

A NEW SPECIES OF TYRANNULET (TYRANNIDAE: PHYLLOMYIAS) FROM ANDEAN FOOTHILLS IN NORTHWEST BOLIVIA AND ADJACENT PERU

Sebastian K. Herzog,1,2,5 Michael Kessler,3 and José A. Balderrama2,4

1 Institut für Vogelforschung "Vogelwarte Helgoland," An der Vogelwarte 21, 26386 Wilhelmshaven, Germany; 2 Asociación Armonía–BirdLife International, Casilla 3566, Santa Cruz de la Sierra, Bolivia; 3 Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abteilung Systematische Botanik, Untere Karspüle 2, 37073 Göttingen, Germany; and 4 Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Cochabamba, Bolivia

Abstract.—We describe Phyllomyias weedeni, a new species of tyrannulet (Tyrannidae) from the Bolivian and Peruvian Andes. The species is morphologically and vocally most similar to widely allopatric P. fasciatus (Planalto Tyrannulet), but vocalizations recorded at the six localities from which it is known differ conspicuously and significantly from those of P. fasciatus, and differences in plumage and measurements are also apparent. Vocalization analysis further suggests that the P. fasciatus complex, which comprises three named subspecies, may consist of more than one biological species. Phyllomyias weedeni inhabits the upper canopy of humid and semi-humid foothill and lower montane forest within a narrow elevational range (700–1,200 m). It appears to prefer irregularly structured canopy dominated by small-leaved trees but has also been found in a mosaic of shade-coffee (Coffea spp.) plantations and remnant forest patches. It occurs at low densities, is apparently patchily distributed, and has an estimated extent of occurrence of ≤10,000 km². Its breeding population is estimated to be well below 10,000 mature individuals, and ongoing large-scale habitat conversion throughout much of the species’ range could pose serious conservation problems. The new species thus qualifies as globally “vulnerable” under IUCN Red List Criteria. Further surveys are needed, especially in southeast Peru, to establish the extent of occurrence and population size of P. weedeni more precisely. Received 20 February 2007, accepted 13 June 2007.

Key words: Bolivian Yungas, globally threatened species, new species, Phyllomyias, Tyrannidae.

Une Nueva Especie de Tyrannidae (Phyllomyias) del Piedemonte Andino del Noroeste de Bolivia y Áreas Adyacentes del Perú

Resumen.—Describimos a Phyllomyias weedeni, una nueva especie de Tyrannidae de los Andes de Bolivia y Perú. Morfológicamente y vocalmente, la especie más parecida es P. fasciatus, ambas siendo ampliamente alopatricas. Sin embargo, las vocalizaciones grabadas en las seis localidades de las cuales se conoce la nueva especie difieren conspicuamente y significativamente de aquellas de P. fasciatus, y las diferencias en el plumaje y medidas morfométricas también son evidentes. Los análisis de vocalizaciones sugieren además que el complejo de P. fasciatus, el cual está constituido por tres subespecies, podría incluir más de una especie biológica. Phyllomyias weedeni habita el dosel superior del bosque húmedo y semi-húmedo de piedemonte y de montaña en un rango altitudinal estrecho (700–1200 m). Aparentemente prefiere dosel con estructura irregular dominado por árboles con hojas pequeñas, aunque la especie también fue encontrada en un mosaico de plantaciones de café bajo sombra y fragmentos remanentes de bosque. Existe a densidades bajas, con una distribución aparentemente fragmentada y su extensión de presencia (área de distribución) estimada no sobrepasa los 10000 km². Se estima que el tamaño de su población reproductiva es notablemente menor a 10000 individuos maduros, y la conversión actual de su hábitat a gran escala dentro de la mayor parte del área de distribución de la especie podría traer serios problemas de conservación. Por ende, la nueva especie califica para la categoría global de amenaza “vulnerable” bajo los criterios de la Lista Roja de la UICN. Se requiere de relevamientos adicionales especialmente en el sureste del Perú para establecer su extensión de presencia y su tamaño poblacional con mayor exactitud.

In June 1989, T. A. Parker III and M. Gell-Mann studied the avifauna of Serranía Pilón, an outlying Andean ridge in Departamento Beni, Bolivia (Fig. 1), along the then newly constructed road from Caranavi to Yucumo (Parker et al. 1991). They observed and sound-recorded several tyrannulets in the genus Phyllomyias in lower montane forest at 850–900 m that they tentatively identified as Phyllomyias fasciatus (Planalto Tyrannulet). Parker et al. (1991) noted, however, that vocalizations of these birds were faster and higher-pitched than

E-mail: skherzog@armonia-bo.org

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those of *P. fasciatus* in southeast Brazil and northeast Argentina and concluded that the Serranía Pilón population may represent an undescribed form. This Andean population received no further study, however, and Ridgely and Tudor (1994) and Fitzpatrick (2004) included it under the species accounts of *P. fasciatus* without mentioning that an undescribed taxon may be involved.

On 2 June 1997, S.K.H. sound-recorded three unfamiliar tyrannulets (*Phyllomyias* sp.) in a canopy mixed-species floc at the edge of humid forest at 1,150 m on Cerro Asunta Pata in the Yungas of Departmento La Paz, Bolivia (Fig. 1), along the road from Charazani to Apolo. The recording was later reviewed by B. M. Whitney, who observed (pers. comm.) that the vocalizations were reminiscent of those of *P. fasciatus* but were well outside that species’ normal variation, and he suggested that they may represent the Beni population that Parker had described to him several years earlier as sounding similar to, but distinctively different from, *P. fasciatus*. S.K.H.’s recordings proved to be identical to those of the presumed *P. fasciatus* made by Parker on Serranía Pilón (B. M. Whitney pers. comm.).

