

A NEW SPECIES OF *PERCNOSTOLA* ANTBIRD (PASSERIFORMES: THAMNOPHILIDAE) FROM AMAZONIAN PERU, AND AN ANALYSIS OF SPECIES LIMITS WITHIN *PERCNOSTOLA RUFIFRONS*

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ABSTRACT.—Ornithological studies undertaken in certain sandy soil habitats of lowland northeastern Peru uncovered a previously undescribed species of *Percnostola* antbird. Elements of its morphology, vocalizations, and behavior indicate that it should be considered a well-differentiated species, closely related to *P. rufifrons*. We present a description of the new species; an analysis of how it differs from the four previously described subspecies of *P. rufifrons*; and a reconsideration of species limits within *P. rufifrons*, employing measures of morphology, vocalizations, and behavior. Under guidelines developed previously (Isler et al. 1998, 1999), vocal differences among the four subspecies (*rufifrons*, *subcristata*, *minor*, and *jensoni*) of *P. rufifrons* were insufficient to support considering them distinct species. However, differences in morphology among most of the four taxa were substantial, and we look forward to genetic studies of *Percnostola* and related groups. The localized and highly specialized habitat preferences of the new species cause grave concern for its conservation.

RESUMEN.—Estudios ornitológicos realizados en hábitats de arena blanca de las tierras bajas del nororiente peruano permitieron el descubrimiento de una nueva especie del género *Percnostola*. Elementos de su morfología, vocalizaciones y comportamiento claramente diferencian esta especie, y sugieren una relación cercana a *P. rufifrons*. Presentamos una descripción de esta nueva especie; un análisis de cómo se diferencia esta especie de las cuatro subespecies previamente descritas de *P. rufifrons*; y una reconsideración de los límites específicos dentro de *P. rufifrons*, empleando medidas de la morfología, vocalizaciones y comportamiento. Siguiendo los lineamientos desarrollados en anteriores publicaciones (Isler et al. 1998, 1999), diferencias vocales entre las cuatro subespecies previamente descritas de *P. rufifrons* (*rufifrons*, *subcristata*, *minor* y *jensoni*) fueron insuficientes para considerarlas especies diferentes. Sin embargo, diferencias morfológicas entre la mayoría de estos cuatro taxones fueron substanciales, por lo que es necesario esperar futuros estudios genéticos de este complejo y de otros grupos relacionados. Las preferencias de hábitat altamente localizadas y especializadas de esta nueva especie son motivo de gran preocupación por su conservación. Received 6 Nov. 2000, accepted 17 Aug. 2001.

Extensive ornithological field studies undertaken in the region north of the Río Marañón in the drainages of the Ríos Tigre and Corrientes in northern Peru (Alvarez 1994) have shown that edaphically based forest heterogeneity in the region is accompanied by unique avian diversity. For example, a previously unrecognized species of *Herpsilochmus antwren* was found to inhabit two distinct, patchily distributed white sand forests in the region, known locally as *irapayal* and *varillal* (Whitney and Alvarez 1998) where a new *Zimmerius* tyrannulet also was discov-

ered (Alvarez and Whitney 2001). Another avian resident of these sandy soil habitats was found to resemble some subspecies of the Black-headed Antbird, *Percnostola rufifrons*, a widespread species in northern Amazonia. However, its distinctive plumage and vocalizations suggested that it was an undescribed species or a new subspecies of *P. rufifrons* which previously had been considered to consist of four subspecies: nominate *rufifrons*, *subcristata*, *minor*, and *jensoni* (Capparella et al. 1997). Capparella et al. suggested that *P. r. rufifrons* and *P. r. subcristata* were specifically distinct from *P. r. minor* and *P. r. jensoni*, but here all four taxa were considered subspecies of *P. rufifrons* for analyses of morphology, vocalizations, and behavior. These analyses demonstrated that the population west of the Río Napo in northern Peru warrants consideration as a new species which we propose to name:

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	<i>P. r. rufifrons</i>	<i>P. r. subcristata</i>	<i>P. r. minor</i>	<i>P. r. jensoni</i>	<i>P. arenarum</i>
FEMALES					
Color of crown (excluding forehead)	Black	Dark reddish brown (5YR3/4) edged dark grayish brown (10YR3/2)	Reddish brown (5YR4/4) edged dark brownish gray (5YR4/1)	Black edged greenish (10Y3/) or bluish (5PB3/) gray	Dark neutral gray (N3<->N4)
Color of upperparts	Dark greenish gray (10Y4/ to 5Y3/2)				Dark neutral gray (N4)
Color of primary edges	Reddish brown (5YR4/4)		Grayish brown (10YR5/2)		Bluish gray (10B5/1)
Color of sides of head	Like underparts			Like upperparts	
Color of flanks	Tinged olive but only slightly darker than belly		Dark olive contrasting strongly with belly		Slightly tinged olive
Color of throat and breast	Yellowish red-brown (5YR5/8<->4/8); slightly paler on throat		Light reddish yellow-brown (7.5YR6/8 to 5/8)		Yellowish red-brown (7.5YR5/8); center of throat white
Color of center of belly	Same as breast		Yellow ochre (10YR7/6)		White
MALES					
Crown of color	Black		Black edged dark gray		Dark gray
Length crown feathers	Long	Medium	Short		
BOTH SEXES					
Length tail	Long			Short	
Iris color	Red			Gray	

FIG. 1. Morphological characters distinguishing taxa in the *Percnostola rufifrons* species group. Color descriptions are based on Munsell Soil Color Charts (1994 edition; Macbeth Division of Kollmorgen Instruments Corp., Baltimore, Maryland) with names modified to make them more descriptive. Data provided for female *P. r. jensoni* refer to the holotype; three paler specimens are more evenly colored (see Capparella *et al.* 1997). Measurement data are provided in Table 1.

Allpahuayo Antbird
Percnostola arenarum sp. nov.

Holotype.—Museo de Historia Natural de la Univ. Nacional Mayor de San Marcos, Lima, Peru (hereafter MUSM), No. 21104, adult (skull "100% ossified") female from Mishana, 03° 55' S, 73° 29' W, on the Río Nanay, Dept. de Loreto, Peru, approximately 100 m elevation, collected 29 October 1998 in *varillal*, *bajo húmedo* (low swampy *varillal*) by JAA, voice tape-recorded previous day (same individual as judged by location). Voice specimen to be archived at the Macauley Library of Natural Sounds (hereafter MLNS), Cornell Laboratory of Ornithology, Ithaca, New York.

