On the sympatric occurrence of two subspecies of Blue-crowned Manakin, Lepidothrix coronata exquisita and L. c. caelestipileata, in south-west Amazonia

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On the sympatric occurrence of two subspecies of Blue-crowned Manakin, *Lepidothrix coronata exquisita* and *L. c. caelestipileata*, in south-west Amazonia

by Edson Guilherme

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Summary.—I present evidence of sympatric occurrence of two subspecies of Blue-crowned Manakin *Lepidothrix coronata* in south-west Amazonia. Specimens collected in eastern Acre in Brazil and northern Bolivia, as well as records from south-east Peru, indicate that *L. c. exquisita* and *L c. caelestipileata* both occur in the south-east of the Inambari centre of endemism, when compared to their respective holotypes. Thus, *L. c. exquisita*, which was considered endemic to central-north Peru, is also present in the lowlands of south-west Brazilian Amazonia and northern Bolivia, whilst *caelestipileata*, previously known from the Juruá–Madeira region in Brazil, is present further south, reaching south-east Peru and northern Bolivia.

Blue-crowned Manakin *Lepidothrix coronata* is a widely distributed frugivorous passerine. It ranges from southern Central America (Costa Rica and Panama) to north-western South America south to northern Ecuador, and across western Amazonia from southern Venezuela and south-east Colombia to Peru and Bolivia (Kirwan & Green 2012). Males possess two plumage patterns. In some populations males are black and in others they are predominantly green. Both black and green males have a blue crown. Females and juveniles are uniform green. Amazonian populations are divided into the *coronata* group (black males) including *L. c. coronata*, *L. c. carbonata* and *L. c. caquetae*, and the *exquisita* group (with green males) comprising *L. c. exquisita, L. c. caelestipileata* and *L. c. regalis* (Kirwan & Green 2012). The *exquisita* group is restricted to south-west Amazonia in the Inambari centre of endemism (Cracraft 1985, Silva *et al*. 2005), with *L. c. exquisita* considered endemic to Peru, *L. c. regalis* endemic to Bolivia, and *L. c. caelestipileata* restricted to south-east Peru and adjacent Acre and Amazonas states in Brazil (Kirwan & Green 2012). Here, I present evidence of the presence of *L. c. exquisita* in Brazil and Bolivia, in sympatry with *caelestipileata* in this part of south-west Amazonia.

To obtain historical records of the distribution of three subspecies of *L. coronata* in south-west Amazonia (Fig. 1), I consulted VertNet (http://www.vertnet.org; accessed 15 December 2021) and GBIF (https://doi.org/10.15468/dl.evws4u; accessed 28 December 2021), as well as specimens in the Museu Paraense Emílio Goeldi (MPEG), Belém. Photos of the holotypes of *L. c. exquisita* (AMNH 493004) and *L. c. caelestipileata* (NMBE 1006262) were provided by the American Museum of Natural History, New York, and Naturhistorisches Museum Bern, respectively (Fig. 2). A photo of an *L. c. caelestipileata* (MZUSP 35743) collected in Acre in 1951 was provided by the Museu de Zoologia da Universidade de São Paulo (MZUSP) (Fig. 3C). I took photos of specimens at MPEG in Belém (Fig. 3A–B) and I was later sent additional photos of these individuals by the museum's curators (Fig. 4).

The compilation of records indicated the occurrence of *L. c. coronata* on the south bank of the Solimões and left bank of the Juruá in the west of the Inambari centre of endemism (see Cracraft 1985; Fig. 1). On the upper Juruá, this subspecies reaches the right bank and extends across central-west Acre (Fig. 1). *L. c. caelestipileata* is present throughout the

