

## McConnell's Flycatcher *Mionectes macconnelli* is more than one species

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**SUMMARY.**—Information on voice, display behaviour, elevational distribution and morphology of McConnell's Flycatcher *Mionectes macconnelli* indicate that the two northern populations, long regarded as a single species, actually comprise two species-level taxa—a widespread lowland form *macconnelli* and a highland form *roraimae*. The two forms are similar in plumage, but differ significantly in wing and tail length, and most importantly in vocalisations and display behaviour. They are separated by elevation, with *macconnelli* found in humid lowland forest up to c.500 m and *roraimae* usually well above 500 m. Another highland taxon, *mercedesfosteri*, differs little from *roraimae* and is not recognised here as distinct, although its voice is unknown. Two isolated populations, one in central Peru, the other in lowland Amazonia are not evaluated, but merit additional study.

During the past few decades a better understanding of mechanisms underpinning reproductive isolation has sparked a re-examination of species limits of many taxa. Avian vocalisations and habitat preferences, in particular, have been shown to be important isolating mechanisms (Zimmer 1997, Isler *et al.* 1999, Zimmer & Whittaker 2000, Whittaker 2002, Salaman *et al.* 2003, Braun *et al.* 2005). This paper documents an example of two morphologically similar forms, *Mionectes m. macconnelli* and *M. m. roraimae*, which we believe have achieved reproductive isolation through voice, behaviour and differences in elevational distribution.

McConnell's Flycatcher *Mionectes macconnelli* is a drab, mostly olive-plumaged Tyrannidae found east of the South American Andes. It was originally described as a subspecies of Ochre-bellied Flycatcher *M. oleagineus* from the Kamakabra River in present-day Guyana (Chubb 1919), and the specific name was incorrectly spelled because it was intended to honour F. V. McConnell. In the same paper, Chubb also described highland *roraimae* from nearby Cerro Roraima, but incorrectly regarded it as a subspecies of *M. oleagineus* as well. Todd (1921) recognised that *macconnelli* was widely sympatric with *oleagineus*, elevated *macconnelli* to species status and treated *roraimae* as a subspecies of *macconnelli*. In the same paper he described a third subspecies, *amazonus*, from the lowlands and foothills of south-eastern Peru and Bolivia. A fourth, *peruanus*, was described by Carriker (1930) from middle elevations on the east slope of the Andes in Junín, Peru. Much later a fifth, *mercedesfosteri*, was described as a subspecies endemic to Cerro de la Neblina on the Venezuela / Brazil border (Dickerman & Phelps 1987). Specimens from Cerro Duida also were assigned to this subspecies (initials R. W. D., NY, '85' on specimen labels). On re-examining all subspecies Fitzpatrick (2004) recognised only three of them, subsuming *mercedesfosteri* into *roraimae* and *amazonus* from Bolivia and southern Peru into nominate *macconnelli*.

Therefore, depending upon one's interpretation of the rather convoluted taxonomic history of *M. macconnelli*, it comprises two or possibly three subspecies in north-eastern South America and two isolated subspecies in south-western Amazonia. This paper discusses only nominate *macconnelli*, which occurs in the lowlands of extreme eastern

