Geographic variation in the Rufous-webbed Tyrant *Polioxolmis rufipennis*, with description of a new subspecies

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The Rufous-webbed Tyrant *Polioxolmis rufipennis* (previously in *Myiotheretes* or *Xolmis*—see Smith & Vuilleumier 1971, Traylor 1977, Lanyon 1986) is a large and conspicuous tyrant flycatcher inhabiting the high Andes of Bolivia and Peru. Although recorded only from few and widely scattered localities, no geographic differentiation has been noted. Zimmer (1937), in his review of Peruvian fluvicoline flycatchers, did not comment on this species, and it is currently recognized as monotypic (Traylor 1979).

In connection with a general study of the population structures of bird species associated with high-elevation remnant woodlands in Peru and Bolivia I examined the great majority of museum specimens of the Rufous-webbed Tyrant, and was surprised to find a clearcut geographic differentiation. This pattern is described here, together with a few biological data on this poorly known bird.

Materials

This study is based on the field experience from travels together with Niels Krabbe and others in 1983/84 and 1987, and on studies of museum specimens by myself.

Examined specimens were birds collected in 1983, -87, -89 for the Zoological Museum, University of Copenhagen (ZMUC), and study skins from: the Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); British Museum of Natural History, Tring (BMNH); Carnegie Museum, Pittsburgh (CMP); Field Museum of Natural History, Chicago (FMNH); Institut Royal des Sciences Naturelles de Belgique, Bruxelles (IRSNB); Louisiana State University Museum of Zoology, Baton Rouge (LSUMZ); Musee de Histoire Naturelle, Paris (MHNP); Museo de Historia Natural de la UNMSM, "Javier Prado", Lima (MHNJP); and the Swedish Museum of Natural History, Stockholm (SMNH). (This species was lacking in some other institutions visited.) Altogether 74 specimens were examined. Measurements taken were exposed culmen, tarsus, wing length (cord), tail length and width of the dark distal tail-bar (measured from the narrowest point, parallel with the shaft, to the distal feather edge, and on the outer rectrix). The wing formula and outline of the dark pattern on the outer tail-feathers were recorded. Capitalized colour names refer to a direct comparison with the colour standards of Ridgway (1912).

Distribution and habitat requirements

In **Peru**, specimen records are from the West Andes in Cajamarca (Huacraruco, Hacienda Taulis, Sendamal and near Celendin), La Libertad (Huamachuco, Quirivilca), Ancash (above Huaylas, Quebrada Pucavado, Rio Pumamarca), Lima (upper Santa Eulalia Valley and Hortical in the Cañete drainage) and Ayacucho (Pampa Galeras, Quebrada Queñua); in the **Central Andes** in Amazonas (Atuén), La Libertad (Tayabamba), Pasco and Junin (Huanuco mountains, Chipa, east of Concepción above Huariaca), Huancavelica (Huancavelica) and in Apurimac (Pomayaco, Runtacocha, Chipimarca); and in the **East Andes** in Cuzco (Cachupata, Abra Malaga, Patallacta) and Puno (Checayani). Sight records from other places in Lima, western Ayacucho and Puno are given in Fjeldså (1987). R. A. Hughes has a sighting as far south as Cruz de Condor in Arequipa.

Bolivian specimen records are from western Oruro (Carangas near Nevada Sajama), in the Cordillera Real of La Paz (4 road km W Pongo, 10 miles N Viloca) and Cochabamba (Choro in Ayopaya), in sheltered valleys along the watershed of the Tunari range in Cochabamba and in the rainshadow of central Cochabamba (Cochabamba, Cerro Blanco, above Tutimayo, Colomi, Salto Pampa, Tiraque, Incachaca, Parrasco near Lopez Mendoza, Cuchacancha) and Samaipata in adjacent Sta Cruz. The species is also recorded in Potosi (Finca Salo, Oploca).