S.K.H. and J.A.B. returned to Cerro Asunta Pata, where they sound-recorded and collected two specimens on 3 September 1998. These birds were located immediately using sound playback, to which they readily responded, and they were collected in exactly the same spot where the species had been recorded in 1997. Despite extensive playback on 3 and 4 September 1998 along ~15 km of road with apparently suitable habitat at 1,050–1,500 m, no other individuals could be detected on Cerro Asunta Pata. However, on 8 October 1998, S.K.H. and J.A.B. located the species on Serranía Pilón, at 850–1,000 m, where it was originally observed by Parker and Gell-Mann. In 2004 and 2005, it was discovered at several additional sites in the foothills of the northern Bolivian Andes (departamentos Cochabamba and La Paz) and in shade-coffee (*Coffea* spp.) plantations in extreme southeast Peru in Departamento Puno (Fig. 1).

All vocalizations recorded are conspicuously and consistently different from those of *P. fasciatus*, and morphological differences are also apparent. Thus, we propose to name this new tyrannulet

**Phyllomyias weedeni**, sp. nov.

*Yungas Tyrannulet*  
*Mosqueta Yungueña* (Spanish)
Holotype.—Colección Boliviana de Fauna (CBF) no. 3428; adult female (skull fully pneumatized); Cerro Asunta Pata, 60 km east-northeast of Charazani (approximately 15°03′S, 68°29′W), Departamento La Paz, Bolivia, elevation 1,150 m; collected 3 September 1998 by S.K.H., prepared by J.A.B. Sound-recorded by S.K.H.; recording archived at Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York (MLNS 127042).

Diagnosis: Morphology.—Closely similar to widely allopatric *P. fasciatus*, the type species of the genus. Differs in plumage from all three subspecies of *P. fasciatus* (and especially from *P. f. brevirostris*) by the strongly contrasting gray crown and olive back, and from *P. f. fasciatus* and *P. f. cearae* (primarily in wing chord and tail length) and similar in size to the nominate subspecies (Table 1). The only other similar congener is *P. griseiceps*, from which it differs by the presence of wing bars.

Diagnosis: Voice.—All known vocalization types (the song or multisyllabic whistle and two types of antiphonal duet) are similar
TABLE 1. Selected measurements (mm) of Phyllomyias weedeni and P. fasciatus. Values are means (± SD for P. f. brevirostris), with range in parentheses.

<table>
<thead>
<tr>
<th>Sex (n)</th>
<th>Wing chord</th>
<th>Tail</th>
<th>Tarsus</th>
<th>Culmen&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Bill tip&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Bill width&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male (1)</td>
<td>55.0</td>
<td>46.5</td>
<td>14.4</td>
<td>10.7</td>
<td>5.2</td>
<td>3.8</td>
</tr>
<tr>
<td>Female (1)</td>
<td>52.5</td>
<td>44.0</td>
<td>13.0</td>
<td>11.2</td>
<td>5.4</td>
<td>3.5</td>
</tr>
<tr>
<td>Male (3)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>56.7 (56.5–57.0)</td>
<td>45.8 (45.0–47.5)</td>
<td>14.3 (13.4–14.9)</td>
<td>10.1 (8.9–10.8)</td>
<td>5.1 (4.8–5.2)</td>
<td>3.9 (3.8–4.0)</td>
</tr>
<tr>
<td>Female (1)</td>
<td>51.4</td>
<td>40.0</td>
<td>13.9</td>
<td>9.3</td>
<td>5.2</td>
<td>3.7</td>
</tr>
<tr>
<td>Unknown (2)</td>
<td>56.0 (54.5–57.0)</td>
<td>45.0 (43.0–47.0)</td>
<td>14.4 (14.0–14.8)</td>
<td>10.5 (10.4–10.5)</td>
<td>5.2 (4.9–5.4)</td>
<td>3.6 (3.4–3.7)</td>
</tr>
<tr>
<td>Male (11)</td>
<td>60.7 ± 2.5</td>
<td>51.0 ± 2.0</td>
<td>15.1 ± 0.4</td>
<td>10.5 ± 0.2</td>
<td>5.2 ± 0.5</td>
<td>3.6 ± 0.2</td>
</tr>
<tr>
<td>Female (17)</td>
<td>57.6 ± 1.6</td>
<td>48.6 ± 1.7</td>
<td>15.0 ± 0.5</td>
<td>10.4 ± 0.7</td>
<td>5.3 ± 0.2</td>
<td>3.7 ± 0.3</td>
</tr>
<tr>
<td>Male (2)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>62.3 (62.1–62.5)</td>
<td>53.5 (53.5–53.5)</td>
<td>14.9 (14.7–15.1)</td>
<td>10.6 (10.5–10.6)</td>
<td>5.4 (5.3–5.4)</td>
<td>4.0 (3.7–4.3)</td>
</tr>
<tr>
<td>Female (5)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>55.5 (55.0–56.0)</td>
<td>46.3 (44.5–47.5)</td>
<td>14.2 (13.7–14.8)</td>
<td>10.3 (9.6–11.2)</td>
<td>5.2 (5.0–5.2)</td>
<td>4.2 (3.8–4.9)</td>
</tr>
<tr>
<td>Unknown (1)</td>
<td>54.0</td>
<td>44.0</td>
<td>14.4</td>
<td>n.d.</td>
<td>n.d.</td>
<td>n.d.</td>
</tr>
</tbody>
</table>

<sup>a</sup>Measured from base at skull.
<sup>b</sup>Measured from anterior edge of nares.
<sup>c</sup>Measured at anterior edge of nares.
<sup>d</sup>n = 5 for bill width.
<sup>e</sup>n = 4 for bill width.