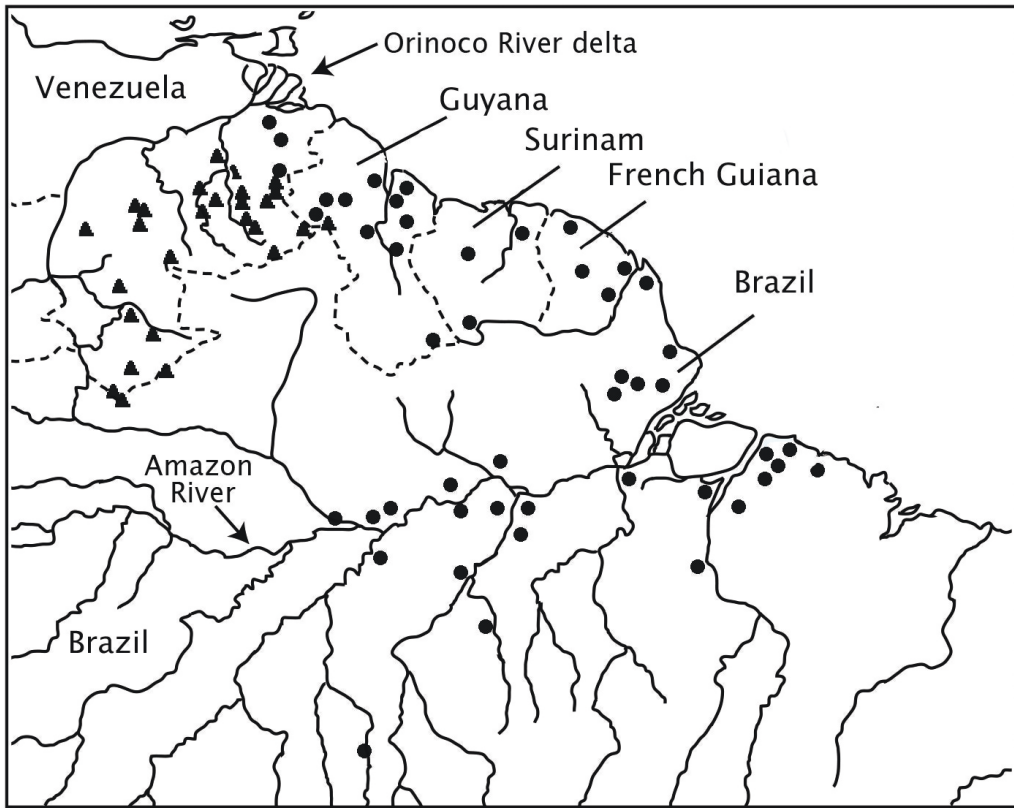


Figure 1. Map showing locality records for *Mionectes m. macconnelli* (solid circles) and *M. m. roraimae* (solid triangles).

Venezuela, the Guianas and the eastern half of Amazonian Brazil, and highland *roraimae*, which is found in the tepuis and río Caura watershed of south-eastern Venezuela and adjacent Guyana (Fig. 1), and has recently also been recorded in adjacent Brazil (M. Cohn-Haft & L. N. Naka pers. comm.).

*Mionectes macconnelli* is quite similar to allied *M. oleagineus* and Grey-hooded Flycatcher *M. rufiventris* (an Atlantic Forest endemic). All three species are characterised by brassy olive upperparts, mainly dull orange-ochraceous underparts and a narrow bill (Ridgely & Tudor 1994). All subspecies of *M. macconnelli* also are quite similar morphologically. *M. m. roraimae* was described by Chubb (1919) as differing from *macconnelli* in being 'rather smaller, paler on the upper-parts, and more brightly coloured on the abdomen, under tail-coverts, axillaries, and under wing-coverts.' Todd (1921) described *roraimae* as similar to *macconnelli*, but more richly coloured throughout, with the uppertail-coverts, throat and upper breast strongly shaded orange-citrine, and yellowish ochre on the lower underparts, axillaries and underwing-coverts, with the wings and tail edged dull orange-citrine. These differences, however, are slight and, while useful for subspecific recognition in the presence of a comparative series of museum specimens, are insufficient, by themselves, for reliable identification in the field. The only published field observations of *M. macconnelli* to date are from a single study of behaviour and nesting of *M. m. macconnelli* north of Manaus, Brazil by Willis *et al.* (1978).

TABLE 1

Measurements of McConnell's Flycatcher (*Mionectes m. macconnelli* and *M. m. roraimae*). *N* = no. of examples. Values are mean  $\pm$  standard deviation, and range. Sexes are combined; wing measured (flat), tail (longest feather). Means of wing measurements and of tail measurements between *macconnelli* and *roraimae* are significantly different (*t*-test, *p* < 0.001)

Taxon	<i>N</i>	Wing	Tail
<i>M. m. macconnelli</i>	14	64.0 $\pm$ 3.03, 58.3–68.4 mm	50.6 $\pm$ 2.90, 46.1–55.7 mm
<i>M. m. roraimae</i> *	66	61.6 $\pm$ 1.90, 57.2–65.3 mm	46.5 $\pm$ 1.85, 44.0–50.7 mm

\*includes measurements from *roraimae* (*n* = 52) and specimens originally described as '*mercedesfosteri*' (*n* = 14). No significant differences between the means of wing measurements (61.7 vs. 61.4 mm) and of tail measurements (46.5 vs. 46.7 mm) of *roraimae* and '*mercedesfosteri*' respectively (*t*-test, *p* > 0.05).

