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A NEW SPECIES OF WOOD-WREN (TROGLODYTIDAE: *Henicorhina*) FROM THE WESTERN ANDES OF COLOMBIA

Una nueva especie de Cucarachero (Troglodytidae: *Henicorhina*) de la Cordillera Occidental de Colombia

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SUMMARY

A new species of *Henicorhina* wood-wren (Aves, Troglodytidae) is described from the Munchique massif of the Western Andes of Colombia. The Munchique Wood-Wren *Henicorhina negreti* is closely related to and probably derived from the Gray-breasted Wood-Wren *Henicorhina leucophrys* of Central and South America. *Henicorhina negreti* appears restricted to a narrow band of extremely wet, stunted cloud forest on the upper Pacific slope, characterized by nearly continuous fog, high epiphyte loads and frequent landslides; it is abruptly replaced in taller forest at lower elevations on this slope by *H. l. brunneiceps,* and on the drier east slope by *H. l. leucophrys*. The new species differs from adjacent forms of *H. leucophrys* in its distinctly barred abdomen, dark juvenal plumage, relatively short tail and longer tarsi. Its song is also very distinct, and the adjacent forms of *H. leucophrys* do not respond to it while they do to each others (despite the fact that the new species occurs between them). Conversely, the new species does not respond to songs of *H. l. leucophrys* or *H. l. brunneiceps*, strongly suggesting that it is reproductively isolated from them and has distinct habitat requirements. Similarities between the ecology of *H. negreti* and that of *H. leucoptera*, another restricted-range endemic sympatric but not syntopic with *H. leucophrys*, are discussed. Possible threats to *H. negreti* due to forest clearance and global climate change are discussed, and we suggest that the species be accorded Critically Endangered status.

Key Words: Colombia, conservation, *Henicorhina negreti*, Munchique Wood-Wren, new species, taxonomy

RESUMEN

Se describe una nueva especie de Cucarachero *Henicorhina* (Aves: Troglodytidae) del macizo de Munchique en la Cordillera Occidental de Colombia. El Cucarachero de Munchique *Henicorhina negreti* está muy emparentado y probablemente se deriva del Cucarachero Pechigrís *Henicorhina leucophrys* de Centro y Sur América. *Henicorhina negreti* al parecer, está restringida a una franja angosta de bosque nublado achaparrado y extremadamente húmedo en la parte alta de la vertiente del Pacífico, caracterizada por muy alto epifitismo y derrumbes frecuentes. La nueva especie es reemplazada abruptamente en bosques más grandes y en elevaciones menores en esta vertiente, por *H. l. brunneiceps* y en los bosques más secos sobre la vertiente oriental por *H. l. leucophrys*. *H. negreti* difiere de las formas anteriores por su abdomen barreteado, plumaje juvenil mucho más oscuro, tarso relativamente más largo y cola más corta. Su canto es también muy distinto y las formas adyacentes

de *H. leucophrys* no responden a éste, aunque si responden entre sí a pesar de que *H. negreti* ocupa una posición geográfica entre ellas; contrariamente *H. negreti* no responde a sus cantos. Lo anterior indica que *H. negreti* probablemente está reproductivamente aislada de *H. leucophrys* y tiene necesidades de hábitat diferentes. Algunas similitudes entre la ecología de *H. negreti* y la de *H. leucoptera,* otro endémico simpátrico, de rango restringido pero no sintópico con *H. leucophrys* son consideradas. La deforestación y el cambio climático global se discuten como posibles amenazas a *H. negreti* y se sugiere que se le otorgue a ésta, la designación de especie Amenazada Críticamente de Extinción.

Palabras clave: Colombia, conservación, Cucarachero de Munchique, especie nueva, *Henicorhina negreti*, taxonomía.

INTRODUCTION

The Chocó Endemic Bird Area (EBA) includes very wet lowland to montane forests situated on the Pacific slope and coastal plain of the Western Andes in Colombia and the main Andean chain in extreme southern Colombia and western Ecuador. This EBA holds 67 endemic bird species and over 100 distinctive subspecies, the world's highest continental concentration of avian endemism (Salaman 2001). However, due to the low elevation of the Western Cordillera ridgeline, its highly disjunct peaks and an absence of substantial massifs above 2500 m, these 67 endemic bird species are concentrated at foothill and premontane elevations. Only two highland (>1800 m) endemics are known from the Chocó EBA: Colorful Puffleg *Eriocnemis mirabilis* and Chestnut-bellied Flowerpiercer *Diglossa gloriosissima*. These and a considerable number of other highland taxa do not range onto the western slope of the main Andean chain farther south, which is separated from the humid upper elevations on the Pacific slope of the Western Andes by the dry Río Patía valley.

An extremely wet climate, difficult terrain, and poor access have historically impeded exploration of the upper elevations of the Western Cordillera, while in recent decades civil unrest has often steered ornithological work to other Andean countries. For these reasons the Colombian Chocó remains one of the biologically least-known regions in the Neotropics (Salaman and Stiles 1996). Increasing attention in the past decade has culminated in the description of three new bird species from the wettest subtropical forests of the Chocó EBA: Chocó Vireo *Vireo masteri* (Salaman & Stiles 1996), Chocó Tapaculo *Scytalopus chocoensis* (Krabbe & Schulenberg 1997), and Cloud-forest Pygmy-Owl *Glaucidium nubicola* (Robbins & Stiles 1999). These discoveries highlight the potential for new discoveries.

Although sporadic collections were made elsewhere in the Colombian Chocó region, most ornithological work during the 20th century was focused on the Pacific slope of Cauca Department, particularly in the region now encompassed within Munchique National Natural Park (NP). Extensive ornithological collections (several thousand birds) were compiled by Kjell von Sneidern, F. Carlos Lehmann and Álvaro José Negret of the Museo de Historia Natural, Universidad del Cauca, Popayán [MHNUC] (Negret 1994), although most efforts were concentrated on the lowland and premontane zones (Bond & Meyer de Schauensee 1940, Negret 1994). In 1967, John Dunning and Kjell von Sneidern visited the highlands of Munchique to photograph birds when they discovered *Eriocnemis mirabilis* (Meyer de Schauensee 1967), which so far is known only from the steep and wet forest-clad slopes of Cerro Charguayaco, the type locality (Mazariegos & Salaman 1999).

Interest in *E. mirabilis* and other rare or threatened species has attracted various visiting ornithologists and birders to Munchique NP. During such visits on 19 August 1978 and 13 February 1984, Hilty's attention was drawn to the song of birds otherwise showing characteristics of Gray-breasted Wood-Wren *Henicorhina leucophrys*. Short tape-recordings were made of these vocalizations. He noted that the song of *H. leucophrys* showed little variation throughout Colombia "…except in w Cauca and w Nariño where [it] sings a remarkably different fife-like series of tinkling notes in many patterns and is perhaps a different species" (Hilty & Brown 1986). Ridgely & Tudor (1989) wrote "… the reported different song type in sw Colombia (in at least part of the range of *H. l. brunneiceps*) is also intriguing". Based on this information, Brewer (2001) suggested incorrectly that this different song might refer to *H. leucophrys brunneiceps*, the Pacific slope subspecies.

Hilty's observations received little attention until May 1996 when, during a brief visit to the Cerro Charguayaco area in Munchique NP, along the road winding through the higher elevations of the park. Coopmans also noticed the unique and distinctive vocalizations of birds looking like *Henicorhina leucophrys*. More surprising was the fact that just a short distance further west, below ca 2200 m, more "typical" *H. leucophrys* songs were heard. Coopmans concurred with Hilty that these individuals surely represented a new taxon, and gathered further evidence on subsequent trips to Munchique NP (April 1997, May 1998, June 1999 and February 2000) and the western slopes of Nariño Department.

Based on this information from Coopmans, Salaman and his team of fieldworkers of the Colombian Evaluation of Biodiversity in the Andes (EBA) Project, Alex Cortés, Andres

Cuervo, Thomas Donegan and Juan Carlos Luna, investigated *Henicorhina* populations across elevational gradients on both slopes of the Western Cordillera below Cerro Munchique in Tambito Nature Reserve, Munchique NP, and surrounding areas (12 km south of Cerro Charguayaco). During 24-27 July 2000, the EBA Project team encountered *H. l. brunneiceps* up to 2250 m on the Pacific slope and nominate *H. l. leucophrys* exclusively on the much drier eastern (Cauca valley) slope. However, at about 2250 m on the Pacific slope, a striking parapatric contact zone was found between *H. l. brunneiceps* and the mystery *Henicorhina*, with unique vocalizations and subtle plumage characteristics distinguishing the two taxa. All three taxa were common within their appropriate habitats, and were frequently heard.

On 26 August 2000, a family party of the mystery *Henicorhina* sp. was tape-recorded and observed in sparse vegetation on a rock face. Upon playback in an adjacent steep stream gully, Salaman and Cortés captured an adult female and recently fledged juvenal, and a further two adult *Henicorhina* sp. were later caught and collected by the team. An hour later, and within four hundred meters of the original locality, an adult male *H. l. brunneiceps* was tape-recorded and trapped, permitting live comparison with the *Henicorhina* sp. prior to collection. The following day, a family group of four *H. l. leucophrys* was mist-netted on the eastern slope of Cerro Munchique and taken to the location of the original captures for direct comparison with the mystery *Henicorhina*, prior to collection. Playback studies of the vocalizations of all three taxa showed strong mutual responses between *H. l. leucophrys* and *H. l. brunneiceps*, but affirmed that neither of these responded to vocalizations of the mystery *Henicorhina* and vice versa.

