



Plate 1. Chestnut-capped Piha *Lipaugus weberi* showing an adult (top right) and a juvenile (lower left). Note the more rufous fringes in the juvenile. Illustration by John P. O'Neill.

A new species of piha (Cotingidae: *Lipaugus*) from the Cordillera Central of Colombia

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The Chestnut-capped Piha *Lipaugus weberi* sp. nov., is described from subandean forest on the northern slope of the Central Cordillera of the Colombian Andes. The new species appears most closely related to *Lipaugus fuscocinereus* of the Northern Andes including the Central Cordillera, but is much smaller, with a distinctive chestnut-brown crown, yellow orbital ring, two modified primaries in the male, an overall darker grey coloration and unique vocalizations. It appears to be restricted to a narrow belt of premontane very humid forests (1500-1820 m asl) where it is fairly common. The restricted range and specific ecological requirements of *Lipaugus weberi* make the species of great conservation concern as the Central Cordillera has been severely deforested and remaining forests are highly fragmented. We present notes on the behaviour, ecology and conservation of this new species.

Se describe *Lipaugus weberi* sp. nov., de bosque subandino de la vertiente norte de la Cordillera Central de los Andes de Colombia. La nueva especie parece estar bastante relacionada con *Lipaugus fuscocinereus* de los Andes septentrionales incluyendo a la Cordillera Central, pero es mucho más pequeña, presenta una distintiva gorra castaño opaco, anillo ocular amarillo, dos remeras primarias modificadas, la coloración gris más oscura y vocalizaciones únicas. Esta especie se restringe a una franja angosta de bosque muy húmedo premontano (1500-1820 msnm), donde es relativamente común. El rango restringido y los requerimientos ecológicos específicos de *Lipaugus weberi* hacen que esta especie sea de gran relevancia para la conservación, más aún debido al estado de deforestación severa de la Cordillera Central, en la cual los bosques remanentes son muy fragmentados. Presentamos anotaciones sobre la ecología, el comportamiento y la conservación de esta nueva especie.

The Central Cordillera of Colombia is a 750 km-long mountain range extending northwards from the bifurcation of the northern Andes at approximately 1° 30'N. It is the highest (average 3000 m) of Colombia's three Andean ranges, as well as the oldest, having attained elevations of over 2000 m in the Miocene period (Hernández-Camacho *et al.* 1992a). The Central Cordillera contains a diverse mosaic of habitats which have produced high biological diversity with high levels of endemism, suggesting some rapid and recent speciation (van Velzen 1992, Hernández-Camacho *et al.* 1992b.), although DNA evidence indicates Andean speciation

pre-dates the Pleistocene (García-Moreno & Fjeldså 2000). Topographical and ecological isolation from other Andean ranges by the Cauca and Magdalena river valleys have accentuated the degree of local endemism. Above 1000 m, the Central Cordillera supports 29 restricted-range bird species, one of the greatest concentrations of montane range-restricted species in the world.

During the late nineteenth and twentieth centuries, good transportation infrastructure encouraged bird collectors to explore the northern Central Cordillera, mainly around Colombia's second city, Medellín, and on the northwestern slope adjacent

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to the lower Cauca valley. Principal collectors in this region included: T. K. Salmon (1872-1878, Sclater & Salvin 1879); M. A. Carriker Jr. (1941-1953, see Graves 1988, 1997), K. von Sneider (1938-1952; Fjeldså & Krabbe 1990); M. A. Serna (1971-1991; Sociedad Antioqueña de Ornitología 1999) and several American Museum of Natural History (AMNH) expeditions (Chapman 1917). Despite notable ornithological attention to the region, the northern premontane slopes (c. 1000-2000 m) of the Cordillera Central remained relatively poorly-known. The Central Cordillera has demonstrated its ability to reveal new species even within recent years (e.g. Graves 1988, Robbins *et al.* 1994, Graves 1997).

From March to June 1999, the regional environmental agency, CORANTIOQUIA (Corporación Autónoma Regional del Centro de Antioquia), commissioned the Universidad de Antioquia Bird Study Group to compile bird inventories at La Forzosa. Surveys mainly concentrated along a ridge at 1700-1820 m asl, where many range-restricted and threatened species were recorded (Cuervo *et al.* 1999). At La Forzosa (1800 m) on 31 March 1999, AMC, JMO, Sandra Galeano and Juan Carlos Luna captured a cotingid of the genus *Lipaugus* which was photographed, measured and released. Several features were noted, which were inconsistent with Dusky Piha *Lipaugus fuscocinereus*, such as a chestnut-brown cap and shorter body length (Cuervo *et al.* 1999). A second individual was captured and released on 23 May 1999 in the same forest, at c. 1500m asl, considered by AMC possibly to represent an undescribed species.

During August 1999, the Colombian Evaluation of Biodiversity in the Andes (EBA) Project conducted a rapid biodiversity assessment of birds, herptiles and plants along an elevational transect on the northeastern slope of the Central Cordillera in Antioquia. After studies at 250 m and 800 m asl, the authors conducted fieldwork at the lower elevations of La Forzosa in pristine forest along a ridge (1550-1600 m asl) and streams "Quebrada Chaquiral and La Soledad" (1500 m asl) from 25-29 August 1999. The La Forzosa *Lipaugus* was one of the most common species in the study area. During four days' fieldwork, we recorded the species on over 50 occasions, making numerous detailed observations and sound-recordings. On 27 August 1999, two individuals were captured in mist-nets and collected. Shortly thereafter the La Forzosa *Lipaugus* specimens were compared by PGWS and F. Gary Stiles with specimens of *L. fuscocinereus* in the collection at Instituto de Ciencias Naturales, Museo de Historia Natural (ICN-MHN). It was immediately apparent

that the La Forzosa *Lipaugus* represented a distinctive new species, which we here name:

***Lipaugus weberi*, sp. nov.**
Chestnut-capped Piha
Piha Antioqueña

HOLOTYPE

Adult male, No. 33412 of the ornithological collection at Instituto de Ciencias Naturales, Museo de Historia Natural (ICN-MHN), Universidad Nacional de Colombia at Reserva La Forzosa, Vereda Roble Arriba, ca. 10 km SW of the town of Anorí, Department of Antioquia, Colombia (6°59'58.3"N; 75°08'33.5"W; 1550 m). Collected 27 August 1999 by Colombian EBA Project '99 and prepared by AMC (original number EBA 076). Sound-recordings deposited with Wildlife Sounds, National Sound Archive (London) (NSA No. WA2000/23). Photographs catalogued with VIREO (No. s50/2/001-004), Academy of Natural Sciences of Philadelphia (ANSP). Stomach contents, an unidentified tick (*Acaro* sp.), and a genetic sample (muscles and liver) preserved and deposited at ICN-MHN. For measurements see Table 1.

ETYMOLOGY

The species epithet is dedicated to Walter H. Weber of Medellín, Colombia, for his enormous and ongoing contribution to Sociedad Antioqueña de Ornitología (SAO) and for promoting Colombian ornithology and conservation. His commitment to Colombian bird conservation and his encouragement of young ornithologists are providing the country with renewed hope. The English name refers to the most contrasting and characteristic morphological feature, the chestnut-brown cap. The Spanish name refers to the Department of Antioquia, the only region in which the species has been found to date.

DIAGNOSIS

Lipaugus weberi exhibits the typical characters of the genus *Lipaugus* (after Ridgway 1907 and Snow 1982), with an overall uniform coloration without strong sexual dimorphism; bill wide at the base with a hooked tip on the maxilla; rictal bristles short; eye diameter wide (7.0 mm); tarsus short and picnaspidean (scutellate-reticulate); unfused toes; tail relatively long (82% of wing chord) with 12 rectrices; size and overall proportions similar to other *Lipaugus*.

Easily distinguished from all congeners by the combination of chestnut-brown crown feathers,

Table 1. Comparison of morphometrics of *Lipaugus weberi*, *L. fuscocinereus* (specimens listed in Appendix), *L. vociferans*, *L. unirufus*, and *L. (Chirocylla) uropygialis*. The mean is given, followed by the standard deviation and sample size. Variation in *L. fuscocinereus* sample numbers is due to partially damaged specimens or impracticalities of measurement. All measurements are in mm with the exception of body mass in grams. See Figure 3 for canonical variate analysis on all biometric data.

