Speckled Hummingbird: more than meets the eye

Speckled Hummingbird *Adelomyia melanogenys* is one of the most widespread species in the Andes, occurring from Venezuela (including the coastal ranges) south to central Bolivia. This is nobody’s idea of a flashy hummingbird: primarily dull brown, with a dark face ‘mask’, it somewhat resembles a small, short-billed hermit *Phaethornis*. This unobtrusive appearance conceals some tangled tales, however. A phylogenetic analysis of DNA sequence data, conducted by Chaves and colleagues (Chaves & Smith 2011, Chaves et al. 2011), recovered significant genetic structure across the wide latitudinal range of Speckled Hummingbird, with six well-defined clades (lineages) within the species. A few years later, Donegan & Avendaño (2015) followed up with a characteristically exhaustive review of geographic variation of plumage, morphometrics, and vocalisations of Speckled Hummingbird, focusing primarily on the Colombian Andes.

One interesting result from the genetic survey was that subspecies *inornata*, of extreme southern Peru and Bolivia, is sister to the five other clades. The name *inornata* might suggest that this subspecies is even plainer than expected, but in reality *inornata* is one of the most well-marked subspecies of Speckled Hummingbird: it is the only taxon with blue speckles on the throat, and it also has a more rufous rump (Zimmer 1951, Donegan & Avendaño 2015). Donegan and Avendaño (2015) also report that the calls of *inornata* are given at a faster rate than in other populations.

Together, these lines of evidence suggest that *inornata* may merit recognition as a species, although Donegan & Avendaño (2015) caution that the ever-popular ‘further study’ is called for. This may be prescient as Zimmer (1951) reported signs of introgression between *inornata* and *chlorospila*, the next population to the north. Contradicting Zimmer, however, is the encouraging sign that Chaves and colleagues included samples from near the type locality of *chlorospila*, and these clearly grouped with northern birds, not with *inornata*. Otherwise, Chaves and colleagues also found that the widespread subspecies *melanogenys*, which, according to some sources (e.g. Zimmer 1951), occurs from Venezuela to southern Peru, is scattered across two of their six clades. At the other extreme, one of the six clades of Chaves et al., named ‘Clade F’, which is restricted to the west slope of the Eastern Andes of Colombia in Santander and Boyacá, does not correspond to any named taxon.

Donegan & Avendaño (2015) took up the challenge represented by the mysterious Clade F, and reviewed the potentially available names. This review is complicated by vague or misleading type localities and lost or unrecognised type specimens, but they tentatively conclude that the name *sabinae* applies to the Santander/Boyacá birds (as already was used for these birds by McMullan & Donegan 2014). Finally, the range of subspecies *melanogenys* (type locality “Bogotá”) needs to be restricted to the region between the Andes of Venezuela and Colombia, to the north, and the northernmost Andes of Peru, to the south. The only available name for birds in the rest of Peru, from just south of the mighty Marañón River south to the range of *inornata*, is *chlorospila*. 
The unobtrusive appearance of Speckled Hummingbird *Adelomyia melanogenys* conceals some tangled taxonomic tales.


2. Speckled Hummingbird *Adelomyia melanogenys*, Reserva Natural de las Aves Reinita Cielo Azul, Santander, Colombia, March 2013 (Luis Urueña; www.manakinnaturetours.com). Location suggests this might be the mysterious ‘Clade F’.


There are three major clades of White-breasted Wood Wren *Henicorhina leucosticta*, with playback experiments on the Central American clade (in Costa Rica) suggesting that Amazonian birds may display the greatest divergence.


7 White-breasted Wood Wren *Henicorhina leucosticta*, Presidente Figueiredo, Amazonas, Brazil, January 2016 (Sergio Gregorio; 500px/sergiogregorio). A bird from the Amazonian clade.


Grey-breasted Wood Wren *Henicorhina leucophrys* appears to contain nine distinct lineages including two elevationally segregated subspecies (*bangsi* and *anachoreta*) in the Santa Marta mountains, Magdalena, Colombia.

9 Grey-breasted Wood Wren *Henicorhina leucophrys bangsi*, San Lorenzo ridge (1,250 m asl), Sierra Nevada de Santa Marta, Magdalena, Colombia, October 2015 (Paulo Cesar Pulgarín Restrepo; www.colombiaavianmalaria.co).