Based on adult and juvenal plumage characteristics from four specimens of each of the *Henicorhina* taxa encountered during the study, differences in vocalizations, the results of the playback experiments, habitat differences and sympatric occurrence with *Henicorhina leucophrys*, the mystery *Henicorhina* clearly represents a new taxon, which meets the requirements for species status under the Biological Species Concept (Johnson *et al.* 1999). We therefore name it:

***Henicorhina negreti* sp. nov.**
Munchique Wood-Wren
Cucarachero de Munchique

HOLOTYPE

Adult female, no. ICN-34016 of the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN-MHN), Bogotá, Colombia; collected and prepared by P. G. W. Salaman (original number EBA-01 # 04) on 25 July 2000, in the "Tambito" Natural Reserve, alongside the border of Munchique National Park (250 meters up the road from 20 de Julio cabin), Municipality of El Tambo, Cauca Department, Colombia (2°30'57.8"N 76°58'29.9"W). The collection locality is at 2350 m elevation on the Pacific slope of the Munchique massif of the Western Andes (Cordillera Occidental) of Colombia, in lower montane rain forest. Tape-recorded in the dense hanging understory on a rock face in primary forest and through playback lured into a mist-net placed nearby in a steep stream gully. Sound-recordings have been deposited with Wildlife Sounds, National Sound Archive of the British Library (London); photographs catalogued with VIREO, Academy of Natural Science of Philadelphia (**Figs 1 & 2,** Front Plate**)**; tissue samples are held at ICN-MHN. For measurements see **Table 1**.

DIAGNOSIS

Henicorhina negreti is a typical member of the genus *Henicorhina*, being a small wren with short, rounded wings (fifth to seventh primaries longest, ninth and tenth shorter than the secondaries), sturdy legs (tarsus about half as long as the folded wing), stubby tail (slightly longer than the tarsus, with 12 rectrices rounded at the tips), and bill decurved toward the tip and moderately compressed anterior to the nostril and shorter than the head (cf. Ridgway 1904).

Table 1. Morphometrics of *H. negreti* type series from dry specimens. All measurements are in mm except body mass, which is in grams.

	Holotype, female	Paratype, male	Paratype, juvenal	Paratype, male
Flat wing chord	55	59	56	58
Body-length	114	117	108	114
Maxilla (tip to skull)	15.2	15.7	13.5	15.9
Bill width (at nostril)	3.4	3.3	3.6	3.6
Bill depth (at nostril)	3.2	3.4	3.2	3.5
Tail-length	27.3	30.8	27.3	27.5
Tarsus-length	25.8	26.1	26.0	25.4
Body mass (in grams)	15.2	16.1	15.4	16.7

Table 2. Comparative differences in colors and plumage patterns between adults of *Henicorhina negreti* and those of the races of *H. leucophrys* found in the Munchique area.

	Henicorhina negreti	***Henicorhina l. leucophrys***	***Henicorhina l. brunneiceps***
Crown	Dark brown (121A, Prout's Brown) with black base and black edges to crown feathers (darker than *leucophrys*).	Dull brown, slightly paler than back (near Cinnamon Brown #33), with some blackish clouding or scaling.	Bright brown (between 121C, Mikado Brown and 34, Russet), slightly duller than back; little dark scaling or clouding.
Upperparts	Bright dark brown to chestnut-brown (223A, Mars Brown to 221A, Warm Sepia)	Bright medium to dark brown (223A, Mars Brown to 223B, Verona Brown)	Rather bright rufous-brown (136, Raw Sienna to 340, Robin Rufous)
Flight feathers	Narrowly and sharply barred with black, more irregularly on rectrices.	Narrowly and usually sharply barred blackish, with less contrast than in *negreti*; more irregularly barred on rectrices.	Narrowly barred with blackish, less distinct and contrasting than in *negreti*
Throat	White with black streaking heavy posteriorly, lighter and sometimes indistinct anteriorly	White with faint or no dark streaking, sometimes with narrow dusky fringes medially	White with indistinct to fairly distinct blackish streaking, less heavy than in most *negreti*
Breast	Medium gray (84-85, Medium to Light Neutral Gray)	Pale gray (85-86, Light to Pale Neutral Gray)	Pale gray (85-86, Light to Pale Neutral Gray)
Sides, flanks	Paler brown than upperparts (223B, Verona Brown to 121B, Brussels Brown)	Paler, brighter brown than upperparts (223B, Verona Brown to 37, Antique Brown), averaging brighter than in *negreti*	Bright rufous-brown (136, Raw Sienna to 38, Tawny)
Abdomen	Pale gray (86, Pale Neutral Gray) with distinct, contrasting black or dusky barring (sometimes partly veiled by pale fringes)	Pale gray (86, Pale Neutral Gray), sometimes marked with brownish; ca 10% show faint traces of darker barring medially, never distinct or contrasting	Pale gray (86, Pale Neutral Gray), immaculate; sometimes washed with buffy or brownish
Soft parts in life	Iris hazel brown; bill black except basal half of mandible which is bluish lead gray.	Iris dark chocolate brown; bill black.	Iris dark brown; bill black.
Characteristics	Overall darker and more obscure upperparts and underparts, with well-marked head, but distinctive barring on pale gray belly.	Crown darker than reddish-brown back and olive-tinged olive; heavier wing barring.	Crown similar to rufous-brown back.

The new species closely resembles the Gray-breasted Wood-Wren *H. leucophrys* but is appreciably darker overall in all plumages. Adults differ from all northern Andean forms of *leucophrys* in their distinctly barred abdomen (only the distant *bolivianus* sometimes approaches *negreti* in this respect) and from sympatric Munchique subspecies of *leucophrys* by their relatively shorter tails and longer tarsi; it differs from nominate *leucophrys* in its more streaked throat, and from *H. l. brunneiceps* in its much darker, less rufescent color dorsally and on the flanks (**Table 2**). Juveniles differ from congeners in being dark sooty blackish below and dull brown above with the facial streaking nearly obsolete (**Table 3**).

Compared with nominate *leucophrys* of the Western Cordillera, *H. negreti* is notably larger in both tarsus and bill length, although birds of this race in the western East Andes (Cordillera Oriental) have similarly long tails (**Tables 4** and **5**). *H. l. brunneiceps* of the Cordillera Occidental is equally large-billed but much lighter and brighter in coloration. *H. negreti* has a strikingly different song from both forms of *leucophrys* found in the region of the type locality (see below) and occurs at higher elevations than *brunneiceps* on the Munchique massif, although *H. l. leucophrys* ranges to similar elevations on the eastern slope.

DESCRIPTION OF THE HOLOTYPE

Adult female with skull 90% ossified, old incubation patch (adult captured from a family group including three recently fledged juveniles), ovary 2.5 mm long, all follicles less than 1

mm diameter and little subcutaneous fat. In the following color description, capitalized color nomenclature and numbers are from Smithe (1971, 1975).

Crown dark brown (near 121A, Prout's Brown), the feathers with sooty fringes giving the effect of indistinct black scaling; sides of crown more extensively black; narrow superciliary white; lores, postocular area and auriculars dull black, cheeks and malar area blackish, mottled with dull white to grayish white passing to white, heavily but indistinctly streaked with black on the throat. Rest of upperparts slightly brighter brown than crown (223A, Mars Brown). Breast and anterior sides gray (between 84 and 85, Medium to Light Neutral Gray), the abdomen paler (86, Pale Neutral Gray); flanks and crissum brown, paler than upperparts (between 223B, Verona Brown and 121B, Brussels Brown); abdomen and median part of flanks barred irregularly with dark gray to blackish. Outer webs of primaries and most secondaries barred narrowly with black, rectrices barred more irregularly with black; inner webs of remiges fuscous. Bare parts in life: iris hazel brown; bill black, except for basal half of mandible bluish lead gray; tarsi and feet bluish slaty gray.

PARATYPES

Two adult males and a juvenal female were collected on 26 August 2000 at Reserva Natural Tambito, adjacent to Munchique NP, between 2350 and 2500 m elevation. The specimens and their tissue samples are held in the ornithological collection at ICN-MHN. Sound recordings have been deposited with Wildlife Sounds, National Sound Archive (London). ICN-34015: adult male (skull fully ossified), collected 25 July 2000, 500 m along the road above 20 de Julio cabin (2°30'57"N 76°58'28"W; 2500 m. by Paul Salaman. ICN-34019: adult male (skull fully ossified; testes 3.7 x 2.1 mm, little subcutaneous fat), collected on 25 July 2000 at the same site by Andrés Cuervo. This specimen is slightly darker gray (84, Medium Neutral Gray) on the breast than the holotype, with heavier black streaking on the lower throat. Dorsally it is darker, more chestnut-brown (221A, Warm Sepia). ICN 34017: juvenal female (skull 0% ossified; ovary <1 mm, little subcutaneous fat), collected on 25 July 2000 by Paul Salaman at the type locality. Part of family party with two other juveniles and both parents (holotype is parental female). This bird (**Table 3**) is much darker than the adults

Table 3. Comparative differences in colors and plumage patterns between juveniles of *Henicorhina negreti* and those of the races of *H. leucophrys* found in the Munchique area.