	Flat wing chord (mm)*	Body-length (mm)	Maxilla (tip to skull) (mm)	Tail-length (mm)	Tarsus-length (mm)	Body mass (g)
<i>L. weberi</i> (male, Holotype)	131	248	20.6	103.5	22.4	72
<i>L. weberi</i> (female)	125	239	22.9	106.8	23.5	72.2
<i>L. weberi</i> (juv. male)	128	220	22.5	108.7	21.1	71.0
<i>L. fuscocinereus</i> (male)	184.9 ± 5.9 [23]	332.8 ± 26.6 [8]	26.42 ± 0.9 [24]	165.0 ± 7.7 [22]	28.0 ± 1.1 [24]	138.01 ± 1.41 [2]
<i>L. fuscocinereus</i> (female)	176.0 ± 4.9 [26]	322.9 ± 20.7 [19]	26.52 ± 1.6 [22]	153.7 ± 7.7 [28]	29.3 ± 1.2 [25]	
<i>L. vociferans</i>	125.2 ± 3.2 [18]	240.2 ± 16.4 [17]	23.2 ± 1.1 [18]	106.0 ± 3.0 [18]	19.9 ± 0.7 [18]	
<i>L. unirufus</i>	126.5 ± 3.8 [3]	233.7 ± 11.0 [3]	25.2 ± 0.8 [3]	105.9 ± 1.0 [3]	21.3 ± 0.9 [3]	
<i>L. (Chirocylla) uropygialis</i>	144.0 ± 8.9 [3]	306.0 ± 8.5 [3]	25.3 ± 0.7 [3]	141.1 ± 3.3 [3]	30.5 ± 0.2 [3]	

overall darker grey plumage, conspicuous yellow orbital ring; and bright yellow gape, tongue and commissure. The overall uniform grey coloration is similar to both Screaming Piha *L. vociferans* from the Amazonian lowlands and Dusky Piha *L. fuscocinereus* from the northern Andean highlands (see Figs. 1). The similarly-sized *L. vociferans* (see Table 1) is more stocky and robust. It has pale grey underparts contrasting with a dark grey back and brownish wings (cf. more uniform dark grey in *L. weberi*) with little cinnamon on the vent and no chestnut on the crown. While *L. weberi* is similar in size to most medium-sized *Lipaugus* (e.g. *L. vociferans* and uniform cinnamon-brown Rufous Piha *L. unirufus*), morphological features are more reminiscent of the much larger *L. fuscocinereus*. *L. weberi* is distinguished from *L. fuscocinereus* by its bare-part and crown coloration differences, and much smaller size. Males of *L. weberi* have only two primaries with stiffened outer remiges, compared to three in *L. fuscocinereus* (p. 6-7 in *L. weberi*, 5-7 in *L. fuscocinereus*; see below). Vocalizations of *L. weberi* are distinctive (see below).

DESCRIPTION OF HOLOTYPE

See Plate 1 and Figs 1 and 2. Adult male with skull fully ossified, left testis 3.5 x 2.0 mm, right testis 1.9 x 1.0 mm, little subcutaneous fat. Weight 72.0 g. Flight feathers and retrices were fresh, indicating recent completion of a moult. For morphometrics of types see Table 1. A subjective colour description is given and followed, wherever possible, by capitalized colour nomenclature and numbers, following Smithe (1975).

Head

Lead grey (Dark Natural Grey, 83) with forehead, cheeks and auriculars medium to dark grey (DNG,

83). Chestnut-brown (Mars Brown, 223A, but darker) crown to upper nape producing a distinctive rusty cap. Crown feathers quite long, with a small number grey-fringed giving a slightly scaly appearance.

Upperparts

Dark grey (between Blackish Neutral Grey, 82 and DNG, 83) extending from the nape and sides of the neck down to the lower back and scapulars, with

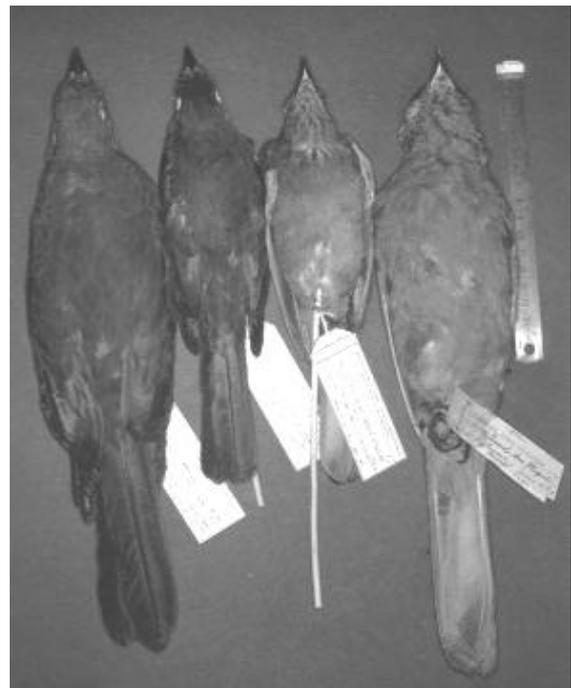


Figure 1. Dorsal view of an adult *Lipaugus fuscocinereus* (far left) and *L. weberi* (centre left) and ventral view of an adult of *L. weberi* (centre right) and *Lipaugus fuscocinereus* (far right). Photo: P.G.W.S.



Figure 2. Dorsal and ventral view of Holotype male *Lipaugus weberi*. Photo: P.G.W.S.

slightly paler grey fringing to nape feathers giving a subtle scalloped appearance. Dark grey extending down the back with an olivaceous-brown (fringes closest to Olive, 30) tinge increasingly darker towards the rump.

Tail

Uniform dark greyish-brown (Vandyke Brown, 121 but slightly greyish).

Underparts

Pale grey (Medium Neutral Grey, 84), darkening (to DNG, 83) on the breast and with silvery lustre (Glaucous, 80) on abdomen. Several individual feathers on the lower breast to mid-belly are broadly tipped olivaceous-brown (near Olive, 30) as on the lower back. Vent and undertail coverts immaculate pale cinnamon-brown (Light Drab, 119C).

Wings

Remiges dark brownish-grey (closest to BNG, 82). Tertials and fringes of secondaries and greater secondary coverts cinnamon-brown (Raw Umber: 23). Leading edge, median and lesser coverts dark grey fading to narrow paler grey tips (between DNG, 83 and MNG, 84). Underwing and axillaries contrasting pale silver-grey (Pale Neutral Grey, 86). Outer webs of primaries 6 and 7 are modified and stiffened with elongated and non-interlocking barb-like projections along the entire length.

Bare parts in life

Iris dark brown; maxilla and mandible uniform black; mouth commissure and narrow uninterrupted orbital ring bright yellowish (Orange Yellow, 18); tarsi and toes dark grey with yellow soles to the feet.

PARATYPES

Adult female (skull fully ossified), No. 33413 of the ornithological collection at ICN-MHN. Collected at the type-locality in an understorey mist-net on a ridge-top at an elevation of 1,550 m on 27 August 1999 by Colombian EBA Project '99 and prepared by PGWS (original number EBA 86). Skull fully ossified, ovaries 8.0 mm (largest ova 0.9 mm), and little subcutaneous fat. Photographs catalogued with VIREO (No. s50/2/005). Stomach contents, parasites and muscles/organs preserved and deposited at ICN-MHN.

Juvenile male (40-50% ossified skull), No. 33797 of the ornithological collection at ICN-MHN. Collected 4 June 2000 by AMC (original number AMC 038) at the type-locality in an understorey mist-net at 1,800 m asl. Testes not enlarged (<5.0 mm), and no subcutaneous fat. For measurements see Table 1.

Parotypic variation

The adult female was undergoing a full body, tail and wing moult, with the three outermost primaries (# 1-3) heavily worn and new primaries emerging at primary #5 and missing #4. Coloration was almost identical to the holotype, but with the following subtle differences: slightly warmer chestnut-brown crown (near MB: 223A), owing to narrower faint black fringe and grey feather tips (probably related to heavier plumage wear) which give a slightly scaly appearance; mantle darker grey and lower back to uppertail coverts less contrasting, being uniform paler olivaceous-brown (near Olive, 30); wings, particularly tertials and outer primaries were faded (sun bleached) and worn, but being replaced by fresh dark greyish-brown (BNG, 82) feathers (as in holotype); and underparts heavily worn (suggesting recent breeding activity) with slightly more individual olive-brown feathers on the belly.

