## Splits, lumps and shuffles Thomas S. Schulenberg

This series focuses on recent taxonomic proposals—descriptions of new taxa, splits, lumps or reorganisations—that are likely to be of greatest interest to birders. This latest instalment, under new authorship, includes new genetic perspectives on relationships in grebes, screech-owls, and antpittas. In other news: Helmeted Woodpecker finds a home at last; evidence is presented for splits in violetear hummingbirds, *Elaenia* flycatchers, wrens, thrushes, and 'Darwin's' finches. Finally, nobody knows quite yet what's going in Orange-billed Sparrows in Panama, but whatever it is, it's something unexpected. Get your lists out!

## Molecular insights into *Podiceps* grebes

Although Eared Grebe Podiceps nigricollis (known as Black-necked Grebe in Europe) is widespread across the Palearctic region, its closest relatives are all Neotropical: Colombian Grebe P. andinus, Silvery Grebe P. occipitalis), Junin Grebe P. taczanowskii, and Hooded Grebe P. gallardoi. Within this group, Colombian Grebe most closely resembles Eared; indeed, originally it was described as a subspecies of Eared and was not widely recognised as a full species until the 1990s. Junin Grebe has been considered to be closely related to Silvery Grebe, but Silvery Grebe itself contains two distinctive subspecies, northern juninensis ('Northern Silvery Grebe' or 'Andean Grebe') and southern occipitalis ('Southern Silvery Grebe' or 'Patagonian Grebe'), which are themselves sometimes recognised as separate species (e.g. del Hoyo et al. 2014).

A welcome molecular perspective on these taxa is presented by Ogawa *et al.* (2015), who used a phylogenetic analysis of mitochondrial DNA (mtDNA) samples from all members of the group. One important—if unsurprising—result is that the New World subspecies of Eared Grebe, *californicus*, is more closely related to Colombian Grebe than it is to the two Old World subspecies. This could mean that the current two-species arrangement is incorrect: the 'right' answer might be either a single species... or three! Whatever, it is unlikely that species limits would be revised without further data.

Another interesting finding was that Junin Grebe and the two distinctive subspecies

of Silvery Grebe all form a single, tightly intermingled genetic complex. Intriguingly, the most divergent genetic lineage within this group is not Junin Grebe, but a sample of *juninensis* from Colombia, which perhaps represents an undescribed taxon. Taken together, these results suggest that members of the Eared Grebe complex have undertaken several very recent, rapid bouts of divergence. Of course, the end products of these divergences are very susceptible to rapid population declines: Colombian Grebe is extinct, and both Junin and Hooded Grebes are Critically Endangered.

## A genetic focus on *Megascops*

Screech owls *Megascops* are classic examples of birds that are difficult to classify by morphology alone. The plumage patterns of these nocturnal species are cryptic, and in many species there are two or more colour morphs; the end result is that variation within a species sometimes seems as great as that between different species. Vocalisations provide a better clue, at least at the species level, although we still await a truly comprehensive look at vocalisations across the genus.

Now enter Sidnei Dantas and colleagues (Dantas *et al.* 2016) who jumped right in with a genetic survey across the screech owls, based on DNA sequence data from both mitochondrial and nuclear genes. Their approach was admirably broad, lacking data from only a single recognised species (Balsas Screech Owl *Megascops seductus*), but including samples of an undescribed species ('Santa Marta Screech Owl', now well known to birders, but still lacking a <u>formal</u> scientific name).