Diagnosis. Morphology.—A medium-sized, sexually dichromatic, typical antbird (Thamnophilidae) most similar to *P. rufifrons*. Female upperparts are dark gray with black wing coverts edged reddish yellow-brown; underparts are primarily reddish yellow-brown and white. The most salient plumage character differentiating the female from females of *P. rufifrons* is the strong contrast between the reddish yellow-brown of most of the underparts and the clear white patch on the center of belly and the whitish center of the chin and

throat. Females also are separable from females of *P. rufifrons* by having the crown and upperparts entirely dark neutral gray and by the lack of a brownish tinge on the gray outer margins of remiges, except for the five outermost primaries. The male is dark gray with throat black and wing coverts black, narrowly edged with white. The male is distinguished from males of *P. rufifrons* by dark gray upperparts that are essentially the same intensity from the crown to the tail. More detailed comparisons of coloration and additional morphological characters distinguishing both sexes of *P. arenarum* from subspecies of *P. rufifrons* are provided in Fig. 1 and Table 1.

Diagnosis. Voice.—Loudsongs of both *P. arenarum* and *P. rufifrons* consist of a series of similar notes that decelerate in pace, more so initially than in the latter half of the vocalization (Fig. 2). However, the notes of the loudsong of *P. arenarum* are shaped like a bowl or a ladle, sloping down in frequency at the beginning and turning up at the end, whereas the frequency of the loudsong notes of all *P. rufifrons* subspecies rises initially and turns down at the end. During "blind" tests in which the source of the sample was ob-

TABLE 1. Measurements (mm) of *Percnostola rufifrons* and *P. arenarum*.^a

	<i>P. r. rufifrons</i>	<i>P. r. subcristata</i>	<i>P. r. minor</i>	<i>P. r. jensoni</i>	<i>P. arenarum</i>
Bill Width	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 4	<i>n</i> = 8
Range	4.7–5.2	4.2–4.6	4.0–4.8	4.3–4.6	3.9–4.8
Mean ± SD	4.9 ± 0.2	4.4 ± 0.2	4.5 ± 0.3	4.4 ± 0.1	4.4 ± 0.3
Bill Depth	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 4	<i>n</i> = 8
Range	5.3–5.9	4.9–5.6	4.9–5.5	4.9–5.2	5.0–5.6
Mean ± SD	5.6 ± 0.2	5.4 ± 0.2	5.2 ± 0.2	5.1 ± 0.2	5.4 ± 0.2
Bill Length	<i>n</i> = 9	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 4	<i>n</i> = 8
Range	11.6–13.0	11.6–13.1	11.4–12.2	10.7–12.8	11.3–11.9
Mean ± SD	12.6 ± 0.5	12.4 ± 0.5	11.9 ± 0.3	11.5 ± 0.9	11.6 ± 0.2
Tarsus Length	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 5	<i>n</i> = 8
Range	27–30	28–30	26–29	28–29	27–28
Mean ± SD	28.6 ± 0.6	29.1 ± 0.8	27.2 ± 0.8	28.2 ± 0.6	27.6 ± 0.5
Tail Length	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 9	<i>n</i> = 5	<i>n</i> = 8
Range	61–66	59–66	48–50	45–52	49–51
Mean ± SD	63.5 ± 2.3	61.7 ± 2.3	49.0 ± 1.0	49.7 ± 3.0	50.0 ± 0.5
Wing Chord	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 6	<i>n</i> = 8
Range	68–73	64–73	64–67	63–69	65–69
Mean ± SD	71.0 ± 2.0	70.6 ± 2.7	65.3 ± 1.0	64.7 ± 2.0	66.6 ± 1.6
Crest	<i>n</i> = 10	<i>n</i> = 2	<i>n</i> = 8	<i>n</i> = 4	<i>n</i> = 7
Approx. Length	15	13	11	10	10

^a Sexes combined. Wing is unflattened wing chord; bill is measured at anterior nostril (see text). Approximate length of crest is the length of a central crown feather whose base is in line laterally with the anterior half of the eye. Because of the possibility of damaging specimens, the length of crown feathers was not obtained more precisely.

scured, all spectrograms of *P. arenarum* loudsongs could be distinguished by the authors from loudsongs of subspecies of *P. rufifrons* by note shape. Also, the overall pace (notes/s) of loudsongs of *P. arenarum* is significantly greater than that of *P. r. minor*, *P. r. subcristata*, and *P. r. rufifrons* (Table 2), but although the pace of loudsongs of *P. arenarum* typically is greater than that of *P. r. jensoni*, the loudsongs of the two taxa do not differ significantly in this characteristic. *P. arenarum* also has a short call that increases in frequency (*n* = 6, Fig. 3A), which also is easily distinguishable from the apparently homologous, chevron-shaped, short call (*n* = 3, Fig. 3C), an example of which was recorded for each *P. rufifrons* subspecies except *P. r. jensoni*. Larger sample sizes would be required to establish differences between *P. arenarum* and *P. rufifrons* in two other calls, a long call (*n* = 3 for *P. arenarum*, *n* = 5 for *P. rufifrons*, and *n* = 2 for *P. r. subcristata*, Fig. 3B and D) and a rattle (*n* = 5 for *P. arenarum*, and *n* = 1 each for *P. r. rufifrons*, *P. r. subcristata*, and *P. r. minor*; Fig. 3E and F), as they did not differ as obviously as the short call. The different lengths of the two rattles express individual variation within each taxon, not dif-

ferences between them. A list of recordings employed for all taxa with site locations, recordists, and archive locations is provided in the Appendix.

