THE BIRDS OF PÁRAMO DE FRONTINO, WESTERN ANDES OF COLOMBIA

Aves del Páramo de Frontino, Cordillera Occidental de Colombia

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ABSTRACT

We conducted an ornithological survey of Páramo de Frontino, the largest páramo in the Western Andes of Colombia and rarely visited by ornithologists. Here we present the first records from this cordillera of *Geranoaetus melanoleucus*, *Hapalopsittaca amazonina*, *Lurocalis rufiventris*, *Grallaria alleni*, *Myornis senilis*, and *Notiochelidon flavipes*, as well as *Uropsalis segmentata*, *Acestrura mulsant*, and *Leptopogon rufipectus*. The latter three had been previously recorded from southern Antioquia, but had remained unpublished. We also obtained significant latitudinal range extensions for 23 species and altitudinal extensions of 300 m or more are given for 26 species. The avian biogeography of the cordillera is discussed and an annotated list given of the species recorded during the survey.

Key words: avian biogeography, Colombia, Páramo de Frontino, range extensions

RESUMEN

Realizamos una exploración ornitológica en el Páramo de Frontino, el páramo más grande de los Andes Occidentales de Colombia y rara vez visitado por los ornitólogos. Presentamos aquí los primeros registros para la cordillera de *Geranoaetus melanoleucus, Hapalopsittaca amazonina, Lurocalis rufiventris, Grallaria alleni, Myornis senilis, Notiochelidon flavipes*, así como de *Uropsalis segmentata, Acestrura mulsanti* y *Leptopogon rufipectus*. Las últimas tres especies habían sido registradas antes en el sur de Antioquia, pero no habían sido publicadas. Obtuvimos ampliaciones significativas de distribución latitudinal para 23 especies y ampliaciones superiores a los 300 m de la distribución altitudinal para 26 especies. Se discuten aspectos biogeográficos de la cordillera, y se incluye un inventario de las especies registradas en la exploración.

Palabras clave: biogeografía aviar, Colombia, extensión de distribución, Páramo de Frontino

INTRODUCTION

The avifauna of the Western Andes of Colombia has received considerable study, but mainly in the southern half of the cordillera (Miller 1963, Orejuela et al. 1979, Hilty & Brown 1986, Echeverry 1986, Negret 1994, 1997, Hilty 1997, Donegan & Dávalos 1999, but see Cuervo et al. 2003). The seven páramos have received relatively little attention by ornithologists. The two largest are Páramo de Frontino and Paramillo, situated some 50 km apart in the northern end of the cordillera.

Chapman (1917) reported on 35 species collected on Paramillo during a ten-day expedition by Leo Miller and Howarth Boyle for the American Museum of Natural History in January and February 1915. Apparently no ornithologist has visited the páramo of Paramillo since. Horacio Echeverry (1986) published a list of the birds of Páramo de Frontino based on his own observations during several visits between 1983 and 1986. In addition, a few museum specimens indicate visits by others. Except for the type specimen of *Coeligena orina* (Wetmore 1953) these specimens remain unpublished. They include some collected by M. A. Carriker, Jr. at 3200 m on 18-27 August 1951 (ICN, USNM), some by T. Cuadros at 3550 m in January 1982, some by M. A. Serna, A. Gómez and M. Peña at 3850 m from 30 December 1989 to 2 January 1990 (all in Colegio San José, Medellín), some by J. M. (full name not known) at 2500 and 3500 m on 4 April 1992, and one by J. J. E. (full name not known) at 3800 m in April (year not given on label) (Universidad de Antioquia).

We here present some of the results of an ornithological expedition we made to the western slope and páramo of Páramo de Frontino for 12 days in August 2004, and discuss the avian biogeography of the Western Andes. For notes on the need for protection of Páramo de Frontino see Flórez et al. (2004) and Krabbe et al. (2005).

STUDY SITES

During the expedition we set up base camps at three different elevations:
Camp 1: 06°27´N, 76°05´W, 3500 m (3300-3900 m). 6-12 August 2004. Open *Espeletia* páramo, elfin woodland and upper reaches of tall humid forest.
Camp 2: 06°26´N 76°05´W, 3150 m (3100-3200 m). 12-15 August 2004. Tall humid forest. This camp was at or very near to the site where Carriker collected the type specimen of *Coeligena orina*.
Camp 3: 06°25´N 76°04´W, 2600 m (2500-2700 m). 15-17 August 2004. Tall humid forest.

We also present here a considerable number of previously unpublished records of birds observed or mist-netted by Gustavo Suárez further south in the Western Andes in southern Department of Antioquia, when these data help to fill the gap between the previously known distributions of these species and our records obtained in the Páramo de Frontino. These records are identified below by the notation GSD.

RESULTS

Ca.155 bird species were recorded at the three camps between 2500 and 3900 m (Anexo 1). Several of the records are noteworthy. The rediscovery of *Coeligena orina* (Wetmore 1953) was published by Krabbe et al. (2005), and the first vocal and genetic material obtained of *Scytalopus canus canus* will be treated in a separate paper. We here present the first records for the Western Cordillera, significant range extensions, and a large number of altitudinal range extensions.

First records for the Western Andes.-
Black-chested Buzzard-eagle (*Geranoaetus melanoleucus*): On 6 August a single adult soaring over the páramo at Camp 1 (3500 m) was observed by NK. Apart from Frontino and Paramillo, the páramos in the Western Andes are probably too small to house this species. The closest known locality is in the Central Andes (Hilty & Brown 1986).

Rusty-faced Parrot (*Hapalopsittaca amazonina*): This species was observed at all three camps. One was seen flying over the páramo at 3500 m on 11 August. At Camp 2 (3150 m) two groups of three and two birds were observed daily 12-15 August. The two, presumably a pair, investigated a hole in a tree for long periods every day, apparently searching for a nest site. At Camp 3 at 2600 m 18 birds were observed daily on 15-17 August as they arrived in small groups in the evening to roost in the forest near the camp. The photographs taken of the pair at the hole (Fig. 1a; see also photos in Flórez et al. 2004) show these birds to have a contrasting golden olive nape, suggesting they may be referable to the recently described subspecies *velezi* (Graves & Uribe Restrepo 1989), hitherto known only from the Central Andes. The species was considered Vulnerable/Rare by Collar et al. (1992).