The first interesting result is that Puerto Rican Screech Owl M. nudipes is not a Megascops at all, but is more closely related to Flammulated Owl Psiloscops flammeolus. Next up, the screech owls proper fall into three main groups: a widespread Neotropical group including Tropical M. choliba, Koepcke's M. koepckeae, White-throated M. albogularis, Bare-shanked M. clarkii, and Whiskered M. trichopsis Screech Owls; an Andean group, composed of Cinnamon M. petersoni, Cloud-forest M. marshalli, Montane Forest M. hoyi, Rufescent M. ingens, and Colombian M. columbianus Screech Owls; and a group that extends from Canada south to the Amazon, including Eastern M. asio, Western M. kennicottii, Pacific M. cooperi, Bearded M. barbarus, Longtufted M. sanctaecatarinae, Peruvian M. roboratus, Tawny-bellied M. watsonii, 'Santa Marta', Blackcapped *M. atricapilla*, Middle American *M.* guatemalae, and Vermiculated M. vermiculatus Screech Owls.

As expected, Dantas and colleagues also present intriguing insights into species-level relationships among screech owls. Variation in song in Tawny-bellied Screech Owl long has intrigued birders, leading a few authorities to recognise two species -(e.g., König & Weick 2008). Everything now is up for grabs, as this paper reports that some populations of Tawny-bellied are more closely related to Black-capped Screech Owl than they are to other populations of Tawnybellied. This all sounds rather messy, but Dantas *et al.* promise us that a more detailed investigation of species relationships of the Tawny-bellied/Blackcapped complex will be forthcoming.

The Middle American/Vermiculated group also presents many taxonomic headaches for the birder, with anywhere from one to five species recognised by different authors. Dantas *et al.* identify four genetic lineages, which they group here into two species: *M. guatemalae*, represented in their study by samples from Mexico; and *M. vermiculatus*, represented by samples from central Panama (*vermiculatus*), Venezuela and Guyana (*roraimae*), and Peru (*napensis*). The type locality of *vermiculatus*, however, is 'Costa Rica'.

All bets are off on the applicability of a name that is tied to such a vague type-locality, but it is worth noting that '*vermiculatus*' from central Panama have a distinctive, very short song, not heard in Costa Rica (or, to my knowledge, anywhere else across the range of the *guatemalae*/ *vermiculatus* complex). These central Panama birds sometimes are recognised as a separate species, 'Choco Screech Owl *Megascops centralis*'. Dantas *et al.* do not attempt to combine vocal and genetic data, but their paper strongly suggests that such a project would lend strong support to species status for *centralis* (or whatever the appropriate epithet may prove to be), separate from *roraimae* and *napensis*.

Finally, Dantas and colleagues report surprisingly strong genetic divergences between their samples of Rufescent Screech Owl from Ecuador and Peru (which currently are considered to be the same subspecies), and between samples of Whiskered Screech Owl from central Mexico and El Salvador. Both cases, they conclude, suggest that "that multiple species-level taxa are involved in each of these groups". Sounds as if yet more work is called for: a familiar tale.

## Nibbling away at hummingbird nomenclature

Over the past several years, Jimmy McGuire and colleagues have published a series of papers on the phylogeny of hummingbirds, based on DNA sequence data. The most recent entry in this series (McGuire et al. 2014) had very broad taxonomic sampling. From the beginning of their efforts, it has been clear that many hummingbird genera are paraphyletic, and that a broad suite of nomenclatural changes are on their way. The first such effort (Remsen et al. 2015) only addresses a small part of this problem, namely the phylogeny and nomenclature within the mango group (Polytminae). Unsurprisingly, the two species of caribs Eulampis are embedded within mangoes Anthracothorax, and so Remsen and colleagues recommend merging Eulampis into Anthracothorax. They also make the case for recognising as separate species the Central American and the South American populations of Green Violetear Colibri thalassinus, based both on genetic and plumage differences. Another armchair tick for many is in the offing!

## A new genus for Helmeted Woodpecker

Helmeted Woodpecker '*Dryocopus' galeatus* is a large, spectacular, and enigmatic woodpecker of the southern Atlantic Forest region. Short (1982) concluded that Helmeted was "beautifully intermediate between *Celeus* and *Dryocopus*". Short classified Helmeted in *Dryocopus*, as has been the norm in recent decades, based on similarities in plumage between Helmeted and Lineated (*D. lineatus*) Woodpeckers; but he noted that in terms of structure, Helmeted was more similar to species of *Celeus*. At that time, Helmeted

### >> SPLITS, LUMPS AND SHUFFLES







**This page:** Research reveals that Junin Grebe and the two distinctive subspecies of Silvery Grebe all form a single, tightly intermingled genetic complex.