Description of holotype.—Color measurements were obtained with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) with a 3.0-mm aperture following the protocol of Graves (1999). Opponent-color coordinates (*L*, *a*, *b*) describe characters in terms of dark to light (0 to 100, low values are dark), red to green (positive if the color is red, negative if green, and near zero if neutral), and yellow to blue (positive if yellow, negative if blue, near zero if neutral), always in this sequence. Entire upperparts from the forehead to the upper surface of the rectrices are dark gray (23.4 + 1.1 + 0.9 on the center of the mantle), almost constant in intensity except slightly darker on the center of the crown (21.7 + 1.0 + 0.8) and slightly paler on the uppertail coverts, which are faintly tinged with reddish yellow-brown (25.2 + 2.2 + 6.6). The gray of the upperparts extends down to below the eyes, but the sides of the head are lighter than the crown and tinged yellow-brown (32.2 + 1.0 + 5.8). Crown feathers are gray to the base, and central crown feathers

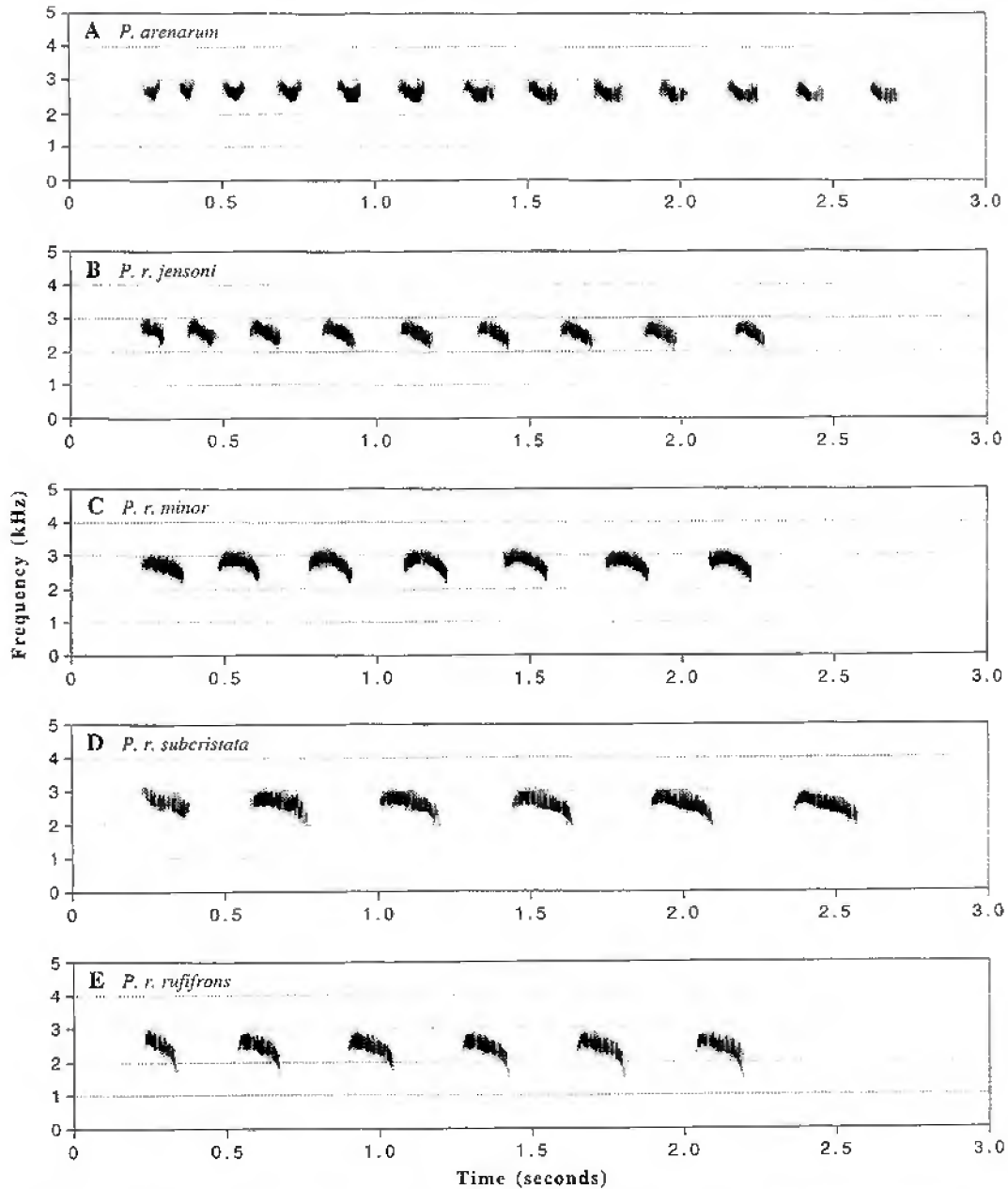


FIG. 2. Loudsongs of taxa in the *Percnostola rufifrons* species group (see Appendix for explanation of archive codes). (A) *P. arenarum*, Mishana, Loreto, Peru (JAA, ISL-JA.8:10). (B) *P. r. jensoni*, Río Apayacu, Loreto, Peru (Wiley ISL-MISC.6:45). (C) *P. r. minor*, opposite Isla Cigarrón, Amazonas, Venezuela (Schwartz MLNS 62051). (D) *P. r. subcristata*, Manaus, Amazonas, Brazil (BMW, ISL-BMW.104:25). (E) *P. r. rufifrons*, Acarai Mountains, Guyana (Braun, ISL-MJB.1:25).

TABLE 2. Pace of loudsongs of subspecies of *Pernostola rufifrons* and of *P. arenarum*. Mean \pm SD; range in parentheses. Sample sizes are number of individuals whose loudsongs were measured.

	Overall pace (notes/s) ^a
<i>P. r. rufifrons</i> (n = 8)	2.58 \pm 0.25 (2.36–3.13)
<i>P. r. subcristata</i> (n = 5)	2.44 \pm 0.12 (2.28–2.56)
<i>P. r. minor</i> (n = 14)	2.97 \pm 0.23 (2.67–3.31)
<i>P. r. jensoni</i> (n = 5)	4.21 \pm 0.17 (4.09–4.50)
<i>P. arenarum</i> (n = 24)	4.94 \pm 0.42 (4.37–5.98)

^a *P. r. jensoni* and *P. arenarum* differ significantly from the other three taxa using tests of significance described in Isler et al. 1998. These require that there can be no overlap of ranges and the smaller set of measurements (a) and the larger set (b) have to meet the requirement $\bar{x}_a + t_{\alpha}SD_a \leq \bar{x}_b - t_{\beta}SD_b$, where t = the t -score at the 97.5 percentile of the t distribution for $n - 1$ degrees of freedom.