10 Grey-breasted Wood Wren *Henicorhina leucophrys anachoreta*, San Lorenzo ridge (2,290 m asl), Sierra Nevada de Santa Marta, Magdalena, Colombia, October 2015 (Paulo Cesar Pulgarín Restrepo; www.colombiaavianmalaria.co).
White-breasted Wood Wren is back in the news

White-breasted Wood Wren Henicorhina leucosticta is one of the commonest and most familiar birds of the understorey of humid lowland forest in the northern Neotropics. Accordingly, most birders probably pay it little attention in the quest for gaudier or more range-restricted ticks. We were advised long ago, however, that White-breasted Wood Wren was likely to contain more than one species.

The first clues to this (as noted in Kirwan 2006) came from a genetic survey of Henicorhina by Dingle et al. (2006) that included 18 samples of White-breasted Wood Wren from across its range. The basic result was quite simple: there are three major clades of this species, corresponding to Central America, South America east of the Andes, and the Chocó. A surprise bombshell, however, was that the Chocó clade was sister to Bar-winged Wood Wren H. leucoptera, rather than to other White-breasted populations. This, of course, strongly suggested that the Chocó birds were a separate species; and, by inference, a case could be made for splitting the two other clades as well. Limitations of the research by Dingle and colleagues were that it relied entirely on mitochondrial DNA, with no input from nuclear genes. Moreover, the geographic sampling, while admirably broad, was also coarse enough to leave open some important questions, such as where the Chocó and Central American clades replace one another.

One would think—certainly one would hope! —that the very encouraging results from Dingle and colleagues quickly would have led to a suite of follow-up genetic studies, but no such luck. An unpublished study by Lelevier (2008), again restricted to mitochondrial DNA but with slightly wider geographic coverage, confirmed the broad outlines of the earlier results. Lelevier added a new twist by identifying that wood wrens in eastern Panama are closer genetically to the Amazonian populations than they are to wood wrens elsewhere in Central America.

The next chapter in the story comes from an older technology, the tried-and-true (albeit tried less often in recent years) method of field playback. Pegan and colleagues (2015) investigated the responses of White-breasted Wood Wrens in Costa Rica to playback of songs from three lineages of the species: sympatric (Central American), Amazonian, and from the Chocó. They found that Costa Rican wood wrens had a highly asymmetric response to playback of songs, all but ignoring the songs of Amazonian wood wrens, while reacting almost as strongly to songs of birds from Chocó as they did to songs of local wood wrens. Pegan et al. noted that this result is not surprising, as an accompanying comparison of songs showed greater similarity between the songs of the Central American and Chocó populations, with Amazonian songs more divergent.

These results strongly suggest that Central American and Amazonian populations are distinct species. Questions still remain—as they so often do!—especially regarding interactions at potential contact zones between the Central American, Darién, and Chocó clades; central Panama in particular now stands out as a region of great interest in this regard. But it is more clear than ever that there are multiple species of White-breasted Wood Wren. Observe and record them where you find them, and wait to see how this all plays out.

Meanwhile, multiple cryptic species uncovered in Grey-breasted Wood Wren

Dingle et al. (2006) also looked at geographic variation in Grey-breasted Wood-Wren, as assessed by analysis of mitochondrial DNA, and detected a familiar pattern: three distinct genetic lineages, which they identified as Central American, Andean, and Chocó. Their use of “Chocó” was a bit of a misnomer, however, as the population they are talking about here is hilaris, the distribution of which is in western Ecuador, just to the south of the Chocó proper. No matter: the really interesting aspect of the distribution of hilaris is that it occurs at mid-elevations in the Andes, immediately below nominate leucophrys. These two subspecies are highly divergent genetically, and have different songs (Dingle et al. 2008, 2010).

Yet another update on this intriguing situation is now in press by Halfwerk and colleagues (2016), who reported on the interactions at a contact zone between hilaris and leucophrys. There is some hybridisation between these two where they meet, although there also is a marked tendency to mate assortatively (i.e. true to type). Additionally, the two song types remained distinct, with only a very low level of songs that were intermediate. In other words, hilaris and nominate leucophrys are behaving very much like two separate species.