The recently fledged (within several months) juvenile male is almost identical in plumage and bare part coloration to the holotype, but with the following differences: dark brownish-grey iris (not dark brown), brighter and broad rufous fringes to the tertials, secondaries, and primaries #7-10; and a little less obvious chestnut-brown crown patch with more greyish feathers at crown edge. The juvenile lacked the modified primaries of the adult male. In *L. fuscocinereus*, four museum specimens (AMNH 173818, AMNH 126595, IAVH 4878, and UMZC 27/Cot/18/c/1) collected in July and September are juvenile birds. All exhibit broad rusty-rufous fringes and tips to the wing feathers, particularly prominent on the greater wing coverts, reminiscent of, but

slightly different from, the pattern observed in *L. weberi*. The juvenile *L. weberi* shows most rufous in the lower flight feathers, whereas in *L. fuscocinereus*, the wing coverts show the most prominent rufous edgings. Juvenile *L. vociferans* have rusty edges and tips to the wing and tail feathers, and may even show a rufous band in the wing primaries, similar to that of many furnariids (J. O'Neill *in litt.* 2000). In *L. vociferans*, it is known that the juvenile rufous wing coverts and rufous-tipped flight feathers are retained until first complete moult, when adult plumage is acquired (Snow 1982). With so few juvenile *L. fuscocinereus* in the collections, juvenile plumage is probably lost rapidly in this species also.

Sexual dimorphism

Amongst *Lipaugus*, only the Rose-collared Piha *L. streptophorus*, shows strong sexual dimorphism. Where data exist, males of most *Lipaugus* apparently average slightly larger than females (Snow 1982). However, for *L. fuscocinereus*, wing chord and tail length differ significantly between sexes ($F_{1,47}=38.609$, $P<0.001$, $F_{1,47}=54.099$, $P<0.021$, respectively). Although there is an overlap of *c.* 7mm, this is a fairly reliable measurement for sexing some *L. fuscocinereus*, (see Table 1).

Snow (1982) compared the tail to wing length proportions for *Lipaugus* with *L. fuscocinereus* (the largest tail averaging 92% of wing chord). Comparing sexes, male *L. fuscocinereus*, with a longer wing chord, average 89.3% while female tails average 94.1% of wing chord. Our limited data suggest a similar sex difference in *L. weberi*, with males 79.0% and females 85.4%.

Previously undocumented sexual dimorphism is reliable for sexing adult *L. fuscocinereus* and *L. weberi* based on the presence or lack of modified outer webs of the primaries (*L. fuscocinereus* [$n = 53$]), although modified primaries were not present on juvenile males. Amongst *Lipaugus* as traditionally treated, only *L. lanioides* was previously noted to have modified primaries (Snow 1982). *Chirocylla* (*Lipaugus*) *uropygialis*, which may also be a congener, has highly modified primaries, although in the female modifications are also much reduced (Remsen *et al.* 1982 and see Taxonomic Affinities below).

Measurements of individuals not collected

An adult of undetermined sex was captured, examined and released on 31 March 1999 (1750 m asl), total culmen (tip to skull) 20 mm; tarsus length 20 mm; flattened wing chord 123 mm; tail length 110 mm. An adult, presumed a male, was captured,

examined and released on 23 May 1999 (1500 m asl), total culmen (tip to skull) 21 mm; tarsus length 20 mm; maximum wing chord 129 mm; tail length 102 mm. (Note: caution is advised in comparing wing chord data between live birds and specimens due to post mortem shrinkage). Little plumage variation has been noted amongst c. 300 sightings in the field.

Field characteristics

Medium-sized bird with thrush-like proportions. Appears uniform slaty-grey, with conspicuous yellowish orbital ring and gape. Chestnut-brown crown feathers appear very dark in poor light, and can be difficult to see in the field. Vent cinnamon-brown. Long tail appears quite forked and is sometimes flicked upwards. Perching posture is slightly more horizontal than in other *Lipaugus*. It is particularly vocal, with a loud piercing call regularly heard throughout the day and year. Flight is fairly noisy.

TAXONOMIC AFFINITIES

From its general morphology, voice and behaviour, the new species can be immediately placed in the genus *Lipaugus*, family Cotingidae. The genus *Lipaugus* Boie 1828, traditionally constituted seven species (*cryptolophus*, *subalaris*, *vociferans*, *unirufus*, *lanioides*, *streptophorus* and *fuscocinereus* [per Snow 1982]), but has recently been shown by phylogenetic analysis of DNA sequences and morphological data to be polyphyletic (Prum 1990). The Andean green pihás, *L. subalaris* and *L. cryptolophus*, are not closely related to the grey or rufous *Lipaugus* spp. (Prum *et al.* 2000). They have been placed in the genus *Snowornis* based on morphological and phylogenetic characteristics (Prum 2001).

All species of the genus *Lipaugus*, as well as other superficially similar genera (e.g. *Chirocylla*, *Snowornis*, *Rhytipterna*, *Laniocera*) have been inspected at AMNH, IAVH, ANSP, UMZC, CAR, USNM, NHM and ICN-MHN. Sound recordings were analysed and compared for most *Lipaugus* species. See Appendix for localities of specimens of *Lipaugus fuscocinereus* examined.

Male *L. weberi* shares the specialized modified primary barbules, used for display wing-whirring, with male *L. fuscocinereus* and *L. lanioides*, as well as both green pihás, *Snowornis subalaris* and *S. cryptolophus*. Modified primaries are absent in *L. vociferans*, *L. streptophorus*, and *L. unirufus*, indicating that they do not undertake the wing-whirring display. The number of modified primaries varies, with two in *L. weberi* and *L. lanioides*, versus three in *L. fuscocinereus*. Both species of *Snowornis* share the modified primaries and yellow eye ring with

L. weberi, however, differ in their largely olive green plumage, yellow underwing and partially concealed black crown patch in male (*subalaris*) or both sexes (*cryptolophus*), which supports their recognition as a genus distinct from *Lipaugus* (Prum 2001).

Syringeal data of the genus *Lipaugus* show that species with loud and highly modulated vocalizations, such as *vociferans*, *unirufus*, *streptophorus* and *fuscocinereus*, all have a pair of intrinsic syringeal muscles (Prum 2001). In contrast, both *Snowornis* species lack intrinsic syringeal muscles, resulting in less piercing vocalizations than *Lipaugus* (Prum 2001). With a loud call of very similar timbre to *L. vociferans*, *L. fuscocinereus et al.*, *L. weberi* almost certainly has derived intrinsic syringeal muscles and should be considered a member of the monophyletic *Lipaugus* clade.

The Scimitar-winged Piha *Chirocylla uropygialis* was originally described in its own genus by Sclater (1888), distinguished only by its autapomorphous wing feather specialization. We establish that *C. uropygialis* also shares the characteristic modified barb of the middle primaries with *L. fuscocinereus*, *lanioides* and *weberi* although this feature is much more accentuated in *C. uropygialis*. Other features such as plumage coloration, vocalizations and general proportions are congruent with *Lipaugus*. Remsen *et al.* (1982), Ridgely and Tudor (1994) and Prum (2001) therefore suggested that *Chirocylla* is probably best placed within *Lipaugus*. In view of these factors we agree that there is no justification for maintaining *Chirocylla* as a genus. We therefore recommend that *uropygialis* be placed within *Lipaugus*, with its closest relatives probably being *L. fuscocinereus* and *L. weberi*. However, we strongly advocate further research on the phylogenetic relationship of *Lipaugus*.