Rufous-bellied Nighthawk (*Lurocalis rufiventris*): One bird was recorded at Camp 2 (3150 m) and three birds at Camp 3 (2600 m). At dusk the birds gave their characteristic loud call and were also seen. Unfortunately, no tape-recordings were obtained. We also heard the species at Mesenia (5°29'N 75°54'W, 2300 m) above Jardín in southern Antioquia Department on 21 August. After its call became known, this difficult-to-collect species has turned out to be widespread in the Andes from Venezuela to Bolivia. It probably ranges continuously through the entire Western Andes of Colombia, but in Colombia it had previously only been recorded from a few scattered localities in the Central and Eastern Andes (Hilty & Brown 1986).

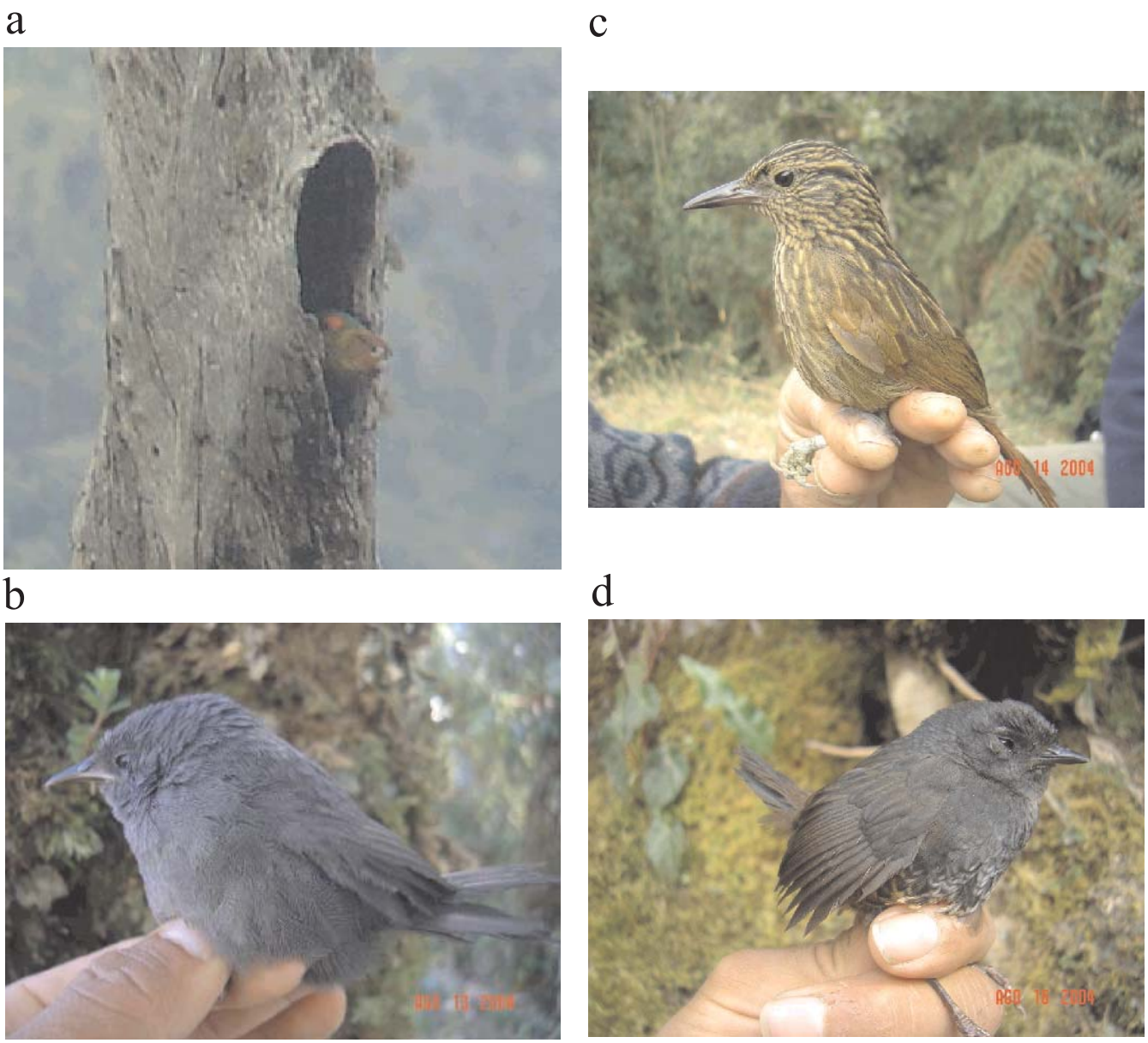

Figure 1. Some noteworthy birds of the Páramo de Frontino. **a.** Rusty-faced Parrot (*Hapalopsittaca amazonina*) at Camp 2. Previously unrecorded in the Western Andes. Photo NK. **b.** Ash-colored Tapaculo (*Myornis senilis*) netted at Camp 2. Previously unrecorded in the Western Andes. Photo JDA. **c.** Striped Treehunter (*Thripadectes holostictus*) netted at Camp 2. First published record from the northern part of the Western Andes. Photo JDA. **d.** Adult female of Spillmann's Tapaculo (*Scytalopus spillmanni*) netted at Camp 3. Extension of range to the northern end of the Western Andes, this population notable for its distinctive calls (see Fig. 2). Photo JDA.

Swallow-tailed Nightjar (*Uropsalis segmentata*): A single bird was heard singing at Camp 3. The only previous record from Western Andes is from southernmost Antioquia (GSD), but the species has probably been overlooked in other parts of the cordillera.

White-bellied Woodstar (*Acestrura mulsant*): A female was observed at Camp 3. The species was only recently found for the first time in the Western Andes, in southern Antioquia (GSD).