whose base is on line laterally with anterior half of eye are approximately 10 mm long. Outer vanes of remiges are dark gray with paler gray margins (28.2 \pm 1.2 \pm 2.6 measured on folded wing) and margins are bluish gray except that the margins of the outermost five primaries are tinged brownish; inner vanes are

the same color as the back except for paler margins. Wing coverts are black (16.2 \pm 1.3 \pm 1.6) with reddish yellow-brown (slightly paler than color of underparts) 2.6-mm deep tips (measured at center of second feather in from outer wing edge) on the greater secondary coverts, 2.3-mm tips on the median secondary coverts, and 2.1-mm tips on the lesser coverts. Primary coverts are unmarked except outermost has thin (<1.0 mm) pale reddish yellow-brown outer edge. Alular quills are thinly (1.2 mm) whitish on outer edges. Underwing coverts are largely light reddish yellow-brown. Chin and center of throat are white tinged with reddish yellow-brown (62.7 \pm 4.1 \pm 25.0). Malar region, sides of throat, and breast are reddish yellow-brown (40.1 \pm 12.2 \pm 34.5). Sides and flanks are reddish yellow-brown infused with dusky (38.0 \pm 4.0 \pm 17.0) in a limited area. Center of belly is demarcated by a 10-mm wide by 15-mm long white patch. Posterior portions of belly and undertail coverts as well as tibial feathers are

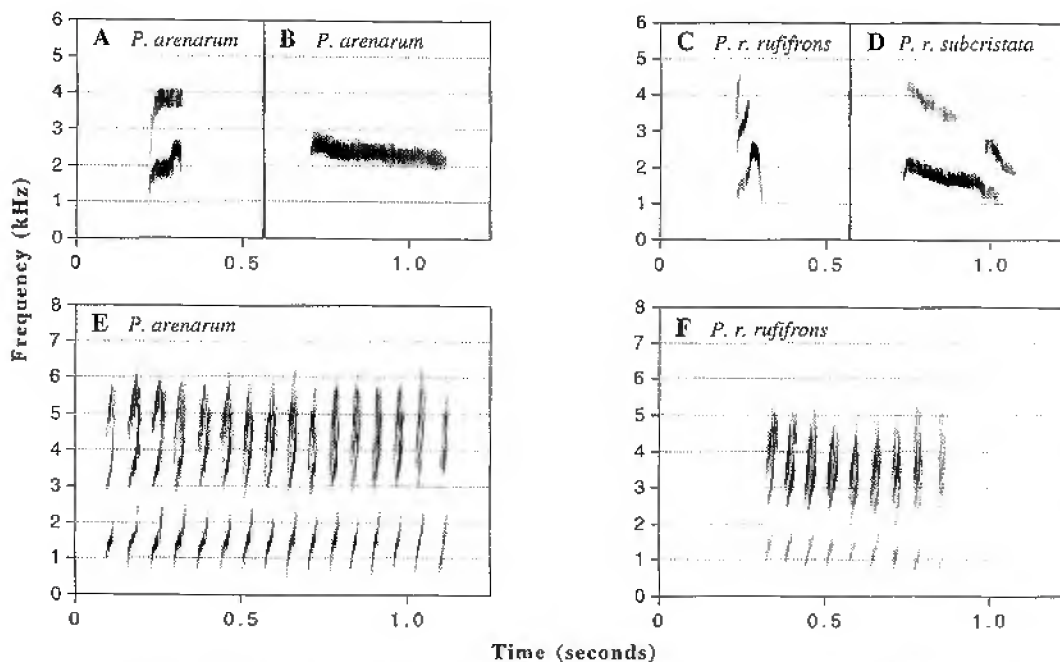


FIG. 3. Calls of taxa in the *Pernostola rufifrons* species group (see Appendix for explanation of archive codes). (A) *P. arenarum* short call, Mishana, Loreto, Peru (JAA, ISL-JA.8:10). (B) *P. arenarum* long call, Mishana, Loreto, Peru (JAA, ISL-JA.8:11). (C) *P. r. rufifrons* short call, Brownsberg Nature Reserve, Suriname (BMW, ISL-BMW.19:19). (D) *P. r. subcristata*, long call, Reserva Ducke, Amazonas, Brazil (Zimmer, ISL-KJZ.29:16). (E) *P. arenarum* rattle, Mishana, Loreto, Peru (JAA ISL-JA.8:14). (F) *P. r. rufifrons* rattle, Serra do Navio, Amapá, Brazil (Whittaker ISL-AW. 9:13).

similarly but less intensely colored than anterior underparts (38.2 + 6.6 + 22.8). Under-side of rectrices is slightly darker gray than upperparts (20.7 + 1.8 + 2.4). Soft parts in life were: iris gray with blackish tint to center, maxilla black with pale commissure, mandible bluish gray, tarsus bluish gray. Body mass was 24.2 g. Skull is "100% ossif." Liver tissue was saved in buffer (# 2-10-98) at the Field Museum of Natural History. Measurements of dried specimen are: wing (unflattened chord) 65 mm, tail 49 mm, tarsus 28 mm, bill length from anterior edge of the nares to tip 11.4 mm, bill depth at anterior edge of the nares 5.5 mm, and bill width at anterior edge of the nares 3.9 mm.

Description of allotype.—Adult male (skull "100% ossified"), MUSM No. 21107. Upperparts are dark gray; darkest on forehead, lightest on mantle; center of crown feathers, especially those nearer the sides of the head, slightly darker than edges. Central crown feathers whose base is on line laterally with anterior half of eye are approximately 10 mm long. Upperpart color measurements are as follows: forehead 15.3 + 0.7 + 0.4, center of crown 19.9 + 0.8 + 0.0, base of nape 21.2 + 1.0 + 0.7, center of mantle 24.0 + 0.7 + 0.1, center of rump 23.0 + 0.4 + 0.2, and uppertail coverts 22.4 + 0.7 + 0.2. Rectrices are dark gray (upper side 22.6 + 1.1 + 2.1, under side 24.7 + 1.7 + 3.1); outer two rectrices on each side have thin (<1 mm) light brownish gray tips. Lores and ear coverts are dark gray (20.5 + 0.7 + 0.6). Chin and throat are blackish (12.5 + 1.0 + 0.7). Remaining underparts are dark gray. Underpart color measurements are as follows: center of breast 23.2 + 0.5 + 0.0, center of belly 24.6 + 0.7 + 1.2, sides and flanks like breast and belly, and undertail coverts 23.0 + 0.9 + 1.7. Greater, median and lesser secondary wing coverts are black (13.3 + 1.5 + 1.3) with narrow (ca 1 mm) white margins at tips. Primary coverts are unmarked except outermost has thin (<1.0 mm) whitish outer edge. Alular quills have thin (<1.0 mm) whitish outer margins. Remiges are dark gray with thin (ca 0.7 mm) paler gray outer edges (color measurement on folded wing: 22.8 + 0.7 + 1.2), browner on distal edges of five outer primaries. Inner webs are brownish gray. Underwing coverts are gray (34.8 + 1.2 + 2.7). Soft parts from field notes were: iris

