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Integrative taxonomy reveals hidden diversity in the *Catharus fuscater* (Passeriformes: Turdidae) complex in Central and South America

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ABSTRACT

We assembled datasets of genetic (genomic ultraconserved elements [UCEs], mtDNA) and phenotypic (morphology, voice) characters to address species limits and taxonomy in the slaty-backed nightingale-thrush *Catharus fuscater* (Passeriformes: Turdidae), a polytypic complex of songbirds with a broad montane distribution in Central and South America. We identified 10 allopatric populations that have been evolving independently for multiple glacial cycles. Genetic structure is broadly correlated with divergence in phenotypic characters, including plumage colour, iris colour, maxilla (bill) colour, and the acoustic structure of vocalizations (calls and songs). We propose an integrative taxonomic revision that recognizes seven species in the complex, including a newly described species from eastern Panama, and four subspecies, of which two are newly described.

Keywords: phylogenetics; Neotropics; nightingale-thrush; systematics

INTRODUCTION

Genetic data have repeatedly confirmed the primary role of geographic barriers in the speciation process (e.g. Winger and Bates 2015, Hazzi *et al.* 2018, McCullough *et al.* 2022). However, there is little consensus about where on the 'speciation continuum' to draw the line, between species and subspecies, when dealing with closely related taxa distributed on opposite sides of potential gene-flow barriers (Mayr *et al.* 1953, Cracraft 1987, Remsen 2005, Zink 2006, de Quieroz 2007, Gill 2014). In the Neotropical highlands, hundreds of polytypic bird species have populations distributed across multiple mountain chains, which are isolated by deep river valleys, and adjacent populations may have divergent phenotypes and/or may not be phylogenetic sisters (Remsen 1984). Describing and classifying this extraordinary diversity is necessary for conservation efforts, and to inform studies of the evolutionary origins and maintenance of avian biodiversity. However, the process of integrative taxonomy is not straightforward because of ideological conflicts related to species concepts and their application, and the need for broad geographic sampling of multiple traits (e.g. Remsen 2005, Zink 2006, Petersen and Navarro-Sigüenza 2006, Winker *et al.* 2007, Cicero *et al.* 2021).

The biological species concept (BSC), which defines species by their degree of reproductive (genetic) isolation, is non-operational in cases of allopatry without invoking additional assumptions, because reproductive isolation is not directly testable (Dobzhansky 1937, Huxley 1940, Mayr 1940, 1942, Mayr *et al.* 1953, Zink 1996, Bock 2004, Remsen 2005, Winker *et al.* 2007). To overcome this challenge, the architects of the BSC assumed a priori that populations with subjectively similar phenotypes would interbreed if given the opportunity and, therefore, consolidated them as polytypic species (Mayr 1940: 256). Subsequently, indirect tests of reproductive isolation were proposed to inform speculations about the probability of interbreeding in hypothetical contact scenarios (e.g. Remsen 2005, Freeman and Montgomery 2017; see below), although these approaches have not been universally adopted.

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For example, Gill (2014) attempted to circumvent the allopatry problem by reversing Mayr's (1940) null hypothesis, by contending that reproductive isolation should be assumed a priori, if allopatric populations are phenotypically divergent (i.e. 'lumpers' should bear the burden of proof). Other scientists abandoned the BSC altogether, by formulating alternative species concepts that focused on criteria of phenotypic and/or genetic diagnosability (e.g. phylogenetic species concept [PSC], Cracraft 1987; evolutionary species concept [ESC], Wiley 1978), or attempting to unify species concepts under more inclusive criteria (e.g. unified species concept [USC]; de Quieroz 2005, 2007).

Playback experiments are one way to rescue the BSC in cases of allopatry, if one assumes that reproductive isolation can be inferred from the response behaviour of the experimental subjects. An audio recording of vocalizations from one population is broadcast on a speaker to members of a second (allopatric) population, and researchers then record whether (and how much) the test subject vocalizes, and whether (and how close) it approaches the speaker. Playback experiments have been described as a simulation of secondary contact, by which researchers attempt to 'ask the birds themselves' if they perceive the stimuli to be conspecific (Freeman and Montgomery 2017). Strong 'territorial' responses to playback purportedly indicate that the populations are conspecific, and weak responses are interpreted as evidence of reproductive isolation. However, this method assumes that the birds are territorial in the traditional sense (i.e. respond aggressively to conspecifics that encroach on their 'defended' space), which may not be true for species with non-monogamous social and genetic mating systems, where intraspecific territorial behaviour is facultative and/or mediated by kinship or social rank (e.g. *Catharus* thrushes; Goetz *et al.* 2003, Heckscher 2007, Halley 2014, Greeney *et al.* 2015, Halley *et al.* 2016). In such cases, without extended monitoring of colour-banded subjects (including both the singers and assessors), the social context needed to properly interpret the variable responses of playback experiments is usually lacking. Even if such data were available, as Freeman *et al.* (2022) acknowledged, there would still be uncertainty about how to interpret behavioural responses because birds may approach the speaker simply out of curiosity (e.g. Hausberger *et al.* 2021).

Another popular but controversial approach to species delimitation in cases of allopatry is to apply an arbitrary threshold ('yardstick') to trigger species rank, which may be based on the level of genetic and/or phenotypic divergence in sympatric congeners (e.g. Helbig *et al.* 2002, Tobias *et al.* 2010, Tobias *et al.* 2021; but see: Isler *et al.* 1998). In geographically widespread groups, this approach requires one to assume that evolution proceeds at a similar rate and/or direction in sympatric and allopatric populations, although they may have divergent life-histories and behaviour and occur in different ecological realms (e.g. Martin 2002, Tenorio and Londoño 2019). Some mitochondrial genes exhibit remarkably clocklike rates of evolution, such that sequence divergence is useful as a proxy for age of divergence (Zink and Barrowclough 2008), but this does not necessarily correlate with the timing of speciation, which is affected by many dynamic, largely time-independent factors, including the strength of stochastic processes like genetic drift, and different modes of natural and social selection (Winker *et al.* 2007, Price 2008).

As species concepts and delimitation methods have matured and diversified, a surprising degree of genetic structure has been uncovered in many montane Neotropical polytypic species (i.e. classified as such under the assumption that allopatric populations would interbreed if the opportunity arose), despite hypothesized opportunities for gene flow at modern and historical range boundaries (e.g. *Chlorospingus* [*flavopectus*] bush tanagers, Weir *et al.* 2008; *Henicorhina* [*leucophrys*] wood wrens, Cadena *et al.* 2019; *Scytalopus* [*magellanicus*] tapaculos, Cadena *et al.* 2020; *Grallaria* [*rufula*] antpittas, Chesser *et al.* 2020). Recent specimen-based studies have also advanced knowledge of geographic variation in phenotypic characters, clarifying the morphological distinctiveness of poorly known taxa (e.g. Halley *et al.* 2017, Halley 2022).

Here, we integrate multiple lines of evidence to review and revise the taxonomy of the enigmatic *Catharus fuscater* (Lafresnaye 1845) complex, a clade of oscine birds (Passeriformes: Turdidae) with a widespread distribution in Central and South America (Clement 2000, Collar 2005, Halley 2020). The complex is traditionally classified as a polytypic species with seven allopatric subspecies, delimited by plumage colour but lacking a quantitative study (e.g. Hellmayr 1934, Clement 2000, Halley 2020), under the implicit assumption that reproductive isolation is incomplete (see above). Taxonomic work on this group has been dormant since Wetmore (1955). However, new and expanded lines of evidence (genetics, morphology, and voice) suggest that allopatric *C. fuscater* populations are more divergent than previously appreciated and species-level diversity may be underestimated (Beltrán and Kattan 2001, Cuervo 2013, Halley *et al.* 2017, Halley 2021). Thus, our objective was to characterize patterns of geographic variation in genetic and phenotypic characters, to reconstruct an evolutionary hypothesis of the complex, and to inform a taxonomic revision.

MATERIAL AND METHODS

Study system

The original description of *Myioturdus fuscater* Lafresnaye 1845 (=*C. fuscater*) by the French aristocrat Baron Nöel Frédéric Armand André de Lafresnaye (1783–1861) was based on a trade skin collected near Bogotá, Colombia. Subsequent research resulted in the description of seven more taxa, based on differences in plumage colour, including some taxa that were described as new species (e.g. Sclater and Salvin 1876, Lawrence '1887'), then demoted to subspecies rank (i.e. subsumed into the polytypic species, *C. fuscater*). In the chronological order of their descriptions, they are: (i) *C. mentalis* Sclater and Salvin 1876 (=*C. f. mentalis*) from the southern Andean highlands of Bolivia and southern Peru; (ii) *C. berlepschi* Lawrence '1887' (=*C. f. fuscater*, *fide* Chapman 1924) from the western slope of the Andes in Ecuador (Ridgway '1887'); (iii) *C. f. hellmayri* Berlepsch 1902 from western Panama and Costa Rica; (iv) *C. f. sanctaemartae* Ridgway 1904 from the Sierra Nevada de Santa Marta in northern Colombia; (v) *C. f. mirabilis* Nelson 1912 from Cerro Pirre in the Darién highlands of eastern Panama; (vi) *C. f. caniceps* Chapman 1924 from the western slope of the northern Peruvian Andes, west of the Río Marañón; and (vii) *C. f. opertaneus* Wetmore 1955 from Antioquia, Colombia.

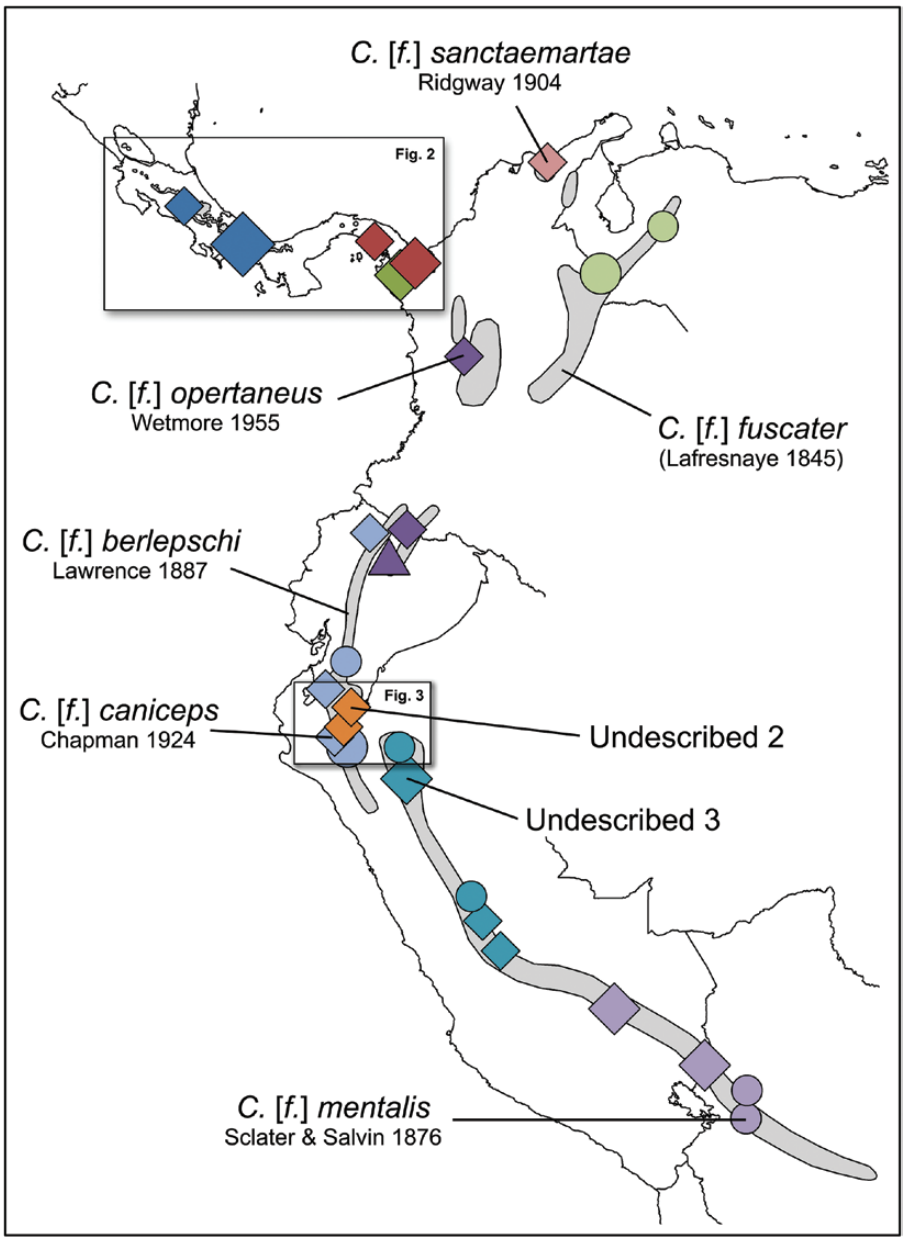

Figure 1. Geographic distribution of the *C.* [*fuscater*] complex in Central and South America. Lines point to type localities. Diamonds denote sampling locations for UCE and *ND2* data. Triangles denote sampling locations for UCE data only. Circles denote sampling locations for *ND2* data only. Shape size is correlated with the number of samples (1–3). The colour-blind friendly palette used here is standardized across figures.

Furthermore, some geographically isolated populations in the *C. fuscater* complex are of uncertain taxonomic affinity. The population on the eastern slope of the Central Andes of Peru (Taczanowski 1884) has been classified as *C. f. caniceps* since the mid-20th century (Bond 1956), but the type series of *C. f. caniceps* was collected in Palambla, Piura, west of the Río Marañón (see: Chapman 1924). Populations in eastern Ecuador have traditionally been classified as *C. f. fuscater*, but are allopatric with the type population, which inhabits the Cordillera Oriental, near Bogotá, Colombia (Lafresnaye 1845). In eastern Panama, specimens from the Serranía del Darién (e.g. Cerro Tacarcuna, Cerro Malí) have been variably classified as *C. f. mirabilis* (Chapman 1924) and *C. f. fuscater* (Hellmayr 1934, Wetmore *et al.* 1984). The affinities of several other isolated populations in eastern Panama are also unclear, including those on Cerro Jefe, Cerro Azul, the Serranía de Majé, and the Serranía de Jungurudó (Chapman 1924, Hellmayr 1934, Wetmore *et al.* 1984, Angehr *et al.* 2004, Renjifo *et al.* 2017).

Molecular data

Taxon sampling

We estimated a nuclear ultraconserved element (UCE) phylogeny with 22 ingroup samples and a mitochondrial (*ND2*) tree with 35 ingroup samples from across the range of the complex (Figs 1–3; Table 1). Both phylogenetic reconstructions used the same two outgroup species (one sample each of *C. dryas* and *C. maculatus*; see: Halley *et al.* 2017), which form the sister-group of the *C. fuscater* complex (Halley 2021). Hereafter, for

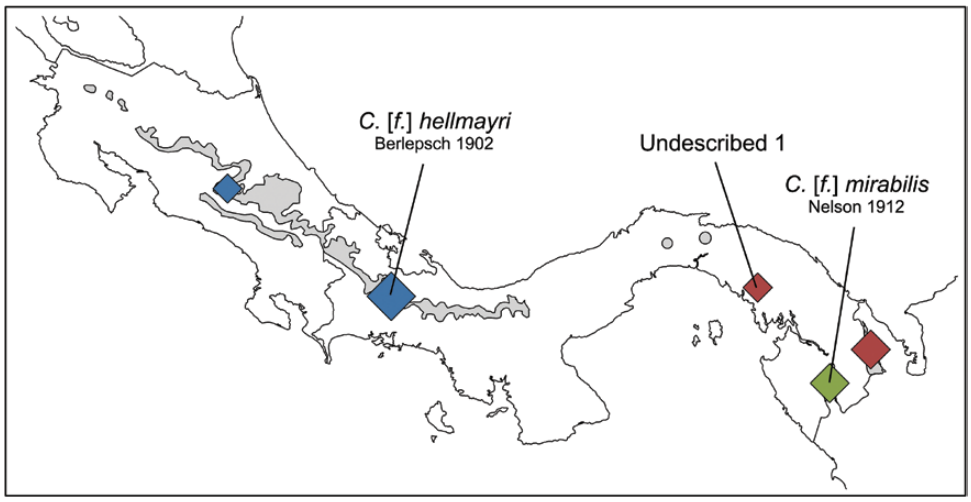

Figure 2. Geographic distribution of the *C.* [*fuscater*] complex in Central America and the Darién region. Lines point to the type localities of each taxon. Diamonds denote sampling locations for UCE and *ND2* data. Shape size is correlated with the number of samples (1–3). Color scheme is standardized across all colour figures.

Figure 3. Genetic sampling locations in southern Ecuador and northern Peru. Satellite imagery created in Google Earth Pro. The Ecuador-Peru border is shown with a thin yellow line in the upper left portion of the map. Diamonds denote sampling locations for UCE and *ND2* data. Circles denote sampling locations for *ND2* data only. Shape size is correlated with the number of samples (1–3). Abra de Porculla (Porculla Pass) is a mountain pass in northern Peru, within the elevational range of the *C.* [*fuscater*] complex, which permits dispersal between the western and eastern slopes. The Río Huancabamba and Río Chinchipe both flow into the Río Marañón, which flows east into the Amazon Basin (denoted by arrows).

convenience, when referring to samples used in this study we refer to the voucher numbers of their respective study skins when possible. If no voucher was available, we used the tissue number or field preparation number, in that order of availability (Table 1).