	***Henicorhina negreti* (ICN 34017)**	***Henicorhina leucophrys leucophrys***	***Henicorhina leucophrys brunneiceps***
Facial area	Crown very dark brown (near 219, Sepia), suffused with blackish; cheeks and malar area dark sooty gray (Blackish Neutral Gray #82) with only faint paler gray to whitish mottling; whitish superciliary thinner than in *leucophrys* (considerably more restricted than in nominate).	Crown dark brown (Cinnamon Brown #33); prominent white superciliary; blackish eyestripe; sides of head/cheeks to malar whitish, streaked blackish, and less well marked than adult.	Crown rufous brown (Verona Brown #223B), bordered laterally with black; with black bases and narrow dark tips to crown feathers; prominent white superciliary; broad black eyestripe; sides of head/cheeks to malar white, streaked black.
Upperparts	Dark brown (219A, Hair Brown) on back and brighter brown (near 121A, Prout's Brown) on rump and upper tail-coverts.	Uniform rufous-buff (Cinnamon #123A).	Rufous-brown (Amber #36).
Underparts	Throat dark gray (Medium Neutral Gray #84) with dusky fringes, becoming solid dark sooty gray (82, Blackish Neutral Gray) on breast, passing to unbarred, dark dull brown (between 119A, Hair Brown and 219, Sepia) on abdomen and flanks	Throat Dark Gray Brown (#20) with slightly off-white streaks; breast darker gray (Light Neutral Gray #85), merging [no contrast] into paler cinnamon brown (Clay Colour #26) on belly and underparts.	Throat white with dark gray streaks giving a chequered gray-and-white appearance; breast to shoulders uniform Pale Neutral Gray (#86); flanks and lower belly to under tail-coverts rufous-brown (Amber #36); tail darker Amber (#36) with thin black barring.
Flight feathers	Faint and indistinct black barring on dark (Black Neutral Gray #82) flight feathers.	Wings dark (Black Neutral Gray #82) with dark cinnamon-brown edges (Cinnamon Rufous #40); tail darker Amber (#36) with thin black barring	Wings edged rufous-brown (Amber #36) with thin black barring.
Soft parts in life	Iris hazel brown; bill black with pale bluish gray lower mandible; tarsi and feet bluish slaty gray.	Iris dark chocolate brown; bill black with pale base to mandible; tarsi and feet dark bluish slaty gray with paler straw yellow soles of feet.	Iris dark brown; bill black; tarsi and feet dark slaty gray.
Characteristics	Overall darker appearance and less facial streaking than adults and juveniles of other taxa.	Overall duller than adult, but with well-marked head features	Crown similar to rufous-brown back.

overall: the crown is dark brown (near 219, Sepia) suffused with blackish, passing to dark brown (219A, Hair Brown) on the back and brighter brown (near 121A, Prout's Brown) on the rump and upper tail-coverts. The black barring on the flight feathers is faint and indistinct. The superciliary is grayish white, and the cheeks and malar area are dark sooty gray with only faint paler gray to whitish mottling, including the chin; the throat is dark gray with dusky fringes, becoming solid dark sooty gray (82, Blackish Neutral Gray) on the breast, passing to unbarred, dark dull brown (between 119A, Hair Brown and 219, Sepia) on the abdomen and flanks.

ETYMOLOGY

The species name honors the late Alvaro José Negret (1949-1998). Alvaro's sudden death on 18 July 1998 robbed Colombia of one of its finest naturalists and conservationists. As a young boy, Alvaro collected birds for the Natural History Museum of Cauca University (MHNUC) under the direction of Carlos Lehmann and Kjell von Sneidern. Following in their footsteps, Alvaro became a professor at Cauca University and then director of MHNUC until his untimely death. He helped maintain and improve a substantial natural history collection with an emphasis on ornithology and environmental education. Alvaro was active in biological research and conservation, particularly in western Cauca and personally protected and managed Tambito Nature Reserve, which boasts over 330 species of birds, including five Threatened species (see below). Above all an avid ornithologist, Alvaro compiled the avifaunal list of Munchique NP and was completing the manuscript of "*Aves Colombianas Amenazadas de Extinción*" at the time of his death. His passing was a great loss for conservation and ornithology in Colombia, at a time when his mighty energy and ability were most needed. The English and Spanish names refer to Munchique National Park, which, together with the adjacent Tambito Nature Reserve, is the only region in which the new species has been recorded to date.

TAXONOMIC AFFINITIES

The genus *Henicorhina* is presently regarded as comprising three species: White-breasted Wood-Wren *H. leucosticta* (Cabanis 1847), of lower elevations, and Gray-breasted Wood-Wren *H. leucophrys* (Tschudi 1844), of higher elevations, are widespread in both Central and South America and replace each other elevationally in many areas. The third, Bar-winged Wood-Wren *H. leucoptera* (Fitzpatrick *et al.* 1977), is a range-restricted and localized species found on outlying mountain ranges in northern Peru and southern Ecuador (Krabbe & Sornoza 1993), and is found syntopically with *H. leucophrys* at a number of localities.

For this study, specimens of all *Henicorhina* taxa were examined, including comparison of *H. negreti* with all 13 *H. leucophrys* subspecies (including seven *H. leucophrys* subspecies from Colombia) and all 11 *H. leucosticta* subspecies including five subspecies from Colombia (following Brewer 2001). Specimens were examined in the following collections: American Museum of Natural History, New York, USA (AMNH); Academy of Natural Sciences of Philadelphia, USA (ANSP); (United States) National Museum of Natural History, USA (USNM); Carnegie Museum, USA (CAR); Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional, Bogotá, Colombia (ICN-MHN); The Natural History Museum, UK (BMNH); the University Museum of Zoology, Cambridge, UK (UMZC); Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH); Museo de Historia Natural, Universidad de Antioquia, Medellín, Colombia (UdeA); Museu de Zoología, Universidade de São Paulo, Brazil (MZUSP); and Museo de Historia Natural, Universidad del Cauca, Popayán, Colombia (MHN-UC).

No apparent hybrids between the two *Henicorhina* species were encountered in the field nor in specimen collections. Although no clear sexual dimorphism in plumage is apparent, *H.*

Table 4. Comparison of morphometrics of unsexed *Henicorhina negreti* and sympatric *H. leucophrys* subspecies based on live measurements (P Salaman, T Donegan). The mean is given, followed by the standard deviation and then the lowest and highest values encountered for each variable. All measurements are in mm except body mass, which is in grams.

	Flat wing chord	Body-length	Maxilla (tip to skull)	Tail-length	Tarsus-length	Body mass (in grams)
Henicorhina negreti (n=4)	**57.0** ± 1.8 (55-59)	**113.3** ± 3.8 (108-117)	**15.1** ± 1.1 (13.5-15.9)	**28.3** ± 1.7 (27.3-30.8)	**25.8** ± 0.3 (25.4-26.1)	**15.9** ± 0.7 (15.2-16.7)
Henicorhina leucophrys brunneiceps (n=142)	**57.2** ± 0.8 (56-58)	**109.6** ± 2.4 (107-113)	**14.7** ± 0.7 (13.8-15.7)	**25.2** ± 1.9 (23.8-25.2)	**24.3** ± 0.6 (23.8-25.2)	**16.3** ± 0.7 (15.7-17.4)
Henicorhina l. leucophrys (n=103) (Salaman 2001)	**58.7** ± 1.5 (57-60)	**111.0** ± 3.6 (107-114)	**14.0** ± 0.9 (13.2-15.0)	**28.1** ± 2.3 (25.5-29.5)	**23.7** ± 0.8 (23.0-24.5)	**14.2** ± 1.2 (12.9-15.2)

Figure 1. An adult and juvenal *H. l. leucophrys* (left) and *H. negreti* (right). Photo: PS.

leucophrys males have longer average measurements for wing chord, maxilla, tail length and tarsus length than females (see **Table 5**). We suspect that measurements of *H. negreti* males also average longer than those of females (see **Table 1**), although a larger sample size would be required to verify this. Within nominate *H. l. leucophrys* in Colombia, measurements show slight clinal variation with birds from the western slope of the Eastern Andes being largest on average, particularly in tail length; only this population has tarsi approaching in length that of *negreti.* Conversely, only in *brunneiceps* is bill size as large as in *negreti,* both being notably larger-billed than populations of *leucophrys*, sex for sex (**Table 5**).

Henicorhina negreti bears stronger morphological and biogeographical affinities to *H. leucophrys* than to the other species of the genus, and is clearly derived from it. Its relationships to the two forms of *leucophrys* occurring in the area present an intriguing problem. The plumage of *negreti* in general is more like that of nominate *H. l. leucophrys,* although it more closely resembles that of *brunneiceps* in its more strongly streaked throat. It is possible that the *leucophrys* population extended to the Pacific face of the cordillera during a relatively dry glacial period of the Pleistocene; increasingly humid conditions during the subsequent interglacial may have produced the cloud forest conditions that permitted the isolation and differentiation of *negreti.* The small size of this founder population perhaps would have facilitated the acquisition and genetic fixation of distinctive morphological features and would have accelerated, through cultural evolution, the development of a different song. The most distinctive plumage feature of *negreti*, the boldly barred abdomen, also occurs, albeit to a much lesser extent, in another subspecies of *leucophrys* (*bolivianus*) and in ca. 10% of nominate *leucophrys* examined, a very faint trace of barring is discernable upon close examination. Thus, the genetic potential to develop a barred abdomen clearly exists in *leucophrys* and this tendency was presumably fixed in *negreti.* The dark juvenal plumage of this form likely evolved in response to the dense, dark and humid forests it inhabits.