...to those of P. fasciatus but differ by a significantly higher overall frequency. Individual notes of the multisyllabic whistle are significantly shorter, differently shaped, and given at a significantly faster pace; a distinctive, accentuated terminal note is usually given with the series, and a truly homologous note appears to be lacking in populations of P. fasciatus. Antiphonal duets also differ diagnostically (vocalizations described in detail below).

Description of holotype.—See color plate on front cover of this issue. Forehead, crown, and nape Dark Olive-Gray with Chagall Yellow. Lores, supercilium, and ear coverts Blackish Brown to Black with yellowish tips. Tertials and wing coverts Deep Yellow. Greater and median secondaries Cerulean Blue. Underwing coverts Cerulean Blue to Light Blue (slightly more intense). Underside of breast feathers closest to Barium Yellow; tips of flank and abdomen feathers between Barium Yellow and Citrine Yellow. Underside of head and upper throat with grayish base and tip; median area whitish, sides of breast with approximately equal amounts of yellowish and grayish tips, therefore appearing somewhat olivaceous. Tertials with grayish base and tip; tips of flank and abdominal feathers between Picnic Yellow and Citron Yellow. Underside of tail with outer webs Light Grayish Olive with Marguerite Yellow edges and inner webs Mineral Gray. Undertail coverts Barium Yellow. Upper side of tail Clove Brown; outer edges of rectrices pale Yellowish Citrine at base, grading into Massicot Yellow toward the tip. Mantle, lower back, and rump Citrine, gradually becoming slightly paler and more yellowish on rump and upper tail coverts. Wing coverts Clove Brown. Greater and median secondary coverts tipped and edged Cream Color to light Cream Color (slightly more yellowish on a few feathers) to varying extents, forming two fairly indistinct wing bars. Lesser coverts indistinctly tipped and edged Citrine. Marginal underwing coverts of the alular area Picnic Yellow (visible in closed wing). Primaries and secondaries Fuscous with basal margin of inner web pale yellowish; outer web of secondaries narrowly edged Primrose Yellow. Tertiaries Clove Brown; outer web edged Cream Color to light Cream Color (edging slightly broader than in secondaries). Soft parts in life: iris brown, maxilla black, mandible black with a pinkish triangle at base and horn tip, tarsus and feet black, soles pale yellow.

Measurements of holotype.—Wing chord 52.5 mm, tail 44.0 mm, tarsus 13.0 mm, culmen from skull 11.2 mm, culmen from anterior edge of nares 5.4 mm, bill width at anterior edge of nares 3.5 mm, body mass 90.0 g (light fat), left ovary 6.0 g × 3.0 mm (right). Holotype, but mantle Dark Citrine and tip of mandible reddish brown. Wing chord 55.0 mm, tail 46.5 mm, tarsus 14.4 mm, culmen from skull 10.7 mm, culmen from anterior edge of nostrils 5.2 mm, bill width at anterior edge of nares 3.8 mm, body mass 8.0 g (no fat), testes 4.0 × 3.0 mm (right) and 5.5 × 2.5 mm (left).

Specimens examined: Skins.—Specimens were examined at the American Museum of Natural History (AMNH, New York) and at the Louisiana State University Museum of Natural Science (LSUMZ, Baton Rouge), and only those measured are listed (all specimens measured by S.K.H.). Plumages of other Phyllomyias spp. with contrasting gray crown and olive back were compared superficially.

Phyllomyias fasciatus fasciatus: Brazil: Bahia, one male and two unsexed specimens (AMNH 243804, 243805, 499953); Bolivia: Santa Cruz, one male (LSUMZ 150862).

Phyllomyias fasciatus brevirostris: Brazil: Minas Gerais, one male and two females (AMNH 316928, 316929, 316930); Paraná,
two males (AMNH 318841, 499951); Rio de Janeiro, one male and two females (AMNH 147003, 147004, 147005); Santa Catarina, one female (AMNH 315230); São Paulo, one male and three females (AMNH 499948, 499950; LSUMZ 69117, 69118).

**Phyllomyias fasciatus cearea**: Brazil: Ceará, one male and two females (AMNH 243807, 243808, 243809); Pernambuco, one unsexed specimen (AMNH 243806).

To increase sample size, additional specimens were measured at the Field Museum of Natural History (FMNH, Chicago) by S. J. Claramunt. To ensure comparability of measurements with those taken by S.K.H., LSUMZ specimens of *P. fasciatus* were measured independently by both observers, resulting in almost identical values.

**Phyllomyias fasciatus fasciatus**: Brazil: Maranhão, one male and one female (FMNH 63201, 63202).

**Phyllomyias fasciatus brevirostris**: Brazil: Minas Gerais, one female (FMNH 191690); Paraná, one male and one female (FMNH 110936, 110937); Rio de Janeiro, one male (FMNH 64241); São Paulo, four males and seven females (FMNS 267410, 267411, 267412, 267413, 267414, 267415, 267416, 267417, 344568, 344569, 344571).

**Phyllomyias fasciatus cearea**: Brazil: Ceará, one male and three females (FMNH 53367, 64236, 64237, 64238).

*Specimen examined: Sound recordings.—Phyllomyias weedeni:* Bolivia: Bení, two recordings; Cochabamba, two recordings (MLNS 127043, 127044); La Paz, two recordings (MLNS 127041, 127042); Peru: Puno, four recordings (including MLNS 127045). Recordings, all made by S.K.H., represent at least 13 individuals and three vocalization types.

**Phyllomyias fasciatus fasciatus**: Brazil: Minas Gerais, one recording (MLNS 108258); Pará, two recordings (P. Boesman). Those recordings represent at least three individuals and one vocalization type.

**Phyllomyias fasciatus brevirostris**: Brazil: Minas Gerais, two recordings (J. Mazar Barnett); Rio de Janeiro, three recordings (MLNS 22172, 30156, 114894); São Paulo, one recording (MLNS 103900); Rio Grande do Sul, five recordings (MLNS 19505, 19808, 19834, 20036, 20063); Argentina: Misiones, one recording (MLNS 34065). Those recordings represent at least 15 individuals and three vocalization types.