Following the examination and comparison of specimens of all *Lipaugus* species, and based on analysis of *Lipaugus* by Snow (1982), we consider that *L. weberi* is most closely related to *L. fuscocinereus*. They share the uniform greyish plumage, and further comparison of vocalizations (see below) and ecological information confirms the close relationship with other congeners, although *L. weberi* is considerably smaller-sized than *L. fuscocinereus* (74% morphometrically; 48% by body mass). Morphometrics of *L. weberi* are presented with *L. fuscocinereus*, *L. vociferans*, *L. unirufus*, and *L. (Chirocylla) uropygialis* in Table 1. The principal morphological characteristics distinguishing *Lipaugus fuscocinereus* and *L. weberi* are compared in Table 2 and illustrated in Figs 1 & 2. Assigning all measured individuals of four *Lipaugus* species

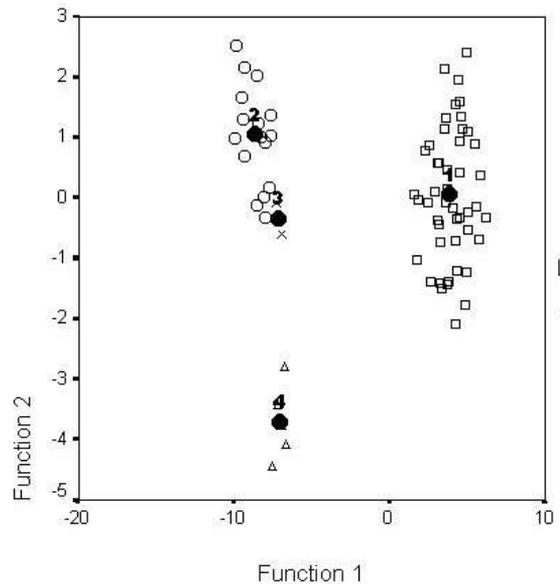


Figure 3: Canonical variate analysis on biometric data (summarised in table 1) for *Lipaugus* species; group centroids (•) *L. fuscocinereus* (○), *L. weberi* (Δ), *L. vociferans* (◻), and *L. unirufus* (x). The degree of accuracy in assigning individuals to all groups is 98.6%, although 100% for both *L. fuscocinereus* and *L. weberi*

(summarised in Table 1) to groups using canonical variate analysis (Fig. 3), a 100% probability accuracy is produced that *L. fuscocinereus* and *L. weberi* are correctly assigned as distinct species. Wing chord, tail and tarsus are the most indicative variables.

Given (i) the highly distinctive nature of *L. weberi*'s morphology, plumage and vocalizations, and (ii) its unique habitat preferences, ecology, and distributional and elevational range within the genus *Lipaugus*, we consider it certain that *L. weberi* meets the requirements for species under the revised

biological species concept (Johnson *et al.* 1999) and the phylogenetic species concept (cf. Zink & McKittrick 1995). We postulate that *L. weberi* is an allopatric replacement of *L. fuscocinereus* in the northern premontane slopes of the Cordillera Central.

DISTRIBUTION

Lipaugus weberi is restricted to a belt of premontane forest between 1500 and 1820 m asl, on the northern slope of the Central Cordillera east of the Nechí river valley, where it is presently known from four localities in Anorí and one in Amalfi (Fig. 4).

La Forzosa (6°59'N; 75°08'W; 1500-1820 m) forest fragment (ca.450 ha), which includes the type-locality at 1,550 m and surrounding forest within the Quebrada Chaquiral and La Soledad watershed ca. 6 km south of Anorí. Observations on 31 March–2 April; 23–26 May; 13–16 July; 26–29 August 1999; 20–22 December 1999, 3–5 June, 28–29 August and 15–17 September 2000 by the authors and many others.

La Serrana (7°05'36.50"N 75°07'49.44"W; 1750 m asl) forest fragment, a disturbed premontane very humid forest ca. 5 km north of Anorí (11 km north of La Forzosa). Observations on 3 October 1999, 19 December 1999; 18 March 2000 and 5–6 June 2000 by AMC, *et al.*

La Condena (7°04' 58.67"N 75°06'04.51"W, 1650–1700 m asl) between the valleys of the Río Porce and Río Anorí within the Quebrada Aguasana watershed, 13 km. north of La Forzosa and 6 km east of la Serrana, apparently continuous forest and one of the largest fragments where the species has been found. Observations on 16 October 1999 and 19–20 March by JMO and AMC.

Table 2. Comparative morphological characters of *Lipaugus weberi* and *L. fuscocinereus*

	<i>Lipaugus fuscocinereus</i>	<i>Lipaugus weberi</i>
Size difference (male) (body/wing/tail length average)	141% larger	71% smaller
Body mass	192% heavier	52% lighter
Head	Uniform dark grey cap.	Chestnut-brown cap.
Upperparts	Darker grey above with more extensive olivaceous areas	Grey with a slightly contrasting olivaceous-grey rump
Underparts	Dusky mottled appearance	Uniform grey with paler belly and cinnamon brown vent
Soft parts	Uniform dark orbital ring	Bright yellow orbital ring
Bill	Black with olive to pale horn below basally; dark commissure	All black; yellow commissure
Wing	Cinnamon-buff wing edges; uniform grey underwing	Dark brownish grey wing remiges; olivaceous-light grey underwing
Modified primary feather outer webs	#5-7 [3]	#6-7 [2]

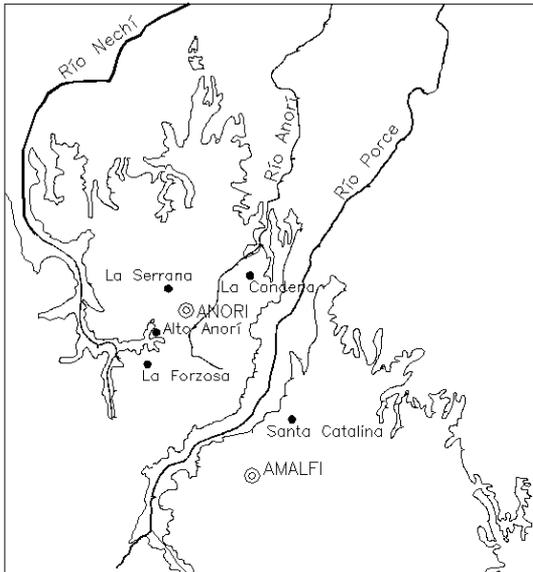


Figure 4. Map of the northeastern Cordillera Central in Dept. of Antioquia. The five localities for *L. weberi* are shown; La Forzosa (type-locality), La Serrana, La Condena, Alto Anorí and Santa Catalina. The 1000-m contour line is shown.

Alto Anorí, in the path to Santa Gertrudis (ca. 7°00'N 75°10'W; 1600–1700 m asl); a large forest fragment of well-conserved primary forest in the southwestern part of Anorí. Observations on 27 August 2000 by J. L. Toro.

Santa Catalina, Vereda Salazar (ca. 6°58'N; 75°02'W; 1500–1600 m), a remnant forest belt of the ridges of the Río Riachón watershed, ca. 10 km northeast of Amalfi. Observations on 27–30 September 2000 by AMC.

Today, *L. weberi* is likely to survive in just a few other forest fragments along the northern and northeastern slopes of the Central Cordillera, e.g. adjacent Municipalities such as Campamento, Angostura, and Guadalupe. We consider it possible that the species was once fairly continuously distributed in premontane forest of the northeastern slope of the Central Cordillera (Fig. 6). Additionally, the subandean forests in the adjacent Serranía de San Lucas contain suitable habitat for the species and remain completely unknown above 1,000 m asl.

The fact that this conspicuous and fairly common new species has not previously been discovered, despite intensive collections about Medellín and the northwestern slope of the Central Cordillera provides strong evidence of a highly localized distribution. The humid premontane forest life zone, between 1200 and 2000 m asl, has a total area of 931 km² in the municipalities of Amalfi and Anorí (CORANTIOQUIA, c/o J. L. Toro in litt.). We estimate approximately 391 km² lies within the

altitude range of *L. weberi* (1500–1820 m). However, the present-day extent of natural mature forest cover within the species altitudinal range in Amalfi and Anorí has been significantly reduced by over 65% to approximately 130 km² (13,000 ha).

L. weberi is not known to be sympatric with any other *Lipaugus*, being allopatric with *L. fuscocinereus* in the highlands and *L. unirufus* in the lowlands. The nearest population of *L. fuscocinereus* to the new species occurs 90 km west in the Western Cordillera on the Paramillo trail, Antioquia Dept. (AMNH 13388) and 220 km south in the Central Cordillera in the Rio Blanco watershed, Caldas Dept (Fig. 5). It is unlikely that *L. fuscocinereus* occurs on the northern slopes of the Cordillera Central as there are few substantial massifs above 2,000 m elevation in the region. Furthermore, historical highland collections in this region have not located the species. *L. unirufus* occurs in the adjacent lowlands and northern Andean foothills, found to 850 m in Municipio Anorí (Donegan and Salaman 1999).