Moustached Antpitta (*Grallaria alleni*):Two individuals were heard and tape-recorded at Camp 2 (3150 m). The subspecies *andaquiensis* is known only from southern Colombia and northern Ecuador, the nominate form only from a small area in the Central Andes of Colombia (del Hoyo et al. 2003). The species was considered Vulnerable by Collar et al. (1992). It is very difficult to collect (pers. obs.) and its song is known by only a few ornithological field workers, so it may have been overlooked in other parts of the Western Andes. This population might prove to be an undescribed subspecies.

The reported specimen(s) from the Western Andes above Cali of an unknown subspecies of Scaled Antpitta (*Grallaria guatimalensis*) (Hilty & Brown 1986) might represent this form.

Ash-colored Tapaculo (*Myornis senilis*): This species was fairly common in dense thickets of *Chusquea* bamboo at Camp 2 (3150 m) and was also recorded below Camp 1 at 3300 m. Tape-recordings of its characteristic song were obtained and two specimens (now housed in ICN) collected (Fig. 1b). Their docile behaviour upon capture and while being handled differed markedly from the lively behaviour of *Scytalopus* tapaculos under similar conditions (own obs.). In Colombia specimen records of this difficult-to-collect species are confined to four scattered localities in the Central and Eastern Andes (Hilty & Brown 1986). In addition there is an unpublished tape-recording (and sighting) by NK from near Medellín (Alto Gallinazo, 6°05'N 75°37'W, 2580 m) in the Central Andes, Depto. Antioquia obtained on 12 June 1994. Only few field workers in Colombia are familiar with its song, and it might prove to be widely distributed in bamboo thickets through all three Andean ranges of Colombia.

Rufous-breasted Flycatcher (*Leptopogon rufipectus*): Two individuals were seen briefly and tape-recorded at Camp 3. Recently reported from southern Antioquia, the first records from the Western Andes (GSD).

Pale-footed Swallow (*Notiochelidon flavipes*): A single bird was observed and heard giving one of its two distinctive calls as it crossed the páramo (3500 m) on 10 August. It was not recorded on the eastern slope, so if it represents a local population rather than being a straggler from the Central Andes, the colony would presumably reside on the more humid western slope. It is usually confined to a narrow elevational band at 2650-3300 m (Ridgely & Greenfield 2001). Although locally distributed in the Andes from Venezuela to Bolivia, it has been found to be much more widespread than formerly believed (see e.g. López-Lanús 1999), after more field workers have become familiar with its vocalizations, as anticipated by Parker & O'Neill (1980) (see e.g. Fjeldså & Krabbe 1990).

Range extensions in the Western Andes.-
Short-tailed Hawk (*Buteo brachyurus*): One bird was observed at Camp 2, one at Camp 3. Formerly known only from the Cordillera Central and the southern half of the Western Andes (Hilty & Brown 1986).

Variable Hawk (*Buteo polyosoma*): Two birds were observed at Camp 2. Formerly known only from the Cordillera Central, west Nariño, and, in the Western Andes, west of Popayán, Cauca (Hilty & Brown 1986) and in southernmost Antioquia (GSD).

Barred Parakeet (*Bolborhynchus lineola*): A group of 12 was observed to cross the páramo daily at Camp 1, where it was also tape-recorded. Formerly recorded only from scattered localities in all three ranges of Colombia, in the Western Andes only in Valle and Cauca (Hilty & Brown 1986) and southernmost Antioquia (GSD).

Barn Owl (*Tyto alba*): One was heard most evenings and seen on a few occasions at Camp 1, another was heard at Camp 2. Known from all three Andean ranges and suspected to be much more widespread than suggested by the few scattered records, which in the Western Andes are only from Valle and Cauca (Hilty & Brown 1986) and southernmost Antioquia (GSD).

White-throated Screech-Owl (*Otus albogularis*): A pair was heard duetting every night at Camp 2 and was tape-recorded. In the Western Andes it had previously been recorded only in Cauca (Hilty & Brown 1986) and southernmost Antioquia (GSD).

Andean Pygmy-Owl (*Glaucidium jardinii*): One was mist-netted at Camp 1 (see photo in Flórez et al. 2004). In the Western Andes it had only been collected above Cali in Valle, whereas a sight record from southern Chocó (Hilty & Brown 1986) probably represents the recently described (Robbins & Stiles 1999) Cloud Forest Pygmy-owl (*Glaucidium nubicola*).

Rufous-banded Owl (*Strix albitarsis*): Two birds were heard at Camp 1, two pairs at Camp 2 (tape-recorded), and one pair at Camp 3. In the Western Andes known from only two sites, one in Cauca (Hilty & Brown 1986) and one in southernmost Antioquia (GSD).

Sword-billed Hummingbird (*Ensifera ensifera*): A single bird was observed flying over Camp 3. Although widespread in the Eastern and southern half of the Central Andes of Colombia, it had only been recorded north to Cerro Tatamá, Valle in the Western Andes (Hilty & Brown 1986).

Striped Treehunter (*Thripadectes holostictus*): Two birds were tape-recorded and netted at Camp 2, one at Camp 3 (Fig. 1c). In the Western Andes it was only recently recorded north to southern Antioquia (Cuervo et al. 2003). Owing to its dense bamboo habitat it is difficult to collect without the use of mist nets. We suspect that its range in all three ranges of Colombia is more continuous than suggested by Hilty & Brown (1986).

Barred Antthrush (*Chamaeza mollissima*): Two birds were heard and tape-recorded at camp 2 at 3200 and 3300 m. This "near-impossible-to-collect" species had only been recorded from the southern ends of the Central and Western Andes in

Colombia, in the latter north to Valle (Hilty & Brown 1986). It probably ranges continuously through the Western Andes. Old "Bogotá" specimens might suggest that it also occurs in the Eastern Andes (Hilty & Brown 1986).