Both *H. leucophrys* and *leucosticta* show considerable variation over their wide ranges, each being divided into a number of subspecies often separated by, or endemic to, isolated mountain ranges or lowland ecoregions. Both may in fact consist of more than one biological species. For example, this is suggested by the presence of two subspecies of *leucophrys* replacing each other altitudinally in the Sierra Nevada de Santa Marta in northern Colombia (Ridgely & Tudor 1989); preliminary analysis of tape-recordings (P. Coopmans) suggests two species could be involved. Also, Winker *et al*. (1996) suggested that the South American and Middle American subspecies of *Henicorhina leucosticta* may represent two distinct species, and that the Central American group itself may include two or more separate species. The monophyly of both *H. leucophrys* and *H. leucosticta* should be reexamined, particularly in the light of the results of recent taxonomic research in other genera such as *Atlapetes* (García-Moreno & Fjeldså 1999).

VOCALIZATIONS

Sound recordings of all *Henicorhina* species and most Andean subspecies of *H. leucophrys* (including *H. l. leucophrys* and *H. l. brunneiceps*) as well as *H. leucoptera* were studied and compared to those of *H. negreti*. As in other members of the genus (cf. Brewer 2001), *Henicorhina negreti* is vociferous and is frequently heard throughout the day and apparently year-round. It is inquisitive and responds strongly to song playback by making rapid darting movements towards the sound source, and producing harsh churring alarm calls (**Fig. 4**). Tape recordings of all three *Henicorhina* taxa have been made by the authors in Tambito Nature Reserve and Munchique NP, including recordings of the holotype (**Fig. 4a**) and paratypes prior to capture. Recordings are deposited with The British Library National Sound Archive (NSA, London) and the Macaulay Library of Natural Sounds (LNS, Cornell).

Spectrograms of *H. negreti* songs (n = 10 individuals) were compared with those of a selection of subspecies throughout

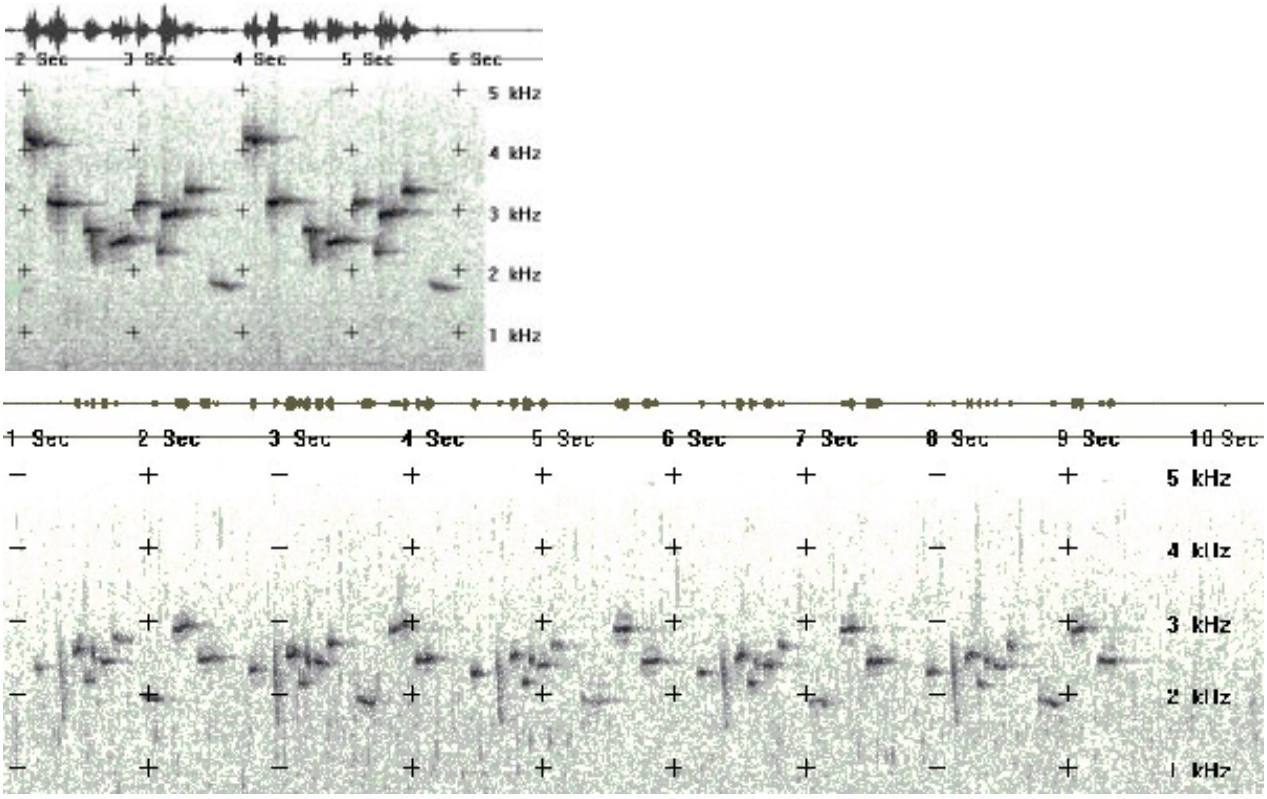
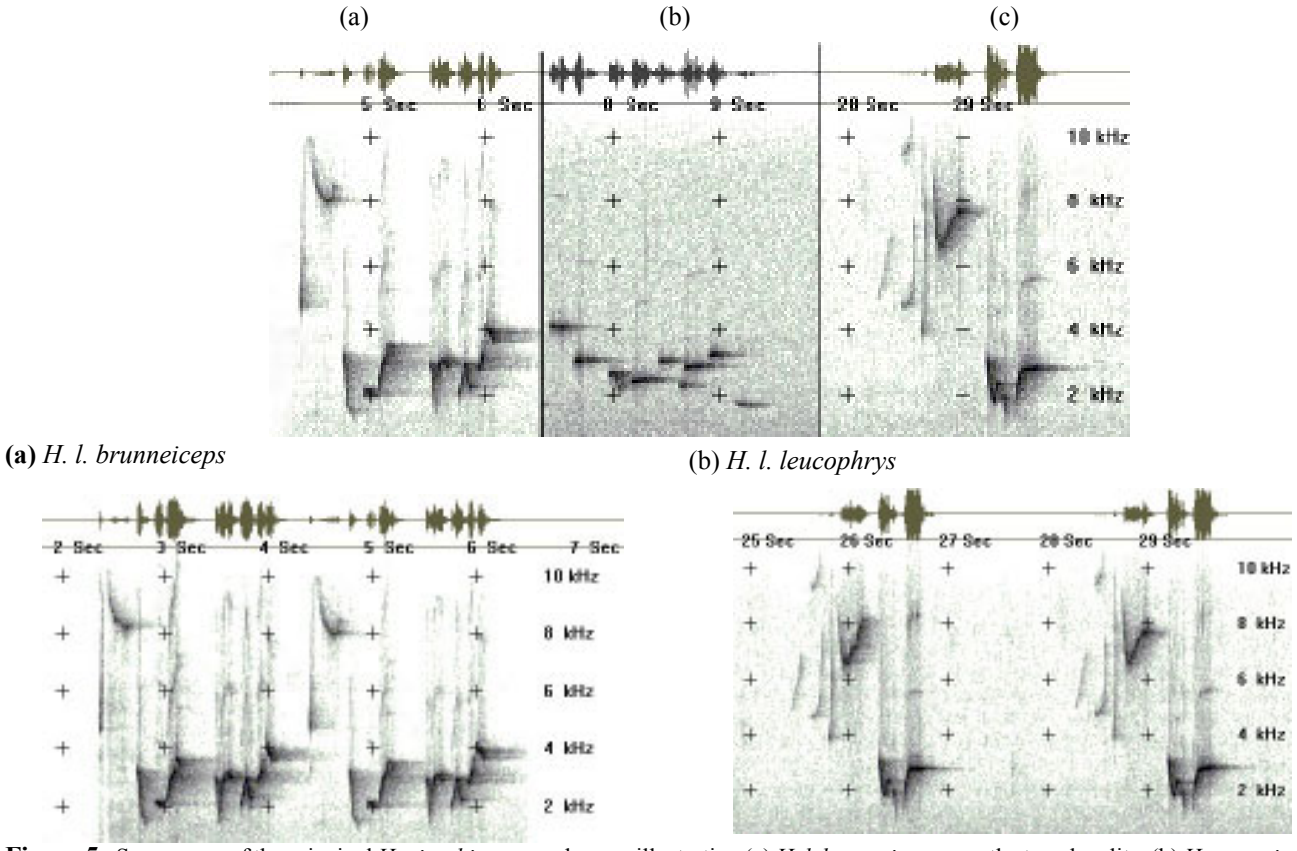


Figure 4. Sonograms of *H. negreti* song (before playback). Recorded by PS and PC at the type-locality. Sonogram PS.