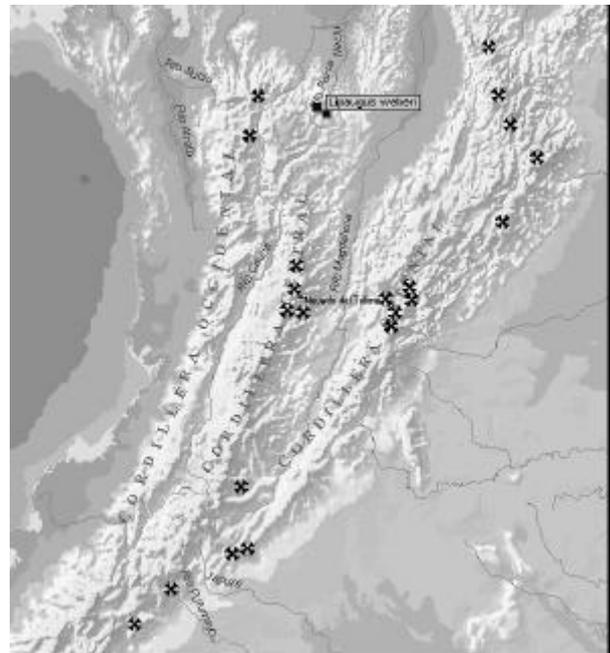


Figure 5. Distribution of *L. fuscocinereus* (X) and *L. weberi* in the Northern Andes of Colombia.

HABITAT

Lipaugus weberi inhabits primary premontane wet forest (*sensu* Holdridge) of the northern slope of the Central Cordillera of Colombia. It is currently known from altitudes of 1500 to 1820 m (Fig. 4), but may



Figure 6. View of primary premontane wet forest at the type-locality of La Forzosa. Photo: PGWS.

range higher (possibly to ca. 2000 m) and almost certainly ranges lower (possibly to ca. 1200 m), corresponding with the range of this life zone in the region (Espinal 1992).

Warm, moist Caribbean air currents converge upon the northern slope of the Central Cordillera over a relatively narrow front. Consequently, frequent mists and high levels of precipitation (2,600-3,500 mm/year) and relative humidity (77-95%) characterize the premontane cloud forests of the region, to which we suspect *L. weberi* is endemic. The dry season is from December to February and wet season from May to October, with a peak in precipitation levels in July-August (Espinal 1992, IDEAM unpubl. data).

The northern Central Cordillera is characterized by a complex topography, dissected by steep river valleys and gorges. Primary forests are characterized by a heterogeneous canopy, from 6-7 m on the ridges, 15-17 m on the slopes, increasing to 20 m along watercourses, with occasional emergent trees up to 30 m. Understorey cover is densest on the steep slopes, dominated by terrestrial herbaceous plants and by epiphytes on ridges. The forests are particularly dynamic, with a high natural treefall rate and

landslides caused by high precipitation on steep slopes with shallow soils.

L. weberi has been found in pristine forest (La Forzosa, La Condena, and Alto Anorí), disturbed primary forest (La Serrana surrounding La Condena and Santa Catalina), and near forest borders, but remains unrecorded in young secondary forest. At La Serrana, selective logging in primary forest had resulted in a more open canopy and colonization by some open country species. In Santa Catalina, the most disturbed forest in which the new species has been found, *L. weberi* is much less frequently encountered than at other sites.

Dominant canopy trees in the new species' preferred habitat include *Guarea* (Meliaceae), *Pouteria* (Sapotaceae), *Protium* (Burseraceae), *Roucheria* (Linnaceae), *Vochysia* (Vochysiaceae), *Virola* (Myristicaceae) and *Clusia* (Clusiaceae) (J. L. Toro *in litt.*). In treefall gaps and forest borders, colonization is led by thickets of bamboo (*Chusquea* sp.), and shrubs of *Miconia* (Melastomataceae) and *Psychotria* (Rubiaceae). Epiphytes (Bromeliaceae, Araceae, Orchidaceae and epiphytic ferns) are notably dense, as well as vines. Palms are an important floristic component, mainly *Dyctiocarium lamarckianum*, *Wettinia kalbreyeri*, *W. fascicularis* and *Geonoma undata*, which are fairly abundant in all strata. Several species of tree ferns (e.g. *Cyathea*, *Dycksonia*) and shrubs and small trees of *Miconia*, *Meriania* (Melastomataceae), *Psychotria*, *Palicourea* (Rubiaceae), *Schefflera* (Araliaceae), *Piper* (Piperaceae) and *Cavendishia* (Ericaceae) are common in subcanopy and understorey communities. The herbaceous species of Gesneriaceae, Heliconiaceae, Maranthaceae, and Araceae are also numerous in the understory (J. L. Toro *in litt.*). The high humidity encourages an abundance of mosses and bromeliads in all strata. The predominant families are Melastomataceae, Clusiaceae, Sapindaceae, Myristicaceae, Rubiaceae, Myrtaceae, Annonaceae, Bromeliaceae, Gesneriaceae, Ericaceae, Myrsinaceae, Lauraceae, and Moraceae (C. E. Gonzalez *in litt.*). Second growth is stunted and dominated by species typical of higher elevations such as *Tibouchina*, *Vismia*, *Weinmannia* and *Escallonia*, with the fern *Pteridium aquilinum* notably abundant.

ECOLOGY AND BEHAVIOUR

The species is conspicuous (principally by voice) and considered locally common at the four localities where it has been recorded in Anorí, particularly between 1550 and 1750 m asl. In Amalfi, where the forest is more fragmented, it is much less common.

We have accumulated more than 300 observations of *L. weberi* in the field, largely in La Forzosa, where fieldwork has been most intensive since March 1999. At least three males appeared to be holding territories along our 300 m mist-net transect in August 1999.

Solitary individuals are usually encountered, perching in the midstorey to lower canopy. Occasionally individuals associate with multi-species foraging flocks in the upper forest strata. Pairs or flocks have only very rarely been observed. *L. weberi* was seen moving across small non-forested gaps (5–15 m wide) and in remnant forest patches at La Serrana, such as along narrow forested ravines beneath deforested slopes, although close to large forest fragments. On exposed branches, *L. weberi* perches in a slightly more horizontal position than other members of the genus. When agitated, it raises the chestnut crown feathers and cocks the tail slightly, exposing its cinnamon-brown vent. Although largely sluggish and inactive throughout the day, one *L. weberi* made loud alarm calls and chased off an approaching Great Thrush *Turdus fuscater* at La Condena.

Diet

L. weberi's diet consists principally of small to medium-sized berries and occasionally large invertebrates. Prior to capture, the holotype was seen feeding from the perch on berries of *Myrsine* sp. (Myrsinaceae), a 7-m high understorey shrub. The holotype's stomach contained many small fruit seeds and pericarps, including a *Myrsine* sp., and a fully intact whitish Lepidoptera larva. The female's stomach contained several small fruit seeds of different species although most related to a purple-pulped fleshy berry, probably of a Rubiaceae shrub (probably *Palicourea* or *Psycotria*). The juvenile's stomach contained green fruit material from a Lauraceae fruit. *L. weberi* has been observed feeding on the berries of *Myrsine coriacea* (Myrsinaceae), *Hieronyma scabrada* (Euphorbiaceae), *Viburnum* sp. (Caprifoliaceae), *Roucheira* sp. (Linnaceae), *Persea* sp. (Lauraceae), *Ilex* sp. (Aquifoliaceae) and *Miconia* spp. (Melastomataceae). Voucher plant specimens were deposited at the Herbarium Universidad de Antioquia (HUA).

Foraging behaviour

Food items were hover-gleaned from the outer foliage of the understorey to subcanopy and, less commonly, taken from a perch. Feeding movements largely comprised short sallies of less than 5 m followed by a hover-flutter and lunge to pluck a berry or stationary invertebrate, before swooping to another exposed

perch and remaining inactive for several seconds. Sometimes the bird grasps a berry before making an acrobatic pirouette, turning its body through 180°, in order to break the pedicel and pull the fruit away from the branch. When gleaning from a fruiting tree, individuals perch in neighbouring trees or perch precariously for short periods on the outer branches of the fruiting tree near clusters of small berries. *L. weberi* has been observed regurgitating seeds. Once, one frenetically bashed a large fruit against its horizontal perch, before consuming the contents.

Occasionally, individuals were observed associating with a multi-species foraging flock, although sometimes only for relatively short periods, perhaps just within an individual's territory. The core species in such flocks included Red-headed Barbet *Eubucco bourcierii*, Buff-fronted Foliage-gleaner *Philydor rufus*, Slate-throated Whitestart *Myioborus miniatus*, Beryl-spangled Tanager *Tangara nigroviridis*, Golden Tanager *Tangara arthus*, Purplish-mantled Tanager *Iridosornis porphyrocephala*, and Yellow-throated Bush-Tanager *Chlorospingus flavigularis*.