gray, bill black, tarsus bluish gray, and soles buff. Body mass was 22.9 g. Length of freshly collected specimen was 147 mm. Measurements of dried specimen (same dimensions as for holotype) are: wing 68 mm, tail 50 mm, tarsus 27 mm, bill length 11.7 mm, bill depth 5.4 mm, and bill width 4.4 mm.

Plumage variation.—Four additional males and two additional females were examined. They were collected by JAA at the type locality or at Nuevo Tarma, 03° 48' S, 74° 21' W, and they are similar to the holotype and allotype except as follows. One female (MUSM 21100) has upperparts from crown to tail slightly tinged brownish; no skull ossification data was provided for this specimen, and it may represent a subadult plumage. One male (MUSM 21103), collected at the type locality, is slightly darker over the entire plumage. Combined measurements for the eight specimens are provided in Table 1. Body mass (all specimens, male and female combined) was: mean = 23.0 g ± 1.0 SD, range 21.3 to 24.3 g, $n = 8$.

Distribution.—Known from only Loreto, Peru, from the drainage of the Río Nanay west to the left bank (as one faces downstream) of the Río Tigre, including Nauta on the left bank of the Río Marañón between those rivers (Fig. 4). The specimen from Nauta, Loreto, Peru, collected by Bartlett in 1865 and currently located at the Museum of Natural History (BMNH 69.5.25.46), was tentatively assigned to *P. r. jensoni* by Capparella et al. (1997). This specimen, a male in poor condition, was carefully reexamined for this paper by C. Milensky who prepared drawings of and photographed the crown feathers. The photographs and drawings were compared to crown feathers of specimens of *P. arenarum*. The bases of the crown feathers of the Nauta specimen are dark gray as in *P. arenarum*, not black as in *P. r. jensoni*.

Etymology.—The name of the new species is derived from "arena" meaning "sand" in Latin, reflecting the podzolic and quartzitic soils of the principal habitat in which the species was found. The English name provides recognition to the Zona Reservada Allpahuayo-Mishana, a newly established national reserve that includes the heart of the known range of *P. arenarum*, and a reserve which

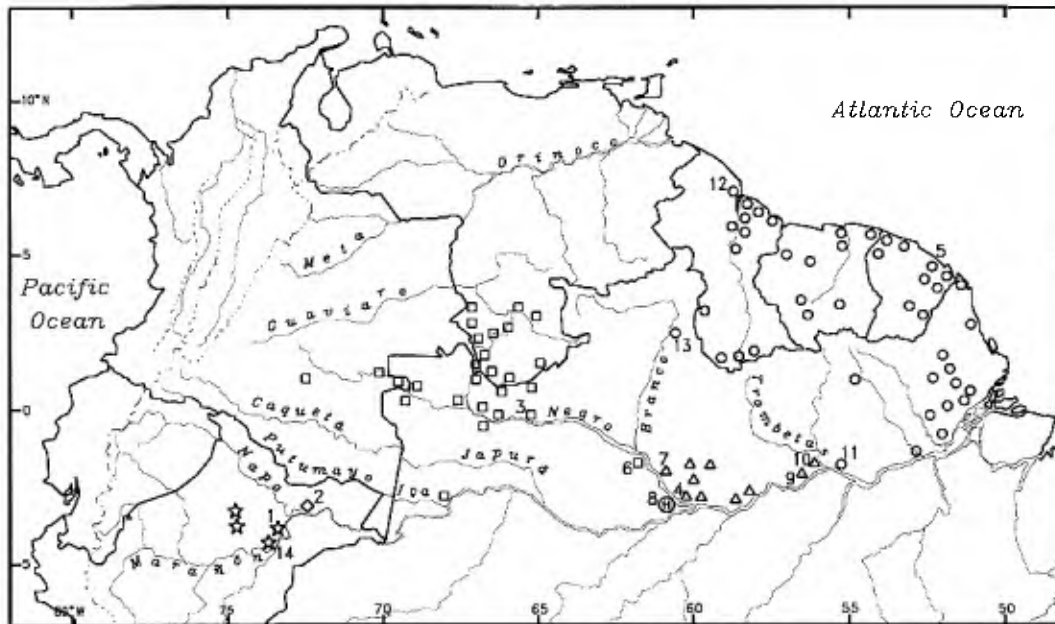


FIG. 4. Distribution of taxa in the *Percnostola rufifrons* species group. Symbols represent the occurrence of taxa within small geographic sectors (see Isler 1997). Symbols: stars = *P. arenarum*, diamond = *P. r. jensoni*, squares = *P. r. minor*, triangles = *P. r. subcristata*, circles = *P. r. rufifrons*, and H in a circle = hypothetical record. Numbers: (1) Mishana, Loreto, Peru, type locality of *P. arenarum*; (2) Quebrada Orán, Loreto, Peru, type locality of *P. r. jensoni*; (3) Santa Isabel = Tapurucuará, Amazonas, Brazil, type locality of *P. r. minor*; (4) Barra do Rio Negro = Manaus, Amazonas, Brazil, type locality of *P. r. subcristata*; (5) Cayenne, French Guiana, type locality of *P. r. rufifrons*. Other localities mentioned in the text are: (6) Parque Nacional de Jaú, Amazonas, Brazil; (7) right bank Rio Apuaú, Amazonas, Brazil; (8) Cacao Pereira, Amazonas, Brazil; (9) Faro, Pará, Brazil; (10) a little to the west of the mouth of the Rio Trombetas, opposite Oriximina, Pará, Brazil; (11) vicinity of Óbidos, Pará, Brazil; (12) Supenaam River, Guyana; (13) Colônia Confiança and Rio Quitanaú, east of the Rio Branco, Roraima, Brazil; and (14) Nauta, Loreto, Peru.