DNA extraction

We extracted whole-genomic DNA from vouchered frozen tissue samples with DNeasy tissue extraction kits and followed the manufacturer's protocol (Qiagen Inc., Chatsworth, CA, USA). For study skin toepads, we collected samples with a

Table 1. List of specimens from which nuclear (UCE) and mitochondrial (*ND2*) data were analysed for this paper, with their respective collection localities, study skin voucher numbers, and tissue numbers (if applicable)

Taxon	Locality	Voucher #	Tissue #	UCE	*ND2*
C. [f.] hellmayri	Chiriquí, Panama	LSU 163711	B26492	X	X
C. [f.] hellmayri	Chiriquí, Panama	UWBM 112336			X
C. [f.] hellmayri	Chiriquí, Panama	UWBM 112340		X	X
C. [f.] hellmayri	Cartago, Costa Rica	N/A	LSU B72031	X	X
Undescribed 1	Darién, Panama	AMNH 811713	toepad	X	X
Undescribed 1	Darién, Panama	AMNH 811714	toepad	X	X
Undescribed 1	Panamá, Panama	UWBM 112249		X	X
C. [f.] mirabilis	Darién, Panama	N/A	LSU B1367	X	X
C. [f.] mirabilis	Darién, Panama	LSU 104645	LSU B1368	X	X
C. [f.] sanctaemartae	Magdalena, Colombia	ANSP 63298	toepad		X
C. [f.] fuscater	Táchira, Venezuela	N/A	kcc113		X
C. [f.] fuscater	Táchira, Venezuela	N/A	kcc89		X
C. [f.] fuscater	Trujillo, Venezuela	N/A	jm125		X
C. [f.] opertaneus	Sucumbios, Ecuador	ZMUC 119587		X	X
C. [f.] opertaneus	Antioquia, Colombia	ZMUC 134855		X	X
C. [f.] opertaneus	Napo, Ecuador	ZMUC 120282		X	
Undescribed 2	Cajamarca, Peru	LSU 97809	LSU B245	X	X
Undescribed 2	Zamora-Chinchipe, Ecuador	ZMUC 128354		X	X
C. [f.] berlepschi	Azuay, Ecuador	ZMUC 128360			X
C. [f.] berlepschi	Loja, Ecuador	ZMUC 118356		X	X
C. [f.] berlepschi	Imbabura, Ecuador	ZMUC 119570		X	X
C. [f.] caniceps	Piura, Peru	AMNH 175531	toepad	X	X
C. [f.] caniceps	Cajamarca, Peru	LSU 170103	B32516		X
C. [f.] caniceps	Cajamarca, Peru	LSU 170104	B32628		X
Undescribed 3	Junín, Peru	KU 114011		X	X
Undescribed 3	San Martín, Peru	LSU 174203	LSU B44436		X
Undescribed 3	Pasco, Peru	LSU 129001	LSU B8001		X
Undescribed 3	Pasco, Peru	LSU 106495	LSU B1656	X	X
Undescribed 3	Amazonas, Peru	FMNH 474413			X
Undescribed 3	Amazonas, Peru	FMNH 474414		X	X
C. [f.] mentalis	Cusco, Peru	FMNH 433744			X
C. [f.] mentalis	Cusco, Peru	FMNH 433745		X	X
C. [f.] mentalis	La Paz, Bolivia	LSU 102856	LSU B100003		X
C. [f.] mentalis	La Paz, Bolivia	ZMUC 118358			X
C. [f.] mentalis	La Paz, Bolivia	N/A	AMNH 2606	X	X
C. [f.] mentalis	La Paz, Bolivia	N/A	AMNH 2496	X	X

sterilized scalpel and processed them in a lab where no modern bird tissues have been handled. We used an extraction technique developed by Andrés M. Cuervo and colleagues (*in litt.*) or a phenol-chloroform extraction protocol followed by bead cleanup (Tsai *et al.* 2019). For the Cuervo and colleagues' extraction method, we soaked toepad samples in absolute ethanol, followed by buffer AE from a QIAamp DNA Micro kit, then minced and added them to a mixture of ATL lysis buffer, proteinase K, and 20 µL of 1M DTT for overnight incubation (56°C) in a rotary oven. The following day, we followed the DNeasy Blood and Tissue Kit protocol with a few exceptions (as follows). In step 1, we added 1 µL of Carrier RNA. In step 2, we added cold 100% ethanol and incubated the mixture for one hour at 4°C. In step 5, we used spin columns from a QIAquick polymerase chain reaction (PCR) purification kit. After eluting the samples from the columns, we concentrated the resulting extract to 100 µL in a SpeedVac. We quantified double-stranded DNA (dsDNA) concentration in all extractions using a real-time qPCR fluorescent detection (Blotta *et al.* 2005) with the Quant-iT™ PicoGreen™ dsDNA Assay Kit (Invitrogen, Eugene, OR, USA).

Ultraconserved element enrichment, sequencing, and library preparation

We submitted DNA extracts to RAPiD Genomics (Gainesville, FL, USA) for library preparation and sequencing of UCEs (Faircloth *et al.* 2012). Libraries were enriched for UCEs using either the 2.5k tetrapod probe kit (2386 UCEs) supplemented

with approximately 100 avian exons, or the standard 5k tetrapod probe kit (5060 UCEs; Faircloth *et al.* 2012), and sequenced with either 100 (2.5k kit) or 150 (5k kit) base pair, paired end reads on an Illumina HiSeq 3000/4000. Mitochondrial sequence data were recovered from off target reads as a byproduct of this process (Amaral *et al.* 2015). After sequencing, we discarded duplicate reads with the python script fastqSplitDups.py (https://github.com/McIntyre-Lab/mcscript) and eliminated adaptors and low quality bases with trimmomatic, implemented in illumiprocessor (Lohse *et al.* 2012, Del Fabbro *et al.* 2013, Faircloth 2013, Bolger *et al.* 2014).

We assembled the trimmed reads using Abyss 2.1.5 (Jackman *et al.* 2017) as implemented in PHYLUCE (Faircloth *et al.* 2012, Faircloth 2016) following the standard UCE pipeline. PHYLUCE matched the assemblies to UCE probes and produced concatenated files for alignment. We used a series of custom scripts to create a single fasta file containing the longest contig from each UCE (https://github.com/juliema/phylogenomics_scripts), and then used this file as a new set of target sequences to match reads with aTRAM v.2.3.0 (Allen *et al.* 2018). This is a pipeline that iteratively assembles reads to form contigs by matching them first to a provided target sequence, then to the results from the previous iteration for subsequent iterations. We assembled contigs for each of our samples using five iterations in aTRAM v.2.3.0 with SPAdes 3.11.1 (Bankevich *et al.* 2012). We then selected the longest contig for each assembled UCE, grouped taxa by UCE, and aligned each UCE using MAFFT (Katoh 2013). Most variation in UCEs occurs in the flanking regions rather than the central probe area, so we selected the longest contig rather than the results from the last iteration. This ensured that the maximum number of informative sites would be utilized, but necessitated additional quality control steps as described below.

We verified each alignment by eye using GENEIOUS 8.0.4 (https://www.geneious.com) and performed two manual types of quality control to reduce errors caused by degraded DNA from toepad tissues (Axelsson *et al.* 2008, Molak and Ho 2011, McCormack *et al.* 2016). We removed any unalignable portions of a contig and scanned (by eye) for individual mismatches within each alignment. We re-coded mismatches as 'N' for toepad samples (Catanach *et al.* 2021). We only retained mismatched base calls when they were identical to any other sequence, regardless of whether the sequence it matched was sourced from a frozen tissue or toepad. If multiple samples had identical, but extremely divergent, sequences from other samples in the UCE probe portion of the alignment, we deleted the entire UCE alignment. UCE probe regions from closely related samples are unlikely to exhibit large amounts of sequence variation because the probes bind to regions that are highly conserved across all tetrapods (Faircloth *et al.* 2012). Libraries prepared from toepad extracts have poorer quality reads and lower coverage than libraries prepared from frozen tissues. Therefore, having high-quality data from frozen tissues as a reference, and implementing these extra quality control steps, enabled us to reduce the 'noise' caused by sequencing error and introduced by the inclusion of low-quality DNA from our toepad-generated sequence data. Finally, we realigned the contigs with MAFFT and trimmed the alignments with trimAL v.1.2 (Capella-Gutiérrez *et al.* 2009) to remove columns of the alignment where over half of the samples contained missing data.

Our study included *ND2* sequences from 22 samples in the ingroup (*C. fuscater* complex) that were generated with Sanger sequencing methods following Voelker *et al.* (2013). We supplemented this dataset with additional *ND2* sequences from 13 samples assembled in GENEIOUS v.8.0.4, by mapping our UCE libraries to two unpublished reference sequences from the Sanger dataset: one from Táchira, Venezuela, and one from Cusco, Peru. We set the 'map to reference' function to medium-low sensitivity, with a maximum of five iterations and no trimming, and manually checked the assemblies by eye. We generated a consensus sequence with a strict 50% threshold and saved all sequences to a single FASTA file. We used the MUSCLE algorithm in SeaView v.4.6.2 (Edgar 2004, Guoy *et al.* 2010) to align all selected reads to the other *C. fuscater* sequences. *ND2* sequences used in this study are deposited in GenBank, and UCE sequences are deposited in the SRA library (see below).

Phylogenetic analysis of ultraconserved element alignment

The UCE dataset included 19 989 parsimony informative sites (about nine per locus on average). We used PartitionFinder 2.1.1 (Lanfear *et al.* 2012, 2017) as implemented on CIPRES (Miller *et al.* 2010) to select the best partitioning scheme. We limited our substitution model test to GTR and GTR+G models, and treated each UCE as a separate partition. We selected models with the lowest second-order Akaike information criterion (AICc) score. Due to computational constraints, we set rcluster_max to 1000 and rcluster_percent to 5.0. The program RAxML v.8.2.12 (Stamatakis 2014) as implemented on CIPRES (RAxML-HPC BlackBox; Miller *et al.* 2010) to be selected, so we used the most commonly selected model (GTR+G) and partitioned the data in accordance with the scheme selected by PartitionFinder (i.e. 1299 partitions). We ran a bootstrap analysis and allowed the program to autocomplete. To simplify text in the discussion of the UCE phylogeny, we reserved use of the terms 'clade', 'monophyletic', and 'sister' for groups of taxa with 100% bootstrap support unless otherwise specified.

Phylogenetic analysis of NADH dehydrogenase subunit 2 alignment

The final *ND2* alignment was 1041 bases with complete sequences from 69% of ingroup samples (24/35). All sequences from these samples included at least 1000 bp, except the following four: LSUMZ 97809 (996 bp), LSUMZ 102856 (975 bp), ANSP 175531 (972 bp), ANSP 63298 (377 bp). In PAUP* (Swofford 2002) we calculated pairwise distances and reconstructed a maximum parsimony (MP) tree with bootstrap values (1000 pseudoreplicates, each with 1000 random additions and maxtrees set to autoincrease). We used RAxML-HPC BlackBox as implemented on CIPRES (Miller *et al.* 2010) to reconstruct a maximum likelihood (ML) tree with bootstrap values (with automated stop criterion) from the unpartitioned matrix, with the GTR+I+G model selected with PartitionFinder 2.1.1 (branchlength = linked; model selection = AICc) as implemented on CIPRES (Miller *et al.* 2010, Lanfear *et al.* 2012, 2017). We used BEAST 2.6.3 (Drummond and Rambaut 2007) as implemented on CIPRES (Miller *et al.* 2010) (40 000 000 generations, sampling every 1000 generations with a burn in

of 25%) to reconstruct a Bayesian inference (BI) tree, estimate divergence times, and calculate posterior probabilities. For divergence-time estimation, we used a strict clock rate for *ND2* (0.029, with 95% HPD = 0.024–0.033 included as a normally-distributed prior) as calculated for Hawaiian honeycreepers (Passeriformes: Fringillidae) based on known ages of the Hawaiian Islands (Lerner *et al.* 2011). Hereafter, unless otherwise specified, when discussing the *ND2* phylogeny, we reserved use of the terms 'clade', 'monophyletic', and 'sister' for groups with ≥ 90% bootstrap support.

Automatic cluster analysis of NADH dehydrogenase subunit 2 data

We compared results from two different automatic clustering algorithms for species delimitation: (i) automatic barcode gap discovery (ABGD, Puillandre *et al.* 2012) and (ii) assemble species by automatic partitioning (ASAP, Puillandre *et al.* 2019). We applied default settings and restricted the analysis to sequences in the ingroup.

Morphological data

Study skins examined

One author (M.R.H.) examined 289 study skins of known sex (N = 163 adult males, 89 adult females, 21 immature males, 16 immature females), and 18 study skins of unknown sex, in the collections of the Academy of Natural Sciences of Drexel University (ANSP), American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CM), Delaware Museum of Nature & Science (DMNH, formerly Delaware Museum of Natural History), Field Museum of Natural History (FMNH), Louisiana State University Museum of Natural Science (LSUMZ), and National Museum of Natural History, Smithsonian Institution (USNM). Each of the following analyses was completed with a subset of these specimens, as noted.

Plumage colour

We assembled (at DMNH) the complete holdings of *C. fuscater* specimens from the collections of ANSP (N = 25), DMNH (N = 13), and FMNH (N = 23), and a portion of the holdings of LSUMZ (N = 25). One author (M.R.H.) examined these 86 specimens under the same light source (flat panel LED) and matched published colour standards (Smithe 1975) to the feathers on the crown, back, undertail coverts, flanks, abdomen, breast, and throat of each specimen. He also scored the absence/presence (0 and 1, respectively) of a thin dark line of feathers connecting the malar regions across the chin.

Maxilla colour

'Black' portions of the maxilla evidently do not fade in study skins, unlike 'orange' parts that fade to yellowish. Therefore, to survey taxonomic variation in the extent of black on the maxilla, one author (M.R.H.) scored maxilla colour as an ordinal variable with five levels (0–4) in a sample of 218 study skins of known sex (N = 120 males, 69 females, 29 immature): (0) no black; (1) small amount of black on the anterior portion of the culmen *or* the nares; (2) small amount of black on the anterior portion of the culmen *and* the nares; (3) black running the entire length of the culmen, connecting the nares; (4) extensive black on the entire maxilla, or on the entire maxilla minus the tomium (cutting edge).

Iris colour

We compiled data from specimen labels and supplemented this dataset by scoring iris colour in a sample of digital photos in the Macaulay Library, Cornell University (ML). We distinguished two general categories of iris colour in our analysis: (i) *white*, which included variable descriptions including 'blanco', 'white', 'whitish', 'grey', 'gris', 'pearl grey', 'pale grey', 'honey grey', 'pale yellow grey', 'pale blue-grey', 'blue-grey', 'blue', 'palest blue', 'blueish white', 'cream white', 'yellow white', 'dull white', 'greenish white', 'milky white', and 'off white'; (ii) *brown*, which included 'brown', 'café', 'dark brown', 'pale brown', 'red-brown', 'hazel', and 'cinnamon brown'.

Vocal data

Audio recordings examined

We analysed songs and calls in 194 audio recordings in the ML and Xeno-canto (XC, http://www.xeno-canto.org) digital archives. We used Raven Pro 1.5 software (Cornell University, Ithaca, NY) with the Hann window function (window size 34 ms, 3 dB bandwidth of 42.3 Hz) to visualize songs and a portion of the call repertoire in a geographically diverse sample of recordings.

Geographic variation in calls

We investigated the acoustic structure of three discrete call types. (i) *Punctuation calls* are uttered at relatively low amplitude, in between songs or bouts of songs. They are of extremely short duration, have a delicate rippling quality, and seem to degrade quickly in the dense vegetation of the forest understory. (ii) *Contact calls* consist of two closely spaced fundamental frequencies and their respective, stacked harmonic overtones. They have a nasal, cat-like mewing or screeching quality. (iii) *Blurred calls* typically rise and/or fall in pitch ('*wree*', '*cree*', '*weep*') and vary among taxa in bandwidth and general structure. They are so named because of their blurry shape on the sonogram, although some low-bandwidth blurred calls have a whistle-like quality. We assumed that calls of each type were homologous among the populations, and thus taxonomically informative. We identified geographic breaks in their acoustic structure by visually sorting them by the shape of the sonogram trace.

Geographic variation in songs

We defined a 'song' as a cluster of two to four pure-tone 'notes' (rarely up to six) with little or no spectral content above the fundamental frequencies (Fig. 4). We defined a 'note' as a continuous trace on the sonogram (i.e. a unimodal waveform with an estimated central frequency and duration). We expanded a method used by Saunders (1961) and produced an exhaustive key of dyadic, triadic, and tetradic frequency contour patterns (hereafter contours, Fig. 5). We used the key to score each song with a two, three, or four-letter code corresponding to its contour shape. Songs with five and six-note contours were rare and only detected in *C. f. hellmayri* (N = 8) and *C. f. mentalis* (N = 1). For this reason, and because they required a considerable expansion of our classification key, we combined them in a single category. More than 99% of songs were classifiable

with our approach (dyadic, triadic, tetradic). We interpreted a lack of shared contours between sister-taxa, and geographically adjacent non-sisters, to be indicative of vocal divergence.

For each recording, we scored one example of each unique song (the first that was not masked by any other sound, Halley *et al.* 2017) and removed recordings of duplicate individuals from the sample (same repertoire recorded at the same site). When multiple examples of the same contour were detected in a single recording, but were composed of different frequencies, we scored them as different (unique) songs. We excluded one recording (ML 515369) because songs from multiple individuals were overlapping and difficult to distinguish from each other, and another recording (XC 128440) because the file was corrupted. We also excluded two songs that were difficult to score because of trills or abnormal frequency structure (XC 2978, 529000).