On 7 March 2001, at 1,450 m elevation in the Sierra de Lema (05°53'N, 61°26'W), Bolívar, south-eastern Venezuela, we first noted that vocalisations of highland *M. m. roraimae* differed from those of lowland *M. m. macconnelli*. Surprised by the dramatic differences in vocalisations, we began a series of systematic playback experiments and behavioural observations on *roraimae*, as well as its lowland counterpart *M. m. macconnelli*. As a result of our observations of playback responses, lek and song behaviour, elevational distribution and minor morphological differences, we believe these two taxa should be treated as biological species.

## Methods

Morphological measurements (Table 1) were compiled from specimens at the Colección Ornitológica Phelps (COP), Caracas (*roraimae*, *n* = 52; *macconnelli*, *n* = 3; *mercedesfosteri*, *n* = 13); Museo de Historia Natural, LaSalle (MHNLS), Caracas (*macconnelli*, *n* = 3); Univ. of Kansas Biodiversity Institute (KUBDI), Lawrence (*macconnelli*, *n* = 6); and the Field Museum of Natural History (FMNH), Chicago (*macconnelli*, *n* = 5; *mercedesfosteri*, *n* = 1). Measurements were made of flattened wing and longest tail feather to the nearest 0.1 mm with dial calipers. *T*-tests were used for statistical comparisons between the means of wing and tail measurements. Measurements of males and females were combined for statistical analysis. Three *M. m. macconnelli* specimens yielded insufficient data for analysis.

Our interpretation of the songs of *Mionectes* is based on the assumption that their vocalisations are inherited, as is the case for other suboscines (Kroodsmá 1989, Kroodsmá & Konishi 1991), and therefore vocal characters are useful for systematic study (Lanyon 1988). For our analysis of vocalisations we used recordings that we made at two highland locations in Venezuela and at one lowland site. For additional comparison we also used, in our trial experiments, recordings of lowland *M. m. macconnelli* made by A. Whittaker north of Manaus, Brazil. All vocalisations of both nominate *macconnelli* and *roraimae* are of birds either at leks or song perches, and are hereafter referred to as 'display calls'.

Initial observations and playback experiments on *roraimae* were conducted by both of us at the 1,450 m location noted above on 7 March 2001 and 18 February 2004, and on 14 March 2005 at a second highland site, at 910 m, in the Sierra de Lema (05°59'N, 61°23'W). Playback experiments with nominate *macconnelli* were made by both of us on 23–24 February 2004 at a lowland site (280 m) in the Santa Fe plot (08°05'N, 61°40'W) of the Imataca Forest Reserve, in Delta Amacuro, Venezuela. DA conducted additional playback experiments with highland *roraimae* in September 2001, August 2002, March 2003, December 2004, and June and December 2005, and with lowland *macconnelli* in June 2005. In August 2005 DA

found two *roraimae* singing at a third forested site (05°02'N, 61°03'W) along a road (1,100 m elevation) between San Francisco de Yuruaní and the village of Paraitepuy del Roraima, and conducted a single playback experiment with these individuals.

Location coordinates were obtained using a hand-held Garmin GPS. Mapped distributions of *M. m. macconnelli* and *M. m. roraimae* are based on (1) museum specimens and their localities in Hellmayr (1927), Phelps & Phelps (1950, 1963), Traylor (1979) and Hilty (2003); (2) documented sound-recordings; (3) records compiled by W. L. Brown for Ridgely & Tudor (1994); and (4) personal data from M. B. Robbins. All heights and distances are estimates.