(a) *H. l. brunneiceps* (b) *H. l. leucophrys*

Figure 5. Sonograms of the principal *Henicorhina* song phrases, illustrating (a) *H. l. brunneiceps* near the type locality, (b) *H. negreti* at the type locality, and (c) *H. l. leucophrys* near the type locality. Recorded by PS & Andres M. Cuervo. Sonogram: PS.

the range of *H. leucophrys*, and in particular to those of *H. l. brunneiceps*, which replaces *H. negreti* at lower elevations on the west slope of the Western Andes (**Fig. 5**). The vocalizations of *negreti* are quite distinct from those of *H. leucophrys*; indeed, the song was the feature that first drew us to the presence of an undescribed species. *H. negreti* songs resemble those of *H. leucophrys* in consisting of a melodic, jumbled series of notes repeated at regular intervals, with each syllable of approximately 100-300 ms in duration. However, those familiar with the "liquid" song of *H. leucophrys* are usually struck by the remarkably melodic nature of the song of *H. negreti*. As in all three other species of the genus, *H. negreti* also has much individual variation in song type.

The *H. negreti* song is typically composed of lengthy repetitions of repeated phrases of 6-12 pure notes. Each repeated phrase lasts approximately 2 seconds, and a typical song can consist of more than 10 repeated phrases, although often curtailed. The final note of a preceding phrase is followed immediately by the first note of the second phrase, giving continuity and musical quality to the song. The notes that comprise the repeated phrase are made at a jumble of frequencies largely in the range of 1.8 - 4.2 kHz, with each note lasting for approximately 50 to 300 ms. The sonagrams (**Figs. 4** and **5**) further distinguish *H. negreti*'s song phrases from those of *H. leucophrys* as follows:

a) The individual notes or syllables of *H. negreti* tend to be "flatter" or purer, i.e. with little frequency change between the beginning and the end of each note (a pure note is visible on a spectrogram as a horizontal line), and longer in duration (up to 300 ms), resulting in the more flute-like nature of the song (average variance between highest and lowest point of each syllable of *H. negreti* vocalizations <0.1 kHz; n = 43 syllables). The syllables of the song of *H. leucophrys* are characterised by slurred liquid notes, which appear on the spectrogram as short sections of hyperbolic, quadratic, cubic, or quartic curves, and which rise and fall between the start and end of each whistle, often including maximum or minimum turning points within a single syllable (average variance between highest and lowest point of note = 1.4 kHz; n = 13 syllables).

b) Some notes in the *H. negreti* song phrase are joined into doublets or sometimes triplets, whereas some other notes are separated from others by a short interval (up to 600 ms), making the phrases sound more deliberate and musical than those of *H. leucophrys*, with a short but distinct pause within the phrase often audible to the human ear.

c) Some *H. l. leucophrys* and H. l. *brunneiceps* song types contain notes up to 8-10 kHz in frequency. Such high pitched notes were not found in *H. negreti* songs.

d) Most *H. negreti* song phrases have one or two pure notes standing out at a frequency between 300 and 800 Hz higher pitched than the previous or following note, adding to the musical quality of the song.

Figure 2. Adult *H. leucophrys brunneiceps* (left) and *Henicorhina negreti* (right). Photo: PS.

Although *H. leucophrys* songs vary throughout the species' range, none of the subspecies with which we are familiar sing with the above combination of features. The song of *H. negreti* stands apart immediately to the experienced ear. Although oscine passerines mostly seem to acquire their songs culturally (Kroodsma 1996), the uniqueness of *H. negreti* songs compared with a wide range of *H. leucophrys* subspecies further supports species status for *H. negreti*. On the other hand, calls of *H. negreti* are mostly churrs similar to those of other members of the genus.

DISTRIBUTION

Henicorhina negreti is presently known from two areas on the uppermost Pacific slope of the Munchique massif of the Western Andes between 2250 and 2640 m (**Fig. 3**):

a) Reserva Natural Tambito (the type locality) and the adjacent 20 de Julio sector of Munchique NP, where it occurs upwards from the 20 de Julio cabin at 2250 m (see above); specimens, observations and tape-recordings on 25–27 July 2000 by Paul Salaman *et al*., and b) Munchique NP, Sector La Romelia, below Cerro Santana on the Pacific slope from the La Romelia Park headquarters (2°38'32"N 76°54'56"W; 2640 m on the Cordillera ridgeline) down (10.9 km by road) to El Planchón,

below Cerro Charguayaco (2°41'N 76°54'W; 2250 m); observations and tape recordings by Steven Hilty and Paul Coopmans (see **Figure 3**).

No *H. negreti* were encountered in the immediate vicinity of the La Romelia cabin (2640 m), probably because the habitat was less suitable (see below). Below 2250 m at the first locality and ca. 2200 m at the second, *H. negreti* is abruptly replaced by *H. l. brunneiceps*; on the eastern side of the ridgeline of the Western Andes, only *H. l. leucophrys* occurs. The range of *negreti* is thus sandwiched between and abruptly bounded by those of two forms of *H. leucophrys* on the Munchique massif. Similar elevational replacements of morphologically very similar but vocally distinctive forms are prominent in *Scytalopus*, another Andean passerine genus (Fjeldså & Krabbe, 1990; Krabbe & Schulenberg 1997).

With knowledge of its conspicuous and easily recognizable song, *H. negreti* should readily be detected if present on the Pacific slope of other peaks in the southern Western Andes, perhaps including Cerro Guapí (2970 m) in Dept. Cauca, Farallones de Cali (3500 m) in Dept. Valle del Cauca, and Cerro Tatamá (3950 m) in Depts. Risaralda and Chocó. It may range higher than heretofore recorded, becuase access to the higher peaks is extremely difficult, resulting in little ornithological exploration in these areas to date. The statement in Hilty & Brown (1986) that birds on the west slope of the Andes in Nariño sing like those in the Munchique area was based on the erroneous assumption that *H. negreti* ranged to lower elevations and extended across the Río Patía valley (separating Colombia's Western Cordillera from the main Andes). This dry valley is an important biogeographical barrier for high-elevation cloud forest birds (Vuilleumier &

Table 5. Comparison of morphometrics of specimens of *H. l. leucophrys* and *H. l. brunneiceps* skins at ICN-MNH and IAVH. The mean is given, followed by the standard deviation and then the lowest and highest values for each variable. Percentages below each data segment refer to the extent to which the male average exceeds the female average for that measurement, expressed as a percentage of the female average. All measurements are in mm. Note that a different data set was used from that presented in Table 4.

	Flat wing chord	**Maxilla (tip to skull)**	**Tail-length**	**Tarsus-length**
Henicorhina l. brunneiceps Males (n = 6)	**53.2** ± 1.0 (52.0 - 54.3)	**18.5** ± 1.0 (16.8 - 19.5)	**24.8** ± 0.8 (23.7-26.0)	**24.7** ± 0.8 (23.6-25.8)
Females (n = 4)	**50.9** ± 2.0 (48.1 - 52.2)	**17.3** ± 0.5 (16.6 - 17.9)	**22.4** ± 0.6 (21.8 - 23.3)	**23.4** ± 0.8 (22.3 - 24.1)
% difference between male and female averages	4.5%	6.9%	10.7%	5.6%
Henicorhina l. leucophrys Cordillera Occidental Males (n = 10)	**53.6** ± 2.0 (50.8 - 56.8)	**17.0** ± 0.9 (15.3 - 18.0)	**24.0** ± 1.0 (22.1 - 25.0)	**25.1** ± 0.9 (23.2 - 26.1)
Females (n = 5)	**52.3** ± 1.6 (50.1 - 54.5)	**16.9** ± 1.1 (15.7 - 18.3)	**23.9** ± 0.4 (23.6 - 24.6)	**23.9** ± 0.9 (22.4 - 24.8)
% difference between male and female averages	2.5%	0.6%	0.4%	5.0%
Henicorhina l. leucophrys western Cordillera Oriental Males (n = 25)	**56.4** ± 1.7 (52.4 - 59.5)	**17.5** ± 0.7 (16.4 - 18.8)	**28.3** ± 1.4 (25.1 - 30.8)	**25.4** ± 0.7 (24.4 - 26.6)
Females (n=20)	**53.3** ± 1.3 (49.3 - 54.8)	**16.8** ± 0.4 (16.0 - 17.5)	**26.6** ± 0.9 (25.1 - 28.2)	**24.5** ± 0.9 (22.9 - 26.7)
% difference between male and female averages	5.8%	4.2%	6.4%	3.7%
Henicorhina l. leucophrys eastern Cordillera Oriental Males (n = 10)	**55.0** ± 3.0 (50.5 - 58.4)	**17.0** ± 0.5 (16.2 - 17.8)	**27.6** ± 1.5 (26.5 - 29.3)	**24.7** ± 1.3 (22.8 - 26.1)
Females (n = 4)	**52.3** ± 2.0 (49.8 - 54.5)	**16.7** ± 0.7 (15.8 - 17.4)	**25.8** ± 0.7 (24.9 - 26.3)	**24.1** ± 0.7 (23.2 - 24.8)
% difference between male and female averages	5.2%	1.8%	7.0%	2.5%

Monasterio 1986), and it is unlikely that *H. negreti* will be found south of it. We have only recorded *H. l. brunneiceps* on this slope in Nariño and in adjacent Ecuador.