**Phyllomyias fasciatus cearea**: Brazil: Ceará, six recordings (P. Boesman, R. Hoyer); Pernambuco, one recording (G. Pereira). Those recordings represent at least seven individuals and three vocalization types.

Spectrograms of all recordings were examined and measured by S.K.H. using RAVEN, version 1.2.1 (Charif et al. 2004).

**Etymology.** We are pleased to name this species in honor of Alan Weeden, in recognition of his support of conservation work throughout South America and, in particular, the conservation of threatened birds in Bolivia. The English name draws attention to the species’ small, geographically restricted range.

**Remarks**

**Morphology.** Of the four taxa measured (Table 1), only for *P. brevirostris* was sample size large enough to statistically examine differences between sexes. Males of *brevirostris* (*n = 11*) had significantly longer wings (*t*-test = 4.10, *P < 0.001) and tails (*t*-test = 3.32, *P = 0.003) than females (*n = 17*), but differences in all other variables were not significant (*P = 0.17* for bill width, *P > 0.53* for the remaining variables in Table 1). We assumed that those relationships also applied to *P. weedeni*, *P. f. fasciatus*, and *P. f. cearea*. One of the two unsexed specimens of *P. f. fasciatus* (Table 1) had wing chord (57.0 mm) and tail (47.0 mm) measurements that clearly identified it as a male, and we treated it as such in the following analyses. The specimen of uncertain sex of *P. f. cearea* (Table 1) was labeled as a male, but measurements (wing chord 54.0 mm, tail 44.0 mm) identified it as a female, and we treated it as such.

Among males, wing chord and tail length of *P. weedeni* were similar to those of *P. f. fasciatus*, whereas measurements of *P. f. brevirostris* and *P. f. cearea* were about 4–7 mm longer than those of the former two taxa (Table 1). Values for females showed similar trends, except for a somewhat shorter tail in *P. f. cearea* (Table 1). These patterns were not reflected in the other morphometric variables (Table 1). Mean tarsus length (both sexes combined), for example, was lowest in *P. weedeni* (13.7 mm), highest in *P. f. brevirostris* (15.1 mm), and intermediate in *P. f. fasciatus* and *P. f. cearea* (14.3 mm and 14.4 mm, respectively).

**Vocalizations.**—Vocal recordings are included in Mayer (2000) and archived at the Macaulay Library of Natural Sounds (see above). The song of *P. weedeni* (Fig. 3A) is a slightly accelerating series of three to five (usually four, 52% of songs measured, *n = 99*) whistled notes that successively decrease in pitch and peak at about 3.4 kHz (first note) to 3.0 kHz (last note). Notes have a clear, smooth quality, present at least two overtones, and lack modulation. The frequency of the first overtone is about 2.8–3.1 kHz higher, and that of the second overtone 5.9–6.2 kHz higher, than the corresponding fundamental note, though the second overtone is very weak and visible in a spectrogram only when a bird is recorded at close range. The longest note is the first note, and the longest internote interval follows the first note, with subsequent notes and intervals becoming successively shorter (Table 2). The song is often (80%) punctuated with a short, sharply pointed terminal note peaking at about 3.8–4.0 kHz (Fig. 3A).

The similar song of *P. fasciatus* is a slow, slightly accelerating series of two to six (usually three or four) whistled notes peaking around 2 kHz (Table 2 and Fig. 3B–D). Notes have a clear, smooth quality, present at least two overtones (three in *P. f. cearea*), and lack modulation. Selected vocal characters (Table 2) of the song of *P. weedeni* were compared statistically with those of *P. fasciatus*. All fundamental notes of *P. weedeni* have a significantly higher (≤2 kHz) maximum frequency (the frequency at which maximum power occurs); *t*-test values: –15.99 to –37.62, all *P < 0.0001*), shorter duration (*t*-test values: –14.90 to –42.57, all *P < 0.0001*) and, virtually all internote intervals (except for the duration of the third internote interval of *P. f. fasciatus*) are significantly shorter (*t*-test values: –6.16 to –11.88, all *P < 0.0001*) than those of all subspecies of *P. fasciatus*. In addition, individual notes of the song of *P. weedeni* successively decrease in pitch, but those of *P. f. fasciatus* remain virtually constant or slightly increase in frequency (Table 2). Note shape also differs between the four taxa (Fig. 3). A principal component analysis (PCA) explicitly corroborated the distinctive nature of the song of *P. weedeni* (Fig. 4A).

Regarding the sharply pointed terminal note, none of the vocalizations of *P. fasciatus* examined has a truly homologous equivalent. Songs of *P. fasciatus* are occasionally (presumably primarily...
at dawn) alternated with a sharply pointed hiccupped double or triple note peaking at about 3.0–3.2 kHz in P. fasciatus, 2.9–3.1 kHz in P. brevirostris (Fig. 3B), and 2.6–2.7 kHz in P. cearae. In P. brevirostris, the average internote interval (n = 20) between the last note of a song and this double or triple note is 1.57 s (range: 0.78–5.20 s). By contrast, the internote interval preceding the terminal note of P. weedeni ranges only from 0.04 to 0.12 s. P. f. fasciatus, in turn, tends to emit a triple note before the song with an average internote interval (n = 11) of 1.47 s (range: 0.57–4.80 s), whereas the mean interval between the last note of a song and the triple note is 4.75 s (range: 2.65–9.63 s). Sample size for P. cearae was too small for analysis.

