

A preliminary bird list from Río Luis, Veraguas province, provides further insight into an avian suture zone in Caribbean Panama

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Presentamos una lista preliminar de las aves colectadas en la costa caribeña de la provincia de Veraguas, Panamá. Encontramos aves no registradas anteriormente en la zona, debido a que sus límites de rango conocidos terminaban al este u oeste de nuestro sitio de colecta. Estas especies incluyen Mosquero Pardo *Cnipodectes subbrunneus*, Colibrí de Julia *Juliamyia julie*, Hormiguero Bicolor *Gymnopathys bicolor bicolor*, Mosquero Aceitunado *Mionectes (oleagineus) assimilis* y las filoespecies occidentales de Buco Barbón *Malacoptila panamensis* y Picolenza Menudo *Xenops minutus*. Nuestros resultados confirman que la costa caribeña de Veraguas, en Panamá, es una zona de sutura importante entre la avifauna de Mesoamérica y Sudamérica.

Several bird species replace each other in the Caribbean lowlands of Panama. Examples include *Manacus* manakins, *Glaucis* and *Anthracothorax* hummingbirds, *Jacana* waders, *Oncostoma* tyrant-flycatchers and *Ramphocelus* tanagers¹⁷. Avian taxonomic turnover can be considered even more widespread when phylogeographic species are considered. Here, examples include *Mionectes* flycatchers¹², *Cantorchilus*⁷ and *Henicorhina* wrens¹, *Arremon* sparrows¹⁰ and *Cyanocopsa* buntings⁴. In fact, abrupt turnover occurs in many

faunal groups, which allowed Bagley & Johnson² to map the location of suture zones for insects, freshwater fish and herpetofauna. However, no precise suture zone was suggested for birds, perhaps because turnover in birds appears to occur broadly across Caribbean Panama.

Gaps in sampling are another reason for the difficulty in locating avian suture zones in Panama. While the country's avifauna is one of the better documented in the Neotropics^{17,19,22–25}, few ornithological surveys in Caribbean Veraguas have been undertaken. This was largely due to difficulty of access, as no roads descended to the Caribbean lowlands from the continental divide, and coastal access has been difficult because of a lack of suitable anchorage along the Caribbean coast of Veraguas²¹. Thus, only a few ornithological expeditions have explored this region¹⁹.

Over the last five years, the government of Panama has begun the construction of a new road (carretera Guabal–Río Luis–Calovébora; Fig. 1) from the town of Santa Fé, on the continental divide in Veraguas province, to Calovébora on the Caribbean coast. This opens up opportunities for further study of the birds of the Caribbean coast of Veraguas province. On 29–31 July 2018, we collected birds along this new road in preparation for more intensive expeditions in the area focusing on turnover within and among bird species in the region.

We established a single field site (08°35'52.8"N 81°12'21.6"W; 170 m elevation) near the town of Río Luis. Vegetation at this site consists of disturbed mature pluvial forest. We exclusively used mist-nets to collect birds. On the final day we used playback to target a few focal, widespread species for comparative genomics work. In total we collected 80 specimens, deposited in the Smithsonian Tropical Research Institute (STRI) Bird Collection,

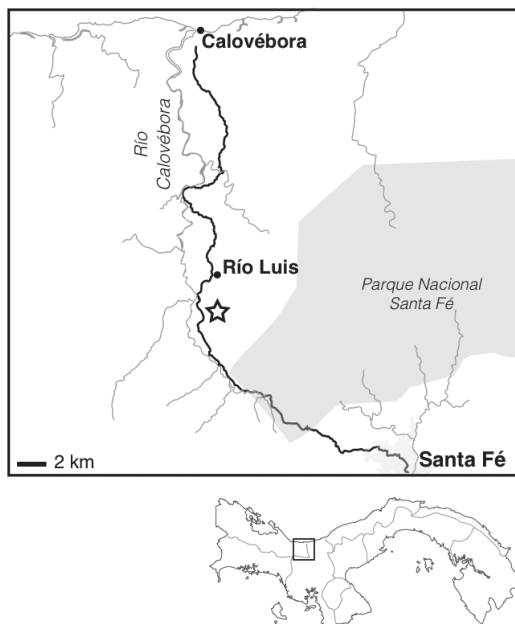


Figure 1. Sampling locality (indicated by the star); black line represents the carretera Guabal–Río Luis–Calovébora, shown at its extent in August 2019.