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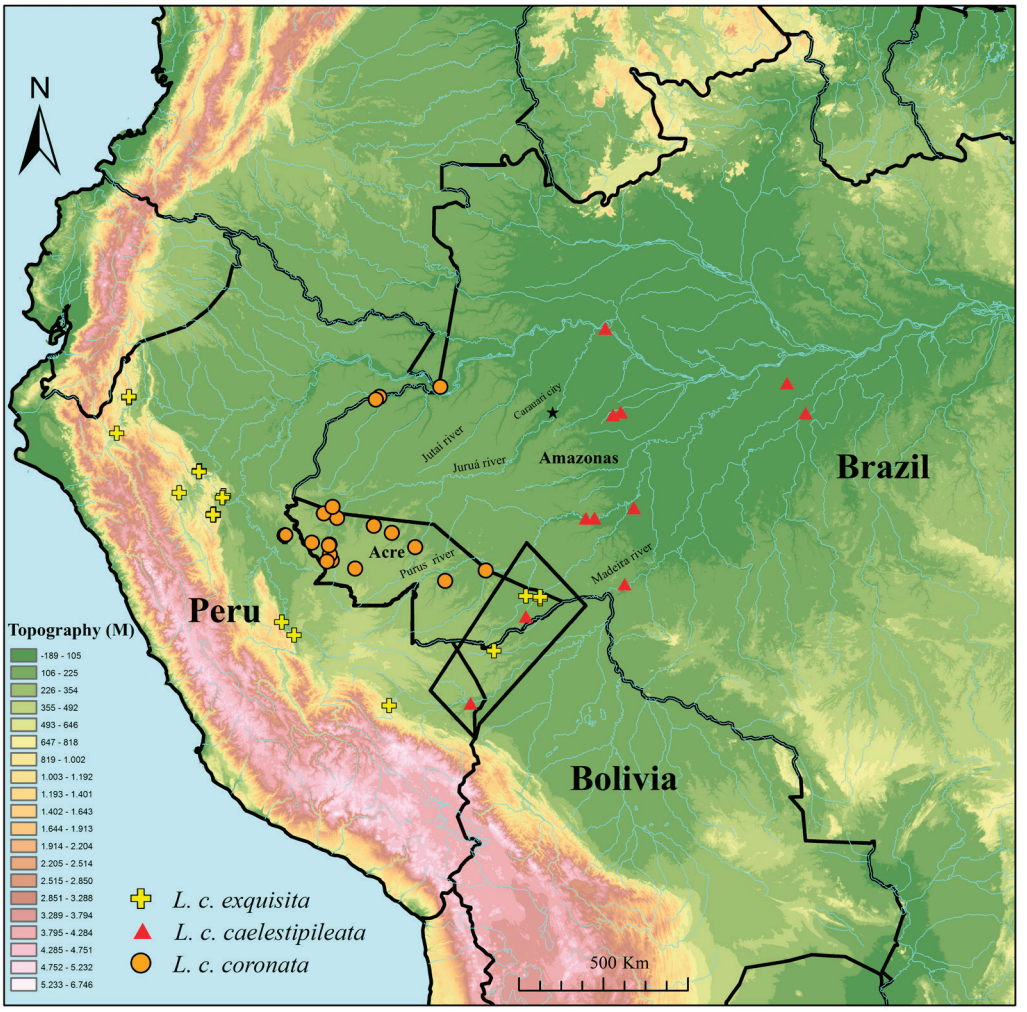

Figure 1. Distribution of three subspecies of Blue-crowned Manakin *Lepidothrix coronata* in south-west Amazonia. The rectangle indicates the region where the taxa *exquisita*/*caelestipileata* occur in sympatry.

Madeira–Juruá interfluvium in the state of Amazonas (Brazil) extending to the border region between Brazil, Bolivia and Peru, south of the Inambari (Fig. 1). *L. c. exquisita* occurs in the Andean foothills of northern Peru to the Amazon lowlands of Peru, Brazil and Bolivia (Fig. 1). In eastern Acre, Brazil, in dpto. Pando in Bolivia and dpto. Madre de Dios in Peru *L. c. exquisita* and *L. c. caelestipileata* occur in sympatry (Fig. 1).

Identification of specimens in the area of sympatry between *exquisita* and *caelestipileata* was confirmed by comparison with their relevant holotypes (Fig. 2). Four specimens from Acre and one from Bolivia (Figs. 3A–B and 4; Table 1) have the crown paler blue and correspond to *exquisita* (Figs. 2B and 4), whereas another collected in the same part of Acre (Fig. 3C; Table 1; Pinto & Camargo 1954) has the brighter blue crown indicative of *caelestipileata* (Figs. 2D and 4; Pinto & Camargo 1954). The straight-line distance between the closest localities of *exquisita* and *caelestipileata* in Acre is only 50 km (Fig. 1). In addition, a specimen at the Museum of Vertebrate Zoology, Berkeley, CA, from dpto. Madre de Dios, Peru, is assigned to *caelestipileata* (Table 1), extending the distribution of this subspecies to the southern boundary of the Inambari (Fig. 1).