JAA, its discoverer, was instrumental in establishing.

DISCUSSION

Distribution of members of the species group.—The distributions of *P. r. rufifrons* and *P. r. subcristata* (Fig. 4) appear to meet at the Rio Trombetas to the east of Faro, Pará, Brazil, as first suggested by Pinto (1947). Otherwise, a large gap in their known ranges occurs south of the Guianas in northern Pará, Brazil, where little collecting was done. Caparella et al. (1997) described the western edge of the range of *P. r. rufifrons* as the Essequibo River in Guyana, but as shown on Fig. 4 there are multiple records to the west of the river starting near the coast on the Supenaam River (Chubb 1921). Sight records (Stotz 1997) from Colônia Confiança and Rio Quitanaú, east of the Rio Branco, Roraima,

Brazil, are assumed to be *P. r. rufifrons* based on proximity to Guyana.

A broad region that includes southern Bolívar, Venezuela, and Roraima, Brazil, west of the Rio Branco, separates the known ranges of *P. r. minor* and *P. r. rufifrons* (Fig. 4). However, the ranges of *P. r. minor* and *P. r. subcristata* come into close proximity along the Rio Negro, Amazonas, Brazil. Recently, *P. r. minor* was found at the Parque Nacional de Jaú, west of the Rio Negro (Borges et al. 2001, C. Marantz pers. comm.). To the east of the Rio Negro, *P. r. subcristata* was found north of Manaus on the right bank of the Rio Apuaú near its junction with the Negro (sight record; M. Cohn-Haft pers. comm.). A specimen of *P. r. subcristata* (AMNH) reported from "Cacau Pereira" (= Cacao Pereira), on the right bank of the Rio Negro opposite Manaus (where no taxon in the complex was

found despite extensive recent field studies; M. Cohn-Haft pers. comm.) was likely to have come from across the river where *P. r. subcristata* is common. Thus, the geographic ranges of *P. r. subcristata* and *P. r. minor* appear to be delimited by the lower Rio Negro, which is extremely wide at this point and which incorporates the group of islands known as the Arquipélago das Anavilhanas, making a formidable barrier between the two taxa.

The region separating the known ranges of *P. r. minor* and *P. r. jensoni* is, for the most part, poorly known ornithologically. The suggestion by Capparella et al. (1997) that the Putumayo/Iça river may mark the extent of the ranges of *P. r. minor* and *P. r. jensoni* requires substantiation, as does the likelihood that the Rio Napo defines the ranges of *P. r. jensoni* and *P. arenarum*. In the regions that appear to separate *P. r. minor*, *P. r. jensoni*, and *P. arenarum*, none of these taxa was found in heavily studied locations such as the Leticia region on the Amazon in Colombia, Quebrada Sucusari on the left bank of the lower Río Napo in Peru, or Libertad on the opposite bank of the Río Napo, but these locations appear to lack sandy soil habitats which may be a requirement of these taxa (as discussed below).

Morphological distinctions among members of the species group.—As with numerous other thamnophilid antbird species (Hellmayr 1929), subspecies of *P. rufifrons* were distinguished primarily by female plumages (Fig. 1) and lengths of crown and tail feathers of both sexes (Table 1). Seven unique morphological character states distinguished *P. arenarum* from all four subspecies of *P. rufifrons* whereas no subspecies of *P. rufifrons* was uniquely distinguished by more than two character states. Of the remaining characters listed in Fig. 1, one (female color of sides of head) was shared by only *P. arenarum* and *P. r. jensoni*, and three were shared uniquely by *P. arenarum*, *P. r. minor*, and *P. r. jensoni*. In contrast, *P. r. minor* and *P. r. jensoni* uniquely shared five characters and were distinguished from each other by two (female color of crown and female color of side of head). Note that Fig. 1 does not separate *P. r. minor* and *P. r. jensoni* by male crown color, even though Capparella et al. (1997) distinguished the two taxa

by the width of gray tips of the male crown feathers. Upon examination of additional specimens of *P. r. minor*, we found overlap with *P. r. jensoni* with respect to this feature, even though in general *P. r. jensoni* male crown feathers have wider gray edges than those of *P. r. minor*. Finally, *P. r. rufifrons* and *P. r. subcristata* resembled each other closely, uniquely sharing seven of the eleven characters listed in Fig. 1 and differing in only two (length of crown feathers and female crown color).

Vocal distinctions among members of the species group.—As described above, three characters (loudsong pace and note shape and short call note shape) distinguished the vocalizations of *P. arenarum* from all *P. rufifrons* subspecies except that loudsong pace was not diagnosable between *P. r. jensoni* and *P. arenarum* (Table 2), and short calls were unrecorded for *P. r. jensoni*. In contrast, we found no diagnosable differences between the vocalizations of *P. r. rufifrons* (32 recordings), *P. r. subcristata* (24 recordings), and *P. r. minor* (24 recordings). The loudsong of *P. r. jensoni* (6 recordings) differed from the other subspecies of *P. rufifrons* on one character, loudsong pace. Lengths of individual loudsong notes of *P. r. jensoni* were significantly shorter than note lengths of the other three subspecies of *P. rufifrons*, but this was considered of dubious value as a character independent of loudsong pace. The small sample of recordings of *P. r. jensoni* calls leaves open the possibility of further differences in vocalizations between it and the other subspecies of *P. rufifrons*.