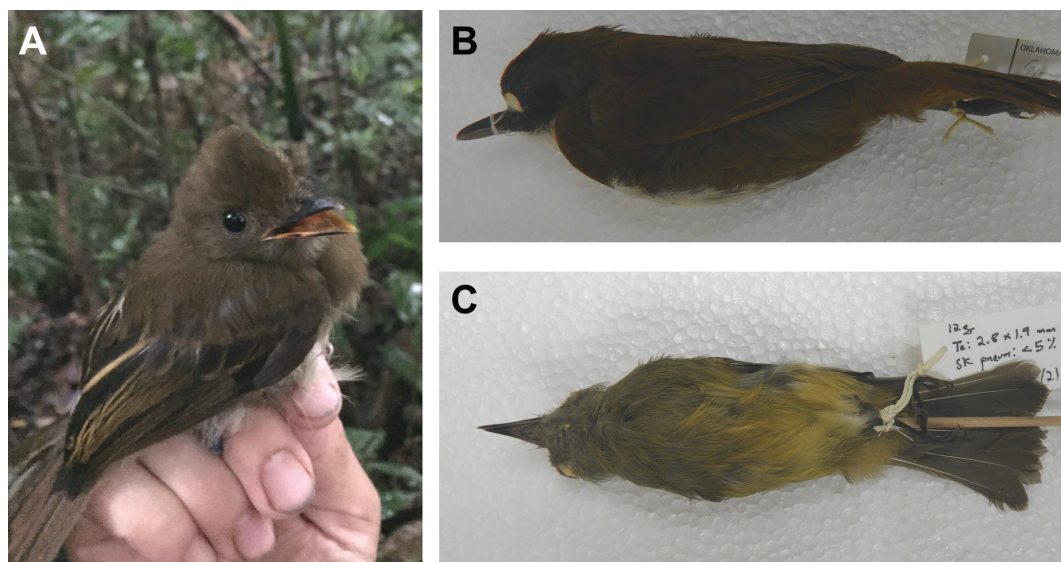


Figure 2. (A) Brownish Twistwing *Cnipodectes subbrunneus* showing characteristic wing posture (Jessica F. McLaughlin); (B) Bicoloured Antbird *Gymnophithys bicolor* showing facial markings of nominate subspecies (Oscar G. López Ch.); (C) Ochre-bellied Flycatcher *Mionectes oleagineus* with *assimilis* plumage (Oscar G. López Ch.)

Naos Island, Panama City, Panama (STRIBC), representing 29 species (Table 1), following the current American Ornithology Society checklist⁵.

The following three taxa are notable for their presence at or beyond their western range limits. We collected two Brownish Twistwings *Cnipodectes subbrunneus* on 29 and 30 July (STRIBC 7885–7886; Fig. 2A). These specimens, and one collected by S. L. Olson at Punta Alegre, Bocas del Toro province in 1990¹³, are the only ones known from west of El Uracillo, Coclé province¹⁷.

A female Violet-bellied Hummingbird *Juliamyia julie* (STRIBC 7887) was collected on 29 July. This species was previously known only from as far west as El Uracillo²³. Although 19th century records exist for Costa Rica and Calovébora (which is due north of Río Luis), both are generally considered to be in error^{18,20,23}.

Finally, we collected four specimens of Bicoloured Antbird *Gymnophithys bicolor* (STRIBC 7890–7893; Fig. 2B), which are assignable to the nominate subspecies based on comparison with the large Panamanian series of this species at STRIBC. Olson¹³ suggested that turnover between this taxon and *G. b. olivascens* probably occurs somewhere between the Valiente Peninsula and Almirante; our record is consistent with this. The nominate subspecies had been collected in Santa Fé previously, but Caribbean slope records were lacking²⁴.