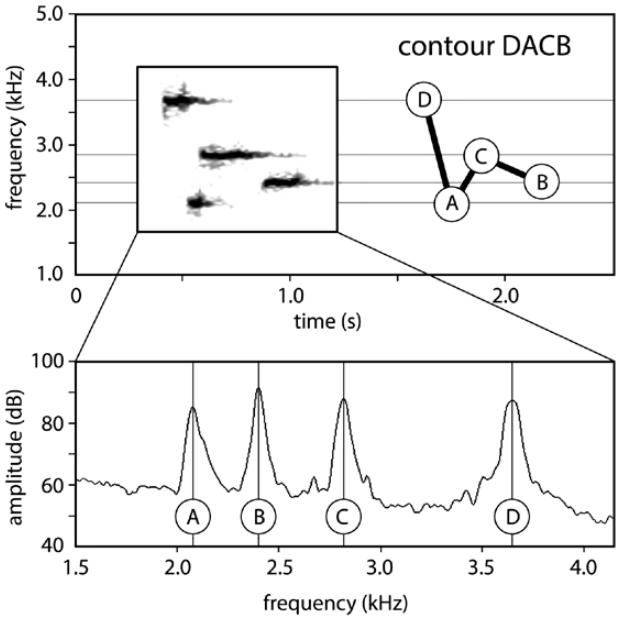

Figure 4. Acoustic structure of *C.* [*fuscater*] songs and classification method. (Lower plot) Each 'note' (single trace on the spectrogram) was labeled with a letter (A–D) corresponding to the ordinal rank of its central frequency (low to high). (Upper plot) The frequency contour of the song is denoted by the temporal sequence of its ranked central frequencies: DACB.

Assumptions about vocal signals

The value of vocal characters in avian systematics may depend on whether the vocalizations in question are innately acquired (i.e. develop normally without exposure to conspecific song), although there is considerable disagreement about this and related subjects (e.g. Payne 1986, Isler *et al.* 1998, Raposo and Höfling 2003, Remsen 2005). Acoustic isolation experiments (e.g. Kroodsma 1982) have not been conducted on any *Catharus* species, to our knowledge, but have been conducted on its sister-group, the monotypic *Hylocichla mustelina* (Lanyon 1979, Whitney and Miller 1987). In isolation, the acoustically complex 'terminal phrases' in *H. mustelina* song, which are structurally like punctuation calls in *C. fuscater*, developed normally in isolation—they are evidently innate, not learned (Lanyon 1979). The 'musical' central phrases, which are structurally like (and maybe homologous with) triadic and tetradic song contours in the *C. fuscater* complex, did not develop normally in acoustic isolation (Lanyon 1979). Therefore, we assumed that *C. fuscater* song contours are learned and, therefore, susceptible to cultural evolution (i.e. decoupled from genetic evolution). This would seemingly render them less reliable as taxonomic characters, although we acknowledge that this assumption may be premature. Despite the potential for cultural evolution, there are no geographic dialects in *H. mustelina* and song-type frequencies are

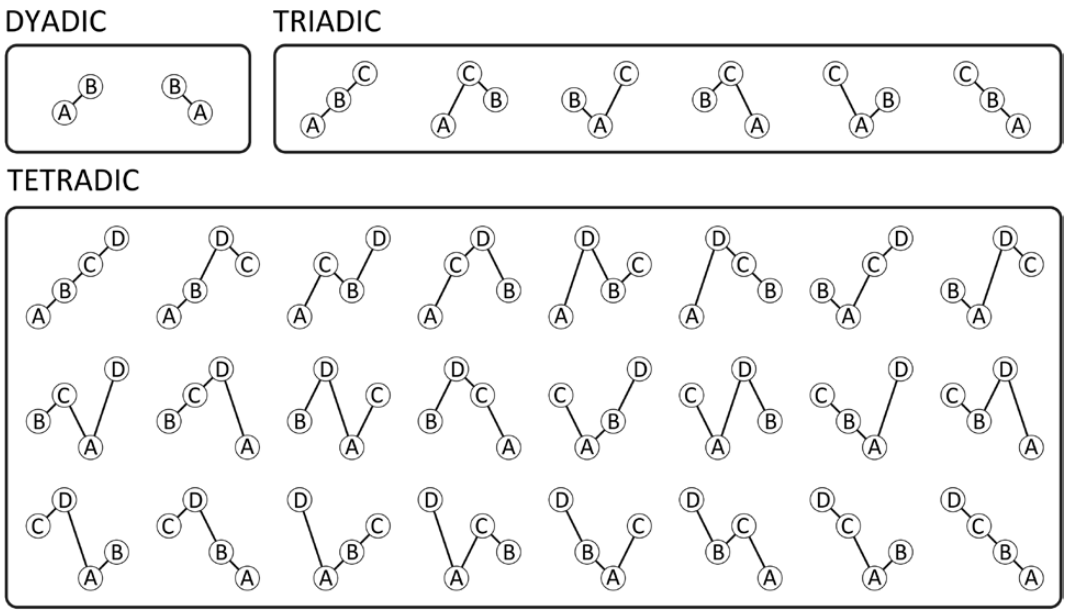

Figure 5. Exhaustive chart of dyadic ($N = 2$), triadic ($N = 6$), and tetradic ($N = 24$) frequency contours used to classify song types in the *C.* [*fuscater*] complex, following Figure 4 schematic. Theoretical sonogram shapes of each contour are shown (i.e., the y-axis denotes frequency, and the x-axis denotes time).

stable in populations at decade timescales (Whitney and Miller 1987, Whitney 1992).

Playback experiments, including some accompanied by taxidermic mount presentations, suggest that vocal divergence among *Catharus* taxa and populations may be correlated with song discrimination, and thus indicative of reproductive isolation among populations (Dilger 1956, Lanyon 1979, Jankowski *et al.* 2010, Freeman and Montgomery 2017, Freeman *et al.* 2022). This may be true, but the social function(s) of 'territorial' song in *Catharus* species remains uncertain. Multiple males provision the offspring of a single female (at the same nest) in *C. bicknelli* (Goetz *et al.* 2003), *C. fuscescens* (Halley 2014, Halley *et al.* 2016), and *C. fuscater* (Greeney *et al.* 2015), and the social and genetic mating systems of *C. bicknelli* and *C. fuscescens* have been described as 'flexible polygynandry' (Goetz *et al.* 2003, Halley *et al.* 2016); no study of the *C. fuscater* genetic mating system has yet been conducted, to our knowledge. In these and possibly other *Catharus* species, territorial behaviour is apparently facultative. A given male will tolerate the presence of some males within its 'territory' (i.e. the polygon defined by singing perches along its periphery), while concurrently excluding other males from the same area (Goetz *et al.* 2003, Heckscher 2007, Halley and Heckscher 2012, Halley 2014, Greeney *et al.* 2015). The 'reason' why any particular male is tolerated or excluded is poorly known, but is probably influenced by genetic relatedness and/or social rank (Heckscher 2007, Halley *et al.* 2016). The frequency of use of different call types and song also varies seasonally and with reproductive context (Heckscher 2018). For these reasons, without more information, we cannot be confident that playback experiments, which do not account for these sources of variation, are actually informative about potential reproductive isolation in the *C. fuscater* complex. More detailed study of colour-banded populations is needed.

Species delimitation

Hereafter, until the taxonomic revision, we place the name '*fuscater*' in brackets to denote uncertainty about species limits, in the main text and all figures and captions. We ranked allopatric populations in the *C.* [*fuscater*] complex as species when the preponderance of evidence indicated that they are diagnosable, independently evolving lineage segments (de Quieroz 2007), which are probably reproductively isolated from each other. Following the approach of Cadena *et al.* (2020), we evaluated multiple lines of evidence to test whether *C.* [*fuscater*] populations 'consistently fulfil expectations characteristic of currently recognized [*Catharus*] species under different species concepts; more fulfilled criteria produce stronger and more comprehensive arguments for species rank'. We asked whether populations were (i) genetically distinct (i.e. reciprocally monophyletic in at least one genetic dataset), as inferred via phylogenetic analysis, (ii) morphologically diagnosable, as determined via standardized comparisons of study skins, and (iii) vocally diagnosable, as inferred by spectrographic analysis of audio recordings of songs and calls. We ranked populations as species when they fulfilled the first criterion (i) and at least one other criterion. We ranked populations as subspecies when they fulfilled only one criterion. For reasons outlined by Halley *et al.* (2017), we did not set operational thresholds based on the degree of genetic divergence between sympatric congeners, for triggering species rank (e.g. Helbig *et al.* 2002, Tobias *et al.* 2010), although the degree of divergence in this system would probably satisfy those criteria. Furthermore, we refrained from basing taxonomic decisions on inferences about reproductive isolation made from the results of playback experiments, although some have advocated for such an approach (e.g. Freeman *et al.* 2022).

RESULTS

Molecular data

Phylogenetic inference with ultraconserved element data

Our final alignment of 22 ingroup and two outgroup samples, representing all taxa except *C.* [*f.*] *fuscater* and *C.* [*f.*] *sanctaemartae* (Table 1), consisted of up to 2199 UCEs per sample and 2 378 390 bases, with all samples having at least 700 296 bases. The *C.* [*fuscater*] complex (ingroup) was monophyletic with respect to the outgroup (*C. dryas* + *C. maculatus*) and composed of eight clades corresponding to allopatric populations with clear geographic boundaries (Fig. 6). Three of these clades did not correspond to named taxa and are referred to below as 'Undescribed' 1, 2, and 3. Three samples from western Panama and Costa Rica formed a clade (hereafter *C.* [*f.*] *hellmayri*) that was sister to the rest of the complex. Within the sister-group of *C.* [*f.*] *hellmayri*, five samples from the Darién region formed a clade (hereafter 'Darién clade') that was sister to a clade that included all South American samples. The Darién clade was itself composed of two reciprocally monophyletic clades, one from Cerro Pirre (hereafter *C.* [*f.*] *mirabilis*) and one from the Serranía del Darién and Serranía de Majé (hereafter 'Undescribed 1').

Within the South American clade, the southernmost subclade, composed of two samples from southern Peru, east of the Río Apurímac, and one sample from northern Bolivia (hereafter *C.* [*f.*] *mentalis*), was sister to a clade containing the rest of the South American samples. Three samples collected on the western Andean slope of Ecuador and north-western Peru, west of the Río Marañón, including a paratype of *C. f. caniceps* (AMNH 175531), formed a clade (hereafter *C.* [*f.*] *berlepschi*) that was sister to a clade composed of three samples from the eastern slope of the Peruvian Andes, between Río Marañón and Río Apurímac (hereafter 'Undescribed 3'). On the eastern Andean slope of northern Peru and southern Ecuador, in the Chinchipe Valley, north to Río Zamora, two samples in a geographically intermediate position between *C.* [*f.*] *berlepschi* (to the west) and Undescribed 3 (to the east) formed a clade (hereafter 'Undescribed 2') that was sister to a clade composed of three samples from northern Ecuador (eastern slope) and the Central Andes of Colombia (hereafter *C.* [*f.*] *opertaneus*). Thus, a longitudinal transect across northern Peru and southern Ecuador shows a 'leapfrog' pattern in the nuclear genome, with a nuclear genetic break on the eastern slope between Valladolid (Zamora-Chinchipe) and Mospa (Napo), Ecuador, probably at the Río Zamora, where Undescribed 2 is replaced by its northern neighbour and phylogenetic sister, *C.* [*f.*] *opertaneus*.

Phylogenetic inference and divergence timing with NADH dehydrogenase subunit 2 data

We recovered *ND2* data for all named and undescribed taxa (Table 1). The topologies of the best BI, ML, and MP trees were identical. The *C.* [*fuscater*] complex was monophyletic with

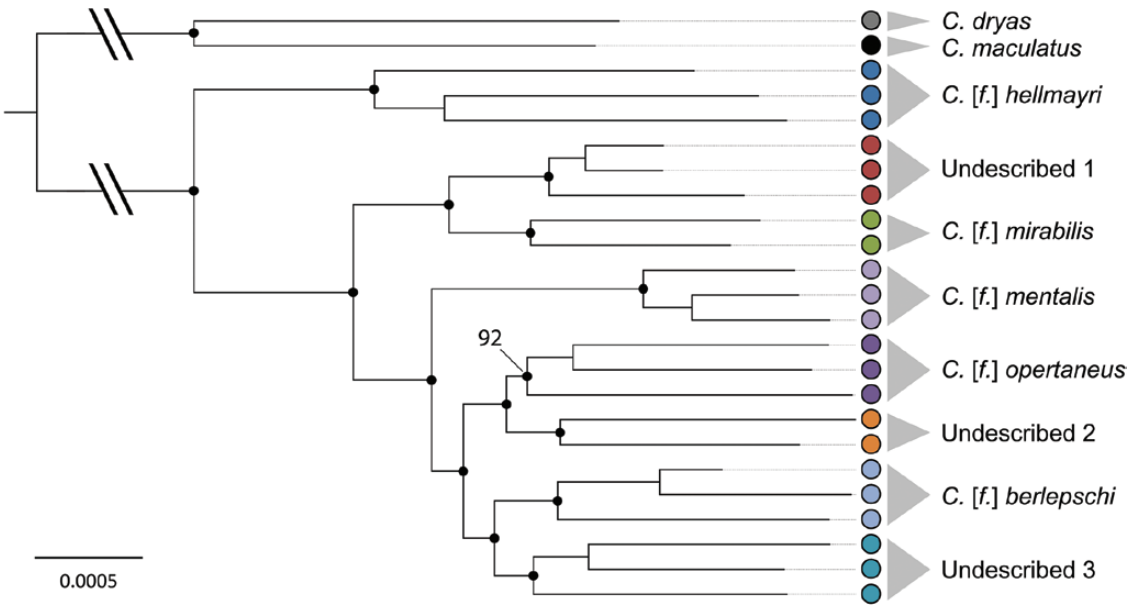

Figure 6. Maximum likelihood (ML) phylogeny of the *C.* [*fuscater*] complex based on a matrix of 2199 UCEs assembled from 24 samples. Black circles denote 100% bootstrap support for critical nodes supporting monophyly of taxonomic groups, with one exception (92%) as noted. Colour scheme of terminal taxa is standardized across figures.

respect to the outgroup (*C. dryas* + *C. maculatus*) and composed of nine clades (plus a single sample of *C.* [*f.*] *sanctaemartae*) corresponding to allopatric populations with clear geographic boundaries (Fig. 7). The *C.* [*fuscater*] complex diverged from the common ancestor of *C. dryas* and *C. maculatus* approximately 5.5 Mya (95% HPD = 4.4–6.7). Mean pairwise uncorrected *p*-distance for between-population sample pairs (N = 535) was 0.066 ± 0.018 (range = 0.008–0.086), an order of magnitude larger than for sample pairs from the same population (N = 60, mean uncorrected *p*-distance of 0.004 ± 0.003, range = 0–0.012). There was low bootstrap support and Bayesian posterior probability for most early nodes in the *ND2* tree (Fig. 7).

Four samples from western Panama and Costa Rica formed a clade (*C.* [*f.*] *hellmayri*) that was sister to the rest of the complex, with a divergence estimate of 3.2 Mya (range = 2.6–3.8). Most nodes separating allopatric populations in the ingroup (55.6%, 5/9) were dated to within 1 Myr after the ancestor of *C.* [*f.*] *hellmayri* diverged from the rest of the complex. Samples from Cerro Pirre (*C.* [*f.*] *mirabilis*) and the Serranía del Darién and Serranía de Majé (Undescribed 1) were reciprocally monophyletic, with an estimated divergence of 1.3 Mya (range = 0.9–1.7). The Darién clade was included in a higher-order clade with two samples from the northern and central Andes (*C.* [*f.*] *opertaneus*: ZMUC 134855 from Antioquia, Colombia, and ZMUC 119587 from Sucumbios, Ecuador, respectively) that diverged from a clade composed of all the rest of the South American samples approximately 2.9 Mya (range = 2.4–3.5). The placement of *C.* [*f.*] *opertaneus* as sister to the Darién clade received limited support (MP = 63; ML = 93; BI = 0.91) and conflicted with the UCE tree. These three taxa were also highly divergent in *ND2*: *C.* [*f.*] *opertaneus* vs. *C.* [*f.*] *mirabilis* (mean uncorrected *p*-distance = 0.069 ± 0.003); *C.* [*f.*] *opertaneus* vs. Undescribed 1 (mean uncorrected *p*-distance = 0.066 ± 0.002).

Samples from western Ecuador and the Huancabamba and Chunchuca valleys of Peru (*C.* [*f.*] *berlepschi*) formed a clade (MP = 98; ML = 98; BI = 1) that was sister to a clade composed of samples from the Chinchipe Valley (Undescribed 2), with relatively shallow divergence (mean uncorrected *p*-distance = 0.010 ± 0.002). Together, *C.* [*f.*] *berlepschi* and Undescribed 2 formed a clade that was sister to a clade (MP = 98; ML = 98; BI = 1) composed of samples from east of the Río Marañón in Peru (Undescribed 3). This *ND2* topology differed from the UCE tree, where Undescribed 3 was sister to *C.* [*f.*] *berlepschi*, and where they together formed a clade that was sister to a clade composed of samples of Undescribed 2, *C.* [*f.*] *opertaneus*, and *C.* [*f.*] *sanctaemartae*. The *ND2* divergence between *C.* [*f.*] *berlepschi* and Undescribed 3 (mean uncorrected *p*-distance = 0.022 ± 0.002) was roughly equivalent to the divergence between Undescribed 2 and Undescribed 3 (mean uncorrected *p*-distance = 0.024 ± 0.001). The placement of the *C.* [*f.*] *berlepschi* + Undescribed 2 + Undescribed 3 clade was unresolved in the *ND2* tree, with respect to the rest of the complex. Samples from Venezuela (*C.* [*f.*] *fuscater*) formed a clade that was sister to a single sequence from the Sierra Nevada de Santa Marta (*C.* [*f.*] *sanctaemartae*), with an estimated divergence of 0.4 Mya (range = 0.1–1.2). The placement of the *C.* [*f.*] *fuscater* + *C.* [*f.*] *sanctaemartae* clade (MP = 98; ML = 100; BI = 1), with respect to the rest of the complex, was unresolved. Samples from Bolivia and southern Peru, east of the Río Apurímac (*C.* [*f.*] *mentalis*), formed a highly divergent clade that was reconstructed as sister to *C.* [*f.*] *fuscater*, but with low support for that placement (Fig. 7; Table 2).