Recordings by SLH were made with a Sony TCM-5000 cassette recorder and are deposited at the Cornell University's Macaulay Library of Natural Sounds (MLNS 172518 and 172549 *M. m. roraimae*; and 172565 and 172572 *M. m. macconnelli*). Recordings by DA were made using a Marantz digital PMD670/U1B recorder. Recordings by M. B. Robbins of *M. m. macconnelli* were made with a Sony Pro-II recorder (MLNS 108004, 108826). Those by A. Whittaker, with a Sony TCM-5000, are at the British Library of Wildlife Sounds (BLOWS, London). Sennheiser ME-67 microphones were used in all cases. Commercially available recordings of *M. m. macconnelli* can be found on a CD (Schulenberg *et al.* 2000) and a CD-ROM (Mayer 2000). Recordings by SLH of *M. m. macconnelli* and *M. m. roraimae* can be accessed via the MLNS website (as can M. B. Robbins' recordings from Guyana). Recordings of *M. m. macconnelli* also can be accessed on the Xeno-canto website ([www.xeno-canto.org/](http://www.xeno-canto.org/)). All of these recordings differ markedly from our recordings of highland *roraimae* and we encourage readers to listen to some of these to better appreciate the differences in the display calls of these two forms. The differences also can be seen in our sonograms (Fig. 2).

Playback experiments were conducted to observe reactions of both highland and lowland forms to the other's vocalisations. To determine reactions we presented an individual with a pre-recorded tape of the other taxon's vocalisation first. Each pre-recorded tape ran to a max. of c.2 minutes, presenting an individual with a minimum of six vocalisations of highland *roraimae*, and a dozen or more vocalisations of lowland *macconnelli*. Each playback trial with the other taxon's vocalisation was repeated at least twice with a buffer period of several minutes between each playback and an additional buffer of several minutes before the taxon's own vocal type was presented. We noted playback response (or lack of) and recorded response as simply strong, moderate or none. A strong response involved immediate approach and vocalisation (usually within 10–30 seconds); a moderate response was characterised by some vocalisation and limited approach usually after c.30–90 seconds of playback. When no approach or song was elicited by playback we noted the response as none. For playback we used our own recordings made at the sites mentioned above. Initially, a recording of lowland *M. m. macconnelli* made by A. Whittaker north of Manaus, Brazil was also used.

## Results

Wing and tail measurements of *macconnelli* were significantly different from those of *roraimae* (Table 1), with lowland *macconnelli* having slightly longer wing and tail lengths. Conversely, wing and tail measurements of the more recently described highland form *mercedesfosteri* were nearly identical to those of *roraimae*, thus supporting Fitzpatrick's (2004) conclusion that this form is unworthy of recognition. We therefore regard *mercedesfosteri* specimens as part of *roraimae* in our analysis but, to avoid confusion, identify them by name enclosed in quotes hereafter. When we played back an unknown vocalisation on 7 March 2001, in the Sierra de Lema, the singer responded immediately, perching close by and behaving nervously as it moved among branches 2.5–6.0 m above ground in

TABLE 2

Summary of playback responses by month. Responses defined as strong, moderate and none for *roraimae* and *macconnelli* to their own and to each other's display vocalisations. Strong implies an immediate response, moderate a slow or delayed response; none indicates no reaction (see text). Date (year) of playback trials are shown at bottom (superscript); each trial consisted of at least two 90-second playback attempts using each song type.

Months <sup>1,2</sup>	Dec.	Feb.	Mar.	Jun.	Aug.	Sep.
<i>roraimae</i> song to <i>roraimae</i>	strong	strong	strong	strong	moderate	none
<i>macconnelli</i> song to <i>roraimae</i>	none	none	none	none	none	none
<i>roraimae</i> song to <i>macconnelli</i>		none		none		
<i>macconnelli</i> song to <i>macconnelli</i>		strong		none		

<sup>1</sup>*roraimae* trials conducted March 2001, February 2004 and March 2005, and *macconnelli* trials February 2004 by SLH & DA.

<sup>2</sup>*roraimae* trials conducted September 2001, August 2002, March 2003, December 2004, and June and December 2005, and *macconnelli* trials June 2005 by DA.

wet premontane forest within an area of predominantly white sandy soil. Visually, we identified the bird as a McConnell's Flycatcher, but realised this vocalisation was unlike anything we knew from this species in the lowlands. While the bird sang we could hear another individual vocalising c.60 m distant. Subsequently, we have found *M. m. roraimae* at other highland sites in the Sierra de Lema region and southward in eastern Venezuela.