At the same time, three taxa were observed beyond the eastern range limits of mtDNA lineages, which may represent biological species. The first is Ochre-bellied Flycatcher *Mionectes*

(*oleagineus*) *assimilis* (STRIBC 7882–7884; Fig. 2C). Three distinct mitochondrial lineages of *M. oleagineus sensu lato* occur in Panama^{9,12}. The westernmost mtDNA lineage is congruent with the subspecies *assimilis*, which ranges from western Panama to south-east Mexico. This taxon differs notably in plumage, bill shape and song from other Panamanian *oleagineus* (MJM unpubl. data), and probably represents a separate species. The presence of *assimilis* at our study site is particularly surprising, given that STRIBC specimens from Santa Fé, Veraguas province, are assignable to the central and south-western mitochondrial lineage, which is more closely related to some Amazonian populations than it is to *assimilis*¹². This extraordinarily sharp divide across unbroken forest in such a small geographic space (c.22 km) reinforces that this region is key to understanding the generation of patterns of cryptic biological variation across Panama.

Based on DNA sequencing, two mtDNA lineages of White-whiskered Puffbird *Malacoptila panamensis* occur in eastern and western Panama, respectively. These more or less agree with the traditionally recognised *inornata* subspecies (south-west Mexico to western Panama) and the nominate (central Panama to north-west Colombia)^{14,23}. MtDNA sequences from our Río Luis specimen (STRIBC 7888) cluster with sequences from Bocas del Toro province, and not those from Colón province east to Darién province, which suggests that mitochondrial turnover in White-whiskered Puffbird must occur in the c.50 km between our field site and western Colón.

Table 1. Species collected at Río Luis, Veraguas province, Caribbean Panama, on 29–31 July 2018.

English name	Scientific name	No. of specimens
Band-tailed Barbthroat	<i>Threnetes ruckeri</i>	4
Long-billed Hermit	<i>Phaethornis longirostris</i>	4
Stripe-throated Hermit	<i>Phaethornis striigularis</i>	1
Bronze-tailed Plumeleteer	<i>Chalybura urochrysis</i>	1
Crowned Woodnymph	<i>Thalurania colombica</i>	2
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	2
Violet-bellied Hummingbird	<i>Juliamyia julie</i>	1
White-whiskered Puffbird	<i>Malacoptila panamensis</i>	1
Black-crowned Antshrike	<i>Thamnophrilus atrinucha</i>	1
Checker-throated Antwren	<i>Epinecrophylla fulviventris</i>	4
Chestnut-backed Antbird	<i>Myrmeciza exsul</i>	6
Bicoloured Antbird	<i>Gymnophrys bicolor</i>	4
Ocellated Antbird	<i>Phaenostictus mcleannani</i>	2
Plain-brown Woodcreeper	<i>Dendrocicla fuliginosa</i>	2
Wedge-billed Woodcreeper	<i>Glyphorhynchus spirurus</i>	4
Plain Xenops	<i>Xenops minutus</i>	1
Golden-collared Manakin	<i>Manacus vitellinus</i>	4
Royal Flycatcher	<i>Onychorhynchus coronatus</i>	3
Ochre-bellied Flycatcher	<i>Mionectes (oleagineus) assimilis</i>	3
Brownish Twistwing	<i>Cnipodectes subbrunneus</i>	2
Bay Wren	<i>Cantorchilus nigricapillus</i>	2
White-breasted Wood Wren	<i>Henicorhina leucosticta</i>	1
Long-billed Gnatwren	<i>Ramphocoenus melanurus</i>	3
Black-striped Sparrow	<i>Arremonops canirostris</i>	1
Orange-billed Sparrow	<i>Arremon aurantirostris</i>	4
Buff-rumped Warbler	<i>Myiophobus fulvicauda</i>	1
Dusky-faced Tanager	<i>Mitrospingus cassinii</i>	2
Tawny-crested Tanager	<i>Tachyphonus delatii</i>	4
Thick-billed Seed Finch	<i>Sporophila funerea</i>	4
Variable Seedeater	<i>Sporophila corvina</i>	1
Buff-throated Saltator	<i>Saltator maximus</i>	2

Likewise, distinct mtDNA lineages of Plain Xenops *Xenops minutus* occur in western and eastern Panama⁸, which refer to the *ridgwayi* and *littoralis* subspecies. The type specimen of *X. m. ridgwayi* is from Tocumen and Wetmore²⁴ considered this subspecies to occur from eastern Panamá province west to the Costa Rican border. Alternatively, Remsen¹⁵ considered this subspecies to occur north-west to Nicaragua. Subspecies *littoralis* is generally thought to range from eastern Panamá province through Darién province to north-west Ecuador²⁴. However, Harvey & Brumfield⁸ found that a bird from El Copé, Coclé province, clusters both in mitochondrial and genome-wide data with birds from eastern Panama. Our Caribbean Veraguas province specimen (STRIBC 7889) has mtDNA that clusters with birds from Colón to

Darién provinces, but most genome-wide markers cluster with birds from Bocas del Toro province (JFM unpubl. data). Thus, we can suggest that the genetic break between these mtDNA lineages probably occurs in Caribbean Veraguas province, suggesting that phenotypic variation between subspecies is decoupled from underlying genomic variation across this divide.