Behavioral distinctions among members of the species group.—Two behavioral characteristics distinguished *P. arenarum* from subspecies of *P. rufifrons*. First, while foraging, *P. r. rufifrons*, *P. r. subcristata*, and *P. r. minor* pumped their tails downward rapidly and raised them slowly (BMW pers. obs.) whereas *P. arenarum* exhibited no stereotyped tail movement while foraging. We lack information regarding tail movements of *P. r. jensoni*. Second, we never observed *P. arenarum* at army ant swarms which, however, occurred rarely in its preferred habitat. Except for *P. r. jensoni*, other subspecies of *P. rufifrons*, especially *P. r. rufifrons* and *P. r. subcristata*, sometimes spend about as much time foraging

over ant swarms as foraging away from ants (Willis 1982) and have been considered "professional" ant followers (Oniki and Willis 1972, Haverschmidt and Mees 1994, Willis and Oniki 1978). With regard to *P. r. jensoni*, R. H. Wiley (pers. comm.) recently followed two army ant raids (at different locations during different years) for 1–2 h each within 100–200 m of locations where *P. r. jensoni* was singing. In neither instance did *P. r. jensoni* join the other species following the ant swarms. It appears that either *P. r. jensoni* did not usually accompany army ants or that the ant raids were outside territories that the birds were reluctant to leave.

Otherwise, behavior of *P. arenarum* resembled that of subspecies of the *P. rufifrons* as described by Willis (1982). Foraging took place almost always ≤ 1 m from the ground as birds moved very quickly, leaping from one sapling or branch to another. They sometimes sallied to the ground to capture prey, and then returned immediately to a perch above the ground, which is typical behavior of *P. r. rufifrons*, *P. r. subcristata*, and *P. r. minor* over ants. As with related taxa, *P. arenarum* also searched for prey by perching on fallen saplings or on the ground, moving with short hops of a few centimeters, head and tail held at and slightly below parallel with the ground. Leaves on the ground were brushed aside or grasped briefly and moved aside with the bill to reveal hiding prey items, although the birds did not manipulate leaf litter with their feet (i.e., no scratching or shuffling). They traveled in pairs or small groups, apart from mixed species flocks, as do subspecies of *P. rufifrons* except when they associate with other species at ant swarms. Pair members sometimes foraged within a few meters of one another but frequently were more than 10 m apart, sometimes up to 40 m, keeping in contact vocally as they moved quickly through their territory. While singing, all members of the species group (lacking data for *P. r. jensoni*) pumped the tail downward with each note in the song. Birds typically sang from slightly elevated perches, up to about 1 m above ground.

Habitat distinctions among members of the species group.—*P. arenarum* was found primarily in a very dense and stunted (canopy height lower than 10 m, often lower than 5 m) terra firme forest, of a type called *varillal* by

local inhabitants, that grows on nearly pure white sandy soil. In every *varillal* in which *P. arenarum* was found, the understory was dominated by saplings of white sand specialists, e.g., the palm *Euterpe catinga* (Palmae) and *Caraipa* spp. (primarily *C. utilis*; Clusiaceae). It sometimes inhabited *varillales* containing emergent trees (*Caraipa tereticaulis*) to 20 m or more, but only if a dense understory predominated. It occurred rarely in a nutrient poor habitat, locally called *irapayal* and consisting of taller forest with a dense understory of the irapay palm (*Lepidocaryum tenue*) that grows on very old, weathered clay soils as well as sandy soils. Occurrence in *irapayales* was extremely local; *P. arenarum* was absent from most stands of this habitat. More information on the edaphic nature and floristic components of *varillales* and *irapayales* was provided by Whitney and Alvarez (1998). The likelihood that *P. arenarum* is confined to these habitats also is supported by its apparent absence from the adjacent intensely ornithologically surveyed region immediately to the east of its known range (between Iquitos and the Río Napo) where these habitats seem to be missing. The habitat of *P. arenarum* possibly is relictual, its distribution reflecting an ancient branching, as was suggested for *Herpsilochmus gentryi*, the other recently described thamnophilid found in the same habitats (Whitney and Alvarez 1998).

Nothing was known previously of the habitat preferences of *P. r. jensoni* as the original description (Capparella et al. 1997) lacked such information. Subsequently, R. H. Wiley (pers. comm.) repeatedly encountered *P. r. jensoni* near the type locality from 1999 to 2000. One population occurred in an *irapayal* on sandy soils where the birds were territorial and fairly numerous. However, *P. r. jensoni* also was found in nearby habitats that were on apparently different soils. Wiley's impression was that *P. r. jensoni* occurs on sandy soils but was not completely restricted to them.

The remaining taxa were found in a variety of habitats with dense understory, including forest edge, second growth, low stands around rock outcroppings, and tree falls and brush piles within forest (Willis 1982, Thiollay 1994, Tostain et al. 1992). It seems likely that sandy soils underlie many of these habitats as

such soils are common in the Guianan shield. In particular, *P. r. rufifrons* was found in savanna forests in the broad sandy plain that borders the Caribbean Sea in Suriname (Haverschmidt and Mees 1994) and in mature mangrove stands of the sandy shore of French Guiana (Tostain 1986), and *P. r. minor* was found to prefer sandy soil forests in Vaupés in extreme eastern Colombia (Hilty and Brown 1986, S. Hilty pers. comm.). However, neither of these subspecies appears to have a narrow or specialized habitat requirement. Although habitat preferences of *P. rufifrons* have not been described in sufficient detail to permit certainty, it appears that *P. arenarum* is more of a habitat specialist.

Conservation.—Unless *P. arenarum* is found elsewhere, the species may occupy one of the most specialized habitat niches in the smallest geographic range of any thamnophilid antbird (another candidate for this unfortunate distinction is the Marsh Antbird *Stymphalornis acutirostris* of southeastern Brazil; Bornschein et al. 1995). The habitats in which *P. arenarum* is found are subject to intense human activity in a region of rapid population growth. Currently, *varillal* is heavily exploited for poles for building houses, and the leaves of the irapay palm are extensively harvested to make thatched roofs. Complicating the threat, the new species has been found only in certain *varillales* and even fewer *irapayales*, despite the intensive ornithological surveys by JAA in the Tigre and Nanay river basins. A critical step in its conservation was the recent establishment of the Zona Reservada Alpahuayo-Mishana, which includes much of the known range of *P. arenarum* and which harbors other species (e.g., *Herpsilochmus gentryi*) restricted primarily to white sand habitats in this region of Amazonia. The important action by the government of Peru in establishing the reserve now must be followed with resources to protect it. Until additional steps are taken to maintain its population, we recommend that *P. arenarum* be regarded as “endangered” as defined by the International Council for Bird Preservation (Collar et al. 1992), i.e., a taxon “in danger of extinction and whose survival is unlikely if causal factors continue operating.”