Following our initial sighting we conducted experimental playbacks, presenting highland *roraimae* with songs from lowland *macconnelli* and vice versa, and we have not observed a single instance in which the singer of one form appeared to recognise or respond to vocalisations of the other (Table 2). On the other hand, playback of *roraimae*'s own voice elicited a strong response in December, February and March, a moderate response in June and August, and none in September (Table 2). Responses of lowland *macconnelli* to recordings of their own voices, and to those of a *macconnelli* recorded near Manaus by A. Whittaker were strong during February visits to a lek, with birds vocalising and approaching immediately to within 1–2 m of the observer. In June 2005, DA revisited this lowland site of *macconnelli* and was unable to locate any birds or elicit any response to playback. One female of highland *roraimae* from Cerro de la Neblina, Amazonas, was reported to have large gonads in February; a second female had moderate-sized gonads in March. The results of our playback responses and the evidence of gonad size are preliminary, but suggest some breeding takes place early in the year.

## Distribution

The distributions of *macconnelli* and *roraimae* (including *mercedesfosteri*) are allopatric based on available data, but additional survey work may determine a few sites where they come together. In Venezuela the closest-known sites where *macconnelli* and *roraimae* approach are two *macconnelli* specimens (MHNLS 3725–3726) from km 104 (c.500 m) on the El Dorado–Santa Elena highway in eastern Bolívar, and our voice recordings and observations of *roraimae* at km 111.5 (910 m) on the same road. These records are separated by an elevational span of c.400 m but a straight-line distance that is probably no more than 5 km.

Lowland *macconnelli* is known from two areas in Venezuela, the Serranía de Imataca in north-eastern Bolívar, and sight records and voice recordings in the foothills of the Sierra de Lema close to the Guyana border (DA pers. obs.). All *macconnelli* records are from the lowlands below 500 m. We found one specimen labelled as *macconnelli* (MHNLS 10295)