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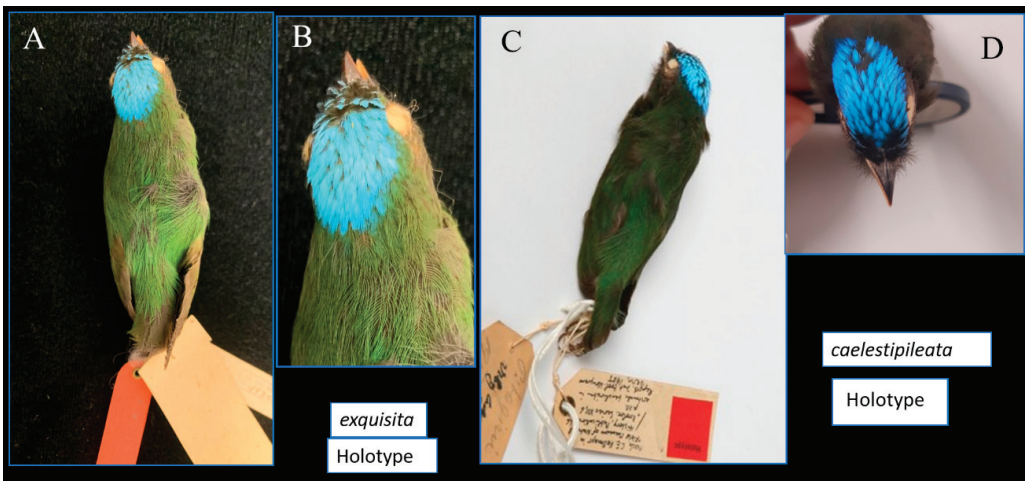

Figure 2. Holotypes of two subspecies of Blue-crowned Manakin *Lepidothrix coronata*. (A–B) *L. c. exquisita* (Hellmayr 1905) (Paul Sweet, © American Museum of Natural History, New York); (C–D) *L. c. caelestipileata* (Goeldi 1905) (Manuel Schweizer, © Naturhistorisches Museum Bern). Note the difference in the blue crown: pale turquoise in *exquisita* and darker and shinier in *caelestipileata*.

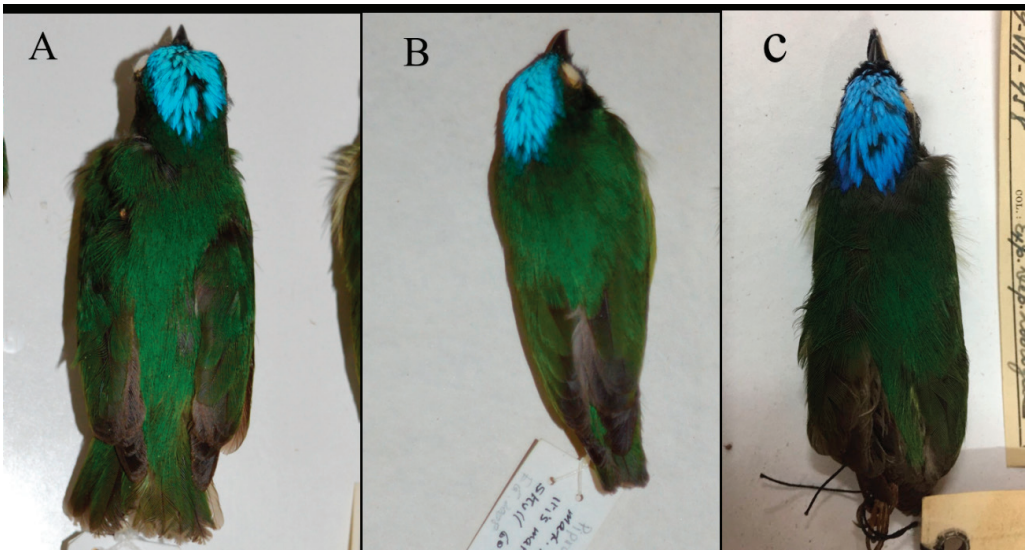

Figure 3. Evidence of sympatric occurrence among two geographic races of Blue-crowned Manakin in south-west Amazonia. (A) *L. c. exquisita*, eastern Acre, Brazil (MPEG 63656) (Edson Guilherme); (B) *L. c. exquisita*, dpto. Pando, northern Bolivia (MPEG 54188) (Edson Guilherme); and (C) *L. c. caelestipileata*, eastern Acre, Brazil (MZUSP 35743) (Luís Fábio Silveira, © Museu de Zoologia da Universidade de São Paulo). Note the difference in crown colour between the specimen of *caelestipileata* (C) versus those of *exquisita* (A–B).