Typically in Peru it occurs at around 4000 m on slopes with light *Polylepis* woodlands surrounded by puna grassland and rocky terrain with occasional cacti, scrubs and *Puyas*. Often the territory includes high rock-walls and narrow rocky ridges adjacent to *Polylepis* patches. In the breeding season, the species seems to be narrowly restricted to the edges of *Polylepis* woods or to areas with scattered, park-like *Polylepis* vegetation, sometimes with the giant bromeliad *Puya raimondii* admixed. In most of Peru, these woodlands are isolated well above the cloud and elfin forests. On the Pacific slope, the *Polylepis* habitats usually lie near the upper fringe of the zone of frequent mists, but well above the relict patches of true cloud forest and also somewhat isolated from shrub-steppe habitats. This isolation of the breeding habitat may be a main reason for the apparent specialization of the Rufous-webbed Tyrant to *Polylepis* woodlands (see Vuilleumier's (1986) view of the evolution of specialization to *Polylepis* in birds).

In Cochabamba in Bolivia most records of Rufous-webbed Tyrants are at 3000–3800 m, from places where the *Polylepis* grows interspersed in a more varied scrubby vegetation, with small acacia-like trees and *Barnadesia* scrub. The valleys in this southern part of the range have a vegetation continuum from lower-temperate thorny scrub mixed with *Polylepis* to pure *Polylepis* shrub on the edge of the Altiplano. The Rufous-webbed Tyrant may hardly reach elevations with pure *Polylepis* stands, maybe because these habitats are, in general, biologically very poor.

The only nest of the Rufous-webbed Tyrant found (15 February 1987, with 2 fledglings) was in a tiny patch of *Polylepis* trees in a small stream ravine on a puna slope. It was a rather flimsy and open cup of stalks and thin twigs placed just below the top of a 5 m-tall tree overhanging the stream.

The Rufous-webbed Tyrant hunts hovering, like a kestrel, or using hanging hover on aerial updraughts (Fjeldså & Krabbe in press). A bird may also watch from a conspicuous perch in a bush-top or a projection on a rocky slope or rock-wall, to glide down to take prey from the ground. In open country it sometimes watches from hummocks and makes short runs and sallies. The need for updraughts and elevated hunting posts may be a main determinant of its selection of rocky walls and ridges in the rolling grasslands and semideserts characterizing the high Andes. However, it is difficult to see how *Polylepis* trees as such can have any significance in relation to the feeding ecology. Thus, although the species seems to have developed a very strong (if not total) attachment to *Polylepis* stands for breeding, it probably roams some distance away from these woodlands when not breeding. Many specimen records from the dry non-breeding season are from places with fields, xeric stream valleys and from humid treeline habitat around 3000 m—in Peru at Huacraruco, Atuén, Pomayaco and Cachupata, and in Bolivia where there are records from humid montane forest habitat at Aduana above Incachaca.

The sparse records of the Rufous-webbed Tyrant to a considerable extent may be a result of a paucity of observations in its steep and difficult habitat. Even in the most suitable habitat, the species holds large territories, and has a very low population density. Many *Polylepis* patches are isolated by tens of kilometers from the next patch. However, the long wings and good flying powers of the Rufous-webbed Tyrant (Fitzpatrick 1985), and its ability to leave the core habitat at least seasonally, should permit some gene-flow contact between local populations. The species must be expected to have been much more widespread previously than today, since the patchiness of forest habitats in part results from human activity, from pre-Incaic times up to the present (Ansion 1986, Fjeldså 1987).

Character variation

Measurements. The sexual dimorphism in measurements is slight through Peru, but increases southwards. For the West Andes from Cajamarca to Lima, the mean wing length of 7 ♂♂ is 131.9, of 6 ♀♀ 128.9 mm; 15 Bolivian ♂♂ have the mean 124.1, 15 ♀♀ 116.3 mm; for the isolated southernmost site, Oploca, 2 ♀♀ have wings 101.5 and 104 mm, 2 ♂♂ 124 and 125 mm. A similar variation is found in other measurements, males being slightly larger than females, a difference that is most pronounced furthest south. The material is insufficient for a sex-separated analysis of character variation; however, it is worth noting that the male: female ratio of museum specimens examined is 0.65 for the Peruvian material, 1.36 for Bolivian material.