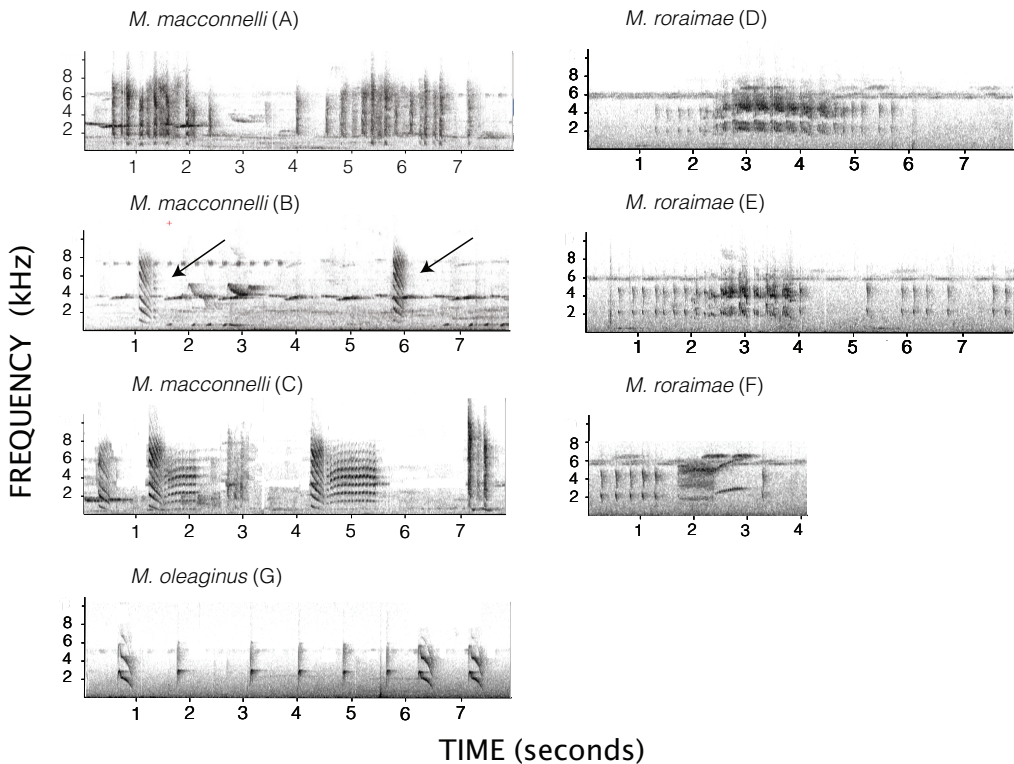


Figure 2. Sonograms of vocalisations of *M. m. macconnelli* (A–C) and *M. m. roraimae* (D–F) forms of McConnell's Flycatcher and allied Ochre-bellied Flycatcher *M. oleaginus* (G) for comparison. Arrows in example B indicate the characteristic buzzy vocalisation of *M. m. macconnelli* during display.

that sometimes lead to another display call, e.g. as in the seven well-spaced notes at end of Fig. 2E. The unmusical display call described above is occasionally followed by a few single notes, then by a weak, upslurred series of thin zipping notes (Fig. 2F), like fingers running along a tiny comb. The notes in this 'comb' phrase recall the buzzy *macconnelli* vocalisation in Fig. 2C, but those of *roraimae* are uttered at a faster rate, are much thinner, weaker and higher pitched, and heard far less often. Display calls of *roraimae* are given at a rate of *c.*1–4 / minute during optimum early-morning hours but increase to a max. of *c.*8 / minute after playback. *M. m. roraimae* may have other calls, but we have not documented them and we believe that its repertoire is less varied than that of *macconnelli* and its call rate much lower.

## Habitat and behaviour

Collection locations, our observations, and those of M. B. Robbins indicate that *macconnelli* and *roraimae* are almost or entirely separated by elevation in eastern Venezuela and Guyana. Both taxa occur inside humid forest with relatively open understorey. However, the forested slopes of the tepuis, where *roraimae* is found, are cooler and wetter and rainfall is probably less seasonal than in the lowlands, where *macconnelli* occurs. All of our observations of *roraimae* are in humid forest on sandy soil near the Gran Sabana or in rocky areas with boulders and large rock outcrops. The lek of *macconnelli* that we located in February was inside humid lowland rainforest with a fairly open understorey and several buttressed trees and large vines. The terrain at the display site was flat to gently sloping

and drained away toward a shallow ravine with dense undergrowth. When calling and displaying, *macconnelli* perched at heights *c.*0.3–2.5 m above ground (rarely to 3 m up) and, as noted by Willis *et al.* (1978), this species is fond of perching and displaying on tree buttresses or vines near buttresses, and usually vocalises when quite close to the ground. *M. m. roraimae*, by contrast, was always observed calling and displaying alone on small branches at heights of *c.*2.5–7.0 m above ground (rarely 1.5–20 m up), thus markedly higher than *macconnelli* and utilising a wider range of perch heights.

At dawn a minimum of six birds occupied the *macconnelli* lek we observed. The entire group displayed within a relatively compact area of *c.*15–30 m. At least three birds spent most of their time within a few metres of each other. It is unknown if the birds in this group, presumably males, occupied small fixed or floating territories during these early-morning calling sessions, but individuals seemed to return to certain perches frequently. Activity levels were high on both mornings of observation and periodically reached almost frantic levels during the first two hours after dawn. Thereafter activity declined, calling became less frequent and, by mid morning, most birds had dispersed. During midday we heard no vocalisations and the display area appeared deserted. We were not able to make afternoon observations, but we did not observe males occupying well-spaced, linear calling territories anywhere in the area, as reported at Reserva Ducke, north of Manaus (Willis *et al.* 1978). However, this could occur during midday or at other places or times of the year.

Typically we have found *roraimae* singly, in loosely associated twos, or less often in well-separated threes or fours. M. B. Robbins (pers. comm.) also reports loose groups of up to four on Ayanganna tepui in Guyana. *M. m. roraimae* has not been found in compact display groups similar to those we observed in lowland *macconnelli*, nor in numbers greater than four. In our experience, calling birds were always well separated from conspecifics (estimated 15–60+ m apart) and on most occasions probably out of sight of each other when vocalising but within hearing distance. We heard *roraimae* giving display calls mainly during early-morning hours but have not observed the level of intense, almost frantic activity in *roraimae* that sometimes characterises *macconnelli*. During late morning the calling sites of *roraimae* were often quiet. Brief playback always elicited a strong response during December, February and March, even if we did not initially hear the birds vocalising. Usually a bird would appear rather high overhead and then descend to call. Response to playback declined in June and August, although two individuals were noted calling spontaneously in August at one site. In September, DA was unable to elicit a response during playback trials.