Automatic cluster analysis of NADH dehydrogenase subunit 2 data

ABDG analysis identified nine groups that corresponded to the allopatric clades described above, while lumping *C.* [*f.*] *berlepschi* and Undescribed 2 (which were not sisters in the UCE tree).

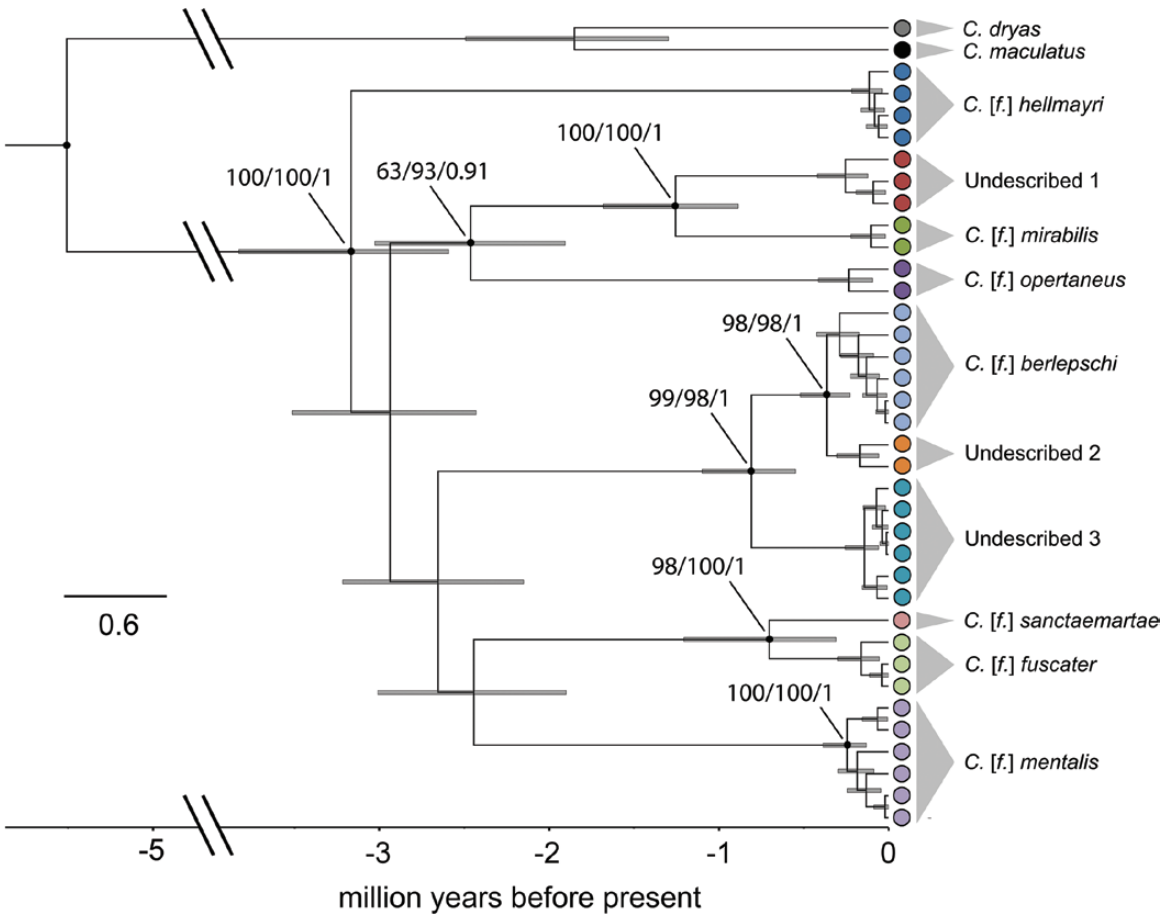

Figure 7. Time-calibrated Bayesian Inference (BI) tree reconstructed from *ND2* sequences of 37 samples of *C.* [*fuscater*] with the GTR+I+G substitution model (see Methods). The topology was consistent with the maximum likelihood (ML) and maximum parsimony (MP) trees. Molecular clock estimates of lineage divergence times were calibrated with *ND2* rates from Lerner *et al.* (2011) and node bars indicate the 95% highest posterior density interval. Branch lengths are proportional to substitutions per site. Support values for well-supported nodes are shown to the upper left of the node (MP/ML/BI). Support values are not shown for nodes with <70 bootstrap support (MP/ML) or <0.90 posterior probability (BI).

ASAP analysis identified seven groups: samples of *C.* [*f.*] *fuscater* and *C.* [*f.*] *sanctaemartae* were combined into one group, and samples of *C.* [*f.*] *berlepschi*, Undescribed 2, and Undescribed 3 were also combined.

Morphological data

Plumage colour

We detected a considerable amount of taxonomic variation in plumage colour, which generally corroborated published accounts (Table 3). We also distinguished three distinct patterns of sexual variation in the adult plumage: (i) monochromatic, wherein adult males and females exhibited no difference in colour, or differed slightly in brightness only; (ii) dichromatic, wherein adult males and females differed in plumage colour; and (iii) polychromatic, wherein the sexes differed in colour and adult males exhibited two colour 'types' (Fig. 8).

Maxilla colour

We detected sexual and taxonomic differences in the colour of the maxilla (Table 4). Juveniles from all populations had uniformly black maxillae, which implies that the juvenile character state may be retained (neoteny) in adults of some taxa (e.g. *C.* [*f.*] *berlepschi* females, *C.* [*f.*] *opertaneus* and Undescribed 2). The taxon with the brightest bill overall, expressing the least amount of black in both sexes, was *C.* [*f.*] *sanctaemartae*. Males had brighter bills than females on average in all taxa except *C.* [*f.*] *opertaneus* and Undescribed 2, in which both sexes had completely black maxillae, like juveniles (Table 4). In Undescribed 3, sexual differences in maxilla colour were very slight and probably non-significant.

Iris colour

We detected three general patterns of iris colour, which were not correlated with age or sex (Table 5): (i) *monochromatic white*, including taxa where 'brown' irides accounted for < 20% of specimens; (ii) *monochromatic brown*, including taxa where 'white' irides accounted for < 20% of specimens; and (iii) *dichromatic*, where both colour types were detected at greater than 20% frequency (Table 5).

Vocal data

Geographic variation in 'punctuation calls'

We detected punctuation calls in recordings of every population. We detected three geographic patterns, hereafter types 1–3 (Fig.

Table 2. Mean uncorrected *p*-distances (±SD) within and between mitochondrial clades (taxa), based on pairwise comparisons of *ND2* sequences from the *C.* [*fuscater*] complex ($N = 35$). Samples of *C.* [*f.*] *berlepschi* and *C.* [*f.*] *caniceps* did not form reciprocally monophyletic clades, and are therefore combined here under the older name (*berlepschi*). Intra-taxon divergence values are shown in boldface

	hellmayri	Undescr. 1	*mirabilis*	*opertaneus*	Undescr. 2	*sanctaemartae*	*fuscater*	*berlepschi*	Undescr. 3	*mentalis*
hellmayri	**0.002 ± 0.001**									
Undescr. 1	0.075 ± 0.001	**0.006 ± 0.003**								
mirabilis	0.076 ± 0.002	0.039 ± 0.002	**0.003**							
opertaneus	0.073 ± 0.001	0.066 ± 0.002	0.069 ± 0.003	**0.008**						
Undescr. 2	0.077 ± 0.002	0.075 ± 0.002	0.069 ± 0.001	0.071 ± 0.003	**0.005**					
sanctaemartae	0.067 ± 0.001	0.072 ± 0.001	0.067 ± 0.004	0.073 ± 0.001	0.061 ± 0.003	—				
fuscater	0.075 ± 0.001	0.073 ± 0.001	0.069 ± 0.002	0.071 ± 0.001	0.063 ± 0.002	0.020 ± 0.002	**0.003 ± 0.002**			
berlepschi	0.076 ± 0.002	0.078 ± 0.003	0.071 ± 0.002	0.075 ± 0.002	0.010 ± 0.002	0.069 ± 0.001	0.065 ± 0.002	**0.005 ± 0.003**		
Undescr. 3	0.068 ± 0.001	0.077 ± 0.001	0.073 ± 0.002	0.071 ± 0.002	0.024 ± 0.001	0.070 ± 0.001	0.065 ± 0.001	0.022 ± 0.002	**0.002 ± 0.001**	
mentalis	0.080 ± 0.003	0.080 ± 0.003	0.082 ± 0.002	0.072 ± 0.001	0.071 ± 0.003	0.079 ± 0.004	0.066 ± 0.003	0.074 ± 0.002	0.069 ± 0.001	**0.005 ± 0.002**

9). In all three types, two fundamental frequencies that are not harmonically related occurred simultaneously, indicating that both syringeal sound sources were engaged in call production. Type 1 ('pulsed/rippling') punctuation calls consisted of a rapid burst of notes that rose and fell in sonographic shapes resembling stacked caret graphemes (^), with a sweeping quality not unlike songs of *C. fuscescens*, albeit much briefer. Type 1 punctuation calls were detected in recordings of *C.* [*f.*] *hellmayri* ($N = 11$ recordings), Undescribed 1 ($N = 1$) and *C.* [*f.*] *mirabilis* ($N = 3$). In contrast, Type 2 ('long/sinuous') punctuation calls consisted primarily of two continuous (non-pulsed) notes (Fig. 9). Type 2 punctuation calls were detected in *C.* [*f.*] *fuscater* ($N = 7$), *C.* [*f.*] *sanctaemartae* ($N = 2$), and *C.* [*f.*] *berlepschi* ($N = 4$). Type 3 ('short/simple') punctuation calls were detected in Undescribed 2 ($N = 1$), *C.* [*f.*] *opertaneus* ($N = 1$), Undescribed 3 ($N = 1$), and *C.* [*f.*] *mentalis* ($N = 1$). A 'Type 3' call was also detected in one recording of *C.* [*f.*] *fuscater* (ML 66349), although this call had a wider frequency bandwidth than typical Type 3 calls (Fig. 9). In general, Type 3 punctuation calls were much briefer and simpler in structure than Type 1 or 2 punctuation calls, and rare in our sample of recordings.

Notably, despite their geographic variability, the structure of punctuation calls was stable at decade timescales. Type 1 punctuation calls in recordings of *C.* [*f.*] *mirabilis* made by T.A. Parker in 1982 (ML 25872) and K. Allaire in 2009 (XC 60762) were nearly identical, about 0.2 s in duration and falling within the 2–5 kHz frequency range. Likewise, the sinuous structure of Type 2 punctuation calls was temporally stable across 56 years, in recordings of *C.* [*f.*] *fuscater* in Venezuela made by P. Schwartz in 1963 (ML 66348, 66349) and D. de Jesus Garcia in 2019 (XC 471156).

Geographic variation in 'contact calls'

Among populations, contact calls varied subtly in the spacing of harmonic overtones, and the shape of the frequency bands (i.e. sloping upwards or chevron-shaped; Fig. 10). The contact calls of *C.* [*f.*] *hellmayri* and Undescribed 1 had the tightest overtone spacing and were similarly shaped (sloping upwards), whereas *C.* [*f.*] *mirabilis* contact calls had wider spacing and a tendency toward an inverted chevron shape, like some South American populations. In shape and the spacing of overtones, the contact calls of Undescribed 2 were more like *C.* [*f.*] *berlepschi* (its mitochondrial sister) than *C.* [*f.*] *opertaneus* (its nuclear sister) (Fig. 10).

Geographic variation in 'blurred calls'

The structure of blurred calls was geographically variable in frequency range, in bandwidth (narrow vs. wide), and in the direction of the frequency modulation. Blurred calls either ascended or descended in frequency, and both types were detected in *C.* [*f.*] *berlepschi* (Fig. 11). Notably, *C.* [*f.*] *berlepschi* and Undescribed 3 gave similar 'check-shaped' blurred calls, whereas the blurred call of *C.* [*f.*] *mentalis* resembled only the upper portion of the 'check-shaped' call (Fig. 11). 'Descending' blurred calls in *C.* [*f.*] *berlepschi* and Undescribed 2 were structurally divergent. However, because our sample size was small, we do not know the extent of variability of blurred calls within populations, or even whether blurred calls occur in the populations of which we lacked recordings (e.g. Undescribed 1, *C.* [*f.*] *mirabilis*).

Table 3. Adult plumage colour variation in the *C.* [*fuscater*] complex based on specimens in the ANSP, DMNH, FMNH, and LSUMZ. Numbers taken from Smithe (1975) denote colours on the crown, back, undertail coverts (tl-covs), flanks, breast, and throat. 'Chin' is scored with two levels (0,1) referring to the absence or presence, respectively, of an unbroken (although sometimes faint) line of darker feathers connecting the malar regions across the chin. Specimens from southern Ecuador and north-western Peru (*C.* [*f.*] *caniceps*) were scored separately from north-western Ecuador (*C.* [*f.*] *berlepschi*), despite showing low genetic divergence, to illustrate plumage colour differences. Specimens from eastern Panama (*C.* [*f.*] *mirabilis*, Undescribed 1) were scored using non-fresh (faded) specimens (see text). Color scores from a 'brown type' unsexed specimen of *C.* [*f.*] *fuscater*, the only study skin of that taxon available for the formal analysis, are included below as 'female'.

Sex	*N*	Taxon	Crown	Back	tl-covs	Flanks	Breast	Throat	Chin
M	5	*C.* [*f.*] *hellmayri*	119[1]	119[1,3]	119A–C/ 27	121[2,4]	79/ 79[2]	119C[4]–79[2]	0–1
	2	Undescribed 1	119[1]	119[1,3]	119C	121[2,4]	119C[4]	119C[4]	1
	2	*C.* [*f.*] *mirabilis*	119[1]	119[1,3]	119B–C	121[2,4]	119C[4]	119C[4]	1
	2	*C.* [*f.*] *sanctaemartae*	119[1]	119[1,3]	119A	121[2,4]	79[2]	79[2]	1
	0	*C.* [*f.*] *fuscater*	–	–	–	–	–	–	–
	0	*C.* [*f.*] *opertaneus*	–	–	–	–	–	–	–
	2	Undescribed 2	219[2]	119A[1]	119B	121[2,4]	91	119D	1
	7	*C.* [*f.*] *berlepschi*	119[1]	119[1,3]	119A–D/ 27	121[2,4]	79/ 119D[4]	119D[4]	0–1
	3	*C.* [*f.*] *caniceps*	219[2]/ 119[4]	119/ 119[1,3]	119B–C/ 27	79–121	119D[5]	119D[5]	0–1
	8	Undescribed 3	119[1]	119[1,3]	119B	121[2,4]	79[2]	119D[4]	0
	9	*C.* [*f.*] *mentalis*	119[1]/ 219[2]	119[1]/ 219[2]	119A	121[2,4]	79[2]/ 91	79[5]/ 91	0–1
F	2	*C.* [*f.*] *hellmayri*	119[1]	119[1,3]	119C	121[2,4]	79[2]	119C[4]	0–1
	1	Undescribed 1	119	119	119B/ 119C	121[2,4]	119C[4]	119C[4]	1
	1	*C.* [*f.*] *mirabilis*	119[1]	119[1,3]	119B	121[2,4]	119C[4]	119C[4]	1
	1	*C.* [*f.*] *sanctaemartae*	119[1]	119[1,3]	119A	121[2,4]	79[2]	79[2]	1
	1	*C.* [*f.*] *fuscater*	219[2]	219[2]	–	121[2,4]	91[5]	91[5]	0
	0	*C.* [*f.*] *opertaneus*	–	–	–	–	–	–	–
	2	Undescribed 2	219[2]	119A[1]	119B	121[2,4]	91	119D	1
	1	*C.* (*f.*] *berlepschi*	119[1]	119[1,3]	27	121[2,4]	79	119D[4]	0
	4	*C.* [*f.*] *caniceps*	219[2]	119	119B–D/ 27	79–121	119D[5]	119D[5]	0
	9	Undescribed 3	219[2]	119	119B/ 27	121[2,4]	119C	119D[4]	0
	5	*C.* [*f.*] *mentalis*	219[2]	119A[1]	119A	121[2,4]	91/ 91[5]	91/ 91[5]	0

Notes: (1) same hue as 119, but approaching darkness value of Jet Black (89); (2) darker than the given value; (3) slightly paler than crown; (4) cooler (less warm) than the given value; (5) paler than the given value.

Geographic variation in song contours

We scored frequency contours for 435 songs in 194 audio recordings from the geographic ranges of 10 allopatric populations: *C.* [*f.*] *hellmayri* (*N* = 179 songs from 58 recordings); Undescribed 1 (*N* = 7 from 5); *C.* [*f.*] *mirabilis* (*N* = 24 from 11); *C.* [*f.*] *sanctaemartae* (*N* = 36 from 22); *C.* [*f.*] *fuscater* (*N* = 88 from 37); *C.* [*f.*] *opertaneus* (*N* = 15 from 11); Undescribed 2 (*N* = 8 from 4); *C.* [*f.*] *berlepschi* (*N* = 46 from 25); Undescribed 3 (*N* = 25 from 16); *C.* [*f.*] *mentalis* (*N* = 7 from 5). We detected a total of 30 contours (excluding single-note songs and treating five- and six-note contours as a single category; see Methods), representing 90.9% of the 33 contours detectable with our method (Fig. 12). The three contours (9.1%) that were not detected were tetradic patterns (ACBD, ADCB, BACD). Details about the distribution of specific contours are discussed below, within the relevant species accounts.