Species status of populations.—Rigorous requirements for establishing species status in

allopatric populations under the Biological Species Concept (BSC) demand that vocal, behavioral, and/or genetic characters distinguish the populations of morphologically similar taxa (Johnson et al. 1999). We developed guidelines for employing vocal characters to assess species limits in allopatric thamnophilid antbird populations (Isler et al. 1998, 1999). The guidelines were derived from analyses of the extent of differences in vocalizations of sympatric pairs of closely related antbird species. Employing these guidelines, the present analysis showed that *P. arenarum* was distinct vocally from *P. rufifrons*. Given that *P. arenarum* also differed from *P. rufifrons* in a number of morphological and behavioral characters, we have no hesitation in recommending that *P. arenarum* be recognized as a distinct species.

Regarding subspecies of *P. rufifrons*, only *P. r. jensoni* exhibited any vocal distinctions (one character deemed inadequate to support species status although calls are yet to be recorded) and possible behavioral differences, although field studies of *P. r. jensoni* were too preliminary to be definitive. The recommendation of Capparella et al. (1997) that *P. r. rufifrons* and *P. r. subcristata* should be considered specifically distinct from *P. r. minor* and *P. r. jensoni* based on morphology was not supported by vocal differences between these two groups of taxa. Given the paucity of vocal distinctions, and in the absence of other substantiated behavioral or genetic evidence, we recommend that *P. r. rufifrons*, *P. r. subcristata*, *P. r. minor*, and *P. r. jensoni* continue to be recognized as subspecies of *P. rufifrons* under the BSC.

Under the Phylogenetic Species Concept (Zink and McKittrick 1995), all four subspecies of *P. rufifrons* would be considered species given the diagnostic morphological differences among them.

Remarks.—Assessments of species limits under any criteria in poorly studied regions of the Neotropics are subject to revision upon additional information, and it is worthwhile to identify particular regions in which field studies might shed light on species limits among subspecies of *P. rufifrons*. Despite the few morphological differences (two characters) between *P. r. rufifrons* and *P. r. subcristata*, given the close proximity of their ranges near

the Rio Trombetas (Fig. 4), it is possible that they intergrade or that they come together without intergradation in parapatry or sympatry; surveys of the Rio Trombetas region could help resolve this question. To the west, further surveys are needed in the region west of the Rio Branco and north of the Rio Negro that separates *P. r. minor* from *P. r. ruffifrons* and *P. r. subcristata*. Geographic ranges of *P. r. minor* and *P. r. jensoni* and of *P. r. jensoni* and *P. arenarum* could be separated by the Río Putumayo/Iça and Río Napo, respectively, and additional field work in the region between the Río Napo and the Río Caquetá/Japurá should aid in understanding relationships among these taxa. Finally, recordings of additional types of vocalizations as well as additional behavioral data for *P. r. jensoni* might provide a basis for its reassessment as a distinct species.

With or without the acquisition of new distributional and behavioral information, genetic studies are needed to facilitate understanding of phylogenetic relationships of the species group, which is of special interest given substantial morphological differences among subspecies of *P. ruffifrons* that is unaccompanied by diagnostic vocal distinctions. Such studies should include a number of possibly related outgroups, as the genus *Percnostola* (sensu Peters 1951) may be polyphyletic.

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APPENDIX

The following list identifies recordings used in this study by taxon, country, state or department, recording location, and recordist. Numbers following the recordist name identify the number of cuts per recordist per location. Acronym for recording archive: MLNS = Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca. ISL = recordings not yet archived in an institutional collection but that have been copied into the inventory maintained by the MRI and PRI. Many of these recordings will be archived by the recordists.

Percnostola r. rufifrons, 32 recordings. BRAZIL: Amapá: Porto Grande (K. Zimmer 4, ISL), Serra do Navio (J. F. Pacheco 3, ISL; K. Zimmer 3, ISL; A. Whittaker 2, ISL). Pará: Porto Trombetas (J. F. Pacheco 2, ISL). GUYANA: Acarai Mountains (M. Braun 4, ISL; C. Milensky 2, ISL), Sipu River (M. Braun 2, ISL). SURINAME: Brownsberg Nature Reserve (T. Davis 2, MLNS; MLI 1, MLNS; BMW 4, ISL), Base of Voltzberg (BMW 1, ISL), Zanderij Airport (BMW 2, ISL).

Percnostola r. subcristata 23 recordings. BRAZIL: Amazonas: Reserva Ducke (J. Pierson 1, ISL; P. Schwartz 1, MLNS; K. Zimmer 4, ISL), Manaus (BMW 4, ISL; K. Zimmer 1, ISL), 60–90 km north of Manaus (R. Bierregaard 4, MLNS; M. Cohn-Haft 4 MLNS; BMW 1, ISL), Presidente Figueiredo (K. Zimmer 3, ISL).

Percnostola r. minor, 24 recordings. BRAZIL: Amazonas: São Gabriel do Cachoeira (M. Cohn-Haft 1, ISL; K. Zimmer 11, ISL), 40 km north of São Gabriel do Cachoeira (BMW 3, ISL), left bank of Rio Negro opposite São Gabriel do Cachoeira (BMW 3, ISL; K. Zimmer 1, ISL). COLOMBIA: Vaupés: Mitú (S. Hilty 2, ISL). VENEZUELA: Amazonas: opposite Isla Cigarrón (P. Schwartz 2, MLNS), Pico San Carlos (P. Schwartz 1, MLNS).

Percnostola r. jensoni, 6 recordings. PERU: Loreto: Río Apayacu (R. H. Wiley 6, ISL).

Percnostola arenarum, 45 recordings.

PERU: Loreto: left bank Río Tigre opposite mouth of Río Corrientes (JAA 1, ISL), upper Río Tigre (JAA 1, ISL; BMW 1, ISL), El Dorado (JAA 5, ISL), El Milagro (JAA 1, ISL), El Tigre (JAA 1, ISL), Expetroleros (JAA 3, ISL); Intuto (JAA 1, ISL), location unknown (JAA 5, ISL), Lores (JAA 2, ISL; BMW 1, ISL), Mishana (JAA 20, ISL), San José (JAA 1, ISL), Varillal Palometa (JAA 1, ISL), Yuto (JAA 1, ISL).