## Discussion

*M. m. macconnelli* and *roraimae* recall closely related species-pairs of birds that behave as elevational replacements in the Andes (Terborgh 1971, 1985, Terborgh & Weske 1975) as well as the Spot-winged Antbird *Percnoscstola leucostigma* / Roraiman Antbird *P. saturata* complex from the tepui mountains (Braun *et al.* 2005). Our evidence of vocal differences between *macconnelli* and *roraimae*, as well as differences in display behaviour, distribution and certain differences in morphology indicate that these two forms should be regarded as distinct biological species.

*M. m. roraimae* is not threatened by habitat loss. It is found across most of the tepui mountain region and the Caura watershed in southern Venezuela, and immediately adjacent Guyana and Brazil. Few roads penetrate this area, rapids prevent or hinder river access, and consequently human population is extremely low. Except for a small number of isolated airstrips, mostly associated with mining, the habitat of *roraimae* remains largely inaccessible to human activities.



A portion of *macconnelli*'s range in Venezuela, including where we observed it, lies within a large forestry reserve east of El Palmar, Delta Amacuro. It remains largely unreported in lowland forest elsewhere in north-eastern Bolívar or southern Delta Amacuro, areas that are becoming increasingly deforested. Overall the species is widespread, but certainly uncommon in lowland rainforest across the Guianas and eastern Brazil where large areas of intact forest remain.

The English name McConnell's Flycatcher has been in widespread use for all forms of this species and is best retained for the nominate form. No English name exists for highland *roraimae*. Group names, i.e. Lowland and Highland McConnell's-Flycatcher respectively, are helpful geographically and retain a historical connection, but imply a shared ancestry that is unproved. M. Cohn-Haft (pers. comm.) noted that because *M. roraimae* and *M. oleagineus* share an orange mouth lining (unlike *M. macconnelli*, which is apparently black throughout its range), *roraimae* and *macconnelli* might not be each other's closest ancestors. With this in mind, we suggest that highland *roraimae* be called Sierra de Lema Flycatcher after the mountain range where we first discovered its unusual song.

In south-western Amazonia, two taxa, *M. m. peruanus* and *M. m. amazonus* occur in the Amazonian lowlands and southern Andean foothills, and also appear to be separated by elevation. *M. m. peruanus* occurs up to 1,200 m on the east Andean slope of central Junín in Peru (Peters 1979, Schulenberg *et al.* 2007) but is poorly known and its voice is apparently unrecorded. Its plumage is brighter olive above than *macconnelli* and tinged ochraceous, with cinnamon-tipped wing-coverts and paler, more buffy-orange underparts, making it the most readily identified taxon of the group.

The distribution of *amazonus*, if accorded subspecies status, includes north-eastern Bolivia (up to 2,400 m) in dptos. Pando, Beni, La Paz, Cochabamba and Santa Cruz, and in south-eastern Peru in Ucayali and Madre de Dios, and possibly along the río Javari. A second cluster of *amazonus* records (Traylor 1979, Fitzpatrick 2004) occurs eastward in central Amazonas, central Pará, and northern Mato Grosso, Brazil. The plumages of birds from these two populations of *amazonus* are so similar to that of *macconnelli* that Fitzpatrick (2004) subsumed all of *amazonus* into *macconnelli* despite the apparent gaps between their ranges. However, Miller *et al.* (2008), found that lowland *M. macconnelli* is polyphyletic with southern Amazonian birds (*amazonus*) sister to all other lowland *Mionectes* including those of the Guiana Shield lowlands. To date, we believe that no DNA sequence data exists for either of the upper-elevation taxa (*peruanus* or *roraimae*). Further study may reveal important differences in *peruanus* as well.

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