Hellmayr (1905) described *exquisita* as having the 'crown of the head beautiful sky blue' and Goeldi (1905) described *caelestipileata* in German as having the crown 'Himmelblauen' (sky blue), but there is a difference between the blue of *exquisita* (turquoise/lighter; Figs. 2A–B and 4) and that of *caelestipileata* (darker/brighter; Figs. 2C–D and 4), which makes it possible to clearly distinguish them (Fig. 4; Hellmayr 1906, 1929) and to state that they occur in sympatry in south-west Amazonia (Fig. 1). The presence of *caelestipileata* in Madre de Dios in Peru was already known (Schulenberg *et al*. 2007, Snow 2020).

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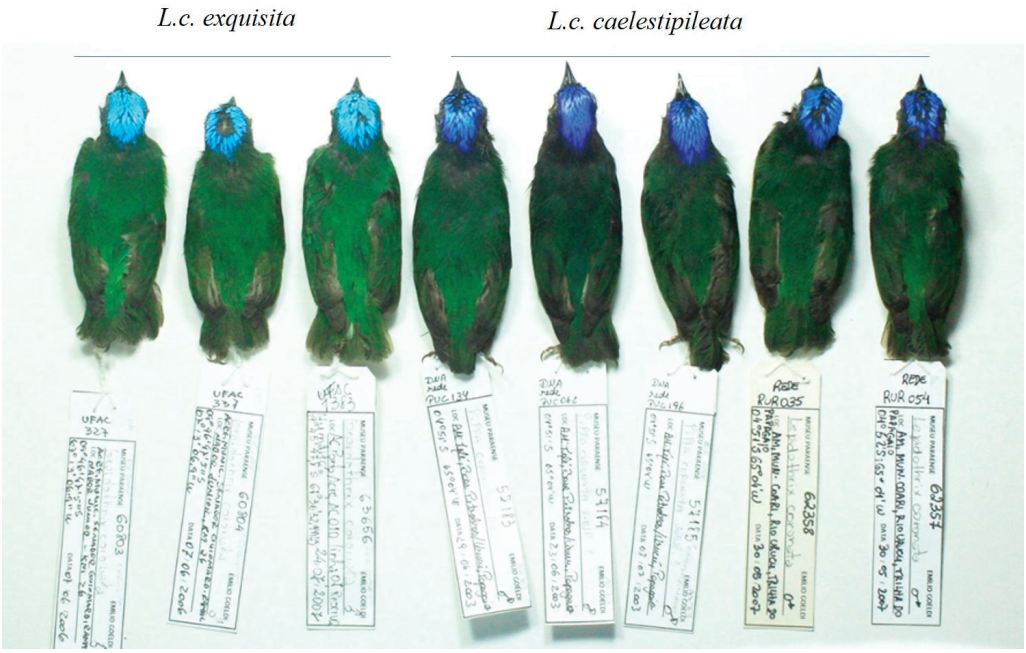

Figure 4. Specimens of *L. c. exquisita* from eastern Acre and *L. c. caelestipileata* from Amazonas, Brazil, at MPEG, showing differences in crown colour, and matching their respective holotypes, taken under the same light conditions (Lincoln Silva Carneiro, © Museu Paraense Emílio Goeldi, Belém)

TABLE 1
Material evidence of sympatry of two subspecies of Blue-crowned Manakin *Lepidothrix coronata* in south-west Amazonia; see Fig. 1 (rectangle). * MPEG = Museu Paraense Emílio Goeldi, Belém; MZUSP = Museu de Zoologia da Universidade de São Paulo; MVZ = Museum of Vertebrate Zoology, Berkeley, CA.