**1** Junin Grebe *Podiceps taczanowskii*, Lake Junín, Junín, Peru, July 2013 (Pete Morris/Birdquest)

**2** ('Northern') Silvery Grebe *Podiceps occipitalis juninensis*, Lagunilla, Jujuy, Argentina, July 2009 (James Lowen; jameslowen.com)

**3** ('Southern') Silvery Grebe *Podiceps occipitalis occipitalis*, Lago Correntoso, Neuquen, Argentina, October 2009 (James Lowen; jameslowen.com)

Facing page: There can be little surprise that a genetic analysis of screech owls *Megascops* raises as many questions as it suggests answers.

**4** Rufescent Screech Owl Megascops ingens ingens, Amazonia Lodge, Manu Biosphere Reserve, Madre de Dios, Peru, October 2008 (Joel Rosenthal; www.flickr. com/joelnrosenthal)

5 Vermiculated (Choco) Screech Owl Megascops (guatemale) centralis, Pipeline Road, Colón, Panama, March 2015 (John van Dort; tinyurl.com/vanDortJohn)

6 Vermiculated Screech Owl Megascops guatemale napensis, Wildsumaco Lodge, Sumaco, Napo, Ecuador, June 2012 (Nick Athanas; www.antpitta.com)

Woodpecker was so poorly known that Short worried that it might already be extinct; it remains a rare bird. It is also now better known, and in particular its vocalisations, unknown to Short, also prove to be similar to those of *Celeus*.

Most recently, no fewer than three separate genetic surveys conclusively place Helmeted Woodpecker in *Celeus*. All three of these studies are based on an earlier genetic survey of *Celeus* by Benz & Robbins (2011); to this, Benz *et al.* (2015) and Dufort (2016) used genetic material from separate old specimens of Helmeted Woodpecker, while Lammertink *et al.* (2015) acquired fresh tissue of this species.

Although all three publications clearly place *galeatus* in *Celeus*, not in *Dryocopus*, there is less consensus beyond that point. Benz and colleagues identify *galeatus* as the sister species of all remaining *Celeus* other than Cinnamon Woodpecker *Celeus loricatus* and Ringed Woodpecker *C. torquatus*. Meanwhile, Lammertink *et al.* consider *galeatus* to be part of a clade that also includes Kaempfer's Woodpecker *C. obrieni*, Rufous-headed Woodpecker *C. spectabilis* and Cream-coloured Woodpecker *C. flavus*. Finally, Dufort simply considers the position of *galeatus* within *Celeus* to be unresolved.

Both Benz *et al.* and Lammertink *et al.* propose that the plumage similarity between Helmeted and Lineated Woodpeckers is no accident; instead, they argue (more extensively in Benz *et al.*) that *galeatus* is a visual mimic of two larger, syntopic species, Lineated Woodpecker and Robust Woodpecker *Campephilus robustus.* The type of mimicry invoked



### >> SPLITS, LUMPS AND SHUFFLES

for Helmeted Woodpecker, interspecific social dominance mimicry, involves a smaller, subordinate species (such as Helmeted Woodpecker) that gains an advantage in minimising competition by mimicking the plumage of larger-bodied syntopic species; this type of mimicry may be relatively common in birds (Prum 2014).

# The Bay-backed Antpitta complex: who's in, who's out

Antpittas are some of most sought-after species of Andean birds (even as they are becoming easier to see, thanks to the proliferation of feeding stations in Colombia and Ecuador). Although it is rather facile to characterise almost all antpittas as little known, this description applies in particular to a series of species that collectively range from Colombia south to Peru, the Bay-backed Antpitta complex. Traditionally, this group has included Yellow-breasted *Grallaria flavotincta*, Whitebellied *G. hypoleuca*, Rusty-tinged *G. przewalskii*, Red-and-white *G. erythroleuca*, and Bay *G. capitalis* Antpittas.