In the antiphonal duet of P. weedeni (Fig. 5A), one bird gives a brief (about 0.09–0.10 s) burry note covering a bandwidth of about 3.5–3.8 kHz. The other member of the pair delivers a louder vocalization comprising three distinctly different elements in irregular succession: three sharp notes in fast (about 0.11–0.12 s) sequence that successively decrease in power, bandwidth, and frequency, peaking at about 4.2–4.3 kHz (first note) to 3.1–3.2 kHz (last note); an approximately 0.18- to 0.36-s series of two or three upslurred, somewhat squeaky whistles peaking at about 3.6–3.7 kHz (first note) to 4.1 kHz (last note); and a sharp but quieter single note peaking at 3.3–3.5 kHz. On the basis of the sound recordings of P. fasciatus available to us, we found evidence for duetting only in P. f. brevirostris and P. f. cearae, which seem to duet much less frequently than P. weedeni. The duet of P. f. brevirostris (Fig. 5B) is less complex and characterized by notably lower frequencies than that of P. weedeni. It comprises a short (about 0.10–0.12 s) burry note (almost lacking in Fig. 5B) consisting of a fundamental note (bandwidth about 1.3–2.6 kHz) and a similarly strong overtone (bandwidth about 2.9–3.9 kHz) given by one bird while the other member of the pair delivers a rapidly trilled series of many louder, clear notes peaking at about 2.9–3.2 kHz (as compared with frequencies around 4 kHz for most notes in P. weedeni). Equivalents of the two or three upslurred whistles and the succession of three sharp notes in the duet of P. weedeni (Fig. 5A) seem to be lacking.

Structurally, the duet of P. f. cearae (Fig. 5C) is of similar complexity to that of P. weedeni, but it differs in its notably lower frequencies and the shape of individual notes (which also applies to the duet of P. f. brevirostris). The duet of P. f. cearae comprises several different elements given in irregular succession: a short (about 0.12–0.13 s) burry note consisting of a fundamental note (bandwidth about 1.1–2.2 kHz) and a virtually identically strong hump-shaped overtone (bandwidth about 2.1–3.4 kHz); a slightly shorter (about 0.08–0.09 s), louder burry note (bandwidth about 3.3–3.5 kHz).
1.3–2.7 kHz); an irregular trilled to hiccupped series of many slightly raspy notes peaking at about 2.1–2.7 kHz; and an approximately 0.28- to 0.30-s series of three clear notes peaking at about 2.0–3.1 kHz, with a conspicuous left-hand tail to the first note.

Both types of burry notes are apparently given by one member of a pair, whereas all other elements seem to be given by the other. When a pair is agitated (e.g., by playback; Fig. 5D), the same elements are given, but much faster and with a higher incidence of the first element, and a fifth element is added: a 0.10- to 0.15-s U-shaped note peaking at about 2.6–2.9 kHz, with a frequency range of about 0.9–1.2 kHz.

Both *P. weedeni* and *P. f. brevirostris* have a second type of antiphonal duet (Fig. 6). That of *P. weedeni* (Fig. 6A) is much more regularly structured than the species’ first type of duet (Fig. 5A). It consists of a rapid (about 0.35–0.40 s) series of notes that can be described onomatopoetically as a raspy “here-we-go,” which is repeated three times in fast succession (left half of Fig. 6A); sometimes the order of notes is changed to “go-here-we” (right half of Fig. 6A). The whole duet is followed or preceded by a combination of a single sharp note with a distinct left-hand tail at the base and a brief trill or purr consisting of 3–4 notes. The second type of duet of *P. f. brevirostris* differs from that of *P. weedeni* in its note structure and in having a more irregular succession of elements (Fig. 6B).

**Distribution and habitat.**—*Phyllomyias weedeni* inhabits a narrow elevational range of about 700–1,200 m and is known only from five localities in the lower Bolivian Yungas and one area in the lower Peruvian Yungas (Fig. 1). The Bolivian localities are (1) Río Cocos, ~3.5 km east of the border between Bolivia and Peru (14°04′ S, 68°51′ W, elevation ~1,000 m), Departamento La Paz, in Parque Nacional y Área Natural de Manejo Integrado Madidi (hereafter “Madidi”), where it was sound-recorded and observed in February 2005 by S.K.H., V. H. García-Solíz, and T. Perkins; (2) the type locality on the northeastern slope of Cerro Asunta Pata (15°03′ S, 68°29′ W, elevation 1,150 m), Departamento La Paz, just inside the Área Natural de Manejo Integrado Nacional Apolobamba (hereafter “Apolobamba”); (3) Ubinichi on the Río Yuyo (15°08′ S, 68°19′ W, elevation ~700 m), Departamento La Paz, ~21 km southeast of the type locality on the border of Apolobamba, where a single bird was sound-recorded by M. A. Troncoso-Joffré and R. Vargas-Rodríguez (recording reviewed by S.K.H.) in January 2004; (4) the east and west slopes of southern Serranía Pilón (15°16′–17°S,
The natural habitat of *P. weedeni* is the upper canopy of evergreen Andean foothill and lower montane forest. On Serranía Pilón, Smith and Killean (1998) found 146 tree species >10 cm diameter at breast height (92 genera in 37 families) at 900 m. Dominant tree families were Fabaceae (or Leguminosae), Moraceae, Rubiaceae, Sapotaceae, Myrtaceae, Euphorbiaceae, Lauraceae, and Meliaceae. Comparable vegetation studies from other sites are lacking, but qualitative observations also showed a predominance of leguminous trees and a high abundance of species of the other families mentioned above, as well as Burseraceae, Flacourtiaceae, and Sapindaceae at Asunta Pata and at the northwestern tip of Cordillera Mosetenes (M. Kessler pers. obs., H. Huyla pers. comm., respectively). At all sites, the canopy was about 20–35 m tall and of an irregular structure, contained numerous trees with small leaves, and was characterized by little to moderate growth of epiphytes. Climatic conditions were fairly dry to moderately humid (about 2,000–2,500 mm mean annual precipitation; Mueller et al. 2002). At the northeastern tip of Cordillera Mosetenes, virtually no vascular epiphytes occurred in the canopy, and the forest was in part semideciduous, which suggests a mean annual precipitation on the order of 1,500–1,700 mm.