Taxon	Country	Locality	Date	Source/catalog number *	Specimen
L. c. exquisita	Brazil	Acre, Ramal Nabor Jr.	07/06/2006	MPEG 60803	male, checked
L. c. exquisita	Brazil	Acre, Ramal Nabor Jr.	07/06/2006	MPEG 60804	male, checked
L. c. exquisita	Brazil	Acre, Reserva Humaitá	20/07/2007	MPEG 63590	male, checked
L. c. exquisita	Brazil	Acre, Reserva Humaitá	24/07/2007	MPEG 63656	male, checked
L. c. exquisita	Bolivia	Pando, Prov. Nicolás Suarez	10/07/1986	MPEG 54188	male, checked
L. c. caelestipileata	Brazil	Acre, rio Iquri	28/08/1951	MZUSP 35743	male, checked
L. c. caelestipileata	Peru	Puerto Maldonado, Madre de Dios	12/01/1982	MVZ 169507	female, unchecked

Although Guilherme (2009, 2012) reported the presence of *exquisita* in eastern Acre based on the four specimens collected in 2006–07 (Table 1; Figs. 3A and 4), the Brazilian Committee on Ornithological Records (CBRO) (Piacentini *et al*. 2015) did not accept this taxon's occurrence in Brazil, alleging that eastern Acre 'comprises precisely the type locality of *L. c. caelestipileata*'. Guilherme (2016) reaffirmed the presence of *exquisita* in eastern Acre based on a comparison of four specimens collected there (Table 1; Figs. 3A and 4) with material attributed to *exquisita* from central Peru. However, the recent version of the CBRO checklist (Pacheco *et al*. 2021) again argued for excluding *exquisita*, ignoring the specimens from Acre (Table 1; Figs. 3A and 4), and also noted that Del-Rio *et al*. (2021) had confirmed

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that birds east of the Juruá are *caelestipileata*. Del-Rio *et al*. (2021) sampled a restricted region (Carauari) of the middle Juruá River *c*.550 km distant from locations where specimens in Acre were collected (Fig. 1).

Phylogeographic studies of Blue-crowned Manakin indicate that the current geographic distribution of the group is related to different vicariance events, such as the uplift of the Andes and formation of the modern drainage network in the Amazon lowlands (Cheviron *et al*. 2005, Reis *et al*. 2019). Some have defended the idea that it is floodplains (*várzea*) along main rivers that limit the occurrence of taxa in the *L. coronata* group (Del-Rio *et al*. 2021), however, neither vicariance nor the presence of floodplains can explain the sympatric presence of these two taxa in the south-east Inambari. Both must have reached the region by dispersing from their core areas, namely the Andean foothills (*exquisita*) and north-central Inambari (*caelestipileata*). This type of biogeographic encounter between parapatric taxa is not uncommon in Acre (Guilherme 2012) and corresponds to the southernmost contact zone in the south-west Amazonian lowlands proposed by Haffer (1997). Maintenance of this distribution pattern among sister taxa in this region may be related to environmental gradients (Tuomisto *et al*. 2003, 2019). In east Peru, north-west Bolivia and south-west Brazilian Amazonia (Acre and Amazonas), *terra firme* ecosystems are predominantly dominated by two forest typologies, those dominated by bamboo and forests with palms (Silveira *et al*. 2008, Carvalho *et al*. 2013). When these taxa meet due to dispersal, they appear to have adapted to use these different habitats thereby avoiding direct (interspecific) competition, occurring in the same geographic region but occupying different habitats (Carneiro *et al*. 2022). Increased ornithological knowledge of the region has shown that some species thought to occur only in the Andean foothills also occur in the adjacent lowlands in Peru, Brazil and Bolivia (Guilherme & Aleixo 2007, Tobias *et al*. 2008, Rego *et al*. 2009, Plácido *et al*. 2018), as well as species known only in the central-northern Inambari that have been recorded further south (Souza *et al*. 2018), just as suggested by Haffer (1997: 283).

Sympatric occurrence of these two subspecies of Blue-crowned Manakin in the south-east Inambari has biogeographic and phylogenetic implications. Relationships and species limits are still under debate within the genus *Lepidothrix* (Dias *et al*. 2018), in particular in the *L. coronata* group (Cheviron *et al*. 2005, Reis *et al*. 2019). If both taxa occur in the same geographic area and maintain their diagnosable morphological characteristics, it is possible that they have already completed their speciation process and are, in fact, species.

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