Chestnut-naped Antpitta (*Grallaria nuchalis*): Fairly common in dense bamboo thickets at Páramo de Frontino. At least six birds were heard and tape-recorded at 3100-3300 m between Camp 1 and Camp 2. Although their songs were fairly similar to songs of the subspecies *ruficeps* of the Eastern and Central Andes of Colombia, and differed distinctly from the single recording available of *obsoletus* of western Ecuador, their subspecific allocation remains to be established. The species was only recently reported for the first time in the Western Andes of Colombia, where it was recorded from southern Antioquia (Cuervo et al. 2003). It is very difficult to collect and probably ranges continuously through the Western Andes.

Slate-crowned Antpitta (*Grallaricula nana*): Fairly common in bamboo thickets between Camp 1 and Camp 2 at 3300 m, where 5 individuals were heard and tape-recorded. A single bird was also tape-recorded at 3150 m at Camp 2. In the Western Andes it had previously been recorded north only to southern Antioquia (Cuervo et al. 2003).

Spillmann's Tapaculo (*Scytalopus spillmanni*): Common in dense undergrowth of tall humid forest at and above Camp 2 to 3300 m, and at Camp 3. A male was tape-recorded and collected at camp 2, and a female (Fig. 1d) was collected at camp 3. Two additional males and a female were tape-recorded and collected in southern Antioquia and immediately adjacent Chocó at Mesenia (5°29'N 75°54'W, 2250-2400 m). These five specimens (deposited in ICN) are the first of the species from Colombia that are vocally documented. There are tape-recordings from the Central Andes (Krabbe & Schulenberg 1997) and recently also from southern Antioquia in the Western Andes (Cuervo et al. 2003). Interestingly, the calls of birds from the Western Andes differ markedly from calls given by birds in the Central Andes and Ecuador (Fig. 2), whereas songs only differ slightly. Genetically the birds from the Western Andes of Colombia are very similar to Ecuadorian birds (D. C. Cadena pers. comm.), which questions the suggestion by Whitney (1994) that calls may be more primitive than songs in the genus.

Ocellated Tapaculo (*Acropternis orthonyx*): One was seen and was heard singing daily at Camp 2. The species was only recently recorded for the first time in the Western Andes, from southern Antioquia (Cuervo et al. 2003).

Chestnut-crested Cotinga (*Ampelion rufaxilla*): One was observed at Camp 2. In the Western Andes only recently recorded as far north as southern Antioquia (GSD).

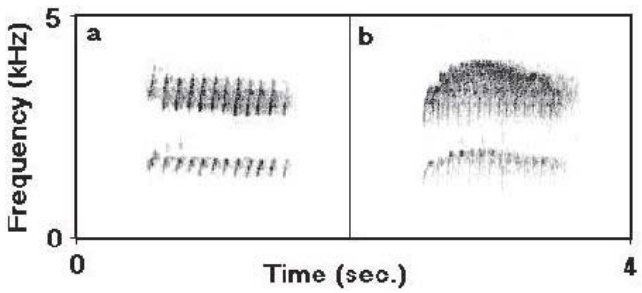

Figure 2. Call of Spillmann's Tapaculo (*Scytalopus spillmanni*) as given in the Western Andes of Colombia (**a**) and Ecuador and the Central Andes of Colombia (**b**).

White-tailed Tyrannulet (*Mecocerculus poecilocercus*): Two individuals were observed by GS at Camp 2. In the Western Andes only recently reported as far north as southern Antioquia (Cuervo et al. 2003).

White-banded Tyrannulet (*Mecocerculus stictopterus*): Two individuals were seen or heard daily at Camp 2 and were tape-recorded. In the Western Andes it had only been recorded north to Cerro Munchique in Cauca (Hilty & Brown 1986).

Streak-necked Flycatcher (*Mionectes striaticollis*): One was observed at Camp 3. In the Western Andes previously recorded north to southern Antioquia (Hilty & Brown 1986).

Rufous-headed Pygmy-Tyrant (*Pseudotriccus ruficeps*): One was seen and tape-recorded at Camp 2, another was seen at Camp 3. Cuervo et al. (2003) reported a range extension north to southern Antioquia in the Western Andes.

Smoky Bush-Tyrant (*Myiotheretes fumigatus*): Two birds were seen and tape-recorded at Camp 2. In the Western Andes it had only been recorded north to southern Antioquia (GSD).

Black-chested Mountain-Tanager (*Buthraupis eximia*): Common at Camp 1 where at least five birds were seen, three were tape-recorded, and two netted and photographed (see photos in Flórez et al. 2004). In the Western Andes the species had been recorded only at Paramillo.

Buff-breasted Mountain-Tanager (*Dubusia taeniata*): One was observed below Camp 1 at 3300 m. Until it was recently reported from southern Antioquia (GSD) this species was known only north to Cauca in the Western Andes (Hilty & Brown 1986).

Plush-capped Finch (*Catamblyrhynchus diadema*): One was observed below Camp 1 at 3300 m, and four, two of which were netted and photographed (Fig. 3a), at Camp 2. Before the recent records from southern Antioquia (GSD) it had only been reported north to Valle in the Western Andes.