Although most of our observations suggest that the species prefers tall upper canopy, Parker et al. (1991) observed birds foraging in crowns of small trees at forest edge, and S.K.H. and J.A.B. lured a pair into 2- to 5-m-tall, open roadside scrub using song playback. However, many Neotropical bird species that inhabit the canopy in unbroken forest descend to lower heights at forest edge (S. K. Herzog et al. pers. obs.). In addition, *P. weedeni* seems to tolerate a certain degree of habitat disturbance. It was about as abundant in traditional polyculture shade-coffee plantations (with *Inga* sp. as the dominant shade tree) in southeast Peru as it was in fairly intact forest on Serranía Pilón, and the species was repeatedly observed at the edges of roads. It is unknown, however, whether *P. weedeni* can sustain viable populations in such disturbed habitats, or whether they represent sink habitats or ecological traps.

It was already suggested by Parker et al. (1991:132) that *P. weedeni* "probably ranges to the north and south [of Serranía Pilón] on the forested slopes of outlying Andean ridges" and that "it should even be looked for in Peru." Cordillera Mosetenes, like Serranía Pilón, indeed is an outlying Andean ridge, but the occurrence of *P. weedeni* at Asunta Pata and Ubinichi shows that the species also ranges into the central part of the east Andean slope in Departamento La Paz. Although it seems likely that *P. weedeni* occurs in areas between the known localities, intensive avifaunal surveys throughout Pilón Lajas have failed to locate the species in the interior of the reserve (Hennessey et al. 2003). T. A. Parker also did not record *P. weedeni* during a survey at Calabatea, a lower montane forest site 6 km north of the type locality (Parker and Bailey 1991, Parker et al. 1991). M. A. Troncoso-Joffré and R. Vargas-Rodriguez (pers. comm.) failed to locate the species at Yuyo and Achiquirí (~21 km and ~32 km southeast of the type locality, respectively), despite song playback, whereas S.K.H. and M.K. (unpubl. data) did not record *P. weedeni* on Serranía Bellavista –20 km northeast of Caranavi. Farther to the north, recent surveys on several outlying foothill mountain ranges in Madidi with apparently suitable habitat within the known elevational range of *P. weedeni* by A. B. Hennessey (pers. comm.; Serranía Sediri, Tequeje, del Tigre; Fig. 1), R. W. Soria-Auza (pers. comm.; Serranía

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**Fig. 4.** Factor scores produced by a principal component analysis confirm (A) the unequivocal distinctiveness of the song (multisyllabic whistle) of *Phyllomyias weedeni* (solid circles) in comparison with that of *P. fasciatus fasciatus* (open circles), *P. f. brevirostris* (open triangles), and *P. f. ceareae* (solid squares) (eight variables included: maximum frequency and duration of the first three notes and duration of the first two internote intervals); and (B) the distinctiveness of almost all songs of *P. f. ceareae* within the *P. f. fasciatus* complex (symbols as in panel A; six variables included: maximum frequency and duration of the first three notes).

67°04′W, elevation 850–1,000 m), Departamento Beni, on the border of the Reserva de la Biosfera y Territorio Indígena Pilón Lajas (hereafter “Pilón Lajas”); (5) the northwestern tip of Cordillera Mosetenes, above the confluence of the Ipiri and Santa Elena rivers (16°03′S, 66°40′W, elevation 700–850 m), Departamento Cochabamba, where it was sound-recorded (MLNS 127043, 127044) and observed by S.K.H. and R. W. Soria-Auza in September 2004.

In extreme southeast Peru, *P. weedeni* was observed and sound-recorded (MLNS 127045) in February and March 2005 by S.K.H., V. H. García-Soliz, and T. Perkins, and again in January 2006 by V. H. García-Soliz (pers. comm.) between the villages of Curva Alegre and Palmerani (14°02′–03′S, 68°54′–57′, elevation 920–1,200 m; locality 6 in Fig. 1), Departamento Puno, within 1–1.5 km of the Bolivian border.
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The northern reaches of Cordillera Mosetenes probably represent the southern distributional limit of *P. weedeni*. Farther south, the evergreen forest of the outer Yungas slopes becomes increasingly wet until a precipitation maximum is reached in the Villa Tunari (Fig. 1) area in Departamento Cochabamba (mean annual precipitation $\geq 6,000$ mm; Mueller et al. 2002). We assume that this habitat is unsuitable for the new species. Moreover, the avifauna on the slopes above Villa Tunari has been fairly well studied (Herzog et al. 2005), and it seems reasonable to conclude that the lack of records indicates the species’ absence from that area.

*P. weedeni* also was not recorded during a 24-day survey on central Cordillera Mosetenes (16°14′S, 66°25′W, elevation 1,180–1,600 m; S. K. Herzog and M. Kessler unpubl. data) in August and September 2003, despite repeated playback of song recordings of *P. weedeni*, and MacLeod et al. (2005) did not locate it on the Río Altamachi at the base of central Cordillera Mosetenes.

**Biogeography.**—Obvious vocal and plumage similarities between *P. weedeni* and *P. fasciatus* suggest a sister relationship. The range of *P. weedeni* is located ~800 km to the west of the closest population of *P. fasciatus* in the Serranía de Huanchaca in extreme eastern Bolivia (Cabot et al. 1988, Killean and Schultenberg 1998), which inhabits semi-humid and, to a lesser degree, deciduous forests in eastern and southern Brazil, eastern Paraguay, and northeast Argentina (Ridgely and Tudor 1994, Fitzpatrick 2004).