It is intriguing to find three *Henicorhina* taxa occurring virtually sympatrically, within 1 km of each other. Indeed, Chapman (1917) remarked: "The occurrence of two forms of *Henicorhina leucophrys* on the western slope of the Western Andes is surprising but is apparently proven by our large series of specimens [21 *H. l. leucophrys* specimens taken in the Western Andes, plus 6 *brunneiceps*]. *H. l. guttata* [*guttata* later synonomized with *leucophrys*, by Chapman (1926)] occupies the middle and upper part, *H. l. brunneiceps* the lower part of the Subtropical Zone". What Chapman did not realize was that *H. l. leucophrys* had been taken only in the middle and upper parts of the much drier eastern slope.

Furthermore, it is interesting to note that Miller and Richardson, working for Chapman, camped along the Río Tambito at 2170 m (6900 feet), very close to the *H. negreti* type locality. They were also close to Cerro Santana ("Coastal Range"), but on reaching the crest of the range were faced with strong winds, electrical storms and dense fog, while "it rained and hailed with great violence" (Chapman 1917). Not surprisingly, they "found few birds" (Chapman 1917), although a total of 652 specimens (registered at AMNH) were collected by Miller and Richardson at three localities near or within the range of *H. negreti*: Cerro Munchique (316; inc. 8 *H. l. leucophrys*), Gallera (103; incl. 1 *H. l. brunneiceps*) and "Coastal Range" (233; no *Henicorhina* specimens) (Darwin Database 2003).

ECOLOGY AND BEHAVIOR

We have accumulated ca 70 observations, ca 25 sound-recordings, and 4 captures of *H. negreti*; 100+ observations, 15 sound-recordings, and 16 captures of *H. l. brunneiceps*; and ca 25 obs., 3 recordings, and 4 captures of *H. leucophrys* in the region of the type locality. Furthermore, the authors have compiled numerous observations, tape-recordings and captures of almost all *Henicorhina* subspecies found in Colombia (in all major mountain ranges) and most other subspecies (including 217 captures of *H. l. brunneiceps*; see **Table 5**).

Henicorhina negreti inhabits stunted montane cloud forest on the Pacific slope of the Western Cordillera of Colombia (**Figure 6**) and is currently known from elevations ranging from 2250 to 2640 m. It is common in naturally disturbed forest with patchy successional habitat, typically preferring an extremely dense understory smothered in epiphytes at forest borders, landslides and along stream gullies. Climatic and topographic extremes, detailed above, are most pronounced above 2250 m on the Western Cordillera, as on Cerro Munchique, Cerro Santana, and Cerro Charguayaco in Munchique NP. The terrain is so precipitous that natural landslides scar the entire landscape, resulting in a habitat mosaic of successional vegetation types, ranging from exposed rock and bare soil to small patches of stunted wet montane forest, with extremely high densities of epiphytic vegetation. The predominant habitat structure is characterized by a low canopy (<5 meters), high stem density, and increased biomass of bryophytes. A dense understory stratum is dominated by epiphytes and terrestrial bromeliads and mosses.

Figure 6. View northwards from Cerro Munchique across primary montane wet forest at the type locality. Note the extent of cloud cover, apparently the key element producing the specific habitat of *H. negreti.* Photo: PS.

A preliminary study of diversity and floristic composition in arboreal and non-arboreal plants at the Tambito Nature Reserve type locality (between 1300 and 2500 m) has been completed by Carlos González (in litt.). A total of 640 plant species, belonging to 269 genera and 110 families, was encountered in a total combined area of 6250 m^2 of Montane Cloud Forest. Of these, 292 species were trees and 348 non-arboreal. 78.9% were dicotyledonous, 12% monocotyledonous, and the remainder were ferns and mosses. The most important canopy families were Melastomataceae (47 species), Lauraceae (34),

and Rubiaceae (30). In mid-story to understory families, the most important groups were Gesneriaceae (63 species), Piperaceae (33), and Orchidaceae (32). The most species-rich tree genera were *Miconia* (25 species), *Nectandra* (10-15), and *Ficus* (10); for non-arboreal plants, these were *Piper* and *Peperomia* (17 species each), *Columnea* (15), and *Anthurium* (18). Palmae are scarce. Early successional stages of landslides are characterized by *Chusquea spp.* bamboo; shrubs and small trees of the Melastomataceae, Rubiaceae, and Ericaceae; and an abundance of dense mats of bryophytes, especially mosses, together with terrestrial bromeliads.

The new *Henicorhina* species, like its congeners, is more often heard than seen. Behavioral and ecological characteristics of *H. negreti* are almost indistinguishable from those of *H. leucophrys*, both being territorial, perky, and inquisitive, making them ideal for field study. Pairs or family parties usually creep about inconspicuously in the densest understory vegetation, often disappearing inside dense moss blankets or epiphyte tangles in search of small to medium-sized arthropods. Birds stay close to the forest floor, typically within 2 m of the ground, infrequently ascending to 3-4 m to investigate epiphyte clumps on tree trunks. *Henicorhina negreti* rarely associates with mixed-species foraging flocks, but occasionally does so for relatively short periods when a flock passes through the territory of an individual, pair, or family group. On two occasions birds were observed associating loosely and briefly with a party of Sepia-brown Wrens *Cinnycerthia olivascens*. The diet of *H. negreti* consists exclusively of small insects, principally Coleoptera and Diptera. No fruits, seeds or other vegetable matter were found in the stomach contents. In sum, the social behavior, foraging and diet of *H. negreti* do not appear to differ appreciably from those of *H. leucophrys* (see Skutch 1960).

Along two km of road, 5-8 territorial pairs or males were registered. Although common, the new species seemed to have lower population densities than did *H. l. brunneiceps*, of which ca 10-14 territorial pairs were encountered per two km transect. Along a one km trail inside forest at 2500 m, the population density of *H. negreti* was considerably lower still, with just one pair found. This may have been because the forest trail ran through less steep terrain (no landslides), and being farther from streams, resulting in suboptimal habitat.

The holotype (female) had a devascularized but still bare incubation patch and was caught in the presence of its mate (adult male) and three recently (< 2 weeks) fledged juveniles, of which one was collected (25 July 2000). Recently fledged juveniles were observed for all three *Henicorhina* taxa during the EBA proyect study in July. A highly vascularized incubation patch was present on an adult female *H. l. brunneiceps* trapped on 25 July 2000 (an individual originally banded in 1997 by Donegan). The capture and collection of the *H. l. leucophrys* family group (adult pair and one juvenal) on 26 July 2000 was noteworthy in that here also the juvenal had recently fledged (<2 weeks). Males of both *H.l. leucophrys* and *H. l. brunneiceps* were in complete molt in late July at Tambito, a few weeks ahead of females, which delay molt while continuing parental care to juveniles (Salaman 2001). No *H. negreti* individual caught during July 2000 was in molt.

Other breeding information for *H. leucophrys* in the region is as follows: fledglings May, Dec (Nariño), April, May (NW Ecuador), nests in March [1], May [2], June [5] (above Cali, Dept. Valle) (Hilty & Brown 1986, Fjeldså & Krabbe 1990). At the Río Ñambí Community Nature Reserve (175 km to the south; see **Table 4**), *H. l. brunneiceps* captures revealed that May and September are peak nesting periods, with fledglings in July-August and November-February and an intensive molt period in August and September (Salaman 2001). Miller (1963) collected breeding condition males from mid-February to early March, found a nest with one egg in May, and collected a juvenal in December. This evidence suggests strongly that *H. leucophrys* in the Munchique area breeds during the wettest period (April-June), and again during the second "wet season" (October-November). Our data for *H. negreti* are consistent with April-June breeding, although further fieldwork would be required to determine if it has a second breeding season like *H. leucophrys*.

LOCAL DISTRIBUTION AND PLAYBACK EXPERIMENTS

We used playback experiments to determine whether two adjacent taxa actually overlapped at any point. *Henicorhina* wrens are typically sedentary (Brewer 2001), although some local seasonal movements have been noted in Guatemalan subspecies of *H. I. leucophrys* (Skutch 1960). Territories are maintained year-round with pairs sometimes engaging in antiphonal duets. Due to their territorial nature, *Henicorhina* species often respond rapidly and aggressively to playback.

H. l. leucophrys versus *H. negreti*

Surveys on the eastern slope of the Western Andes below Cerro Munchique revealed the presence of several family groups of *H. l. leucophrys*, although with low population densities. Much of the original habitat has been replaced with *Pinus, Eucalyptus* and *Cupressus*, with *H. l. leucophrys* now confined to remnant streamside thickets. Using playback along a *c*. 3 km transect, five *H. l. leucophrys* males were heard holding territory between 2300 and 2500 m, exclusively on the eastern slope of the Cordillera despite repeated song playback experiments on the western slope. *Henicorhina negreti* was found at the same elevations as *H. l. leucophrys*, but exclusively on the Pacific (western) slope, the delimitation between the two taxa thus following the Western Andes ridgeline. We recorded *H. negreti* up to *c*. 200 m linear distance from the ridgeline on this slope, and recorded *H. l. leucophrys* up to *c*. 800 m linearly from the

ridgeline on the other slope. However, despite repeated playback of the songs of both taxa along a 500 m transect across the ridgeline, we did not find *H. l. leucophrys* and *H. negreti* territories abutting, nor did we hear songs of one taxon from the other's territory. We consider it highly likely that *H. negreti* and *H. l. leucophrys* territories exist in close proximity where natural habitat is continuous across the ridge crest. However, little suitable habitat remains on the eastern slope adjacent to the ridgeline in the study region (see below).