Species delimitation

Rationale for taxonomic revision

The *C.* [*fuscater*] complex is an ancient radiation of underappreciated complexity. Allopatric populations (hereafter 'taxa') are genetically divergent, differ in multiple phenotypic traits, and multiple lineages have been evolving independently since the Late Pliocene or Early Pleistocene (2–3 Mya). In plumage colour, the taxa in this complex exhibit an unprecedented and confusing degree of sexual and geographic variation, including subtle patterns of sexual polychromatism (*C.* [*f.*] *mentalis*), dichromatism (*C.* [*f.*] *fuscater*, Undescribed 1, Undescribed 3), and monochromatism (*C.* [*f.*] *hellmayri*, *C.* [*f.*] *mirabilis*, *C.* [*f.*] *sanctaemartae*, *C.* [*f.*] *berlepschi*, *C.* [*f.*] *opertaneus*, Undescribed 2). One taxon (Undescribed 3) is evidently divergent in the juvenile plumage (see below). Iris colour is monochromatic (white or brown) in some taxa, but dichromatic in other taxa, evidently to different degrees, and it is not indicative of age or sex in any taxon. White irides are rare among the Turdidae and in *Catharus* are only found in the *C.* [*fuscater*] complex (Clement 2000). Taxa in this complex also differ in the neotenous expression of black on the maxilla, which (when present) presumably obscures the signalling function of the bright red/orange bill (e.g. Bright and Waas 2002). Vocally, we found taxonomically informative variation in the acoustic structure of three different call types, which are presumed to be innate (not learned). We also found evidence that the acoustic structure of punctuation calls has been stable across multiple decades. Differences in the distributions of song

Figure 8. Side view of polychromatic adult plumages in *C.* [*f.*] *mentalis* (from left to right): 1, FMNH 433742, a 'grey' male with enlarged testes; 2, FMNH 433738, a 'brown' male with enlarged testes; 3, FMNH 364458, a 'brown' male with testes not enlarged; 4, FMNH 433740, an adult female with an enlarged ovary. Adults of both colour types (FMNH 433742, 433738) were collected at the same site in November 2001. Photograph by M.R.H.

Table 4. Taxonomic, sexual, and age-related variation in the extent of black on the maxilla, scored with five levels (see text) in a geographically broad sample of *C.* [*fuscater*] study skins ($N = 295$). The endpoints of the scale are no black (0) and completely black (4). Means (±SD) are shown for adults of each sex, and immatures (both sexes combined)

Taxon	Adult males		Adult females		Immatures	
	N	Score	*N*	Score	*N*	Score
C. [*f.*] *hellmayri*	43	2.23 ± 1.04	21	2.62 ± 1.2	9	4.0 ± 0.0
Undescribed 1	14	1.43 ± 0.65	10	2.80 ± 1.14	1	4.0
C. [*f.*] *mirabilis*	10	1.5 ± 0.53	4	2.75 ± 0.96	0	–
C. [*f.*] *sactaemartae*	16	0.75 ± 1.13	15	1.47 ± 1.13	1	4.0
C. [*f.*] *fuscater*	18	1.39 ± 0.70	4	3.0 ± 1.15	5	4.0 ± 0.0
C. [*f.*] *opertaneus*	1	4.0	1	4.0	1	4.0
Undescribed 2	2	4.0 ± 0.0	2	4.0 ± 0.0	0	–
C. [*f.*] *berlepschi*	12	3.58 ± 0.90	3	4.0 ± 0.0	6	4.0 ± 0.0
C. [*f.*] *caniceps*	16	2.63 ± 1.09	12	4.0 ± 0.0	7	4.0 ± 0.0
Undescribed 3	10	3.60 ± 0.52	9	3.89 ± 0.33	1	4.0
C. [*f.*] *mentalis*	14	2.29 ± 0.91	7	3.57 ± 0.79	8	4.0 ± 0.0

frequency contours, which are presumably learned (not innate) and thus susceptible to cultural evolution, were more subtle. In song, the most diagnosable groups were *C.* [*f.*] *hellmayri*, which had a greater diversity of tetradic song contours than any other taxon, and *C.* [*f.*] *fuscater* and *C.* [*f.*] *sanctaemartae*, which sang more ascending dyadic songs (AB) than any other taxon.

Social and reproductive behaviour in the genus *Catharus* is complex and apparently unusual among Neotropical thrushes (Stutchbury and Morton 2001, Greeney *et al.* 2015, Halley *et al.* 2016). At present, we have a poor understanding of how much divergence is necessary for vocalizations to be perceived as 'different enough' (heterospecific) by the birds themselves, much less how such vocalizations are interpreted in social contexts (*contra* Dilger 1956, Freeman *et al.* 2022). We encourage researchers to apply conservative interpretations of behaviour until more data are available. Few studies of colour-banded populations have been conducted to date (e.g. Beltrán and Kattan 2001, Greeney *et al.* 2015) and the influences of kinship and social dominance hierarchies on patterns

Table 5. Taxonomic variation in iris colour, scored with two levels (brown vs. white, see text) in a sample of *C.* [*fuscater*] study skins and digital photos ($N = 340$). Populations in which brown irides were detected in < 20% of specimens were categorized as 'monochromatic white' (mono white). Populations in which white irides were detected in < 20% of specimens were categorized as 'monochromatic brown' (mono brown). Populations in which brown and white irides were both detected at greater than 20% frequency are categorized as 'dichromatic'. The complete list of specimens and digital photos is provided in the Supporting Information, Table S1.

Taxon	Category	Total	Brown		White	
		N	*N*	%	*N*	%
C. [*f.*] *hellmayri*	mono white	230	4	1.7	226	98.3
Undescribed 1	mono white	8	0	0	8	100
C. [*f.*] *mirabilis*	mono white	2	0	0	2	100
C. [*f.*] *sanctaemartae*	mono white	34	4	11.8	30	88.2
C. [*f.*] *fuscater*	mono white	17	2	11.8	15	88.2
C. [*f.*] *opertaneus*	mono brown	7	7	100	0	0
Undescribed 2	dichromatic	5	2	40	3	60
C. [*f.*] *berlepschi*	mono white	37	1	2.7	36	97.3
C. [*f.*] *caniceps*	dichromatic	12	4	33.3	8	66.7
Undescribed 3	dichromatic	19	9	47.4	10	52.6
C. [*f.*] *mentalis*	mono brown	23	19	82.6	4	17.4

of cooperative parental care, vocal behaviour, and territoriality have barely been explored (e.g. Heckscher 2007, Halley 2014, Greeney *et al.* 2015, Halley *et al.* 2016, Dyrcz *et al.* 2015).

Here, we have demonstrated an exceptional degree of genetic and phenotypic variation in the *C.* [*fuscater*] complex, which exceeds the predictions of the traditional null hypothesis of the BSC as applied to allopatric populations (e.g. Mayr 1940; but see: Gill 2014). Each of these taxa easily satisfy the most inclusive criteria for species rank (USC; de Quieroz 2005, 2007), and in most cases they satisfy the criteria of the PSC (Cracraft 1987), ESC (Wiley 1978), and many other species concepts, including most interpretations of the BSC in allopatry. Nevertheless, we acknowledge that our sample sizes of genetic and/or vocal data were too small to confidently assign species rank to some taxa (i.e. under the criteria outlined in the Methods), although we suspect that additional research will support doing so. For example, we lacked UCE data for *C.* [*f.*] *sanctaemartae* and *C.* [*f.*] *fuscater*, and had only one sample of *C.* [*f.*] *sanctaemartae* in the *ND2* dataset—too few samples to even establish its identity as a clade, although this was already accomplished by Cuervo (2013). Similarly, too few specimens and recordings were available to determine whether *C.* [*f.*] *opertaneus* and Undescribed 2 (sister-taxa in the UCE tree), and *C.* [*f.*] *berlepschi* and Undescribed 3 (sister-taxa in the UCE tree), were vocally divergent from each other, although in both cases available (genetic) evidence is sufficient to distinguish them as sister subspecies. Despite these limitations, our data considerably advance a scientific knowledge of geographic variation in the *C.* [*fuscater*] complex, sufficient to conservatively revise the taxonomy and set the stage for future systematics and population genetics research.

Therefore, we propose a taxonomic revision that elevates seven taxa, formerly treated as subspecies, to species rank. We also formally describe one new species (Undescribed 1) and two new subspecies (Undescribed 2, Undescribed 3), which were not previously recognized as taxonomic units. We follow a 'linearized' phylogenetic arrangement in the remainder of the paper, which, probably for biogeographic reasons, approximately parallels the geographic distribution of taxa from north to south. To supplement the revision, we also propose new English names for each species and recommend the retirement of the name 'Slaty-backed nightingale-thrush' to avoid confusion with past uses.

Order Passeriformes

Family Turdidae

Catharus hellmayri Berlepsch 1902

Talamanca nightingale-thrush

(Fig. 13)

Catharus fuscater hellmayri Berlepsch 1902: 69; Ridgway 1907: 24; Carriker 1910: 748; Nelson 1912: 24; Hellmayr 1934: 464; Slud 1964: 301; Wetmore *et al.* 1984: 155; Ridgley and Gwynne 1989: 352; Phillips 1991: 112; Clement 2000: 299; Collar 2005: 700; Halley 2020; Halley 2021.

Catharus fuscater Salvin 1867: 132; Lawrence 1868: 9; Frantzius 1869: 289; Salvin 1870: 180; Salvin and Godman 1879: 5 (in part); Ridgway 1881: 333; Zeledon 1885: 104; Bangs 1902: 50; Meyer de Schauensee 1964: 317 (in part); Powell 1979; Stiles and Skutch 1989: 368; Loiselle and Blake 1991; Young *et al.* 1993; Wolfe *et al.* 2009; Bueter *et al.* 2009; Jankowski *et al.* 2010; Kounek *et al.* 2013.

Catharus hellmayri Sharpe 1902: 182; Davis 1972: 176.

Type material

Monotypic species. SMF 53156 (holotype), study skin, adult male, collected by E. Gounelle in 'Panama, Veragua, Chiriquí'. This specimen was not examined in this study. Label data were provided by G. Mayr (*in litt.*).

Geographic range

Northern mountains of Costa Rica (Rincón de la Vieja, Miravalles, Tenorio) to west-central Panama (Parque Nacional Santa Fé, Veraguas).

Adult specimens examined

Catharus hellmayri ($N = 64$): Costa Rica ($N = 34$): Cartago (five males, two females): 'Aqinares' (=Aquiares): AMNH 391543 (male); Cervantes: USNM 49152 (female); Juan Vinas: CM P28231 (male); Navarro: AMNH 391541 (male), AMNH 391542 (female); Santa Cruz de Turrialba: AMNH 391544 (male); Tierra Blanca: CM P11045 (male); Heredia (seven males, one female): Cariblanco de Sarapiquí: ANSP 67249, CM P25349, P25362, P25368, USNM 199697 (males), AMNH 503920 (female); unknown site about 24 km. N. of San José: AMNH 391539, AMNH 391540 (males); San José (13 males, six females): Carrillo: AMNH 503916–503918 (males); Guayabo: AMNH 391536 (male); La Guaria de Dota: USNM 209929 (male), USNM 209928 (female); La Hondura: AMNH 391537, CM P26384, P26393, P26414, P26423, P26434,

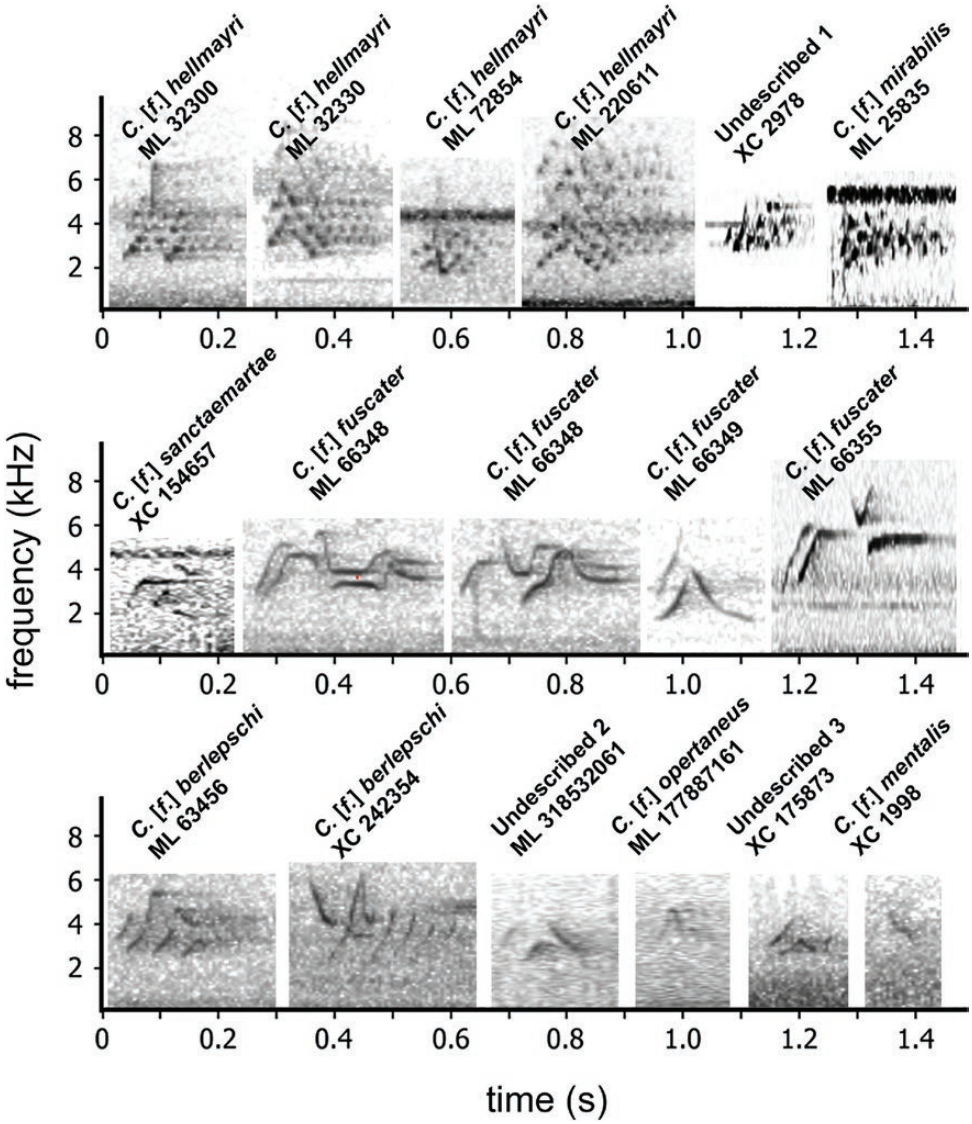

Figure 9. Taxonomic variation in the structure of 'punctuation calls', visualized in RavenPro 1.5 (Cornell University). We recognize three groups based on shared acoustic structure: (Type 1) pulsed/rippling: *C.* [*f.*] *hellmayri*, Undescribed 1, *C.* [*f.*] *mirabilis*; (Type 2) long/sinuous: *C.* [*f.*] *sanctaemartae*, *C.* [*f.*] *fuscater*, *C.* [*f.*] *berplepschi*; (Type 3) short/simple: Undescribed 2, *C.* [*f.*] *opertaneus*, Undescribed 3, *C.* [*f.*] *mentalis*.

P26445, P26535 (males), AMNH 391538, CM P26108, P26550, P26581 (females); unknown locality (one female): USNM 68172. Panama (N = 30): Chiriquí (11 males, seven females): Boquete: AMNH 503911–503913, FMNH 24305 207592 207595, USNM 188572 188573 (males), FMNH 53580, USNM 188570, USNM 188571, AMNH 503814 (females); 12.6 km north of Los Planes, Gualara-Chiriquí Grande Road: USNM 607605 (male), USNM 607614 (female); unknown site 23.3 km north of Los Planes, Gualara-Chiriquí Grande Road: USNM 607617 (male); Reserva Forestal Fortuna: FMNH 470768 (male), FMNH 470767 (female); Veraguas (seven males, six females): AMNH 246360–246366 (males), AMNH 187643, AMNH 246367–246371 (females).

Immature specimens examined

Catharus hellmayri (N = 8): Costa Rica (N = 6): Heredia (three females): Cariblanco de Sarapiquí: AMNH 503919, CM P25344, P25363 (females); San José (two males): Guayabo: AMNH 391534, 391535 (males); Unknown Province: Cusoua, La Palma: USNM 85546 (male). Panama (N = 2): Chiriquí (two females): Boquete: FMNH 207593 207594 (females).