One unresolved taxonomic question regarding these antpittas is how many species should be recognised in this group, with some authors (e.g. Meyer de Schauensee 1966) suggesting that all of these could be considered conspecific. Another question is whether there might be additional species that belong to this assemblage, and, if so, which.

Both questions were investigated by Winger et al. (2015), who prepared a phylogeny using traditional sequencing of mtDNA genes, and also genotyping by sequencing to assess variation across a much larger spectrum of the genome. One of the most unexpected results is that Yellowbreasted Antpitta, which has been considered by some to be merely a subspecies of White-bellied Antpitta, is not a member of this complex at all! Instead, Winger and colleagues identify Yellowbreasted as the sister species to Brown-banded Antpitta G. milleri. Also not a member of this complex is White-throated Antpitta G. albigula. On the other hand, the Bolivian endemic Rufousfaced Antpitta G. erythrotis is the sister to Redand-white Antpitta, and so hereby joins the Whitebellied Antpitta complex.

Relatively shallow genetic breaks are reported within White-bellied Antpitta across the Zamora Valley in Ecuador, and within Red-and-white Antpitta between the Cordillera Vilcabamba and points farther south in Peru. More intriguing is a somewhat larger break within Bay Antpitta across the Chanchamayo Valley in Peru, between 'northern *capitalis*' (i.e., the known populations of Bay Antpitta) and a recently discovered 'southern *capitalis*' on the west side of the Apurímac Valley, which differs from the northern birds both in plumage and in voice. The mysterious 'southern *capitalis*' does not yet have a formal name, but we can look forward to new information on this ... subspecies? species? ... to be published elsewhere.

## **Splitting Lesser Elaenia**

Lesser Elaenia *Elaenia chiriquensis* is one of the most widely occurring members of the genus, with a distribution that extends from Costa Rica south to northern Argentina and southern Brazil. Three subspecies are recognised: nominate *chiriquensis* of Costa Rica and Panama; *albivertex*, which is widespread in South America east of the Andes; and *brachyptera*, of the Chocó region of western Colombia and Ecuador.

The late Paul Coopmans discovered that the vocalisations of brachyptera were different from those of other populations. Although Coopmans was not able to publish a thorough analysis of vocalisations across Lesser Elaenia, Ridgely & Greenfield (2001) suggested that brachyptera might merit recognition as a species. That supposition has been confirmed by Rheindt et al. (2015), who examined both vocalisations and genetic data (DNA sequences, from both mitochondrial and nuclear genes) across all three subspecies. Nominate chiriquensis and albivertex transpire to be very similar, both genetically and vocally, but brachyptera differs significantly in both character sets. Rheindt and colleagues recommend that brachyptera be recognised as a separate species, 'Coopmans's Elaenia'. A final twist to the story is confirmation that 'Coopmans's Elaenia' is not a Chocó endemic, but also occurs on the east slope of the Andes of Ecuador; field observers should be on the lookout for it as well in adjacent regions of Colombia and Peru.

## Plain Wren: more than meets the eye?

Plain Wren *Cantorchilus modestus* is widespread in Central America, occurring from southern Mexico south to central Panama. There is no clear consensus on how many subspecies to recognise, with anywhere from three to five being accepted by different authorities.

Subspecies *zeledoni* of the Caribbean slope of Costa Rica and western Panama long has been recognised as the most divergent, and has been accepted by some authors as a separate species (Brewer 2001). The two other principal subspecies are *elutus* (Panama) and *modestus* (Mexico to southwestern Costa Rica; subspecies *roberti* and *vanrossemi* are recognised by some authors for populations in Caribbean Honduras and in El Salvador, respectively).