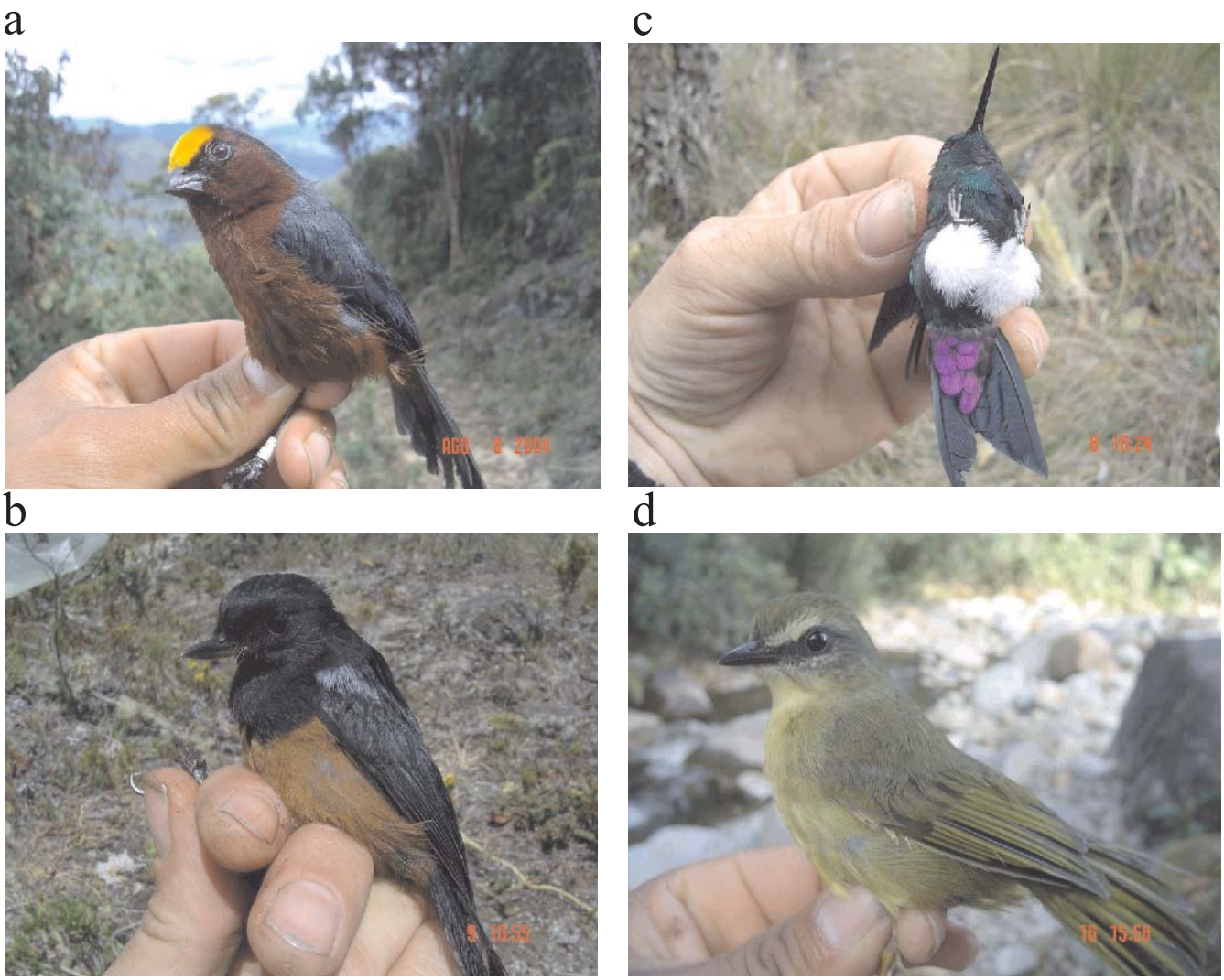

Figure 3. Noteworthy records and distinctive subspecies of birds from the Páramo de Frontino. **a.** Plush-capped Finch (*Catamblyrhynchus diadema*) netted at Camp 2. There are no previously published records from the northern end of the Western Andes. Photo JDA. **b.** Chestnut-bellied Flowerpiercer (*Diglossa gloriossisima*) netted at Camp 1. Endemic to the Western Andes. Photo NK. **c.** Glowing Puffleg (*Eriocnemis vestitus paramillo*), a subspecies endemic to the two northernmost páramos in the Western Andes. Netted at Camp 1. Photo NK. **d.** Citrine (Richardson's) Warbler (*Basileuterus luteoviridis richardsoni*) a very distinct subspecies endemic to the Western Andes. Photo NK.

Two probable sightings of interest are here regarded as hypothetical pending confirmation of the identifications and collection of specimens, because they might represent undescribed taxa:

Golden-breasted Puffleg (*Eriocnemis mosquera*): A single individual of what appeared to be this species was observed by PF at Camp 1. In Colombia it was known only from the Central Andes and the southern portion (north to Cauca) of the Western Andes, although old "Bogotá" specimens might suggest its occurrence in the Eastern Andes (Hilty & Brown 1986). Owing to the local distribution of several species in the genus it remains possible that the observed bird represents an undescribed taxon.

Grass Wren (*Cistothorus platensis*): One individual of what appeared to be this species was observed by GS at Camp 1. Strangely, no other was recorded, despite ample suitable habitat. Owing to the large northward range extension represented by this record (in the Western Andes known only north to Cauca) and the possibility that it represents an undescribed taxon, we prefer to treat it as hypothetical.

Altitudinal range extensions.- Numerous species were recorded at higher elevations than previously reported in Colombia. Some of these, such as hummingbirds and fruit-eating birds, might be seasonal at higher elevations. In the following list we only mention the 26 altitudinal range extensions of 300 m or more. The species name is followed

by the highest elevation we found it and then in parenthesis the highest elevation previously reported. The latter is that given by Hilty & Brown (1986) unless another reference is indicated.