The local variation in wing- and tail-length is given in Table 1. Other measurements show a similar pattern of differentiation. Clearly, birds from the northern part of the range average largest (despite the low fraction of males in the data), those from the East Andes zone of Bolivia small. There is much individual variation in southern and central Peru.

Omitting 4 specimens from near the borderline (3 from Puno, 1 from Oruro), the average wing-length, with standard deviation, is 129.1,

TABLE 1
Local variation in wing and tail length (mm), and width of the tail bar (mm), in the Rufous-webbed Tyrant *Polioxolmis rufipennis*

	n	Wing	Tail	Tail bar
Cen. Andes of Amazonas + Libertad	2	131, 133	92, 93.4	23.5, 24
W. Andes of Cajamarca + Libertad	10	129.4–133	86.2–99	17.5–24.7
Ancash to W Ayacucho	8	127–135	92–97	19–28
Pasco, Juin + Huancavelica	4	128–132	91.3–96.8	19.5–23
Apurimac	6	120–130.5	95.5–110.5	22–25
Cuzco	3	126.5–130	88.5–97	19–23
Puno	3	117–131	?	6–8
W. Oruro	1	134	96.2	18
E. Cordilera of N. Bolivia	6	119.2–126.5	85.9–90	6–18
Tunari area	11	113–126.2	84–90.6	9–16
Lower Cochabamba	11	112.5–128	83–88.8	11–16
Potosi	4	101.5–125	88–91.5	11–16

s.d. ±3.5 mm for Peru, 120.5 ±6.2 mm for Bolivia. The calculated joint non-overlap for the 2 series is 82% for the wing-length (82% for ♂♂, 87% for ♀♀), 90% for tail length. Comparing birds from the West Andes with those from the East Andes of Bolivia, there is no overlap at all. The wing formula did not show clearcut regional differences.

Colours. Bill and feet are black (gape pale olive towards flesh), the eyes brownish white to pale grey-brown (unlike the dark-eyed *Myiotheretes* and *Cnemarchus*, though a fledgling had dark brown eyes, with yellow mouth and cutting edges of both mandibles). The plumage is generally dark sooty grey, lightest below, becoming pinkish buff on the central belly and vent; the underside of wings and tail are extensively cinnamon-rufous, except for a dark distal bar and dark central pair of tail-feathers. The juvenile plumage (3 specimens, January–February) is slightly warmer hued, the throat less clearly streaked, but the breast appearing slightly spotted, owing to a faint buffy tinge on the feather edges.

There is an absolutely constant geographic difference. Peruvian birds (and the one from western Oruro) were deep neutral grey above, giving a very uniform, smooth, bluish slaty impression. All Bolivian birds and specimens from Puno Peru (Azangaro) are slightly lighter and duller grey, as if slightly tinged brownish, and the feathers of the breast often have definitely lighter, more buffy feather-sides causing faint streaking. This state is approached only in juvenile birds from Peru.

The tail-bar (as defined in the introduction) is 17.5–30 mm wide (mean 22.0, s.d. ±3.0 mm) in most of Peru, against 6–16 (18) mm (mean 12.1 ±2.9 mm) in Puno and Bolivia (Table 1). Variations in the outline of the bar (e.g. whether the dark colour curves up along the shaft or inner edge of the feather, or not) do not follow a geographic pattern.

Discussion

The character expression is fairly constant in northern Peru and southwards in the West Andes, while birds from the East Andes zone of Bolivia show other character states (with a greater variance owing to more marked

sexual dimorphism). Birds from Apurimac to Puno in southern Peru show somewhat variable size; however, if also the colouration is considered, the differentiation is very abrupt. Regarding the width of the tail-bar, only one bird from Cordillera Real in La Paz (bar 18 mm wide) causes overlap with birds from north of the Raya pass between Puno and Cuzco. Three birds from Puno are transitory by size, but have narrow tail-bars. Birds from Cuzco show slightly narrower tail-bars than those from further north. Gene flow could be expected to take place easily all the way along the East Cordillera from La Paz to Cuzco.