Audio recordings examined

Catharus hellmayri (N = 63): Costa Rica (N = 51): Alajuela: Bosque de Paz Biological Reserve: XC 107128; Monteverde: XC 220593; Parque Nacional Juan Castro Blanco, sector Volcán Viejo: ML 64132091; Volcán Tenorio: XC 166201, 166202; Cartago: Orosi: XC 169247; Parque Nacional Tapantí: ML 48406801, XC 274444, 274445, 274447, 274448; Heredia: Braulio Carrillo, Carretera: ML 28234; Puntarenas: Monteverde: ML 28202, 28263, 28264, 28269, 32268, 32300, 32309, 32327, 32328, 32330, 32701, 32715, 53950, 53951, 56198, 72831, 72839, 72844, 72850, 72854, 74195, 76697,

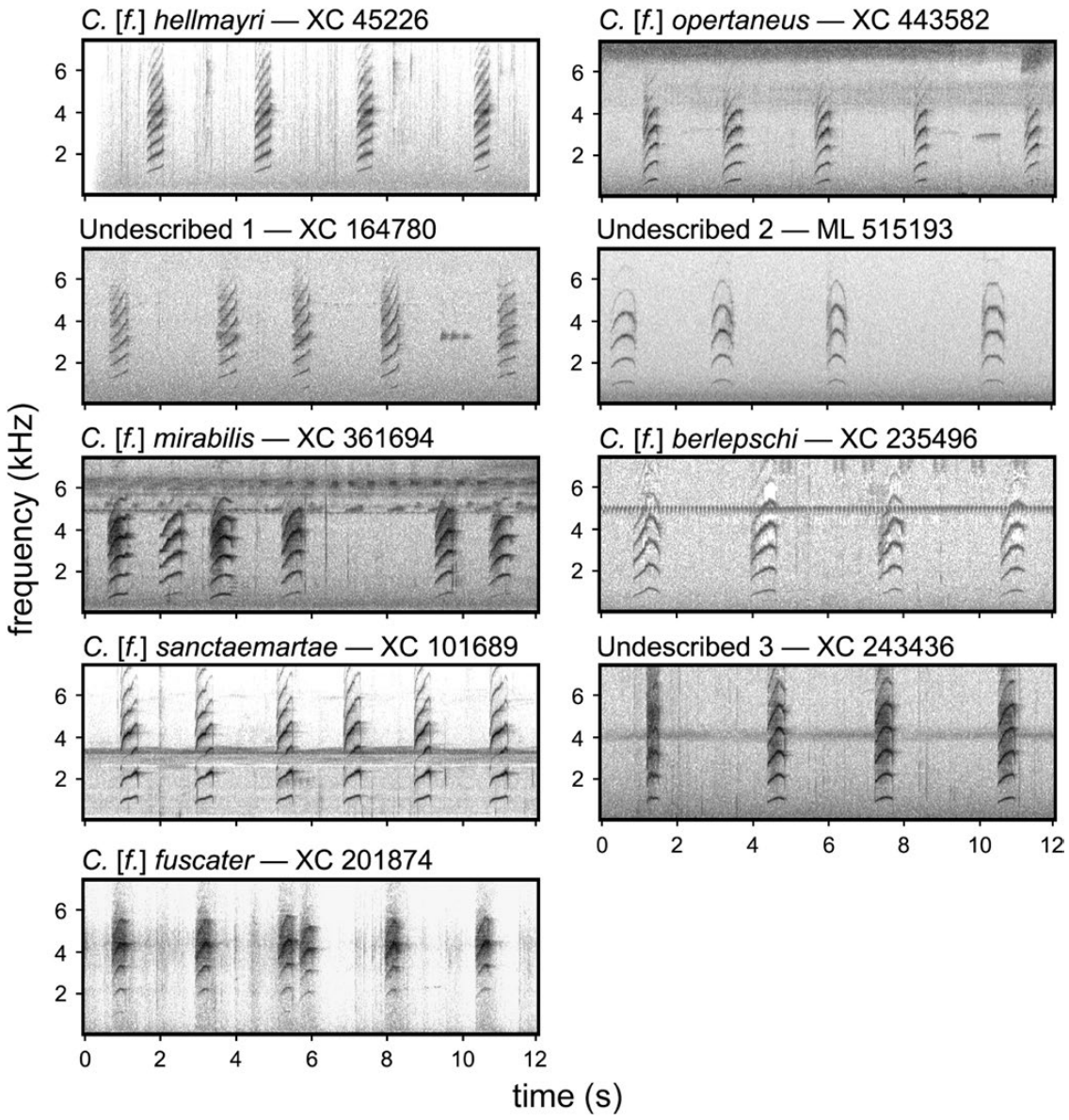

Figure 10. Taxonomic variation in the structure of 'contact calls', visualized in RavenPro 1.5 (Cornell University). No recording of contact calls in *C.* [*f.*] *mentalis* was available.

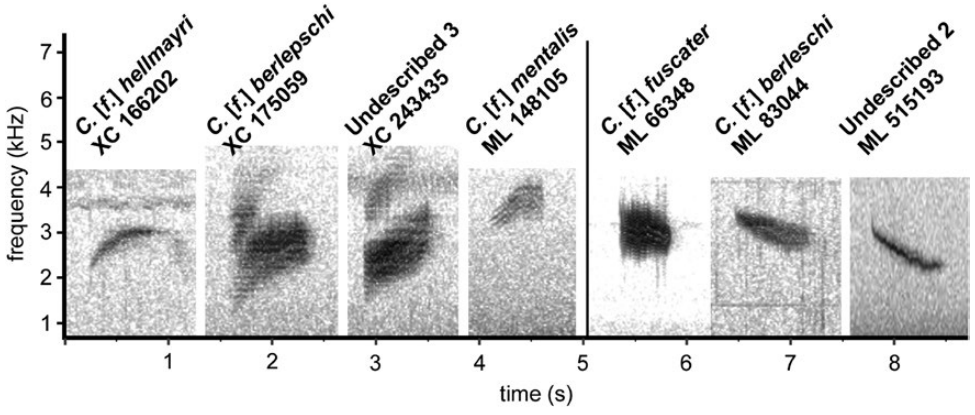

Figure 11. Taxonomic variation in the structure of 'blurred calls', visualized in RavenPro 1.5 (Cornell University). The black line divides calls that modulate upward in frequency (left) and downward in frequency (right); both types were detected in *C.* [*f.*] *berlepschi*.

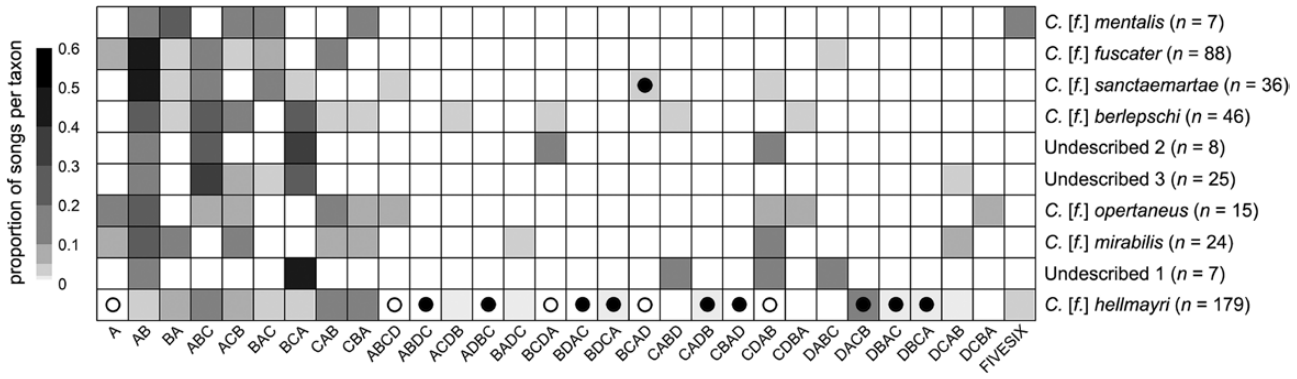

Figure 12. Heat map showing frequency distributions of song contours within each population. Dyadic, triadic, and tetradic song contour names follow Fig. 5. Single-note songs are shown in the first column (A) and songs with five or six notes were combined into a single category, shown in the last column (FIVESIX). Open (white) circles denote song contours that were not detected in *C.* [*f.*] *hellmayri*, despite it having a much larger sample size than other taxa. Closed (black) circles denote contours that were only detected in one taxon.

76699, 76703 209231 209234 209242 209244, 219846, 220560, 220582, 220611, 220633, XC 45226, 137776, 593699; San José: Monserrat de Coronado: ML 59585321; San Gerardo de Dota: XC 107125, 107127. Panama (N = 12): Chiriquí: Boquete: XC 133595; Continental Divide, along Gualaca-Chiriquí Rd.: ML 54410; Kakintú: XC 112998; Los Planes, Fortuna Field Station: ML 54207, 54225, 54391, 54427; Reserva Forestal de Fortuna: XC 271146, 271147, 367649; Ngäbe-Buglé: Cerro Colorado: XC 78388, 145618.

Diagnosis

Genetics: In both phylogenetic reconstructions, samples from the range of *C. hellmayri* formed a clade that was sister to the rest of the ingroup. ABGD and ASAP analyses both identified *C. hellmayri* as an independent genetic cluster. The estimated divergence time between *C. hellmayri* and the rest of the complex was 3.2 Mya (range = 2.6–3.8) and it was highly divergent from its closest geographic neighbours, *C.* [*f.*] *mirabilis* (mean uncorrected *p*-distance = 0.075) and Undescribed 1 (mean uncorrected *p*-distance = 0.076).

Morphology: Study skins of *C. hellmayri* have darker ventral plumage than any other taxon, except *C.* [*f.*] *sanctaemartae* (Fig. 13); less black on the chin than *C.* [*f.*] *sanctaemartae*; and shorter tails on average than any other taxon (see: Hellmayr 1934).

Voice: Catharus hellmayri is distinguished from the South American taxa by its Type 1 punctuation call structure (Fig. 9), 'tightly spaced' contact call structure (Fig. 10), and greater diversity of song contours (Fig. 12). It was the only taxon with a narrow-bandwidth blurred call that rose in pitch (Fig. 11). The song contour DACB accounted for 15% of songs in *C. hellmayri* (N = 27/179), but was not detected in any other clade.

Etymology

The proposed English name references the Cordillera de Talamanca, which encompasses nearly the entire range of *C. hellmayri*.

Catharus arcanus sp. nov.

Darién nightingale-thrush

(Figs 13, 14; formerly Undescribed 1)

urn:lsid:zoobank.org:act:25B3DB71-FE5E-4FBF-A2CE-8D270CBA7250.

Catharus fuscater Meyer de Schauensee 1964: 317 (in part).
Catharus fuscater fuscater Wetmore *et al.* 1984: 157; Ridgely and Gwynne 1989: 352; Clement 2000: 299 (in part); Collar 2005: 700 (in part); Renjifo *et al.* 2017.
Catharus fuscater hellmayri Clement 2000: 299 (in part).
Catharus fuscater mirabilis Clement 2000: 299 (in part).
Catharus fuscater subsp.? Phillips 1991: 112.
'Unnamed-1' Halley 2021: 132.

Type material

Monotypic species. FMNH 470769 (holotype), study skin, adult male, collected by J. Klicka (preparator), G.M. Spellman, and J.M. DaCosta on Cerro Chucantí, 17 km south-west of Chimán, Panamá province, Panama (8.7958°, –78.4630°, elev. 1200 m), on 16 February 2006.

Geographic range

Serranía de Majé, Panama, and along the Serranía del Darién from Cerro Azul in the west, to Cerro Tacarcuna in the east (Wetmore *et al.* 1984, Cuervo 2013, Renjifo *et al.* 2017).

Adult specimens examined

Catharus arcanus sp. nov. (N = 25): Panama: Panamá (one male, one female): Cerro Chucantí: FMNH 470769 (male); NW slope of Cerro Jefe: LSUMZ 164300 (female); Darién (14 males, nine females): unspecified locality on Cerro Tacarcuna, eastern slope: AMNH 136159–136165 (males), AMNH 136166 (female); unspecified locality on Cerro Tacarcuna, slope unknown: AMNH 136171, 811713, LSUMZ 80201 (males), AMNH 136167–136170, AMNH 811714 (females); La Laguna Camp on Cerro Tacarcuna: USNM 469735 (male), USNM 486474 (female); unspecified locality on Cerro Malí: USNM 484791, USNM

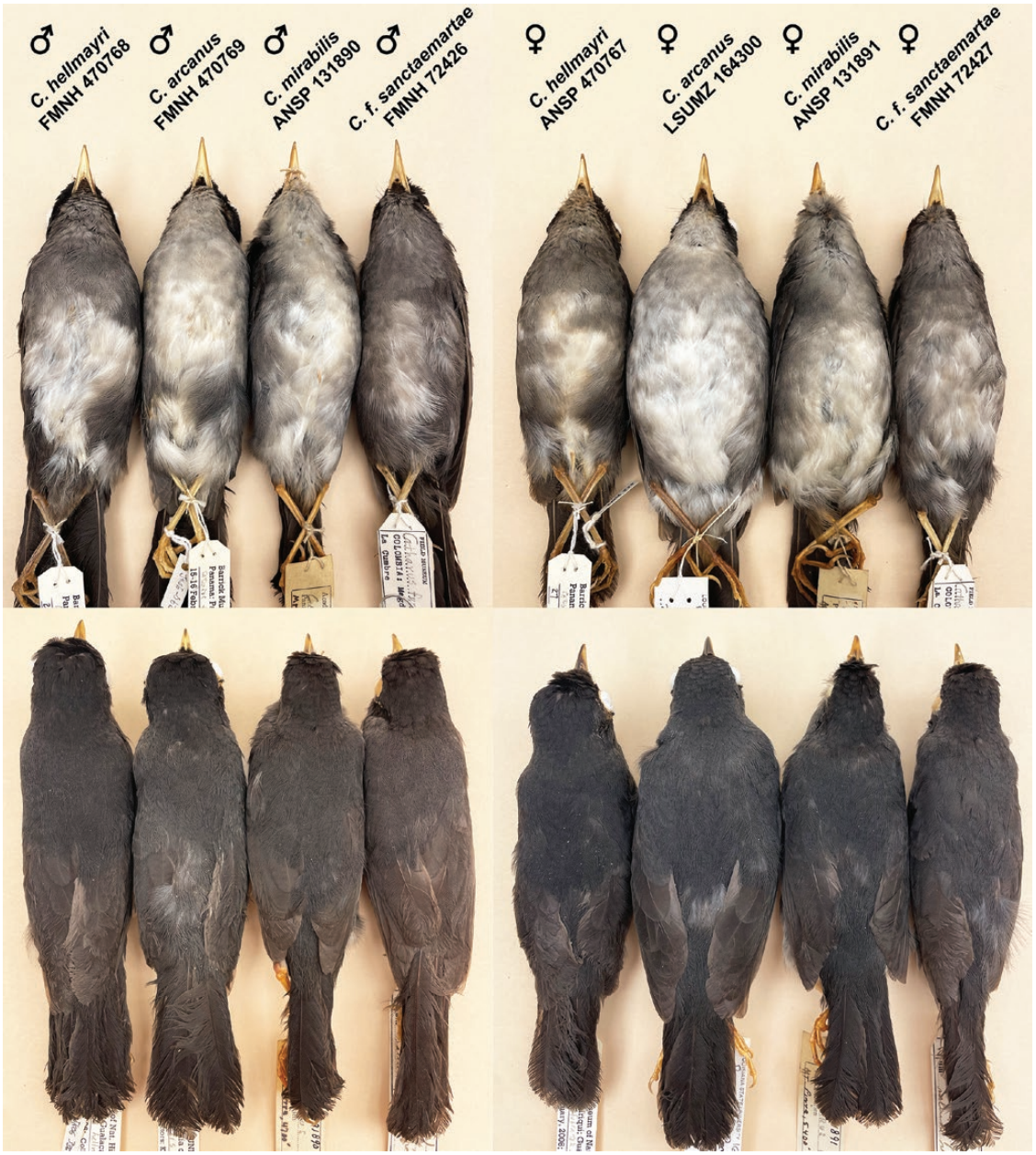

Figure 13. Dorsal and ventral views of the adult plumages in *C. hellmayri*, *C. arcanus* sp. nov., *C. mirabilis*, and *C. f. sanctaemartae*. Photograph by M.R.H.

484792 (males), USNM 484793 (female); unspecified locality on ridge west of Cerro Malí: USNM 486473 (male).

Immature specimens examined

Catharus arcanus sp. nov. ($N = 1$): Panama: Darién (one male): La Laguna Camp, Cerro Tacarcuna: USNM 486475 (male).

Audio recordings examined

Catharus arcanus sp. nov. ($N = 6$): Panama: Darién: Cerro Chucantí: ML 137736401, XC 2976–2979, 164780.

Diagnosis

Genetics: In both phylogenetic reconstructions, samples of *C. arcanus* sp. nov. formed a clade that was sister to *C.* [*f.*] *mirabilis* of Cerro Pirre (mean uncorrected *p*-distance = 0.04 ± <0.01). In the UCE tree, these taxa were reciprocally monophyletic and formed a clade that was sister to all South American taxa. ABGD and ASAP analyses both identified *C. arcanus* sp. nov. and *C.* [*f.*] *mirabilis* as independent genetic clusters. The estimated divergence time between *C. arcanus* sp. nov. and *C.* [*f.*] *mirabilis* was 1.3 Mya (95% HPD = 0.9–1.7).