A more comprehensive genetic survey of Grey-breasted Wood Wren was conducted by Caro et al. (2013). This study had very wide geographic
coverage, but, surprisingly, did not include representatives of hilaris. These researchers identified no fewer than nine (!) genetic lineages within this species. The focus of this study, however, is on a situation in the Sierra Nevada de Santa Marta, in northern Colombia, that parallels the story from western Ecuador.

In the isolated Santa Martas, there are two elevationally segregated subspecies, lower-ranging bangsi and, at higher elevations, anachoreta. Todd & Carriker (1922) treated these as belonging to separate species, but for most of the 20th century both were demoted to the rank of subspecies of Grey-breasted. The genetic work by Caro and colleagues, based on phylogenetic analysis of DNA sequence data from both mitochondrial and nuclear genes, reveals that bangsi and anachoreta are not closely related to each other. The songs of the two differ (Caro et al. 2013); there is discrimination to tape playback (Caro et al. 2013, Burbidge et al. 2015); and the two taxa are locally sympatric at intermediate elevations (Caro et al. 2013).

These two clearly are different species, although there is a question over how to classify them. Everyone agrees that anachoreta is a species endemic to the Santa Martas (McMullan & Donegan 2014; Cadena et al. 2015), but the status of bangsi is less clear. It too is considered by McMullan & Donegan (2014) to be a Santa Marta endemic, but Cadena et al. (2015) are more cautious, holding out the possibility that it is conspecific with its closest relative, manastarae of the Serranía de Perijá on the Colombia/Venezuela border.

There also are discussions to be had over appropriate English names for the Santa Marta populations. McMullan & Donegan proposed “Bangs’ Wood Wren” for bangsi and “Santa Marta Wood Wren” for anachoreta, whereas Cadena et al. (2015) considered the etymological origins of anachoreta and suggested “Hermit Wood Wren” for this species. My own preference would be for anything other than “Santa Marta”, to reduce the risk of confusion with another local endemic, Santa Marta Wren Troglodytes monticola; but time will tell which name (if either!) catches hold.

Finally, both bangsi and anachoreta (and presumably hilaris as well) are embedded deep within the ‘Grey-breasted Wood Wren’ complex. Elevating one or more of these to the rank of species implies that several other species of ‘Grey-breasted Wood Wren’ will need to be recognised before we are through. Even though Grey-breasted Wood Wren is spitting out cryptic species left and right, however, nobody yet has tackled the bigger picture of just where this will end. We are left hoping that research groups involved so far continue their efforts to unravel the mysteries of wood wren evolution.

### Three-way split in Black-billed Thrush

Black-billed Thrush *Turdus ignobilis* is a common, widespread species in northern South America. It primarily occurs east of the Andes, but also is present in inter-Andean valleys in Colombia. The species epithet *ignobilis* indicates that this bird never has gotten any respect: it is a classic ‘trash’ bird, drab in appearance and occupying gardens, forest edge, and other ‘less desirable’ habitats. Nevertheless, this thrush is worth a second (and third) look.

An analysis of phenotypic and genetic variation across its range by Cerqueira et al. (2016), however, reveals that perhaps we have been too quick to take this thrush for granted. Cerqueira and colleagues discovered that the six subspecies of Black-billed Thrush are not each other’s closest relatives. Instead, the three northwestern subspecies, which occur in the northern Andes and on the tepuis, are sister to Lawrence’s Thrush *T. lawrencii* of Amazonia; subspecies debilis, which is widespread in the lowlands of western Amazonia, is sister to Marañon Thrush *T. maranonicus*; and the two eastern subspecies, which are restricted to white-sands habitats, are basal to the debilis and maranonicus pair. *Et violà*, three species result: *T. ignobilis* (including subspecies goodfellowi and murinus); *T. debilis* (monotypic); and *T. arthuri* (including subspecies cururuensis).

Cerqueira et al. proposed that *T. ignobilis* retain the English name “Black-billed Thrush”, that *T. arthuri* be named “Campina Thrush”, and that *T. debilis* be called “Varzea Black-billed Thrush”. In my view, “Campina Thrush” is a fine choice, but “Varzea Black-billed Thrush” is a mouthful, and we already have one Varzea Thrush (the recently described *T. sanchezorum*). Meanwhile, retaining “Black-billed Thrush” also runs the risk of confusion for anyone who hasn’t yet internalised the message about the split (which is a real problem, as it takes field guides years to catch up). Other name options would be “Drab Thrush” for *T. ignobilis* (again taking that epithet to heart!), and simply “Amazonian Thrush” for *T. debilis*.
There is evidence for splitting Black-billed Thrush into three species.