Tawny-breasted Tinamou (*Nothocercus julius*) 3500 m (3100 m); Black Vulture (*Coragyps atratus*) 3600 m (2700 m); Short-tailed Hawk (*Buteo brachyurus*) 3150 m (2500 m); Black-and-chestnut Eagle (*Oroaetus isidori*) 3700 m (3300 m); Ruddy Pigeon (*Columba subvinacea*) 3150 m (2800 m); Barred Parakeet (*Bolborhynchus lineola*) 3600 m (2600 m); Barn Owl (*Tyto alba*) 3500 m (3000 m); Andean Pygmy-Owl (*Glaucidium jardinii*) 3500 m (2800 m); Rufous-banded Owl (*Strix albitarsis*) 3500 m (3000 m); Green-fronted Lancebill (*Doryfera ludovicae*) 3150 m (2700 m); Collared Inca (*Coeligena torquata*) 3300 m (3000 m); Buff-tailed Coronet (*Boissonneaua flavescens*) 3150 m (2800 m); Brown-billed Scythebill (*Campylorhamphus pusillus*) 2600 m (2100 m); Azara's Spinetail (*Synallaxis azarae*) 3300 m (3000 m); Pearled Treerunner (*Margarornis squamiger*) 3500 m (3000 m); Striped Treehunter (*Thripadectes holostictus*) 3150 m (2700 m); Long-tailed Antbird (*Drymophila caudata*) 3150 m (2700 m); Moustached Antpitta (*Grallaria alleni*) 3100 m (2100 m); Chestnut-naped Antpitta (*Grallaria nuchalis*) 3300 m (3000 m); Slate-crowned Antpitta (*Grallaricula nana*) 3300 m (repeatedly between 2900 and 3000 m: Stiles & Rosselli 1998); Chestnut-crested Cotinga (*Ampelion rufaxilla*) 3150 m (2700 m); Rufous-headed Pygmy-tyrant (*Poecilotriccus ruficeps*) 3150 m (2700 m); Black-throated Tody-tyrant (*Hemitriccus granadensis*) 3500 m (3100 m); Pale-footed Swallow (*Notiochelidon flavipes*) 3500 m (3000 m); White-sided Flowerpiercer (*Diglossa albilatera*) 3500 m (3100 m); Blue-capped Tanager (*Thraupis cyanocephala*) 3300 m (3000 m).

Five species listed for the higher parts of Páramo de Frontino by Echeverry (1986) were not found by us. These were Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*), Bar-winged Cinclodes (*Cinclodes fuscus*), Andean Tit-spinetail (*Leptasthenura andicola*), Barred Fruiteater (*Pipreola arcuata*) and Streak-throated Bush-tyrant (*Myiotheretes striaticollis*). Bar-winged Cinclodes and Andean Tit-spinetail are otherwise unreported for the Western Andes, so although these records are possible, we hesitate to accept them without evidence in the form of photographs, tape-recordings, or specimens. The remaining species might well occur rarely or seasonally, and should be looked for in future visits.

DISCUSSION

The Western Andes of Colombia are much lower than the Central and Eastern Andes. Only seven areas hold peaks that reach above the present treeline, and four passes are at elevations slightly lower than 2000 m, rendering the flora and fauna of páramo and treeline habitats effectively fragmented, not only under present conditions but also during the considerably colder climates of the late Pleistocene. This has caused the evolution of a large endemic flora and fauna. The avifauna, with its generally great mobility, shows less endemism than the plants, but a number of forms that are widespread in the Andes, such as Bar-winged Cinclodes (*Cinclodes fuscus*), Andean Tit-spinetail (*Leptasthenura andicola*), Streak-backed Canastero (*Asthenes wyatti*), Many-striped Canastero (*Asthenes flammulata*), thistletails (*Schizoeaca* spp.), Red-rumped Bush-Tyrant (*Cnemarchus erythropygius*), Scarlet-bellied Mountain-Tanager (*Anisognathus igniventris*), Plain-colored Seedeater (*Catamenia inornata*), and Plumbeous Sierra-Finch (*Phrygilus unicolor*) have not been able to colonise these páramos (see above concerning putative sight records of Bar-winged Cinclodes and Andean Tit-spinetail on Páramo de Frontino).

Only five species, Dusky Starfrontlet (*Coeligena orina*) (see photos in Flórez et al. 2004), Colorful Puffleg (*Eriocnemis mirabilis*), a yet undescribed species of tapaculo (*Scytalopus* sp. nov.) (see Cuervo et al. 2003), Munchique Wood-Wren (*Henicorhina negreti*) (see Salaman et al. 2003), and Chestnut-bellied Flowerpiercer (*Diglossa gloriossissima*) (Fig. 3b) are endemic to the Western Andes. Four of them are found only at high elevations, whereas the tapaculo is restricted to the Pacific slope and is probably isolated by competing congeners rather than unsuitable habitat (see Krabbe & Schulenberg 1997).

Of the ten subspecies endemic to the Western Andes four, *Eriocnemis vestitus paramillo* (Glowing Puffleg) (Fig. 3c), *Metallura williami recisa* (Viridian Metaltail), *Scytalopus canus canus*) (Páramo Tapaculo), and *Anisognathus lacrymosus intensus* (Lacrimose Mountain-Tanager) are confined to high elevations; four, *Nothocercus bonapartei intercedens* (Highland Tinamou), *Andigena nigrirostris occidentalis* (Black-billed Mountain-Toucan), *Basileuterus luteoviridis richardsoni* (Citrine Warbler) (Fig. 3d) and *Chlorospingus semifuscus livingstoni* (Dusky-bellied Bush-Tanager) to middle elevations, and two, *Grallaria guatimalensis chocoensis* (Scaled Antpitta) and *Thryothorus mystacalis saltuensis* (Whiskered Wren) to lower elevations on the Pacific slope. Following Winkler & Christie (2002), diagnosis by Krabbe & Schulenberg (2003), and Fitzpatrick (2004) we do not consider *Piculus rubiginosus pacificus*, *Grallaricula flavirostris ochraceiventris*, *Zimmerius chrysops molestus* and *Mionectes striaticollis selvae* to be valid taxa.

The well-documented climatic fluctuations in the Eastern Andes of Colombia (Hooghiemstra & Ran 1994) suggest that the treeline was lowered from 3400 m to nearly 1800 m in the Eastern Andes several times during the last 2 million years. The lack of many highland birds in the páramos and subpáramos of the Western Andes might be an indication that

the cooling here was more moderate, probably owing to the influence of the humid Pacific air masses.