Variation in morphometrics, plumage colour, and genetics (mtDNA) across the range of the species were investigated by Saucier *et al.* (2015). One unexpected result of this study is that an isolated population in Belize differs in both bill size and in plumage from adjacent Plain Wrens in Guatemala, and presumably represents an undescribed subspecies. The proposed subspecies *roberti* and *vanrossemi*, however, are best merged into *modestus*.

The genetic surveys yielded some surprises, including the detection of a very low level of gene flow between zeledoni and modestus. Saucier and colleagues speculate that this introgression may be a recent development, as increased deforestation allows for limited contact between two populations that previously were allopatric. Even more surprising is that the populations of south-west Costa Rica, previously assumed to be of the northern *modestus*, are identical to *elutus* of Panama. These authors suggest that the range of elutus be expanded northward into Costa Rica. Saucier et al. were not able to document contact between *modestus* and *elutus*, but they assume that these two taxa must meet somewhere, as suitable habitat seems to be continuous throughout the region; even so, they could find no evidence of gene flow between these two.

Assessing these genetic data, and briefly reviewing earlier research on the duetting patterns of these wrens by Mann *et al.* (2003), Saucier *et al.* recommend recognising each of *modestus*, *elutus*, and *zeledoni* as a full species. Subspecies *zeledoni* already has a well-established English name ('Canebrake Wren'); there is no widely used English name for *elutus*, but I suggest that Panama Wren (Hellmyar 1934) might be appropriate: despite the documentation of the taxon's presence in Costa Rica, *elutus* still is primarily a Panamanian species.

### **Support for Grayson's Robin**

Rufous-backed Robin *Turdus rufopalliatus* is a common and familiar thrush, endemic to western Mexico (and rare but regular as a non-breeding visitor to the south-western United States). A duller version of this robin, *graysoni*, breeds on the Tres Marías Islands, off the Pacific Coast of Mexico. Currently *graysoni* is classified as only a subspecies

of Rufous-backed Robin, but it was recognised as a species by early authors (*e.g.*, Ridgway 1907) and even a few modern sources (Phillips 1981, 1991). Montaño-Rendón *et al.* (2015) reinvestigated the taxonomic status of *graysoni*, with genetic data (phylogenetic analysis of mtDNA sequences). The authors determined that *graysoni* and the mainland populations are reciprocally monophyletic, with no gene flow between the two.

An intriguing part of this story is the presence of *graysoni* in coastal Nayarit, on the mainland opposite to the Tres Marías Islands. The presence of *graysoni* on the mainland has been known for a long time (Phillips 1981), but it still is not clear whether it has a small breeding population on the mainland, or if it is only a non-breeding migrant here. In any event, no evidence has yet been found of gene flow between island and mainland populations. In concert with the duller plumage and different morphometrics of *graysoni*, and the absence of any signs of introgression between them, Montaño-Rendón *et al.* (2015) recommend recognising *graysoni* as a species.

### **Darwin's finches revisited**

One might think that 'Darwin's finches' had been studied to death, in view of the monumental, decades-long investigations by Peter and Rosemary Grant into the fine-scale dynamics of evolution in the birds (e.g. Grant & Grant 2008, 2014). But the development of a larger perspective—the phylogenetic relationships across the Darwin's finch radiation—has proved to be a greater challenge; indeed, so great were the frustrations of early genetic surveys of the group that some authors have argued that only a single species (!) of *Geospiza* should be recognised (e.g. McKay & Zink 2014).

Efforts to unravel this Gordian knot have continued, and—finally—are shedding new light on the problem, with some surprising results. The most detailed portrait of Darwin's finches comes from Lamichhaney *et al.* (2015), who prepared a phylogeny of this radiation using whole-genome re-sequencing. A paper by Farrington *et al.* (2014), using more traditional sequencing of several mitochondrial and nuclear genes, produced a phylogeny that is less detailed yet fully consistent with the work of Lamichhaney and colleagues.