Morphology: Adult study skins of *C. arcanus* sp. nov. are paler on the dorsal surface than similarly-aged skins of *C. hellmayri* and *C.* [*f.*] *mirabilis*, in both sexes (Fig. 13). Unlike adult females of *C.* [*f.*] *mirabilis*, which had darker crowns than mantles, there was no contrast between the pale crown and mantle of the *C. arcanus* sp. nov. adult female (LSUMZ 164300), which had an enlarged ovary (11 × 5 mm), 100% pneumatized skull, and no bursa. Ventrally, study skins of *C. arcanus* sp. nov. and *C.* [*f.*] *mirabilis*

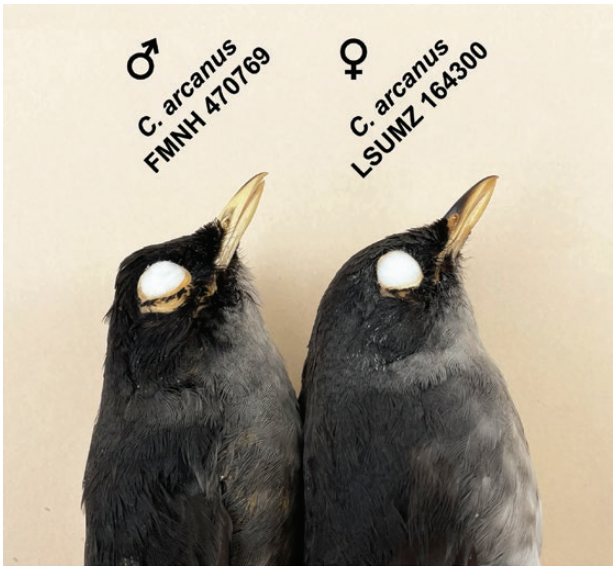

Figure 14. Side view of the adult plumages in *C. arcanus* sp. nov.. Photograph by M.R.H.

were paler than *C. hellmayri* (Fig. 13). Like *C.* [*f.*] *mirabilis* (and to a lesser extent *C. hellmayri*, see: Ridgley and Gwynne 1989), *C. arcanus* sp. nov. has a yellowish wash on the ventral surface in life, that renders the breast 'olive' and abdomen 'pale yellow' (*fide* E. Eisenmann, on the label of AMNH 811714). Similar notes were written on the labels of LSUMZ 80201 ('Yellowish olive instead of grey underneath in fresh specimens') and AMNH 811713 ('olive yellowish instead of grey underneath'). This character distinguishes these three taxa from all South American populations, but the yellow wash fades quickly after death. After a few years, museum skins of *C. arcanus* sp. nov. have no trace of yellow in the ventral plumage and the 'olive' fades to cooler than Light Drab (119C). To our knowledge, no fresh (<5 years old) material of *C. arcanus* sp. nov. or *C.* [*f.*] *mirabilis* exists in any collection.

Voice: Catharus arcanus sp. nov. is distinguished from the South American taxa by its Type 1 punctuation call structure (Fig. 9), and from *C.* [*f.*] *mirabilis* by its 'tightly spaced' contact call structure (Fig. 10). Our dataset lacked recordings of blurred calls from *C. arcanus* sp. nov., and too few recordings were available to adequately determine whether *C. arcanus* sp. nov. and *C.* [*f.*] *mirabilis* are divergent in song. Notwithstanding, the only triadic song contour (BCA) detected in *C. arcanus* sp. nov., which accounted for 43% of songs ($N = 3/7$), was not detected in *C.* [*f.*] *mirabilis*. Of the three tetradic contours detected in *C. arcanus* sp. nov. (CABD, CDAB, DBAC), only one (CDAB) was detected in *C.* [*f.*] *mirabilis* (Fig. 12).

Description of the holotype

FMNH 470769 weighed 37.9 g before it was prepared. The testes were slightly enlarged (2 × 1 mm) and the skull was completely pneumatized. In 2022, the entire dorsal surface of FMNH 470769 was darker than Sepia (119), with the crown being slightly darker than the back and rump. The undertail coverts were Light Drab (119C) and the flanks were darker and cooler than Vandyke Brown (121). The breast and throat were darker than Light Drab (119C). A fine black line connected the malar regions across the throat.

Etymology

The scientific name is derived from masculine Latin adjective *arcanus* (mysterious, secret), referring to the retiring nature of the species. The proposed English name references the Serranía del Darién, which encompasses most of its geographic range.

Comments

The sister-species *C. arcanus* sp. nov. and *C.* [*f.*] *mirabilis* are separated by only 125 km on the Isthmus of Panama and there is no major water barrier between them. The palynological record in lowland Panama, from the Last Glacial Maximum (LGM), includes elements of the montane flora that now occur > 1000 m higher in elevation (Bush and Colinvaux 1990). Given these facts, and the age of the divergence, it seems likely that these mountain-bound species had opportunities for secondary contact in the Darién lowlands during the LGM, and have already passed historical 'tests' of sympatry.

Catharus mirabilis Nelson 1912

Pirre nightingale-thrush

(Fig. 13)

Catharus fuscater mirabilis Nelson 1912: 24; Deignan 1961: 430; Ridgley and Gwynne 1989: 352; Phillips 1991: 112; Clement 2000: 299 (in part); Collar 2005: 700; Halley 2020; Halley 2021.
Catharus fuscater fuscater Hellmayr 1934: 465.
Catharus fuscater Meyer de Schauensee 1964: 317 (in part); Robbins *et al.* 1985.

Type material

Monotypic species. USNM 232933 (holotype), study skin, adult male, collected by E.A. Goldman (original no. 15534) at 1585 m elevation on Cerro Pirre, Darién, Panama, near the head of the Río Limón, on April 18 1912 (see: Deignan 1961: 430). Nelson (1912) also listed the following specimens, which are paratypes ($N = 11$): USNM 232600, 232927–232932, 232934–232936. The type series was examined by M.R.H. on 23 October 2013.

Geographic range

Endemic to Cerro Pirre, Darién province, Panama, where it is fairly common on the eastern slope from 1000 to 1500 m (Robbins *et al.* 1985).

Adult specimens examined

Catharus mirabilis ($N = 14$): Panama: Darién (10 males, four females): Cerro Pirre: USNM 232927–232933, 232936, ANSP 131889, 131890 (males), USNM 232600, 232934, 232935, ANSP 131891 (females).

Audio recordings examined

Catharus mirabilis ($N = 15$): Panama: Darién: Cerro Pirre: ML 25790, 25807, 25814, 25835, 25872, 60762, 105199, 286837, 286854, 286865, XC 10493, 220586–220588, 361694.

Diagnosis

Genetics: In both phylogenetic reconstructions, samples of *C. mirabilis* formed a clade that was sister to *C. arcanus* sp. nov. (mean uncorrected *p*-distance = 0.04 ± <0.01). In the UCE tree, these taxa were reciprocally monophyletic and formed a clade that was sister to all South American taxa. ABGD and ASAP analyses of *ND2* data both identified *C. mirabilis* and *C. arcanus* sp. nov. as independent genetic clusters. The estimated divergence time between these sister-taxa was 1.3 Mya (95% HPD = 0. 9–1.7).

Morphology: Study skins of *C. mirabilis* were darker, and in adult females showed more contrast between the mantle and crown, than *C. arcanus* sp. nov (Fig. 13). Study skins of *C. mirabilis* and *C. arcanus* sp. nov. were ventrally paler than *C. hellmayri* specimens collected the same year (Fig. 13). As mentioned previously, the ventral surface of *C. mirabilis* is 'distinctly yellowish … on the under parts of the head, neck, and body' (Nelson 1912), similar to *C. arcanus* sp. nov. and (to a lesser extent) *C. hellmayri*. This rapidly fading character distinguishes these three taxa from the South American taxa.

Voice: Catharus mirabilis was distinguished from all other taxa by the combination of a Type 1 punctuation call structure (Fig. 9) and 'widely spaced' contact call structure (Fig. 10). Our dataset lacked recordings of blurred calls from *C. mirabilis*. Too few recordings were available to determine whether *C. mirabilis* and *C. arcanus* sp. nov. are divergent in song. Of the three triadic contours (ACB, CAB, CBA) detected in *C. mirabilis*, none were shared with *C. arcanus* sp. nov.. Of the three tetradic contours (BADC, CDAB, DCAB) detected in *C. mirabilis*, only one (CDAB) was detected in *C. arcanus* sp. nov. (Fig. 12).

Comments

According to published descriptions, the eggs of *C. mirabilis* ('very pale greenish white, spotted lightly with dots of cinnamon-brown, which are grouped to form a faintly-indicated cap on the summit of the blunt end', Wetmore *et al.* 1984: 157) are patterned differently than the eggs of *C. hellmayri* ('pale blue, thickly speckled and dotted and blotched over the entire surface with light chestnut-rufous', Carriker 1910: 748). Egg colour and pattern have been used previously to distinguish morphologically similar *Catharus* species (e.g. *C. occidentalis* and *C. frantzii*; Phillips 1969). More research is needed.

Etymology

The proposed English name refers to Cerro Pirre, where *C. mirabilis* is endemic.

Catharus fuscater (Lafresnaye 1845)

Cordilleran nightingale-thrush

(Fig. 13)

Myioturdus fuscater Lafresnaye 1845: 341.

Catharus fuscater Sclater 1859b: 324 (in part); Salvin and Godman 1879: 5 (in part); Seebohm 1881: 285 (in part); Bangs 1899: 108; Allen 1900: 183; Berlepsch 1902; Sharpe 1902: 181; Meyer de Schauensee 1966: 412 (in part); Meyer de Schauensee 1970: 342 (in part); Hilty and Brown 1986; Ridgley and Tudor 1989: 109 (in part); Boesman 1998; Hilty 2003, Naveda-Rodríguez and Bisbal 2008; Biancucci and Martin 2010; López-O. *et al.* 2014; Remsen *et al.* 2023 (in part).

Catharus fuscater sanctae-martae Ridgway 1904: 112; Todd and Carriker 1922: 405; Hellmayr 1934: 465; Meyer de Schauensee 1950: 922; Meyer de Schauensee 1964: 317 (in part).

Catharus fuscater fuscater Bangs 1930: 332; Hellmayr 1934: 465; Meyer de Schauensee 1950: 922; Meyer de Schauensee 1964: 317; Ginés *et al.* 1953: 188; Wetmore 1955; Hilty and Brown 1986: 543; Fjeldså and Krabbe 1990: 554 (in part); Clement 2000: 299 (in part); Collar 2005: 700 (in part); Halley 2020; Halley 2021.

Catharus fuscater sanctaemartae Cracraft 1985: 57; Hilty and Brown 1986: 543; Ridgley and Tudor 1989: 109; Fjeldså and Krabbe 1990: 554; Clement 2000: 299; Collar 2005: 700; Strewe and Navarro 2003; Halley 2020; Halley 2021.

Type material

Catharus f. fuscater: MCZ 76525 (holotype), study skin, collected 'ad Bogotám' (=Bogotá, Colombia) and exported to France, where it was accessioned (original no. 3544) into the private collection of Lafresnaye (see: Bangs 1930: 332; Halley 2021: 64). The precise type locality remains uncertain, because many 'Bogotá' trade skins were not collected in the immediate vicinity of the city. This specimen was not examined in this study.

Catharus f. sanctaemartae: CM 8797 (holotype), study skin, adult male, collected by 'Mrs H. H. Smith' (=Amelia 'Daisy' Woolworth Smith) in 'Elheibano' (=El Líbano, see: Paynter 1997: 132), Magdalena, Colombia, on 22 April 1899; chosen from a series of 10 skins reported by Allen (1900), of which the remaining nine skins are paratypes: AMNH 72219–72224, 72226, 72227, 97770. For this study, MRH examined the holotype on 8 February 2023.

Geographic range

Catharus f. fuscater: Sierra de Perijá of Venezuela (Zulia), northern Andes of Venezuela (southern Táchira to southern Lara) and Colombia (Cesar and La Guajira), eastern Andes of Colombia (Norte de Santander south to Bogotá); inhabits montane forests between 1500 and 2900 m (Hilty 2003).

Catharus f. sanctaemartae: Sierra Nevada de Santa Marta of north-eastern Colombia; inhabits forests of the Subtropical Zone from 600 to 2100 m (Ridgway 1904, Todd and Carriker 1922).

Adult specimens examined

Catharus f. fuscater (*N* = 24): Colombia (*N* = 20): Boyacá (three males): Peña Blanca: CM P59638, P59738, P59739 (males); Casanare (one male): Río Negro: CM P59940 (male); La Guajira (four males, one female): Laguna de Junco, Cerro Pintado, Sierra Perijá: USNM 374606, 374607 (males); La Africa, south of Villanueva, Sierra Perijá: USNM 374611, 374612 (males), USNM 374609 (female); Magdalena (two males, one female): Monte Elias, Sierra Negra, south-east of

Fonseca: USNM 369688, 369689 (males); Sierra Perijá, above Airoca: USNM 374608 (female); Norte de Santander (five males, two female): Buenos Aires, on the Abrego-Sardinata highway: USNM 397776, 398778, 398779 (males), USNM 398780 (female); Las Ventanas: CM P57684 (female); Ocaña: CM P55137 (male); Pueblo Nuevo: CM P55260 (male); Santander (one male): Cachirí: CM P58600 (male); Unknown Department: ANSP 16106 (unsexed). Venezuela ($N = 2$): Mérida (one male): La Cutata: AMNH 503904 (male); Trujillo (one male): Guamito: CM P88902 (male).

Catharus f. sanctaemartae ($N = 33$): Colombia ($N = 33$): Magdalena (eight males, eight females): Cuchilla de San Lorenzo: CM P41731, USNM 387888, 387889 (females); El Líbano: AMNH 72224, 72226, CM P8797 (males), AMNH 72220, 72227, CM P8834 (females); La Cumbre: FMNH 72426 (male), FMNH 72427 (female); Las Taguas: CM P37834 (male); Pueblo Viejo (N slope on Río San Miguel): CM P44941 (female); San Miguel: ANSP 63298, CM P45092 (males); unspecified locality: CM P38599 (male); Cesar (nine males, eight females): Chendua, on the Río Guatapurí: USNM 387891, 387893–387896, 387900 (males), USNM 384177, 384179, 387892, 387897–387899 (females); Pueblo Bello, Chinchicua, San Sebastián Track: USNM 387902, 387903 (males), USNM 387901 (female); San José, on the Río Guatapurí: USNM 384178 (male); Valparaíso: AMNH 72219 (female).

Immature specimens examined

Catharus f. fuscater ($N = 5$): Colombia: Magdalena (two males, one female): Monte Elias, Sierra Negra, south-east of Fonseca: USNM 369692, 369691 (males), USNM 369690 (female); La Guajira (one female): La Africa, south of Villanueva, Sierra Perijá: USNM 374610 (female); Norte de Santander (one female): Buenos Aires, on the Abrego-Sardinata highway: USNM 398777 (female).

C. f. sanctaemartae ($N = 0$).

Audio recordings examined

Catharus f. fuscater ($N = 37$): Colombia ($N = 17$): Boyacá: Garagoa: XC 562817; Miraflores: Reserva Sucuncuca: ML 178609131; Cesar: Serrania del Perijá: Chamicero del Perijá Proaves Reserve: ML 104944281, 104944491, XC 693383, 693385; Manaure: ML 204647 204669 204676 192628511, XC 511581; Sabana Rubia Rd.: XC 201876; Meta: San Juanito: XC 523041; Santander: El Tope: ML 89839571. Venezuela ($N = 20$): Lara: Parque Nacional Yacambú: XC 220582, 220583, 220591; Mérida: Cardenal Quintero: XC 387113; El Morro (Aricaqua Rd.): XC 220580; La Azulita Rd (near Mérida): ML 55724, 66350; La Carbonera: ML 66351–66356; Pico Humboldt Trail: ML 55730; UAL Forest Trail: ML 64833; Santo Domingo: XC 105423; Táchira: Matamula: XC 220579; Páramo Zumbador: ML 66348, 66349; Trujillo: Parque Nacional Guaramacal: ML 151295441, 157081451, XC 220581, 471156.

Catharus f. sanctaemartae ($N = 28$): Colombia: Magdalena: Cuchilla de San Lorenzo: ML 211710, 211778, 515400, 515410, XC 45455, 45456, 56808, 56810, 74777, 220584, 235616; Reserva Natural El Dorado: ML 215345031, XC 16014, 43477, 43478, 43550, 75357, 101689, 143821, 154657, 165105, 312974, 312975, 316751, 465174, 481613 191687 191688.

Diagnosis

Genetics: In the *ND2* reconstruction, samples from the range of *C. f. fuscater* formed a clade that was sister to a single sequence of *C. f. sanctaemartae* (mean uncorrected *p*-distance = 0.02 ± <0.01), with an estimated divergence of 0.7 Mya (95% HPD = 0.31–1.21). This corroborates Cuervo (2013), who found that *C. f. fuscater* and *C. f. sanctaemartae* were sisters, with broader sampling of *ND2* sequences from within the range of *C. f. fuscater*. ABGD analysis of *ND2* data identified *C. f. sanctaemartae* as an independent genetic cluster, but ASAP analysis merged it with *C. f. fuscater*. We lacked UCE data for *C. f. fuscater* and *C. f. sanctaemartae*, so further research will be needed to confirm their sister relationship, to determine their placement in the broader phylogeny of the complex, and to evaluate whether *C. f. sanctaemartae* is deserving of species rank.

Morphology: Unlike *C. f. sanctaemartae*, the phenotype of *C. f. fuscater* shows puzzling patterns of dichromatism. An unsexed specimen (ANSP 16106) from 'Santa Fe [de Bogotá]' in 'New Grenada' closely resembles 'brown type' males and female specimens of *C.* [*f.*] *mentalis* (e.g. FMNH 433738, 433740) and an individual from Cesar, Colombia, has a brownish dorsal surface (ML 4670402810). In contrast, *C. f. fuscater* adults in the CM collection, collected in Santander and Norte de Santander, Colombia, show no brown on the dorsal surface, although in only one case were multiple individuals collected at the same site. Specimens of *C. f. sanctaemartae* have darker ventral plumage than any other taxon, including *C. f. fuscater* (Fig. 13), rivalled only by *C. hellmayri*, from which it is distinguished by having more black on the chin (Todd and Carriker 1922) and a longer tail (Hellmayr 1934). We lacked fresh specimens of *C. f. sanctaemartae*, so were unable to thoroughly evaluate the claim that males are 'darker and more richly coloured' than females (i.e. a reported difference in brightness, not hue; Allen 1900, Todd and Carriker 1922). However, no clear differences in plumage colour or brightness are evident in male and female specimens collected by Carriker on 16 May 1925, at La Cumbre, Magdalena, Colombia (FMNH 72426, 72427).