Breeding

Most female cotingas undergo a complete post-breeding moult, whilst males, that undertake no parental care, begin moulting while females are nesting (Snow 1982). For example, male and female *L. unirufus*, *L. vociferans*, and *L. lanioides* average two to three months' difference between moults (Snow 1982, Willis & Oniki 1998). The female paratype was in full body, wing and tail moult on 27 August, whilst the male holotype had recently completed moulting, indicating that a similar moult strategy probably occurs in *L. weberi*. Neither sex had enlarged gonads. On 18–20 March 2000, a pair was frequently seen foraging very closely, contrasting with the solitary habits usually observed. A wide repertoire of vocalizations was heard and recorded at this time. The recently fledged juvenile was collected on 4 June 2000. All the indications are that the breeding season is in the first half of the year, perhaps from March, when the breeding period for most passerine birds in the region starts.

VOCALIZATIONS

Like other members of the genus, *L. weberi* is particularly vociferous. It calls frequently throughout the day and year-round. It is inquisitive and responds strongly to whistled imitations and playback, making short sallies across the area of imitation and producing variations of the typical call. Calling is relatively sporadic, although as in *L.*

unirufus (Snow 1982), the explosive call is often elicited by an extraneous loud noise like the fall of a branch or old palm leaf. An extensive series of song recordings has been made, including recordings of the holotype immediately before capture. Additional vocalizations were heard and recorded; several have been deposited with Wildlife Sounds, National Sound Archive (London).

The song is highly distinctive: a loud, piercing *sreeck*, audible at up to *c.* 100 metres inside dense forest (Fig. 7a). A typical song bout will commence with a brief slightly rising introductory note at *c.* 2-3 kHz. The main phrase is a brief (0.35 seconds, s.d. 0.08, *n* = 21) rising scream from 2.23 kHz (s.d. 0.37) to 5.85 kHz (s.d. 0.59) that abruptly descends to 1.125 kHz (s.d. 0.10). This phrase is typically repeated with one-second intervals. Typical of the genus (Snow 1982), there are minor variations of the phrase, but these are barely discernible by ear. When a bird is agitated, such as following playback, the interval between calls is shortened to 0.36 second (s.d. 0.28, *n* = 9).

The song of *L. fuscocinereus* is distinct from that of the new species, although they share similar

commencement and frequency ranges (see Fig. 7b). The introductory phrase is brief (0.48 seconds), slightly rising between 2.2-2.8 kHz. The main phrase (*n* = 5) described as *whee-a-wheee* is typically 1.4 seconds, but may be longer, with embellishments on the trailing end. It commences similarly to *L. weberi*, with a rising scream from 2.26 kHz to 5.59 kHz. However, rather than the abrupt termination of the call as in the new species, *L. fuscocinereus*' call descends and rises over 0.33 seconds from 2.89 kHz to 5.67 kHz, then trails off over 0.75 seconds to 2.83 kHz.

Three other calls of *L. weberi* have been noted. Non-singing birds were observed on two occasions making a low-pitched, relatively quiet nasal *gluck-gluck*, apparently a contact or alarm call (Fig. 8). A second probable contact call, *cu-wheé* or *chew-wit*, was also heard and recorded (Fig. 8), with the first phrase having strong resonance at 1.2, 2.5, and 3.8 kHz and overall 0.47 seconds duration. On landing at a perch, a discrete nasal chirpy call of short duration (0.16 seconds) was occasionally heard.

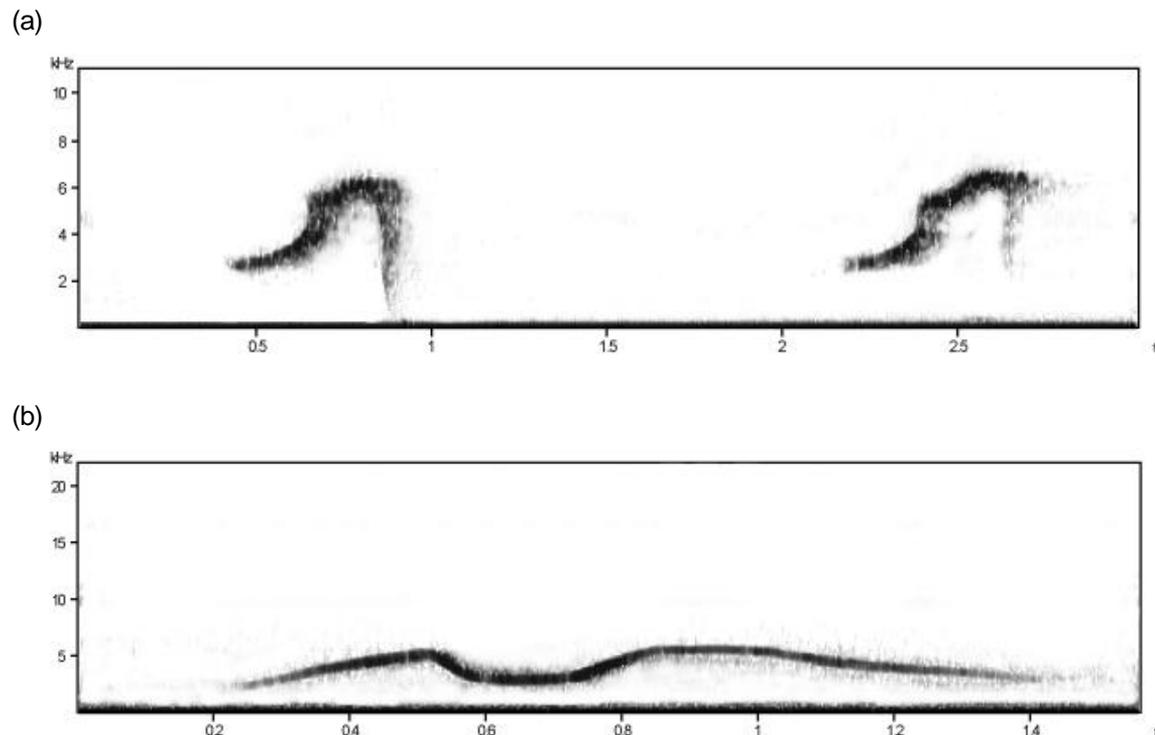


Figure 7. Sonograms illustrating the song of *Lipaugus weberi* (a) and *Lipaugus fuscocinereus* (b). Recorded by (a) AMC at type-locality and (b) Niels Krabbe [IIB 22] single call recorded at dusk in September 1990; Cordillera de los Guacamayos, Napo, Ecuador (00°37'S 77°49'W, 2,100 m). Note that the temporal scale is different. Sonogram: PGWS.

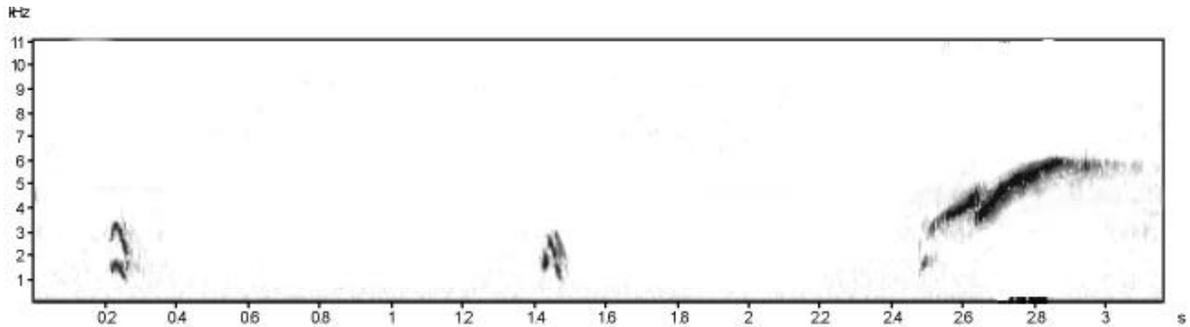


Figure 8. Sonograms illustrating call note type A (nasal “gluck-gluck”) and aggressive “cu-wheé” call of *Lipaugus weberi*. Recorded by AMC. Sonogram: PGWS.

Most *Lipaugus* species have closely- or loosely-associated lek displays, e.g. *vociferans* and *fuscocinereus*. *L. fuscocinereus* has been recorded calling and wing-whirring at a communal lek of 3–5 males in the Central Cordillera of Colombia (López-Lanús 2000). On 6 June 2000 at La Serrana, a very active individual was recorded singing continuously from the subcanopy, 8 m above the ground. The bird had the crest raised and the throat feathers erected, while both wings were slightly extended downwards. After playback, it became more excited as it flew to the playback area. In the final part of this flight, as the bird was ascending to a higher perch, it produced a mechanical wing-whirring sound. The sound was reminiscent of the flight sound of the Sickle-winged Guan *Chamaepetes goudotii*, which was also compared to the wing-sound produced by *L. fuscocinereus* (López-Lanús 2000). However, *L.*

weberi's wing-whirring is less strident than *L. fuscocinereus*; has considerably fewer wing beats (five verses twelve in *fuscocinereus*); and a much more rapid wing verberation rate (one per 0.036 seconds versus 0.23 seconds in *fuscocinereus*) (Fig. 9b). Interestingly, both species sing in flight when wing-whirring. Wing-whirring is probably an important element of lek display for both the new species and *L. fuscocinereus*.