The most striking discovery is that Sharpbeaked Ground Finch *Geospiza difficilis* includes three distinct lineages that are scattered across the Darwin's finch radiation: violà, Sharp-beaked Ground Finch is transformed from one into three species! One of these lineages is represented



There are genetic and plumage grounds for splitting the Central American and South American populations of Green Violetear *Colibri thalassinus*.

7 Green Violetear Colibri thalassinus thalassinus, Parque Nacional Cerro Verde, Sonsonate, El Salvador, November 2012 (Alex Navarro; tinyurl.com/AlexNavarro)

8 Green Violetear *Colibri thalassinus cyanotus*, El Dorado Reserve, Sierra Nevada de Santa Marta, Magdalena, Colombia, January 2015 (Dušan Brinkhuizen; www.sapayoa.com)

9 Green Violetear *Colibri thalassinus crissalis*, Huembo, Pomacochas, Peru, April 2015 (Peter Hawrylyshyn; www.flickr.com/pahyyz)





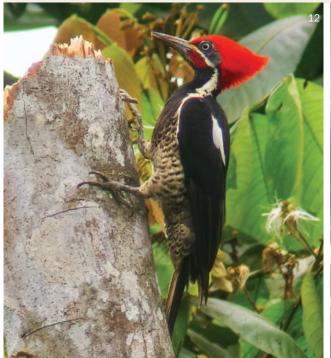
Three recent assessments concur that the correct genus of Helmeted Woodpecker is Celeus rather than Dryocopus.

**10** Helmeted Woodpecker *Celeus galeatus*, San Pedro, Misiones, Argentina, August 2013 (Martjan Lammertink; www.pbase.com/picidpics). Colour-banded male fitted with antennae to track movements.

**11** Male Helmeted Woodpecker *Celeus galeatus*, San Pedro, Misiones, Argentina, October 2013 (Martjan Lammertink; www.pbase.com/picidpics).

**12** Lineated Woodpecker *Dryocopus lineatus fuscipennis*, Rio Silanche Bird Sanctuary, Pichincha, Ecuador (Nick Athanas; www.antpitta.com). This is one of the two species that Helmeted Woodpecker *Celeus galeatus* is thought to mimic.

**13** Pale-crested Woodpecker *Celeus lugubris*, Santa Olga, Formosa, Argentina, July 2008 (James Lowen; jameslowen.com). A closer relation to Helmeted Woodpecker *C. galeatus* than Lineated Woodpecker *Dryocopus lineatus*, it transpires.





### >> SPLITS, LUMPS AND SHUFFLES

by subspecies *septentrionalis*, which occurs on two small islands (Darwin and Wolf) in the northwestern part of the Galapagos Archipelago.

A further wrinkle is that the two other lineages do not map cleanly onto the existing subspecies framework in this ground finch. One lineage is entirely restricted to another small island, Genovesa. The population on Genovesa has been included in nominate *difficilis*, but the type specimen of *difficilis* is from a different island (Pinta). Fortunately a name, *acutirostris*, is available for the birds of Genovesa, and so that would become our second newly recognised species. The third lineage includes nominate *difficilis* from Pinta, as well as the populations of two larger islands (Fernandina and Santiago) that have been called *debilirostris*.

The story is not over, however. Lamichhaney et al. also found that Large Cactus Finch Geospiza conirostris contains two unrelated lineages. Therefore, both nominate conirostris of Española and propinqua of Genovesa should be accorded species rank. A third subspecies, darwini, was not included in this study; and indeed, there seems to be some confusion as to whether or not darwini is a valid taxon at all: apparently no form of Large Cactus Finch is resident on the islands (Darwin and Wolf) from which darwini is reported to occur (Wiedenfeld 2006). Finally, both Lamichhaney et al. and Farrington et al. find evidence that tree finches Camarhynchus are embedded within ground finches Geospiza.