11 Black-billed or “Drab” Thrush *Turdus (i) ignobilis*, La Ceja, Antioquia, Colombia, January 2012 (Priscilla Burcher; tinyurl.com/prisburcher).

12 “Campina” Thrush *Turdus (ignobilis) arthuri*, Paramaribo, Suriname, October 2014 (Jean-Claude Jamoulle; tinyurl.com/J-CJamoulle).

13 “Varzea Black-billed” or “Amazonian” Thrush *Turdus (ignobilis) debilis*, Manaus, Amazonas, Brazil, October 2015 (João Sérgio Barros; tinyurl.com/JoaoSouza).

A broad survey of the genomes of six species of ‘capuchinos’ *Sporophila* has revealed some potential species-specific markers.

14 & 15 Male Dark-throated Seedeater *Sporophila ruficollis*, Barra do Quaraí, Rio Grande do Sul, Brazil, December 2010 (Márcio Repenning; tinyurl.com/marcio_repenning).
Assuming that it is accepted as a genuine species, the ‘authorities’ will need to decide which of two competing descriptions of Iberá Seedeater should take precedence.

16 Male Iberá Seedeater ‘Sporophila digiacomoi/digiacomoorum’ or S. iberaensis, Corrientes, Argentina (Carlos Figuerero).

17 Male Iberá Seedeaters ‘Sporophila digiacomoi/digiacomoorum’ or S. iberaensis (Aldo Chiappe; plate reproduced with permission from López-Lanús ‘2015’).

The American Ornithologists Union does not (yet!) split “Fuertes’s” Oriole Icterus (spurius) fuertesi from Orchard Oriole Icterus spurius; recent research identifies consistent but minor differences in vocalisations.

18 Orchard Oriole Icterus spurius, Petén, Guatemala, March 2008 (Christopher L. Wood).

19 Probable Orchard Oriole Icterus spurius, Tuxtla Gutiérez, Chiapas, Mexico, December 2014 (Mario A. Espinosa; tinyurl.com/quetzalpr). This individual combines plumage characteristics of both Orchard at Fuertes’s Oriole Icterus (spurius) fuertesi.

20 Orchard (Fuertes’s) Oriole Icterus (spurius) fuertesi, Camino a Las Barrancas, Veracruz, Mexico, March 2007 (Stephen Davies; tinyurl.com/chlorophonia).
Breakthrough in unraveling the ‘Capuchino’ radiation?

The ‘capuchinos’ are a group of small-bodied *Sporophila* seedeaters; as a group, capuchinos occur from Mexico south to northern Argentina, but the greatest diversity is in Paraguay, southernmost Brazil and northern Argentina. Capuchinos have presented many taxonomic headaches over the years. Some species are similar to others (or, in the case of females, completely indistinguishable!), and a few species also have rare colour morphs, such as Tawny-bellied Seedeeater *S. hypoxantha* (Areta & Repenning 2011b) and Dark-throated Seedeeater *S. ruficollis* (Areta et al. 2011). Most species otherwise are clearly delineated by distinctive male breeding plumages, and recent field work has documented that capuchinos also sort out by breeding habitat and song (Areta 2008, Areta & Repenning 2011a, Areta et al. 2011). And so, with a few notable exceptions, such as Entre Rios Seedeeater *S. zelichi*, there is broad agreement on which capuchinos should be recognised as species.

Efforts over the years to use genetic approaches to investigate the relationships within the capuchino group have crashed and burned, however, revealing only little more than that the bulk of the capuchino group radiated very rapidly and very recently (Lijtmaer et al. 2004, Campagna et al. 2012). Campagna is not easily dissuaded, however, and has made yet another effort to crack the capuchinos. The most recent study (Campagna et al. 2015) is not a phylogeny of the group; instead, this team conducted a broad survey of the genomes of six species of capuchinos (a so-called genomic scan), searching for species-specific markers.