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**Fig. 5.** Antiphonal duets of *Phyllomyias weedeni* and *P. fasciatus*. (A) *Phyllomyias weedeni*, from Bolivia: La Paz, Cerro Asunta Pata; 3 September 1998, recorded by S.K.H. (B) *Phyllomyias f. brevirostris* from Brazil: Rio de Janeiro, Parque Nacional do Itatiaia; 16 November 1980, recorded by T. A. Parker (MLNS 22172). This is a partial (perhaps primarily male) vocalization; the short, burry notes given by the other member of the pair are almost lacking in this example. (C) *Phyllomyias f. cearae* from Brazil: Pernambuco, Altinho; 23 December 2006, recorded by G. Pereira. (D) *Phyllomyias f. cearae* after playback from Brazil: Pernambuco, Altinho; 23 December 2006, recorded by G. Pereira.

**Fig. 6.** A second type of antiphonal duet of *Phyllomyias weedeni* and *P. fasciatus brevirostris*. (A) *Phyllomyias weedeni*, from Bolivia: La Paz, Cerro Asunta Pata; 2 June 1997, recorded by S.K.H. (B) *Phyllomyias f. brevirostris* from Brazil: Minas Gerais, Parque Estadual do Rio Doce; 25 December 1996, recorded by J. Mazar Barnett.
The distribution pattern exhibited by the two forms thus represents further evidence for the well-documented biogeographic link between the Andes and southeast Brazil (see, e.g., Fitzpatrick and O’Neill 1979; Sick 1985, Willis 1992). Behavior.—Owing to the species’ overall low abundance and preference for the upper canopy, little is known about its behavior. Phyllomyias weedeni was almost always observed in pairs except in early March in southeast Peru, when most birds detected were single. On one occasion at Palmareri, S.K.H. observed and sound-recorded a presumed family group of three P. weedeni in mid-February, and at Cerro Asunta Pata he once observed and tape-recorded three birds in a canopy mixed-species foraging flock (flock cohesion appeared to be rather loose) in early June, and heard a fourth nearby. All four birds vocalized vigorously, including both the song and antiphonal duets. It was unclear whether this behavior represented a type of group display, as reported for P. fasciatus by Fitzpatrick (2004), or a territorial dispute between neighboring territory-holders. The mixed-species flock contained, among other species, Campostoma obsoletum (Southern Beardless-Tyrannulets), Thraupis palmarius (Palm Tanager), and Tanager chilenus (Paradise Tanager). A pair tape-recorded by R. W. Soria-Auza (pers. comm.) at the northwestern tip of Cordillera Mosetenes also appeared to participate in a canopy mixed-species flock, but the flock was too distant to determine its composition.

Primarily, P. weedeni were seen perched in a nearly horizontal posture, with their head somewhat raised and tail slightly cocked. When the birds are excited by playback, perch posture can be more angled, halfway between horizontal and upright. A singing bird observed by S.K.H. held its wings slightly drooped and slightly lowered the tail simultaneously with each whistled note. Another bird occasionally displayed short, fast upward movements of the tail while engaged in antiphonal duetting.

Foraging maneuvers consisted mainly of short aerial sallies ("sally-strike"); Remsen and Robinson (1990), in all directions, to flying insects in the upper canopy, and birds tended to land on a new perch after each Sally. One bird observed by S.K.H. flew straight up to ~50 cm above its perch, caught a small insect in flight, and returned to the same perch, only to fly off and out of sight a few seconds later. Although our sample size is small, these observations contrast with the foraging behavior of P. fasciatus, which is reported to perch- and hover-glean (Fitzpatrick 2004) and to feed regularly on mistletoe berries (Loranthaceae; B. M. Whitney pers. comm.).

Intrageneric relationships.—As described above, plumage and external morphology of P. weedeni and P. fasciatus are similar; no other member of this genus is nearly so closely matched. Vocalizations of these two underscore their apparent sister relationship. For almost all known vocalization types of P. weedeni, a homologous equivalent is found in P. fasciatus. However, homologous songs (multisyllabic whistles) and antiphonal duets are diagnostically different (Table 2; Figs. 3–6) and represent unequivocal markers for the two forms.

There is some geographically structured variation in the vocalizations of P. fasciatus that seems to correspond to the known geographic ranges of the three subspecies. The northernmost taxon, P. f. ceareae, occurs in northeast Brazil, extending from Ceará and Rio Grande do Norte south to Sergipe, whereas the nominate subspecies is reported to extend from Maranhão and western Bahia in eastern Brazil southwest to southern Mato Grosso and extreme eastern Bolivia; P. f. brevirostris, in turn, occurs in the Atlantic forest region of southeast Brazil, eastern Paraguay, and southeastern Argentina (Fitzpatrick 2004). Precise range limits, however, seem to be poorly known, as is exemplified by P. Boesman’s recordings of P. f. fasciatus from Pará (see above), which apparently represent a new distributional record for this taxon.

Differences in the song (multisyllabic whistle) between subspecies are most pronounced in P. f. ceareae, all of whose fundamental notes have a significantly lower maximum frequency (the frequency at which maximum power occurs; t-test values: −8.17 to −13.85, all P < 0.0001; for sample sizes, see Table 2) than those of P. f. fasciatus and P. f. brevirostris (the fourth note of P. f. brevirostris was excluded from analysis owing to a sample size of n = 5). Phyllomyias f. ceareae further differs from P. f. brevirostris in duration of the first and second notes (t-test = −4.96 and −4.92, respectively; P < 0.0001) and in the duration of the first and second internote intervals (t-test = 6.10 and 6.30, respectively; P < 0.0001), and from P. f. fasciatus in the duration of the second (t-test = 3.57, P < 0.001) and third internote intervals (t-test = 6.55, P < 0.0001) (for sample sizes, see Table 2). The distinctiveness of the song of P. f. ceareae is largely confirmed by a PCA, though slight overlap with the other two subspecies is apparent (Fig. 4B) for two to three songs from Pernambuco. In addition, songs of P. f. ceareae comprise up to six notes (35% of songs measured had more than 4 notes), whereas the maximum number of notes per song in the other two subspecies was four. Differences in the frequency, structure, and note shape of the antiphonal duet (see above; Fig. 5B–D) further emphasize the vocal distinctiveness of P. f. ceareae.