There is indirect evidence that colonisation of the Western Andes in some cases happened by jump dispersal across the Cauca Valley rather than through continuous suitable habitat. One form of Lacrimose Mountain-Tanager (*Anisognathus lacrymosus olivaceiceps*) occurs in the north ends of both cordilleras, whereas the form *palpebrosus* is found further south in the Central Andes and the form *intensus* further south in the Western Andes (to which it is endemic). Possibly relict, but also more likely the result of jump dispersal, is the distribution of a subspecies of Golden-crowned Tanager (*Iridosornis rufivertex caeruleoventris*), which is found in the north ends of both Central and Western Andes, while the subspecies *ignicapillus* (sometimes merged with the nominate race) occurs further south in both cordilleras, as well as a form of Brown-capped Vireo (*Vireo leucophrys disjunctus*), with a similar (but lower elevational) distribution, with *dissors* occurring further south in both cordilleras. The same could be the case for Andean Siskin (*Carduelis spinescens nigricauda*), with *spinescens* occurring further south (but see Robbins et al. 1994).

A number of highland birds are found in the Central Andes, but only in the northern half of the Western Andes. Two of them, Glowing Puffleg (*Eriocnemis vestitus*) and Viridian Metaltail (*Metallura williami*) have evolved distinct subspecies in the Western Andes. Others have not, including Crowned Chat-Tyrant (*Ochthoeca frontalis*), Brown-bellied Swallow (*Notiochelidon murina*), Rufous Wren (*Cinnycerthia unirufa*), Black-chested Mountain-Tanager (*Buthraupis eximia*), and Black-headed Hemispingus (*Hemispingus verticalis*). Treeline vegetation is sparse in the southern end of the cordillera, perhaps too limited in extent to support viable populations of some of these species, but the presence of Chestnut-bellied Flowerpiercer on Cerro Munchique indicates that some of the others could potentially occur there. Their apparent absence from the southern end of the Western Andes might be explained by a scenario of jump dispersal from the Central Andes to the northern end of the Western Andes.

For some species with similar, but somewhat lower elevational distributions, the scenario of jump dispersal seems even more likely. These include Green-crowned Brilliant (*Heliodoxa jacula*), Mountain Avocetbill (*Opisthoprora euryptera*), Gorgeted Woodstar (*Chaetocercus heliodor*), White-bellied Woodstar (*Chaetocercus mulsant*), Dusky Piha (*Lipaugus fuscocinereus*), Black-collared Jay (*Cyanolyca armillata*), and Red-bellied Grackle (*Hypopyrrhus pyrohypogaster*). In particular the latter two seem unlikely to have been missed by early collectors in the southern half of the Western Andes.
An interesting case is a form of Black-throated Flowerpiercer (*Diglossa brunneiventris vuilleumieri*) (see photo in Flórez et al. 2004 mislabelled as Chestnut-bellied Flowerpiercer) found in the high páramos in the north ends of both cordilleras. Despite extreme isolation from other forms referred to *D. brunneiventris*, the closest being Venezuela (sometimes considered a distinct species) and Peru (Fjeldså & Krabbe 1990), these two populations are so similar that they cannot be told apart. They might represent unchanged relicts of a once continuous population, but a scenario of more recent jump dispersal should not be discarded.

The odd distributions of Solitary Eagle (*Harpyhaliaetus solitarius*) and Lazuline Sabrewing (*Campylopterus falcatus*) that are shown by Hilty & Brown (1986) to be distributed only in the Eastern Andes and the northern end of the Western Andes, but not in the Central Andes, deserve to be addressed. The Lazuline Sabrewing probably reached the Western Andes through jump dispersal. It possesses high dispersal abilities, as indicated by a recent successful colonization of the Santa Marta Mountains (Strewe & Navarro 2004), and Hilty & Brown (1986) suspected that it occurs in the northern end of the Central Andes. The population of Solitary Eagle in the Western Andes may be relictual. If the species is indeed genuinely absent from the Central Andes, it could have disappeared in recent times, perhaps even as a result of human activities.

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Anexo 1. Birds recorded on Páramo de Frontino 6-17 August 2004. Number of individuals recorded.

Species	Camp 1	Camp 2	Camp 3
Nothocercus julius	1s (T)	2s (TNS)	
Cathartes aura		1	2
Coragyps atratus	3	x	x
Accipiter ventralis		1 (3000 m)	
Geranoaetus melanoleucus	1 adult		
Buteo magnirostris			1
Buteo brachyurus		1	1
Buteo polyosoma		2	
Oroaetus isidorei	1 adult (3700 m)		
Polyborus plancus			2
Falco sparverius		1 (3000 m)	
Gallinago nobilis	2 (T)		
Columba fasciata	C (T)	C (T)	C (T)
Columba subvinacea		2s (T)	2s (T)
Bolborhynchus lineola	12 (T)		
Hapalopsittaca amazonina	1	5 (T,Photographs)	18 (T)
Amazona mercenaria		1group (T)	
Piaya cayana			2
Tyto alba	1	1c	
Otus albogularis		2s (3100, 3200 m) (T)	
Glaucidium jardinii	1 (N)		
Strix albitarsis	2s	4s (T)	2s
Lurocalis rufiventris		1s	3
Caprimulgus longirostris[1]			
Uropsalis segmentata			1s
Streptoprocne zonaris		10 (T)	
Cypseloides rutilus			3 (2800 m)
Doryfera ludoviciae		1	1 (N)
Colibri coruscans	1 (T)	1	1
Adelomyia melanogenys			3 (N)
Lafresnaya lafresnayi	4 (3300 m) (N)	4 (N)	3 (N)
Coeligena torquata	2 (3300 m) (N)	4 (N)	4 (N)
Coeligena orina	5 (N)	3	
Ensifera ensifera			1
Boissonneaua flavescens		3	3
Heliangelus exortis		5 (N)	5 (N)
Eriocnemis vestitus	20 (N,S)		
Eriocnemis mosquera ?	1		
Ramphomicron microrhynchum	5	1	
Metallura williami	4 (3700 m)		
Metallura tyrianthina	4 (N,S)	6 (N)	
Acestrura mulsant			1female
Trogon personatus	1s (3300 m) (T)	2 (N)	2 (T)
Momotus aequatorialis			2
Aulacorhynchus prasinus		4 (T)	3
Andigena nigrirostris		4 (T)	1
Piculus rivolii		1	
Melanerpes formicivorus		4 (T)	4
Veniliornis dignus			1
Campephilus pollens		2 (T)	
Dendrocincla tyrannina			1c (T)
Xiphorhynchus triangularis			2
Lepidocolaptes lacrymiger		3	5