The good news is that indeed some genetic markers were found between the species; the bad news is that these markers were few, so few that it is difficult to be certain whether these markers in fact are species-specific (the long-sought phylogenetic ‘signal’), or whether the patterns that were detected are randomly distributed (‘noise’ in the phylogenetic system). This may be a path forward, however, if future studies are able to sample larger portions of the genome, and perhaps also larger numbers of individuals per species. We wish researchers luck!

Speaking of capuchinos, another one joins the party

In an unusual series of events, two different and nearly simultaneous publications surfaced, each of which is a description of the same proposed new species of capuchino seedeeater: *S. digiacomoi* López-Lanús ‘2015’ (actually published in 2016) and *S. iberaensis* Di Giacomo and Kopuchian 2016. In one of several odd twists, *digiacomoi* is named in honour of two brothers, Adrián and Alejando Di Giacomo; hence, this epithet should be amended to *digiacomoi*. (And yes, Adrián Di Giacomo both described this species, and has it named, in part, after him.) Fortunately, all parties agree on the same English name, Iberá Seedeeater.

This new species is similar to Dark-throated Seedeeater *S. ruficollis*, but the breeding male differs by having grey restricted to the crown, rather than extending onto the nape, and in having dusky restricted to the throat instead of also covering the upper breast (López-Lanús ‘2015’, Di Giacomo & Kopuchian 2016). It also differs from Dark-throated by having a dusky nuchal collar, and in vocalisations (López-Lanús ‘2015’).

As its English name suggests, the breeding range of this new seedeeater is centred on the Iberá wetlands in Corrientes, Argentina, with a handful of records from Paraguay and one from southern Brazil (López-Lanús ‘2015’, Di Giacomo & Kopuchian 2016). It remains for others to determine which of these two competing descriptions can claim precedence, and be accepted as the valid name for the proposed new species. For that matter, time will tell if Iberá Seedeeater is accepted as a species at all. Some of the features attributed to *diacomicoomrrum/ iberensis* are similar to those of the mysterious *caraguata* seedeeater, which Areta et al. (2011) puzzled over at length before concluding that it represented a colour morph of Dark-throated Seedeeater. In any event, now that Iberá Seedeeater has a scientific name or two, the increased attention that it surely will receive should help elucidate its status.

Vocal divergence in Fuertes’s Oriole

Fuertes’s Oriole *Icterus fuertesi* is an isolate of the widespread Orchard Oriole *I. spurius*, with a very restricted breeding range in northern Mexico. Female Fuertes’s often is indistinguishable from Orchard, but the male is noticeably different: it has the same pattern as male Orchard Oriole, but is ochre and black, rather than chestnut and black. Many authorities consider Fuertes’s to be only a well-marked subspecies of Orchard (e.g. Howell & Webb 1995, Jaramillo & Burke 1999), but others accord it species rank (Fraga 2011).

One of the arguments favoring its treatment as a species is that the song of Fuertes’s Oriole is said
to be different from that of Orchard (Jaramillo & Burke 1999, Fraga 2011). Hagemayer et al. (2012) and Sturge et al. (2015) present the first detailed comparative analyses of the songs of Fuertes’s and Orchard orioles, and report no significant song differences between the two. Sturge and colleagues take things one step farther, however, and also investigate the calls of both orioles. Here lie the differences! The calls of Fuertes’s Oriole are longer in duration and the frequency (pitch) is more modulated, usually with a significant point of inflection in frequency that makes the call almost sound like two notes (rather than one). All of this is good to know, but in most ways it leaves us pretty much where we started: Fuertes’s and Orchard orioles are two taxa with consistent but minor differences between them, and disagreements over whether to recognise one species, or two, are likely to continue.

ACKNOWLEDGMENTS

Thanks to Nick Athanas, Priscilla Burcher, Stephen Davies, Mario A. Espinosa, Carlos Figuero, Sergio Gregorio, Jean-Claude Jamoule, Caroll Perkins, Paulo Cesar Pulgarin Restrepo, Márcio Repenning, João Sôrgio Barros, Joseph Tobias, Luis Urueña, Christopher L. Wood and Phil Yates for providing photographs, to several others for offering images that were not ultimately used, and to Brooke Keeney for sourcing and organising these submissions. Thanks to Aldo Chiappe for granting permission to reproduce his plate published in López-Lanús (‘2015’).

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