While our survey of the avifauna of the Río Luis area was brief and incomplete, our results reinforce the notion that the Caribbean slope of Veraguas province is an important suture zone where a Mesoamerican avifauna meets that of eastern Panama and South America. This continental-level turnover may at least partially explain the exceptionally high levels of beta-diversity observed in many Panamanian ecological assemblages^{3,6,11}. At the same time, we call for urgent ornithological investigation of this area. The same road which has opened up this area to ornithological surveys will probably also be accompanied by the degradation and destruction of habitat via forest fragmentation, potentially leading to declines in the local avifauna¹⁶. Thus, the next few years present a critical window in which to study this area.

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References

1. Aguilar, C., De León, L. F., Loaiza, J. R., McMillan, W. O. & Miller, M. J. (2016) Extreme sequence divergence between mitochondrial genomes of two subspecies of White-breasted Wood-wren (*Henicorhina leucosticta*, Cabanis, 1847) from western and central Panamá. *Mitochondrial DNA A DNA Mapp. Seq. Analysis* 27: 956–957.
2. Bagley, J. C. & Johnson, J. B. (2014) Phylogeography and biogeography of the lower Central American Neotropics: diversification between two continents and between two seas. *Biol. Rev. Cambridge Philos. Soc.* 89: 767–790.
3. Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., Tishechkin, A. K., Winchester, N. N., Roubik, D. W., Aberlenc, H., Bail, J., Barrios, H., Bridle, J. R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte de Rocha, W., De Bakker, D., Delabie, J. H. C.,