Species	Camp 1	Camp 2	Camp 3
Campylorhamphus pusillus			1 (T)
Synallaxis azarae	3 (3300 m) (N)	4	2
Hellmayrea gularis	7 (T,N,S)	3 (N,T)	
Margarornis squamiger	4 (N)	6 (N)	6 (N,S)
Premnornis guttuligera			1s (T)
Pseudocolaptes boissonneaua	4 (N)	2 (N)	2
Thripadectes flammulatus			1 (N)
Thripadectes holostictus		2 (N,T)	1 (T)
Drymophila caudata		2s (N,T)	
Chamaeza mollissima	2s (3200,3300 m)		
Grallaria squamigera	1s		
Grallaria alleni		2s (3100 m) (T)	
Grallaria nuchalis	2s (3300 m) (T)	4s (T)	
Grallaria rufula	5s (T)	2s (N)	5s (N)
Grallaricula nana	5s (3300 m) (T)	1s (T)	
Myornis senilis	1s (3300 m) (T)	5s (T,N,S)	
Scytalopus latrans		2s (T,N,S)	1s (T)
Scytalopus canus	10s (3300-3500 m) (T,N,S)		
Scytalopus spillmanni	2s (3300 m)	4s,c (T,N,S)	5s,c (T,N,S)
Acropternis orthonyx		1s	
Ampelion rubrocristatus	3 (3300 m)	2	
Ampelion rufaxilla		1	
Pipreola riefferii			4 (T,N)
Lipaugus fuscocinereus		4s (T,N)	2
Pachyramphus versicolor			1c (T)
Phyllomyias nigrocapillus		2c (T)	3c
Zimmerius chrysops			5
Mecocerculus leucophrys	20 (T,N,S)	6	
Mecocerculus poecilocercus		2	
Mecocerculus stictopterus		2 (T)	
Serpophaga cinerea			4
Mionectes striaticollis			1
Leptopogon rufipectus			2 (T)
Pseudotriccus ruficeps		1 (T)	1
Poecilotriccus ruficeps		2 (N)	
Hemitriccus granadensis	1		
Myiophobus flavicans			2 (T)
Pyrrhomyias cinnamomea		4 (N)	4
Sayornis nigricans			4
Ochthoeca fumicolor	10 (N,T)		
Ochthoeca rufipectoralis	2 (3300 m) (N)	8	2
Ochthoeca cinnamomeiventris		2 (N)	4 (T)
Ochthoeca frontalis	4 (N,S)		
Ochthoeca diadema		6 (T,N)	1 (N)
Myiotheretes fumigatus		2s	
Myiarchus cephalotes			5 (-2900 m) (T)
Myiodynastes chrysocephalus			1
Tyrannus melancholicus			2
Notiochelidon flavipes	1		
Notiochelidon cyanoleuca		5	3
Cyanolyca armillata		5 (T)	3
Cyanocorax yncas		1	4
Cinclus leucocephalus			2 (N)
Cinnycerthia olivascens			4s (N,T)

Species	Camp 1	C amp 2	Camp 3
Cistothorus platensis ?	1		
Troglodytes solstitialis		4 (N,T)	2 (T)
Henicorhina leucophrys		8 (T,N)	6c,s
Myadestes ralloides			5s (N,T)
Catharus fuscater			1s
Turdus fuscater	10 (N,T)	10 (N,T)	10
Turdus serranus			1
Cyclarhis nigrirostris			1s (T)
Vireo leucophrys			1
Vireo olivaceus[2]			
Cacicus leucoramphus		5 (T)	5
Myioborus miniatus			2 (T)
Myioborus ornatus	8 (T)	10	10
Basileuterus luteoviridis			5s (T,N)
Basileuterus nigrocristatus	1s (3300 m)	3 (T,N)	
Basileuterus coronatus	1s (3300 m)	6 (T,N)	6s (T,N)
Conirostrum sitticolor	2 (N)	2	
Conirostrum albifrons		4	4 (T)
Diglossa cyanea	4 (3300 m)	6 (N)	4
Diglossa gloriossissima	10 (3300-3700 m) (T,N,S)		
Diglossa brunneiventris	20 (3500-3700 m) (N,S)		
Diglossa albilatera	4 (N)	6 (N)	4
Tangara xanthocephala			2
Tangara labradorides			2
Tangara nigroviridis			4
Tangara vassorii	2 (3300 m)	4	5
Tangara heinei			2
Iridosornis rufivertex	4		
Anisognathus lacrymosus	10 (T,N)	8	4
Anisognathus somptuosus			4
Buthraupis montana	4 (3300 m)	6 (T,N)	
Buthraupis eximia	5 (T,N)		
Dubusia taeniata	1 (3300 m)		
Thraupis cyanocephala	1 (3300 m) (N)	6	8
Piranga rubriceps		1	6
Sericossypha albocristata			6 (2800 m)
Cnemoscopus rubrirostris	6 (3300 m)	8	6
Hemispingus atropileus	4 (3300 m) (N)	15 (T,N,S)	2
Hemispingus verticalis	5		
Chlorornis riefferii		4 (N)	1
Catamblyrhynchus diadema	1 (3300 m) (N)	4 (N)	
Atlapetes schistaceus	20 (T,N,S)	10 (N)	8
Buarremon torquatus	2	3 (N)	
Buarremon brunneinucha		2 (N)	2 (N)
Catamenia homochroa	1 (N)	5 (T,N)	
Zonotrichia capensis	2 (T)	2 (N)	4
Carduelis spinescens	70 (T)		
Carduelis xanthogaster			3

N = Netted and photographed, T = Taped, S = Specimen, C = Common (over 10 daily), x = present but not counted c = call, s = song, ? = hypothetical.

Notes:
1: Shown for Páramo de Frontino on distribution map in Hilty & Brown (1986).
2: Specimen in Universidad de Antioquia collected in April by JJE at 3800 m.