Repeated playbacks of both song and alarm calls of *H. negreti* in or near territories of *H. l. leucophrys* never evoked a noticeable response from the residents, whereas playbacks of songs and calls of both this taxon and *H. l. brunneiceps* invariably elicited strong aggressive responses, with individuals immediately approaching and stalking the cassette player. Conversely, in areas near the ridgeline *H. negreti* responded vigorously to its own songs and calls but appeared to ignore those of both taxa of *H. leucophrys*.

H. l. brunneiceps versus *H. negreti*

Intensive playback experiments of the songs of all three *Henicorhina* taxa were conducted between 2140 and 2350 m on the Pacific slope to test the hypothesis that *H. negreti* and *H. l. brunneiceps* occurred syntopically. At five sites from 2140 m to 2220 m large numbers of *H. l. brunneiceps* were recorded, which responded immediately to playback of the subspecies' own song and that of *H. l. leucophrys*. Repeated playback of the song of *H. negreti* at these sites elicited no response. At 2240 m, *H. l. brunneiceps* were heard downslope (at *c*. 2220 m) and *H. negreti* upslope (at *c*. 2260 m). Interestingly, further song playback of the vocalizations of both species at 2240 m did not attract *H. l. brunneiceps* significantly further upslope, or *H. negreti* significantly further downslope. Above 2260 m only *H. negreti* was encountered. However, the highest elevation *H. l. brunneiceps* male, which had previously been agitated by song playback, could still be heard distantly downslope from the lowest *H. negreti* territory at 2260 m. Repeated playback of *H. l. brunneiceps* at sites above 2260 m elicited no response from either *H. l. brunneiceps* or *H. negreti*. Playback of alarm calls made concurrently likewise revealed negative responses between the two species. Thus, the elevational replacement of *H. l. brunneiceps* with *H. negreti* at the *c*. 2250 contour is clearly established.

ECOLOGICAL NICHE SEPARATION

The general conclusion from the playback experiments is that although the range of each *Henicorhina* taxon abutted with that of at least one other taxon, at no location was more than one taxon found. The reason for this striking spatial division appears to be sharp delimitations of distinctly different habitats within short distances along the respective contact zones. The physical geography of Tambito Nature Reserve has been

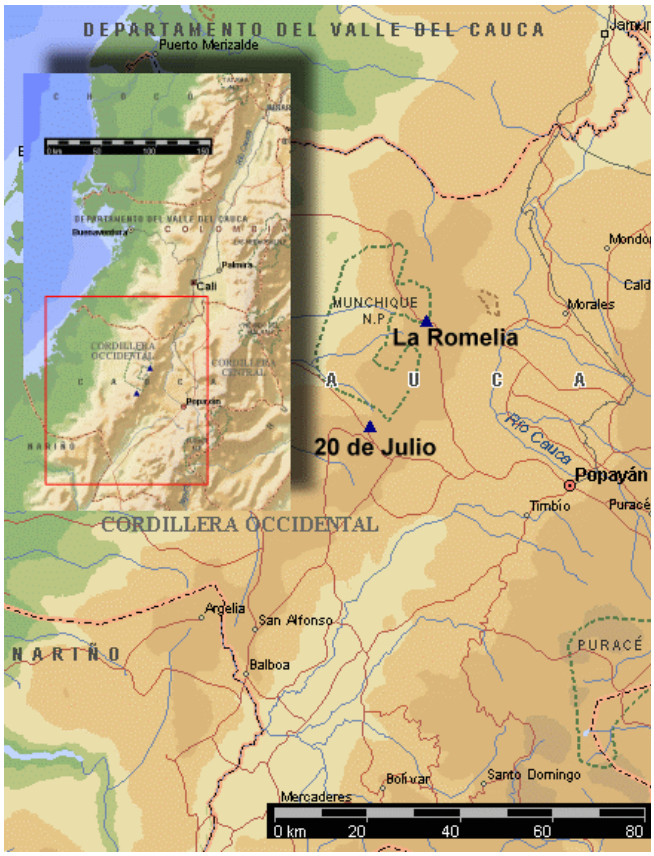


Figure 3. Map of western Colombia, showing the distribution of *H. negreti* (blue triangle = localities in which *H. negreti* has been found.

studied intensively by the Project HERB team led by Mulligan (see further http://www.kcl.ac.uk/herb). This Project has been monitoring and modeling climatic, hydrological and ecological processes in the reserve since 1997 in order to understand the structure and function of tropical montane cloud forest (TMCF) ecosystems and their interaction with environmental change. Data collected by Project HERB are analyzed below in conjunction with the playback experiment data and other ecological information in order to understand more fully the ecological relationships of *Henicorhina* taxa in the region of the type locality.

H. l. leucophrys versus *H. negreti*

A mountain pass at 2550 m elevation on the Popayán to 20 de Julio road crosses the ridgeline separating the western and eastern slopes of the Western Andes and marks a pronounced climatic and ecological shift as high rainfall and wet forest on the Pacific slope immediately give way to the much drier and less humid forest of the east slope. Munchique Carpintería (2°46N 76°93W), lying just east of the ridgeline at 2500 m, has an annual rainfall of 3313 mm, whereas at the same elevation on the western slope annual rainfall amounts to 8268 mm, not including moisture from cloud water interception,

which accounts for at least an additional 9% (González 2000). Considering the almost threefold change in rainfall within just a few kilometers across the cordillera's ridge, drastic and sharp changes occur in the associated habitats and in the ecological characteristics of both slopes. Indeed, the ridge of the Cordillera is an important biogeographical barrier for many species, and forms the limit of the Chocó Endemic Bird Area (Stattersfield *et al*. 1998). The change in climate across the ridge crest, and the sharp change in forest characteristics, clearly coincide with the separation of *H. negreti* and *H. l. leucophrys* and presumably drive that separation. A further indication of the effects of this climatic shift is that only on the drier Cauca Valley slope were conifer plantations able to be established.

H. l. brunneiceps* versus *H. negreti

The sharp separation between *H. l. brunneiceps* and *H. negreti* at or around 2250 m elevation on the Pacific slope is more intriguing. Altitudinal replacement of *brunneiceps* by *negreti* typically takes place within an elevational range of less than 50 m (or less than 100 m in real distance). At first glance, no obvious significant biotic or abiotic discontinuities act as physical or ecological barriers to gene flow, possibly facilitating parapatric speciation between *leucophrys* and *negreti*. However, on closer examination it appears that *H. negreti* is restricted, through ecological pressures, to a more extreme and wet environment typified by the upper slopes of the Pacific versant of the Western Andes.

Rainfall increases and temperature decreases relatively continuously with elevation in the Tambito area (although there are minor local mesotopographic and aspect-related effects). The average increase of annual total rainfall with elevation for Tambito is 4.05 mm/m with 3800 mm/yr at 1374 m and 7600 mm/yr near the type locality (2200 m) (González 2000). The average decrease of temperature with elevation is 0.55°C/ 100 m, with annual average temperature at 2250m being around 10.9°C, and at 2600 m around 9°C (Mulligan 2000). No known non-linearities in these environmental parameters coincide with an elevation of 2250 m.

In terms of the water balance the elevation at which rainfall is equal to potential evaporation is approximately 700m (below the Tambito reserve boundary), with water surpluses above and water deficits below this altitude. The water balance at 2250 m is around 4250 mm producing a very wet environment. There are no major shifts in topographic characteristics around the 2250 m elevation, although a 25 m resolution Digital Elevation Model reveals that slopes tend to be steeper at 2000-2300 m (33° on average, n=14372) than at 2300-2600 m (28° on average, n=12058). In terms of the arboreal vegetation, however, transition is dramatic around the 2250 m mark. In plots above this elevation over 85% of the trees have a diameter at breast height (DBH) of less than 10cm and none have a DBH over 15cm. At all lower elevations above 1300 m only 60% of with the trees had a DBH of less than 10cm. The forest structure is thus quite spindly above 2250 m compared with lower elevations (Jarvis *et al*. in prep.).

By far the strongest apparent physical discontinuity around 2250m is that of ground-level fog. Below 2200m measurements of fog interception by wire harps indicate relatively infrequent and low intensity fog interception (less than 4 mm/day), whereas sites above 2200 m show fog interception of greater than 7 mm/day, indicating more persistent and intense fog presence (González 2000). These empirical findings support field observations of enhanced fogginess, soil and plant wetness, and increased epiphytic growth above 2200 m which may, in turn, contribute to the type of change in forest structure indicated above (Letts *et al*. submitted). This increased wetness has important habitat implications in addition to those already mentioned; soil moisture and water-logging are major factors in the initiation of landslides, especially on significant slopes (Garland and Olivier 1993). Vascular epiphyte biomass in tropical montane cloud forest tends to be around 5-15 t dry matter ha^{-1} (Veneklaas *et al*. 1990, Wolf 1996). Because epiphyte water storage capacity has been estimated at 5.9 times their dry weight, this means that significant epiphytism coupled with significant wetting by fog interception (see further Jarvis, 2000) can lead to additional canopy loads of between 30 and 90 t ha^{-1}, which is likely to increase the propensity for treefall and landslide activity, potentially opening up the canopy to a much greater extent than below the cloud base. The habitats below 2200 m are quite different because they receive cloud inputs less frequently and at lower intensities and are more able to dry out daily, resulting in lower levels of epiphytism, lower treefall rates, and different arboreal structures.