The wing-whirring noise made by male *L. fuscocinereus* and *L. weberi* is brought about by rapid movements of the primaries, with modified outer webs producing the sound. The differences between the two species' wing-whirring sounds are probably related to the different number of primaries with elongated and stiffened barb-like projections (3 in *L. fuscocinereus*; 2 in *L. weberi*), and due to size differences between the two species.

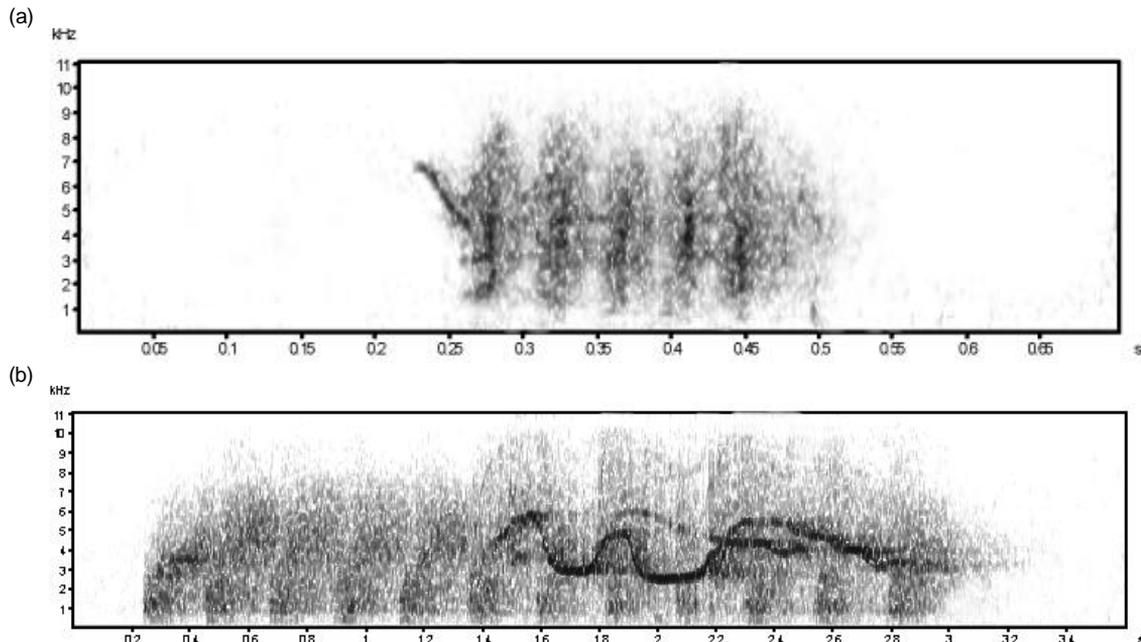


Figure 9. Sonograms illustrating the wing-whirring display and accompanying vocalizations of *Lipaugus weberi* (a) and *L. fuscocinereus* (b). Note that the temporal scale is different. Recorded by (a) AMC and (b) Bernabé López-Lanús. Sonogram: PGWS.

CONSERVATION

The Andes of Colombia, and particularly the Central Cordillera, have undergone almost complete ecological change, representing one of the most human-altered landscapes in South America (van Velzen 1992, Renjifo 1999). Surviving forested areas are now highly fragmented and isolated. The most critical biome for conservation action in Colombia is the premontane ecosystem, which is almost completely deforested outside protected areas (van Velzen 1992, Sánchez & Hernández-Camacho 1995).

Of the 29 bird species restricted to the Cordillera Central, 16 are globally threatened (Stattersfield *et al.* 1998). Furthermore, no protected area in the Central Cordillera encompasses sizeable areas of premontane forests despite a high concentration of endemic bird species at these elevations. Forest cover in the Cordillera Central is estimated at 5% (Carrizosa 1990), but we estimate the extent of forest in the premontane zone to be just 3–4%.

Lipaugus weberi is a forest-dependent species that must have been seriously affected by forest loss and fragmentation because of its narrow geographic and altitudinal range and its specific habitat requirements. Large frugivorous birds, such as cotingas, are particularly susceptible to population declines and extinction over time following habitat fragmentation, due to their dependence on the spatial and temporal variability of food resources according to tree species phenology (Terborgh & Winter 1980, Loiselle & Blake 1992). We suspect *L. weberi* has been extirpated from much of its already small former range. Forest fragmentation has isolated *L. weberi* populations and may ultimately affect genetic structure.

Threats

The northern slopes of the Central Cordillera and adjacent Serranía de San Lucas are extremely rich in fine mineral deposits. Since the 19th century, northeastern Antioquia has been heavily colonized by gold-miners and subsequently farmers, especially coffee-growers and cattle-ranchers. Colonization was particularly intense above 1,000 m, where a cooler climate and rich soils support productive cattle ranching and plantations of coffee, plantain, tangerine, maize and sugar cane. In the 1930s, the coffee boom attracted a further wave of colonizers to the region, which is now the heart of the Colombian coffee-growing industry.

Continued forest degradation and clearance for construction, agriculture and commercial plantations in this region are having profound and long-term environmental impacts. Forest exploitation occurs

despite the classification of "logging-prohibited" areas such as La Serrana – areas which are inadequately enforced. In the mid-1990s, a large tract of native forest near the Anorí type-locality, was replaced with commercial plantations of exotic tree species such as *Pinus* and *Cupressus*. In Amalfi, the premontane forests have almost completely been converted into pastures for cattle ranching, and the remaining forests are heavily disturbed owing to the exploitation of three palm species (*Wettinia kalbreyeri*, *W. fascicularis* and *Dyctiocarum lamarckianum*). The strikingly lower abundance of *L. weberi* in Amalfi compared to the other localities is probably due to earlier colonization and more prolonged resource exploitation than the relatively recent human activities in Anorí. The most profound human effects are focused along the inter-municipal roads to Amalfi and Anorí from Yarumal and Medellín. Throughout the Central Cordillera, human population pressures continue to mount, with the already grave conservation situation expected to worsen further over coming years (Fig. 10).

An aerial survey of Serranía de San Lucas by the authors in July 2000 revealed that the largest tract of premontane forests in the Central Cordillera has recently been colonized by substantial numbers of gold-miners and land stakeholders. Although the authors were able to survey the foothills of Serranía de San Lucas in 1999 (Donegan and Salaman, 1999), three attempts to survey the montane areas have been aborted due to the security situation.

Action taken

Substantive conservation action is hampered by the now highly-fragmented forest landscape. However, CORANTIOQUIA have been promoting the conservation of remaining forested areas, such as La Forzosa and La Serrana, focusing on land purchase schemes of important watersheds that supply drinking water to towns.

Owing to the dedication and foresight of one local farmer, Luis Ángel Ramírez, a 320 ha block of primary forest at La Forzosa (1500–1820 m asl), has long been protected with all forms of human intervention prohibited, despite immense social and economic pressures. The La Forzosa type-locality is of exceptional biological importance, containing populations of several threatened birds including Black Tinamou *Tinamus osgoodi*, Red-bellied Grackle *Hypopyrrhus pyrohypogaster*, Multicolored Tanager *Chlorochrysa nitidissima* and Black-and-gold Tanager *Bangsia melanochlamys* (Cuervo *et al.* 1999). Based on rapid biodiversity surveys by the EBA project and



Figure 10. Deforestation at Type-locality (left) and aerial view (right) of deforested premontane zone of the Northern Andes, 15 km east of the type-locality of La Forzosa near Amalfi, northeast Antioquia. Photo: PGWS.

CORANTIOQUIA, a vulnerability assessment and conservation feasibility plan for the area of Anorí, including La Forzosa, was produced (Donegan & Salaman 1999). This report elaborated the urgent need for protection and detailed results of surveys, with ornithological data providing a strong impetus for conservation. Shortly after the CORANTIOQUIA surveys, the La Forzosa type-locality was formally protected by

CORANTIOQUIA, and an expansion programme is planned to establish forest corridors with the other remnants of primary vegetation. La Serrana is managed by the Anorí municipal government, but lacks adequate control and enforcement against illegal loggers, in spite of being the catchment area of the aqueduct of Anorí. No conservation activities have been developed in Amalfi.