### Cryptic speciation in Orangebilled Sparrow? Or ... 'despeciation'?

Orange-billed Sparrow Arremon aurantiirostris is a common, widespread sparrow that is distributed from southern Mexico south to northern Peru. No fewer than eight subspecies have been described, three of which occur in Panama: *rufidorsalis* in western Panama (Bocas del Toro); widespread nominate *aurantiirostris*; and *strictocollaris* in eastern Panama (San Blas and the Darién).

López *et al.* (in press) examined the complete mitochondrial genome of two specimens of Orange-billed Sparrow from central Panama, discovering that these showed a whopping 6.3% average sequence divergence. A further investigation, using data from a single mitochondrial gene but from a larger sample of specimens, documented a divergence between samples from western Panama (Bocas del Toro) and eastern Panama (San Blas and Darién); samples from central Panama were represented in both the western and eastern lineages.

López and colleagues propose two explanations for these unexpected results. One is that the two Orange-billed Sparrow groups "represent cryptic co-occurring lineages that do not interbreed", i.e. there are two species that meet and narrowly overlap in central Panama. This of course is the explanation that would set listers' hearts ablaze (or, alternatively, frustrate those who have only seen one of the taxa). The second explanation is that the two lineages are "reproductively compatible despite mitochondrial divergences that often indicate partial or complete reproductive isolation in birds". That outcome would be a big wet blanket for list-focused birders, but presents an interesting case study for evolutionary biologists. Something similar was reported by Block et al. (2015) in Spectacled Tetraka Xanthomixis zosterops of Madagascar. In the Tetraka, Block and colleagues found no fewer than four deeply divergent lineages based on mitochondrial DNA, up to three of which were sympatric. A phylogeny of the lice associated with Tetrakas also indicated deep divergences, matching the mitochondrial lineages. Nonetheless other genetic evidence indicated that these Tetraka populations were freely interbreeding, or, as Block et al. described, "despeciating". In other words, populations that were on the path to divergence now have reversed course, and are now coalescing. It will be very interesting to see how this story on Orange-billed Sparrow in Panama plays out!

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Phylogenetic analysis sheds light on relationships between members of the Bay-backed Antpitta complex.

14 Rufous-faced Antpitta Grallaria erythrotis, Manuel Maria Caballero, Santa Cruz, Bolivia, November 2013 (Paul Jones; www.flickr.com/paulbjones)

**15** White-bellied Antpitta Grallaria hypoleuca, Cabañas de San Isidro, Cosanga, Ecuador, June 2011 (Nick Athanas; www.antpitta.com)

**16** Yellow-breasted Antpitta *Grallaria flavotincta*, Refugio Paz de Las Aves, Pichincha, Ecuador, December 2010 (Nick Athanas; www.antpitta.com)





**Above:** Following recent research, 'Darwin's finches' prove even more complicated than even the Grants revealed. Sharp-beaked Ground Finch *Geospiza difficilis*, for example, may comprise three species.

**17** Sharp-beaked Ground Finch of the subspecies *debilirostris*, Volcano Sierra Negra, Isla Isabela, Galápagos, Ecuador, September 2013 (Oleg Chernyshov; www.flickr.com/olegchernyshov)

**18** Sharp-beaked Ground Finch of the subspecies *difficilis*, Isla Genovesa, Galápagos, Ecuador, November 2012 (Roger Ahlman; www.pbase.com/ ahlman)

**19** Plain Wren *Cantorchilus modestus*, Posada Rural Cabañas Las Orquídeas, Zapotal, Miramar, Puntarenas, Costa Rica, May 2014... but which taxon? (Jorge Eduardo Chinchilla Arroyo; tinyurl. com/JorgeChinchilla)

**20** Orange-billed Sparrow Arremon aurantiirostris, Canopy Lodge, El Valle de Antón, Coclé, Panama, May 2015 (Beth Hamel; tinyurl.com/hawkperson). Is this sparrow speciating or despeciating?