The variation is not simply correlated with climate, as both morphological groups range from semi-humid to arid climates. Considering the dispersal potential and lack of particularly large range disjunctions in southern Peru (except probably on the Pacific slope), the pattern of differentiation is difficult to explain. As the habitat was clearly more widespread in the past than today, there is no obvious explanation in the near past. Maybe the topography and climatic oscillations, in combination, caused larger disjunctions sometimes in the far past than today. This is suggested by the phytogeographic patterns with some *Polylepis* species typical of the Peruvian cordilleras (*P. subsericans, incana* and *racemosa*), and other species typical of Bolivia and the altiplanos and southern Peru (*P. besseri, tarapacana* and *tomentella*) (see Simpson 1986 and new distributional records in Fjeldså 1987). However, a specific scenario of differentiation is difficult to hypothesize before the population structure has been worked out for additional *Polylepis*-adapted birds.

I will classify the populations as follows:

Polioxolmis rufipennis rufipennis Taczanowski, 1874 Proc. Zool. Soc. London: 134 Maraynioc, Peru. Type formerly Warshaw Museum, now lost.

Diagnosis. Large (wing 120–135 mm, mean 129.1, s.d. ±3.5 mm), above Deep Neutral Grey to Slate Colour, slightly lighter below, but on the whole appearing very uniform dark, almost bluish. Dusky tail-bar wide, 17.5–30 mm on the outer rectrix.

Range. Locally distributed in the temperate zone of the West and Central Cordilleras of the Andes from Lambayeque, Cajamarca and Amazonas in the north to Cordillera Vilcabamba in Cuzco, and on the west slope very locally south of Lima to Arequipa, Peru, and at Carangas near Nevada Sajama in western Oruro, Bolivia.

Polioxolmis rufipennis bolivianus subsp. nov.

Type. SMNH Stockholm A561808, leg. 13 June 1938 by A. M. Olalla, on Cerro Blanco (3800 m), Cochabamba, Male.

Diagnosis. Generally small (wing 101.5–131 mm; mean 120.5, s.d. ±6.12 mm), dull grey, appearing buff- or brown-tinged rather than bluish, and with the dark bar on the outer rectrix only 6–16 mm wide (measured where the bar is narrowest). The individual colour variation is slight, although some birds have conspicuously paler (more buffy) feather-edges on the breast, which gives a suggestion of spots or streaks.

Description of the type. Above Hair Brown, but remiges showing Light Drab outer webs, and thin whitish edges distally. Becomes slightly paler

below, with Pallid Drab-Grey supralore and streaks on the Light Mouse Grey throat; darkest zone of breast Mouse Grey, with indications of lighter and buffier feather-edges centrally, lower belly and vent buffy white. Under wing-coverts Pinkish Buff, remiges and rectrices Cinnamon (inclining towards Avellaneous) with dusky distal bar, which is c. 11.5 mm wide on the right outer rectrix, but diffusely demarcated (the left outer rectrix has a malformation distally). Culmen 19.4 mm, tarsus 27.8 mm, wing cord 124.3 mm, tail 90.6 mm.

Other specimens examined. 12 in AMNH, 6 in ANSP, 5 in CMP, 6 in MHNP, 3 in LSUMZ, 3 in MHNP, 3 in SMNH. Compared with 43 specimens of the nominate subspecies in AMNH, ANSP, BMNH, CMP, FMNH, IRSNB, LSUMZ, MHNJP and ZMUC.

Range. Puno in southeastern Peru and into Bolivia, along the East Cordillera of La Paz to the Tunari Range of Cochabamba; also in semi-arid central Cochabamba and into adjacent Sta Cruz, and by Oploca in Potosi.

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