Significant differences between P. f. brevirostris and the nominate subspecies exist in the maximum frequency of the first note (t-test = 2.11, P = 0.037), the duration of the first (t-test = 5.99, P < 0.0001) and second (t-test = 3.73, P = 0.0003) notes, and the duration of the first internote interval (t-test = −4.48, P < 0.0001) (for sample sizes, see Table 2). Principal component analysis, however, did not confirm these differences (Fig. 4B).

Although limited by sample size, an examination of differences in morphology underlines the outcome of the vocalization analysis. Female P. f. brevirostris (n = 17) have significantly longer wings (t-test = 3.38, df = 21, P = 0.003) and tails (t-test = 3.49, df = 21, P = 0.002) than female P. f. ceareae (n = 6), whereas male P. f. brevirostris (n = 17) have significantly longer wings (U-test = 1.00, Z = 2.74, P = 0.006) and tails (U-test = 0.00, Z = 2.87, P = 0.004) than males of the nominate subspecies (n = 4). For differences between P. f. fasciatus and P. f. ceareae in both variables, see Table 1.

These results strongly suggest that P. fasciatus consists of more than one biological species and that P. f. ceareae possibly merits species status. Definite recommendations for taxonomic limits, however, and determination of taxon ranges within the P. fasciatus complex, await analysis of a larger, more geographically complete sample of specimens and recordings to determine whether variations in vocalizations and morphology documented by the present analysis may be clinal. Such data are especially required from areas where two or all three taxa may come into contact, to reveal whether intergradation exists (and, if so, to what degree).

Conservation.—Phyllomyias weedeni appeared to be exceedingly rare at Asunta Pata and Ubinichi. During a two-week survey at Asunta Pata in 1997 (S. K. Herzog and M. Kessler unpubl. data; but...
see Herzog et al. 2002), the species was observed just once, and upon returning to the site in 1998 it could be found only in exactly the same spot as in 1997, despite the use of playback of its vocalizations, to which it responded quite readily. Moreover, an extensive avifaunal inventory on Cerro Asunta Pata by LSUMZ in 1993 (S. W. Cardiﬀ and J. V. Remsen, Jr. pers. comm.) did not encounter P. weedeni.

On Serranía Pilón, Parker et al. (1991) had two encounters (ﬁve individuals) with the species during a four-day survey in June, whereas S.K.H. and J. A.B. found three pairs (two on the east, one on the west slope) using tape playback along ~9 km of road in October. By contrast, M. A. Troncoso-Joﬀrê and R. Vargas-Rodrguez (pers. comm.) detected nine individuals along 4 km of road on the west slope (890–970 m) in December 2003, which indicates that some seasonal variation in detectability and responsiveness to playback may exist in P. weedeni.

At the northwestern tip of Cordillera Mosetenes, three pairs and a distantly vocalizing bird were located by S.K.H. and R. W. Soria-Auza over a 12-day period along ~4 km of trails. One bird was heard very faintly by S.K.H. at a distance of about 200–300 m. In response to playback of a song recording, the same bird, together with its presumed mate, approached and was lured into the canopy directly above the observer. This observation suggests that P. weedeni could have a territory size on the order of ≥10 ha.

Between Curva Alegre and Palmerani in southeast Peru, eight individuals were detected over a three-day period in a mosaic of shade-coffee plantations and degraded remnant forest patches along a winding road covering a linear distance of ~6 km (≥10 km by road). By contrast, on the Río Cocos in Bolivia, about 5–6 km east of Palmerani, only three individuals were encountered over nine days along 4.5 km of trails in pristine lower Yungas forest.

Not only does P. weedeni occur at low densities, it also appears to have a very small range and a rather patchy, fragmented distribution. Its maximum range size, based on the six known localities, is about 30,000–35,000 km². However, about half of this area falls outside the elevational distribution of the species, and in a number of areas, P. weedeni has not been observed despite intensive ﬁeld work and the presence of apparently suitable habitat at the right elevation (see above). Thus, it seems unlikely that its effective extent of occurrence exceeds 10,000 km² and its area of occupancy could be well below this value. In light of the species’ low density and apparent patchy distribution, the breeding population of P. weedeni must be very small, and we estimate that it probably is well below 10,000 mature individuals.

Although the species apparently persists in mosaics of shade-coffee plantations and remnant forest patches, the ongoing large-scale conversion of forest habitat to subsistence farming throughout much of the range of P. weedeni (see Ibisch and Mérida 2003) poses serious conservation problems. Given its seemingly small population size, small extent of occurrence, and patchy distribution, P. weedeni qualiﬁes for the category of globally “vulnerable” under the following IUCN Red List Criteria: B1a and B1b (extent of occurrence estimated to be <20,000 km²; known to exist at ≥10 locations, and continuing decline projected in extent of area of occupancy, extent and quality of habitat, and number of mature individuals) and C2a (population size estimated at <10,000 mature individuals, and a continuing decline projected in mature individuals with no subpopulation estimated to contain >1,000 mature individuals) (BirdLife International 2004). Clearly, further surveys are needed, especially in southeastern Peru, to establish the extent of occurrence and population size of P. weedeni more precisely than is possible at present.

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