One out of five *H. l. brunneiceps* banded and released in 1997 within 400 m of the *H. negreti* type locality (near 20 de Julio cabin), was retrapped almost 3 years later in 2000 at almost the same spot. This illustrates the highly sedentary nature of *Henicorhina* populations (as noted by Brewer 2001). It appears that the contact zone with *H. negreti* and *H. l. brunneiceps* is stable and well-established (i.e. coexistence with no temporary movements).

Comparison of ecological niche separation between *H. leucoptera* and *H. leucophrys*

In northern Peru and adjacent Ecuador, another pair of *Henicorhina* Wood-Wrens, *H. leucophrys* and *H. leucoptera* (Bar-winged Wood-Wren), occur in close proximity but seem to partition habitats much as do *H. negreti* and *H. leucophrys*. *Henicorhina leucoptera* is a restricted-range species found on outlying ridges on the east slope of the Andes, apparently inhabiting stunted forest at middle elevations there (Fitzpatrick *et al*. 1977). Recent fieldwork has shown that in several localities, the two species are sympatric but not syntopic. Near

Nuevo Mundo, at the SW end of the Cordillera del Condor, Dpto Cajamarca, Peru, they seemed to separate by habitat, with *leucoptera* inhabiting habitat dominated by scrub (1-2 m) with occasional trees (<3 m), particularly in ravines, at about 2200 m, whereas *leucophrys* was ubiquitous in the wet taller forest nearby (T. Mark, *in litt*). Nearby, in Porvenir Canyon, *H. leucoptera* occurred on a ridge (1800 m), in an area of regenerating scrub (ca.2 m height) dominated by ferns and dispersed 3-meter trees on sandy soils and only 1 km from *H. leucophrys* in tall forest (1690 m). At 2100 m, *H. leucoptera* was found frequently in 4-5 m tall trees and 3 m tall grass (T. Mark, *in litt*.). In the mountains west of Moyobamba in Dpto San Martín, Peru, niche space appeared to be partitioned by the two species as well. *Henicorhina leucoptera* only inhabits the interior of larger patches of stunted, heavily moss/epiphyte-laden forest from 1700-2500 m (primarily from 1700-1900 m, although one was netted at 2500 m). *Henicorhina leucophrys* is more general in habitat use from 1350-2900 m, but inhabits similar stunted forest above 2500 m and will invade the edges of lower patches of the habitat where *H. leucoptera* was also encountered (Davis 1986, D. F. Lane, *in litt*.). In the Cordillera Azul in southwestern Dpto Loreto, Peru, *H. leucoptera* occurs in the absence of *H .leucophrys*, but even here where one might assume the species to experience "ecological release", *H. leucoptera* is restricted to stunted ridgetop forest from 1250-1750 m (Davis 1986, D. F. Lane, *in litt.*). *H. leucoptera* thus appears to be restricted to poor soils plus scrub or impoverished stunted forest (T. Mark, *in litt*.).

Songs of *H. leucoptera* differ less strikingly from those of *H. leucophrys* than do those of *H. negreti*. Comparison of tape recordings of *H. leucoptera* made in the Cordillera Azul with those of *H. leucophrys* from elsewhere in Peru suggest that song of the former is more rapid, richer in quality, less elaborate, and tends to lack high-pitched introductory notes (D. F. Lane, *in litt*.). At this site, within-individual song variation was noted, much as in *H. leucophrys*, with at least three song types from one individual. Furthermore, this species appears to give occasional syncopated pair duets, which are not commonly given by *H. leucophrys*. Scold notes were different, however: drier and more grating in *H. leucoptera*, richer and more liquid in *H. leucophrys* (D. F. Lane, *in litt.*). The scold notes taped in San Martín were similar to those given by *H. leucoptera* in the Cordillera Azul, where one or two additional call notes were tape recorded that were not noted in San Martín (D. F. Lane, *in litt.*).

The interactions between *H. leucoptera* and *H. leucophrys* in Peru and between *H. negreti* and *H. leucophrys* in Colombia are similar in that in both regions, complete species replacements take place within extremely short distances (c. 100 m linearly). The intriguing manner in which *H. leucoptera* and *H. leucophrys* overlap elevationally on the same slope has not yet been recorded between *H. l. brunneiceps* and *H. negreti*, perhaps because we have only studied these taxa together at primary forest sites.

CONSERVATION

Henicorhina negreti is currently known from only two protected areas: Munchique National Natural Park and Tambito Nature Reserve. Munchique NP, on the Pacific slope of the Western Andes, encompasses 44000 ha of wet foothill to montane cloud forest between 500 and 3012 m. Following the discovery of the Colorful Puffleg *Eriocnemis mirabilis*, the area was declared a Flora and Fauna Sanctuary in 1967 and a National Natural Park in 1977. Tambito NR, created and operated by the late Alvaro José Negret through Fundación ProSelva; it includes ca. 3000 ha of very humid premontane forest between 1200 and 2550 m. Both areas are of critical conservation importance, containing the highest concentration of threatened bird species of any site in Colombia (Wege & Long 1995), and encompassing the only known locality for *E. mirabilis*. A total of ten Globally Threatened species, ten Near-Threatened species and at least 20 Chocó endemics have been recorded in Tambito Nature Reserve and Munchique National Park (Wege & Long 1995, Donegan & Dávalos 1999). *Henicorhina negreti* shares similar habitat and elevational range with *E. mirabilis* and the Tanager-Finch *Oreothraupis arremonops*, all being restricted to almost perpetually mist-shrouded wet montane forest on steep terrain. Both Munchique National Park and Tambito Nature Reserve have been submitted as Important Bird Areas (Salaman, *et al*. in litt. 2003).

The current protected status of all *H. negreti* localities appeared ideal for the conservation of the species. However, forest clearance actively continues within the park's borders, and the future of Tambito NR appeared uncertain following Alvaro José Negret's death. Although the NP office in Popayán appears well-funded and well-staffed, this has not translated into practical conservation action because budget cuts have led to the 20 de Julio National Park cabin no longer being staffed or maintained. Increased governmental support for the environment is not considered likely, as Colombia's current economic, political and social problems have caused recent governments to further reduce the Ministry of the Environment (MMA) budget.

Although *H. negreti* prefers successional habitats, forest clearance represents a threat to the species since local decreases in humidity, which often follow deforestation, could render higher-elevation habitats more suitable for *H. leucophrys* subspecies: *Henicorhina leucophrys* has already shown its propensity to invade habitat at elevations which in better-preserved forest are occupied by *H. leucoptera* in Peru (see above), and may therefore pose a threat to *H. negreti*. Even the extreme topography is no savior, because during the recent

dry El Niño summer of 1997 local farmers ignited wildfires across the then unusually dry montane and premontane forest, for maize planting and cattle grazing. The current trend of Global Climate Change due to human-induced changes in the atmosphere could also pose a similar long-term threat to *H. negreti,* because its narrow elevational range is dependent upon specific climatic conditions. If the global warming acts to decrease the humidity of the limited habitat of *negreti*, then invasion by *H. leucophrys* might also be favored. Clearly, continued monitoring of the new species' population and its environment is warranted.

International and local non-governmental involvement and support in conservation efforts of Munchique are acutely required. For example, the Munchique area deserves Important Bird Area status. Munchique is accessible via road from Popayán, one of Colombia's finest colonial cities, which also serves as a base for the important San Agustín and Tierradentro archeological sites, as well as other protected areas including Puracé NP and the recently established Serranía de los Churumbelos NP. Therefore, the potential for ecotourism in the area is great. Improving ecotourism and research facilities would greatly assist Tambito Nature Reserve's long-term future, although this is difficult at present given Colombia's current civil conflict.

Action proposed

Henicorhina negreti is facing an extremely high risk of extinction and is therefore recommended for IUCN Red List status as **Critically Endangered** based on the following criteria:

B1: range size estimated at less than 100 km^2 [Critical];
C2a: small population (<2500 individuals) [Endangered].
Further studies to determine the distribution and population size of *H. negreti* are a high priority for its conservation, and would be of great help in the development of a specific management plan for the Munchique region. Research and conservation initiatives in Munchique should also consider Colorful Puffleg *Eriocnemis mirabilis*, Bicolored Antvireo *Dysithamnus occidentalis*, and Tanager Finch *Oreothraupis arremonops*. 'Rapid assessment' ornithological surveys are needed in remaining montane forest tracts along the Cordillera, particularly in southern Cauca Dept. (e.g. Cerro Guapí), Chocó / Risaralda Depts (Cerro Tatamá), and Antioquia Dept. (Cerro Caramanta, Páramo de Frontino, and Paramillo NP). Such surveys are likely to contribute important new information on the region's avifauna, which remains surprisingly little known.

In 2003 Fundación ProAves-Colombia (www.proaves.org) signed a permanent lease for managing the 20 de Julio National Park cabin to protect the vital southern flank of Munchique National Park from colonization and to monitor timber extraction on the road. ProAves is improving the cabin facilities at 20 de Julio for park guards and researchers as well as maintaining two nature trails. Ornithologists and visitors are welcome to stay at the 20 de Julio cabin and can be shown a number of stunning endemics and threatened species, including *H. negreti*. For further information, please contact secretario@proaves.org.

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