- Dejean, A., Fagan, L. L., Floren, A., Kitching, R. L., Medianero, E., Miller, S. E., Gama de Oliveira, E., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S. P., Roisin, Y., Schmidt, J. B., Sørensen, L. & Leponce, M. (2012) Arthropod diversity in a tropical forest. *Science* 338: 1481–1484.
4. Bryson, R. W., Chaves, J. A. & Smith, B. T. (2014) Diversification across the New World within the “blue” cardinalids (Aves: Cardinalidae). *J. Biogeogr.* 41: 587–599.
 5. Chesser, R. T., Burns, K. J., Cicero, C., Dunn, J. L., Kratter, A. W., Lovette, I. J., Rasmussen, P. C., Remsen, J. V., Stotz, D. F. & Winker, K. (2019) Check-list of North American birds (online). <http://checklist.aou.org/taxa>.
 6. Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Núñez V., P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H. C., Losos, E. & Hubbell, S. P. (2002) Beta-diversity in tropical forest trees. *Science* 295: 666–669.
 7. González, M. A., Eberhard, J. R., Lovette, I. J., Olson, S. L. & Bermingham, E. (2003) Mitochondrial DNA phylogeography of the bay wren (Troglodytidae: *Thryothorus nigricapillus*) complex. *Condor* 105: 228–238.
 8. Harvey, M. G. & Brumfield, R. T. (2015) Genomic variation in a widespread Neotropical bird (*Xenops minutus*) reveals divergence, population expansion, and gene flow. *Mol. Phyl. & Evol.* 83: 305–316.
 9. Loaiza, J. R., Aguilar, C., De León, L. F., McMillan, W. O. & Miller, M. J. (2016) Mitochondrial genome organization of the Ochre-bellied Flycatcher, *Mionectes oleagineus*. *Mitochondrial DNA* 27: 890–891.
 10. López, K., Angeli, C., Aguilar, C., Loaiza, J. R., De León, L. F., McMillan, W. O. & Miller, M. J. (2016) Extreme mitogenomic divergence between two syntopic specimens of *Arremon aurantirostris* (Aves: Emberizidae) in central Panama suggests possible cryptic species. *Mitochondrial DNA Part A* 27: 3451–3453.
 11. Miller M. J. (2014) A distinctive avian assemblage (Aves: Passeriformes) in western Darién, Panama is uncovered through a disease surveillance program. *Rev. Biol. Trop.* 62: 711–717.
 12. Miller, M. J., Bermingham, E., Klicka, J., Escalante, P., do Amaral, F. S. R., Weir, J. T. & Winker, K. (2008) Out of Amazonia again and again: episodic crossing of the Andes promotes diversification in a lowland forest flycatcher. *Proc. Biol. Sci.* 275: 1133–1142.
 13. Olson, S. L. (1993) Contributions to avian biogeography from the archipelago and lowlands of Bocas del Toro, Panama. *Auk* 110: 100–108.
 14. Rasmussen, P. C. & Collar, N. J. (2002) Family Bucconidae (puffbirds). In: del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) *Handbook of the birds of the world*, 7. Barcelona: Lynx Edicions.
 15. Remsen, J. V. (2003) Family Furnariidae (ovenbirds). In: del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, 8. Barcelona: Lynx Edicions.
 16. Renjifo, L. M. (1999) Composition changes in a subandean avifauna after long-term forest fragmentation. *Conserv. Biol.* 13: 1124–1139.
 17. Ridgely, R. S. & Gwynne, J. A. (1992) *A guide to the birds of Panama, with Costa Rica, Nicaragua, and Honduras*. Second edn. Princeton, NJ: Princeton University Press.
 18. Schuchmann, K.-L. (1999) Family Trochilidae (hummingbirds). In: del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) *Handbook of the birds of the world*, 5. Barcelona: Lynx Edicions.
 19. Siegel, D. C. & Olson, S. L. (2008) *The birds of the Republic of Panamá*, 5. Shipman, VA: Buteo Books.
 20. Slud, P. (1964) The birds of Costa Rica: distribution and ecology. *Bull. Amer. Mus. Nat. Hist.* 128: 1–430.
 21. US Hydrographic Office (1902) *The navigation of the Gulf of Mexico and Caribbean Sea*, 2. Fourth edn. Washington DC: Government Printing Office.
 22. Wetmore, A. (1965) *The birds of the Republic of Panamá*, 1. Washington DC: Smithsonian Institution Press.
 23. Wetmore, A. (1968) *The birds of the Republic of Panamá*, 2. Washington DC: Smithsonian Institution Press.
 24. Wetmore, A. (1972) *The birds of the Republic of Panamá*, 3. Washington DC: Smithsonian Institution Press.
 25. Wetmore, A., Pasquier, R. F. & Olson S. L. (1984) *The birds of the Republic of Panamá*, 4. Washington DC: Smithsonian Institution Press.

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Appendix I. Specimens of Bicoloured Antbird *Gymnopithys bicolor* at STRIBC examined for subspecies identification.

STRIBC number	Province
STRIBC7342	Coclé
STRIBC7344	Coclé
STRIBC7355	Coclé
STRIBC0847	Colón
STRIBC0848	Colón
STRIBC0849	Colón

STRIBC number	Province	STRIBC number	Province
STRIBC0850	Darién	STRIBC2956	Colón
STRIBC0851	Panamá	STRIBC2957	Colón
STRIBC0852	Coclé	STRIBC2958	Veraguas
STRIBC0853	Colón	STRIBC3047	Colón
STRIBC0854	Coclé	STRIBC3048	Colón
STRIBC0855	Coclé	STRIBC3049	Colón
STRIBC0856	Coclé	STRIBC3050	Colón
STRIBC0857	Coclé	STRIBC3499	Coclé
STRIBC0858	Bocas del Toro	STRIBC3770	Colón
STRIBC0859	Bocas del Toro	STRIBC3774	Darién
STRIBC0860	Bocas del Toro	STRIBC3775	Darién
STRIBC0861	Bocas del Toro	STRIBC3854	Colón
STRIBC0862	Bocas del Toro	STRIBC3904	Darién
STRIBC0863	Bocas del Toro	STRIBC3906	Darién
STRIBC2550	Veraguas	STRIBC4147	Comarca Emberá-Wounaan
STRIBC2551	Colón	STRIBC4226	Comarca Emberá-Wounaan
STRIBC2954	Colón	STRIBC4807	Darién
STRIBC2955	Colón	STRIBC4815	Darién