Action proposed

Lipaugus weberi is recommended for IUCN Red List status as Endangered based on the following criteria:

B1: extent of occurrence estimated $<100 \text{ km}^2$, being severely fragmented [Critical];

B2d: rapid population decline inferred owing to quality habitat loss [Endangered]; and

C2a: small population ($<2,500$ individuals) with severe fragmentation at all sub-populations <250 [Endangered].

We consider that the most important conservation priorities for *L. weberi* are establishing and enforcing protected areas of forest where the new species is present and conducting field surveys in other areas where *L. weberi* is suspected to occur.

The protection of the few large tracts of forest remaining in the region must be energetically pursued, particularly in Serranía de San Lucas where the species is strongly suspected to occur. All premontane forests at Amalfi will be expatriated within the very near future, and small protected forest fragments in Anorí provide only marginal long-term security for the premontane biodiversity in the region. It is therefore essential to determine the extent of the species' distribution and its regional population status, which would greatly assist the formulation of a management plan. This is most efficiently undertaken by rapid ornithological investigations in premontane and montane forests across the region, particularly in remaining forest tracts east of the Río Porce and in Serranía de San Lucas to the northeast. These surveys would also contribute important new information on the rest of the region's endangered and poorly-known avifauna.

The EBA Project team are grateful to Corporación Autónoma Regional del Centro de Antioquia (CORANTIOQUIA), for assisting and providing scientific permission and for financing the first faunal survey of the La Forzosa forest by the Bird Study Group of Universidad de Antioquia (in particular, thanks to C. Delgado, J. C. Luna, S. Galeano, A. Palacio, A. Vasco, P. Lopera, M. Castaño and A. Patiño). Special thanks are due to Juan Lázaro Toro, for introducing us to the region and for providing invaluable support in the field and with the

botanical assessment; this discovery owes much to him. We are very grateful for advice and assistance from the following: Carlos E. González, Sociedad Antioqueña de Ornitología (SAO), Centre of Bioacoustics, University of Texas A&M University, M. Gonzalo Andrade, Luis M. Renjifo, Richard O. Prum, Bette A. Loiselle, Carla Restrepo, James Van Remsen Jr., Richard Ashcroft, Daniel Cadena, Bernabé López-Lanús, Ali G, Luis Ángel Ramírez, and the UMATAs of Anorí and Amalfi. We are grateful to Robert Prys-Jones (NHM), Paul Sweet (AMNH), Nate Rice (ANSP), J. Angle (USNM), Robin Panza (CAR), Ray Symonds (UMZC), Mauricio Álvarez (IAVH) and F. Gary Stiles (ICN-MHN) for permission to examine specimens and Bernabé López-Lanús and Niels Krabbe for sound recordings. Nora Ochoa kindly assisted us with producing maps and GIS staff of CORANTIOQUIA provided forest cover data. The EBA expedition to La Forzosa was only made possible by generous financial support by British Ornithologists' Union, Royal Geographic Society, Cambridge Expeditions Fund, Percy Sladen Memorial Fund, People's Trust for Endangered Species and many others, accredited in the EBA website (www.proaxis.com/~salaman). Special thanks to John P. O'Neill for the exquisite frontispiece and to Walter H. Weber for his tireless encouragement for our research and conservation efforts. The manuscript has been greatly improved from discussions and comments by F. Gary Stiles, Jon Fjeldsá, John P. O'Neill, Niels Krabbe, David Wege, Richard Prum, Robert Ridgely, and reviewed by David Snow and Gary Graves.

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Received 8 November 2000; revisions accepted 13 March 2001

APPENDIX

Localities and specimens of *Lipaugus fuscocinereus* examined at the American Museum of Natural History (AMNH), New York, USA; (United States) National Museum of Natural History (USNM), Washington D.C., USA; Carnegie Museum (CAR), Pittsburgh, USA; Academy of Natural Sciences of Philadelphia (ANSP), Philadelphia, USA; Instituto de Ciencias Naturales, Museo de Historia Natural (ICN-MHN), Colombia; The National History Museum (NHM), Tring, UK; Instituto Alexander von Humboldt (IAVH), Villa de Leyva, Colombia; and University Museum of Zoology, Cambridge (UMZC), UK.

AMNH 112420, Laguneta, W. Quindio, 10,300 ft, Col., female; AMNH 112421, El Eden, E. Quindio, Col, 8300 ft, Col., male; AMNH 112423, Salento, W. Quindio, 9000 ft, Col., female; AMNH 122393, El Roble (near Fusugasuga), Col., 8000 ft., male; AMNH 122394, El Roble (near Fusugasuga), Col., 8000 ft., male; AMNH 126595, Subia, Cundinamarca, Col., juvenile (?); AMNH 130044, Loja, Ecu, 7000 ft, Col., male; AMNH 130045, Zamora, Loja, Ecu., 2000 ft., female; AMNH 132249, Choachi, Bogotá, 3,200 m, Col., male; AMNH 133882, Paramillo trail, Antioquia, West Andes, 10,000 ft, Col., male; AMNH 173068, Near Baeza, Ecu., 5000 ft, male; AMNH 173815, Baeza, Ecu., female; AMNH 173817, Baeza, Ecu., males; AMNH 173818, Baeza, Ecu., juvenile (?); AMNH 176178, Baeza, Ecu., male; AMNH 180554, Baeza, Ecu., female; AMNH 180556, Baeza, Ecu., female;

AMNH 183740, Sumaco, Arriba, Ecu., male; AMNH 183741, Sumaco, Arriba, Ecu., male; AMNH 183745, Sumaco, Arriba, Ecu., female; AMNH 35513, Ambato, Ecu, male; AMNH 43718, "Bogotá", male; AMNH 494211, "Bogotá", female; AMNH 494212, "Bogotá", male; AMNH 494213, no location, male; AMNH 494214, Baeza, Ecu.; AMNH 494215, Banos, Ecu., female; AMNH 494216, Banos, Ecu., female (?) NHM 1912.12.29.43 (formerly AMNH 112422), Salento, Quindio, above 9000ft., Col., male; NHM 1925.12.24.562, Baeza, E. Ecu., male; NHM 1925.12.24.563, Baeza, E. Ecu., female; NHM 1940.12.5.386, Huila, N. Oriente, NE Ecu., female; NHM 54.1.25.39, "New Grenada", Col. male; NHM 88.1.13.1524, Parrudaki, Col.; NHM 88.1.20.559, Vicinity of Bogotá, Col. female; NHM 88.1.20.560, Alegria, Antioquia, Col., female; NHM 88.1.20.561, Baisa, Ecu. male; NHM 88.1.20.562, Baisa, Ecu. immature; CAR 137367, Moscopan, Cauca, Col., 2485 m, male; CAR 58629, Cachiri, Santander, Col., female; CAR 59394, La Pica, Santander, Col., female; CAR 59481, La Pica, Santander, Col., male; CAR 60225, Boca de Monte, Boyacá, Col., female; CAR 70436, Sancodo, Caldas, Col., female; ICN-MHN (EBA 028), Tataui, Churumbelos, Cauca, Col., 2200 m, male; EBA (capture), El Doron, Churumbelos, Cauca, Col.; ICN-MHN 8990, Tijeras, Moscopan, Cauca, Col., 2750 m, male; ICN-MHN 8991, San Miguel, Cundinamarca, Col., female; USNM 101269, Guayaquil, Ecu., female; USNM 101270, Guayaquil, Ecu., female; USNM 101271 ("*L. fuscocinereus guayaquilensis*" - HOLOTYPE), Guayaquil, Ecu., female; USNM 376734, Moscopan, Cauca, Col., 2700 m, male; USNM 376736, Moscopan, Cauca, Col., 2800 m; USNM 411683, Hcda. Las Vegas, Santander, Col., 6000 ft., female; USNM 47059, Vicinity of Bogotá, Col., male; IAVH 4878 Cabaña La Ilusión, Parque Nacional Natural Cueva de los Guácharos, Huila, Col., juvenile; IAVH 5712 Quindio, Municipio Salento, Rincon Santo, Parque Nacional Natural los Nevados, Col., male; UMZC 27/Cot/18/c/1 No location, immature; UMZC 27/Cot/18/c/2 "Bogotá", Col., female.