relative, *P. ruficeps*, we cannot directly demonstrate its essential reproductive isolation, an important component of the above def-

inition but one that cannot be experimentally verified or rejected. Nonetheless, the following four points provide, when taken together, strong inferential evidence that justifies species status for *P. luluae*: (1) complete divergence from *P. ruficeps* in color of belly and pattern of the sides and front of the face, the latter an area of the body typically critically involved in intersexual communication in birds and likely, therefore, to be crucial in pair formation; (2) differences in advertising song and calls that could potentially serve in reproductive isolation; (3) an unusual degree of stability in color pattern (Johnson 2001), compared with the highly variable *P. ruficeps*, suggesting pronounced genetic cohesiveness and evolutionary independence from related lineages; and (4) total geographic isolation from *P. ruficeps*, guaranteeing the sharing of a common fertilization system by populations constituting *P. luluae*.

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