Voice: The combination of Type 2 punctuation calls (Fig. 9) and 'widely spaced' contact calls (Fig. 10) in recordings of *C. f. fuscater* and *C. f. sanctamartae* distinguish them from *C. hellmayri*, *C. arcanus* sp. nov., and *C. mirabilis*. Punctuation calls were more elaborate and variable in *C. f. fuscater* than any other South American taxon (Fig. 9). An exceptional set of *C. f. fuscater* recordings (ML 66348 –66356) by P. Schwartz features individual birds responding to playback by cycling through repertoires of multiple, distinct Type 2 ('long/sinuous') punctuation calls, and one recording features a Type 3 ('short/simple') punctuation call, reminiscent of the calls of *C.* [*f.*] *opertaneus*, Undescribed 2, Undescribed 3, and *C.* [*f.*] *mentalis*, but with a greater frequency range (see Fig. 9). The descending blurred call detected in *C. f. fuscater* recordings was similar in frequency to, but wider in bandwidth than, the blurred calls of *C.* [*f.*] *berlepschi* (Fig. 11); no recordings of blurred calls were available for *C. f. sanctaemartae*. In song, the ascending dyadic contour (AB) was more prevalent in *C. f. fuscater* and *C. f. sanctaemartae* than in any other taxa (Fig. 12).

Of the four triadic contours detected in *C. f. fuscater* (ABC, ACB, BAC, CAB), two were shared with *C. f. sanctaemartae* (ABC, BAC). Of the three triadic contours detected in *C. f. sanctaemartae* (ABC, BAC, BCA), two were detected in *C. f. fuscater* (ABC, BAC). The only tetradic contour detected in *C. f. fuscater* (DABC) was not detected in *C. f. sanctaemartae*, which had three tetradic contours of its own (ABCD, BCAD, CDAB). The rare contour BCAD, detected in only one recording of *C. f. sanctaemartae* (ML 215345031), was not detected in any other taxon.

Comments

Lafresnaye's (1845) holotype (MCZ 76525) was evidently a grey type based on his description, 'une coloration noirâtre et grise sans la moindre nuance de brun ou de roux' ('a blackish and grey colouring without the slightest hint of brown or of red'). Study skins of *C. f. fuscater* from Boyacá, Colombia at the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), and at the Instituto Alexander von Humboldt (IAvH), have 'dark brown to greyish brown' backs (Beltrán and Kattan 2001), and thus probably represent both colour types. The within-population frequencies of each type are difficult to determine without more data. More study is needed with fresh material.

Catharus berlepschi Lawrence 1888

Trans-Andean nightingale-thrush

(Figs 15–18)

Catharus fuscater Sclater 1859a: 136, 1859b: 324 (in part); Berlepsch and Taczanowski 1884: 283; Salvin 1895, Goodfellow 1901: 309; Meyer de Schauensee 1966: 412 (in part); Meyer de Schauensee 1970: 342 (in part); Ridgley and Tudor 1989: 110 (in part); Clements and Shany 2001: 193; Solano-Ugalde *et al.* 2007; Schulenberg *et al.* 2007 (in part); Kikuchi 2009; Schmitt *et al.* 2013; Astudillo *et al.* 2015; Remsen *et al.* 2023 (in part).

Catharus berlepschi Lawrence '1887' (=1888; see: LeCroy 2005: 39): 503; Ridgway '1887': 504; Sharpe 1902: 182.

Catharus fuscater caniceps Chapman 1924: 14; Hellmayr 1934: 466; Bond 1956: 241; Fjeldså and Krabbe 1990: 554 (in part); Collar 2005: 700 (in part); Halley 2020.

Catharus fuscater fuscater Fjeldså and Krabbe 1990: 554 (in part); Clement 2000: 299 (in part); Ridgley and Greenfield 2001: 660 (in part); Collar 2005: 700 (in part).

Catharus fuscater berlepschi Halley 2021: 132.

***Catharus berlepschi nebulus* ssp. nov.** (formerly Undescribed 3).

urn:lsid:zoobank.org:act:EAE392CC-A763-4E5E-8F6F-68921515C9A2.

Catharus fuscater Taczanowski 1874: 504; 1879: 222; 1882: 4; 1884: 483.

Catharus fuscater caniceps Fjeldså and Krabbe 1990: 554 (in part); Clement 2000: 299 (in part); Collar 2005: 700 (in part).

'Unnamed-3' Halley 2021: 133.

Type material

Catharus b. berlepschi: AMNH 39096 (holotype), study skin, adult male, collected by Joseph Siemiradzki in Cayandeled (approximately –2.117°, –78.98°; see: Paynter 1993: 34), Chimborazo, Ecuador, on 23 January 1883 (see: LeCroy 2005: 38). Siemiradzki collected four males and a female, which Berlepsch and Taczanowski (1884: 283) classified as *C. fuscater*. Berlepsch then sent one of the males (AMNH 39096) to Lawrence, who described it as a new species. For this study, M.R.H. examined the holotype on 20 June 2013.

Catharus b. caniceps: AMNH 175530 (holotype), study skin, adult male, collected by H. Watkins (no. 6011) at Palambla (approximately –5.23°, –79.37° ; see: Stephens and Traylor 1983: 153), Piura, Peru, on 16 September 1922 (see: LeCroy 2005: 39). For this study, M.R.H. examined the holotype on 20 June 2013.

Catharus b. nebulus ssp. nov.: FMNH 474413 (holotype), study skin, adult male, collected and prepared by David E. Willard on Cerro Monte Alegre (–6.5850°, –77.5617°, elev. 2400 m), Amazonas, Peru, on 23 June 2010. When it was prepared, the holotype weighed 37.5 g. Its testes were not enlarged (1 × 0.5 mm) and the skull was 50% pneumatized. In 2022, the entire dorsal surface was darker than Sepia (119), with the crown slightly darker than the back and rump. The undertail coverts were Dark Drab (119B) and the flanks were darker and cooler than Vandyke Brown (121). The breast was darker than Glaucous (79) with faint mottling. The throat was cooler than Drab-Grey (119D), contrasting with the breast.

Geographic range

Catharus b. berlepschi: Western Andes in Ecuador (Carchi, south to El Oro).

Catharus b. caniceps: Western Andes in Ecuador (El Oro), south to north-western Peru (Cajamarca, La Libertad), and the Huancabamba and Chunchuca valleys, west of the Río Marañón.

Catharus b. nebulus ssp. nov.: Eastern slope of the Peruvian Andes from Amazonas (east of Río Marañón) south to Cusco (north-west of Río Apurímac), including Chachapoyas (Amazonas), Tambillo (Huamanga), and Chilpes (Junín) between 1770 and 2290 m (Taczanowski 1884).

Adult specimens examined

Catharus b. berlepschi ($N = 11$): Ecuador ($N = 11$): Carchi (two males, one female): west slope near Maldonado-Tulcán Rd, along Río La Plata: ANSP 181213 181214 (males), ANSP 181212 (female); Chimborazo (three males): Chunchi: ANSP 59755–59757 (males); Pinchincha (three males): Chiriboga: DMNH 59252, 62883 (males); Mindo: AMNH 503903 (male); El Oro (two males, two females): Salvias: AMNH 167890 (male); Zaruma: ANSP 83643 (male), AMNH 130154, ANSP 83644 (females); El Chiral: AMNH 167888 (male).

Catharus b. caniceps ($N = 33$): Ecuador ($N = 6$): Loja (three males, three females): Alamor: AMNH 167894 (female); Celica: AMNH 167891, 167893 (males), AMNH 167892 (female); San Bartolo: AMNH 172116 (male), AMNH 172117 (female). Peru ($N = 27$): Piura (four males, four females): Palambla: AMNH 175530–17533 (males), ANSP 116437, 116438, AMNH 175534, 175535 (females);

Figure 15. Ventral and dorsal views of the adult male plumages in *C. b. berlepschi*, *C. b. caniceps*, *C. o. tenebris* ssp. nov., *C. b. nebulus* ssp. nov., and *C. mentalis*. Photograph by M.R.H.

Lambayeque (one female): Porculla: ANSP 116441 (female); Cajamarca (six males, one female): Chira: ANSP 116442, 116443 (males); Quebrada Lanchal: LSUMZ 170101, 170102 (males), LSUMZ 170103 (female); Quebrada La Palma: LSUMZ 170104 (male); Cajabamba: AMNH 503909 (male). La Libertad (eight males, three females): Seques, north-east of Pacasmayo: AMNH 236066, 236068–236070 (males), AMNH 236067 (female); Taulis, north-east of Pacasmayo: AMNH 236071, 236072, 236075, 236076 (males), AMNH 236073, 236074 (females).

Figure 16. Ventral and dorsal views of the adult female plumages in *C. b. berlepschi*, *C. b. caniceps*, *C. o. tenebris* ssp. nov., *C. b. nebulus* ssp. nov., and *C. mentalis*. Photograph by M.R.H.

Catharus b. nebulus ssp. nov. ($N = 19$): Peru ($N = 19$): Amazonas (two males, four females): 33 km NE of Ingenio: LSUMZ 82159 (female); Cerro Montealegre: FMNH 474413 (male); La Lejia, north of Chachapoyas: AMNH 235051 (male); Leymebamba: ANSP 109278 (female); 20 km E of La Peca: LSUMZ 88630, 88631 (females); Huánuco (three males): Cayumba Alto: FMNH 299304 (male); Cordillera Carpish: LSUMZ 78972, 80744 (males); Junín (one male): Rumicruz: AMNH 174319 (male); Pasco (four males, four females): Playa Pampa: LSUMZ 129006, 129007, 129011 (males), LSUMZ 129002, 129005 (females); Santa Cruz: LSUMZ 106496 (male), LSUMZ 106495, 106497 (females); San Martín (one female): 22 km ENE of Florida Pomacochas: LSUMZ 174203 (female).

Immature specimens examined

Catharus b. berlepschi (*N* = 5): Ecuador (*N* = 5): Carchi (two females): west slope near Maldonado-Tulcán Rd., along Río La Plata: ANSP 181215 181216 (females); Pinchincha: Chiriboga: DMNH 62882 (male); Mindo Arriba: AMNH 180632 (male); El Oro (two males): Salvias: AMNH 167889 (male); Zaruma: AMNH 130153 (male).

Catharus b. caniceps (*N* = 3): Peru (*N* = 3): Piura (one male, one female): Palambla: ANSP 116439 (male), CM 119947 (female); Cajamarca (one male): Chugur, 65 km north-west of Cajamarca: AMNH 236065 (male); Quebrada Lanchal: LSUMZ 170100 (female).

Catharus b. nebulus ssp. nov. (*N* = 1): Peru (*N* = 1): San Martín (one male): 22 km ENE of Florida Pomacochas: LSUMZ 174204 (male).

Figure 17. Side view of adult plumages in *C. b. nebulus* ssp. nov. Photograph by M.R.H.

Audio recordings examined

Catharus b. berlepschi (*N* = 20): Ecuador (*N* = 20): Azuay: Cuenca: Molleturo, Corona de Oro Rd.: XC 602205; Yunguilla Reserve: ML 135902, 135926, 76216901, XC 19999; Loja: near Celica: XC 67875; Reserva Utuana: ML 141950781, XC 67874; Pichincha: Bellavista, Tandayapa: XC 128440, 13227, 4214; Mindo: XC 545139, 546525; Mindo Cloud Forest: ML 139115; Old Mindo-Nono Rd., before Tandayapa: ML 63456; Recinto 23 de Junio: ML 216745971, XC 186913; Reserva Paz de Aves: XC 30933; Tandayapa Bird Lodge: XC 32386, 54902.

Catharus b. caniceps (*N* = 4): Peru (*N* = 4): Cajamarca: Chotas, Bosque Protector Pagaibamba: XC 108771; Sallique: Quebrada Lanchal: ML 515357, 515369; Piura: Ayabaca, Bosque de Cuyas: XC 231.

Figure 18. Ventral and dorsal views of juvenile plumages in *C. hellmayri*, *C. b. nebulus* ssp. nov., and *C. b. berlepschi*. Photograph by M.R.H.

Catharus b. nebulus ssp. nov. (*N* = 18): Peru (*N* = 18): Amazonas: Camino Atuen: ML 398834941; Camp Lowbrow: ML 304312761; Fundo Alto Nieva: ML 72665721; La Llantera cerca de Afluente: ML 272483101; above Leimebamba: XC 175873; Utcubamba: Bagua Grande, ACP Bosque Berlín: ML 129649691, XC 123919; Huánuco: Paty Trail: XC 243435, 243436, 243437; Pasco: Bosque Shollet: ML 228217101, 289516811; Oxapampa: ML 269963401, 376022481; San Martín: Abra Patricia: ECOAN Lodge: XC 30494, 144628; Ucayali: Oventeni: ML 138773; Ulcumano Ecolodge: ML 287691191.

Diagnosis

Genetics: In the UCE tree, samples from (i) western Ecuador and north-western Peru, encompassing the type localities of *C. berlepschi* Lawrence 1888 and *C. f. caniceps* Chapman 1924, and (ii) eastern Peru from Amazonas south to the Río Apurímac (*C. b. nebulus* ssp. nov.), formed reciprocally monophyletic clades. Together, these clades formed the sister-group of a clade composed of samples of *C.* [*f.*] *opertaneus* and Undescribed 2. We treat these major sister-groups as polytypic species: *C. berlepschi* (including *C. b. berlepschi, C. b. caniceps, and C. b. nebulus* ssp. nov.) and *C. opertaneus* (including *C.* [*f.*] *opertaneus* and Undescribed 2, see below). The subspecies *C. b. berlepschi* and *C. b. caniceps* were not genetically diagnosable, despite their plumage colour differences. A sample of *C. b. berlepschi* from the Yunguilla Valley, Azuay, Ecuador (ZMUC 128360) was more similar to a paratype of *C. f. caniceps* (AMNH 175531) than a sample of *C. b. berlepschi* from Imbabura, Ecuador (ZMUC 119570). In the *ND2* tree, these three samples, plus one sample each from the Huancabamba and Chunchuca valleys (i.e. east of the Abra de Porculla, an east–west pass through the Western Cordillera at 2145 m) and a sample from Loja, Ecuador, formed a clade with low within-clade divergence (mean uncorrected *p*-distance = 0.005 ± 0.004). Samples from across the range of the eastern Andean group (*C. b. nebulus* ssp. nov.) also formed a clade in the *ND2* tree with low within-clade divergence (mean uncorrected *p*-distance = 0.002 ± 0.001). The divergence between these sister-clades (*C. b. berlepschi* + *C. b. caniceps*, vs. *C. b. nebulus* ssp. nov.) was an order of magnitude greater (mean uncorrected *p*-distance = 0.022 ± 0.002) than the mean divergence within either clade. ABGD analysis of *ND2* data merged *C. berlepschi* with Undescribed 2 (uncorrected *p*-distance = 0.01 ± <0.01), although these were not sister-groups in the UCE tree, while treating *C. b. berlepschi* and *C. b. nebulus* ssp. nov. as independent genetic clusters. ASAP analysis merged *C. b. berlepschi, C. b. nebulus* ssp. nov., and Undescribed 2.

Morphology: Study skins from the range of *C. berlepschi* in the western Andes were sexually monochromatic in the adult plumage and exhibited a north–south colour cline. At the northern end of the cline, adults had dark dorsal plumage (darker than Sepia, 119), medium-light ventral plumage (Figs 15, 16; Table 3), and completely black maxillae (Table 4), whereas southern adults (*C. b. caniceps*), including in the Huancabamba and Chunchuca valleys, were paler on the flanks, breast, and throat (Figs 15, 16; Table 3) and had dichromatic irides (Table 5). Specimens from Zaruma, El Oro (ANSP 83643, 83644) had somewhat intermediate characters between the endpoints of the plumage colour cline, and are here listed under the nominate form, *C. b. berlepschi*. Adult study skins of *C. b. nebulus* ssp. nov. were dichromatic in iris colour and more similar in plumage colour to *C. b. caniceps* than *C. b. berlepschi*. A juvenile specimen identified as *C. b. nebulus* was morphologically divergent from *C. b. berlepschi* and *C. b. caniceps* (see below), but this requires further investigation to confirm.

Voice: The blurred calls of *C. b. berlepschi* and *C. b. nebulus* ssp. nov. had a 'check-like' sonogram shape, which distinguished them from all other taxa in the complex, including Undescribed 2, which had a downward sloping blurred call that was narrower in bandwidth (Fig. 11). The subspecies *C. b. berlepschi* and *C. b. nebulus* ssp. nov. differed in punctuation call structure (Type 2 vs. Type 3, respectively). In song, of the five triadic contours (ABC, ACB, BCA, CAB, CBA) detected in *C. b. berlepschi*, four (ABC, ACB, BAC, BCA) were shared with *C. b. nebulus* ssp. nov.; of the four tetradic contours (ACDB, BCDA, CABD, CDBA) detected in *C. b. berlepschi*, none was shared with *C. b. nebulus* ssp. nov., and only one (BDAC) was shared with Undescribed 2.

Etymology

We propose the English name 'Trans-Andean nightingale-thrush' for the polytypic *C. berlepschi* because it is the only species in the complex that occurs on both slopes of the Andes. The scientific name *C. b. nebulus* ssp. nov. is derived from Latin feminine noun *nebula* (mist, fog), referring to its montane forest habitat.

Comments

We placed the name '*C. f. caniceps*' into the synonymy of *C. berlepschi* because, in both reconstructions, genetic samples from western Ecuador and north-western Peru formed a clade that encompassed the type localities of both taxa, and the older name has priority. Based on the shallow *ND2* divergence between samples from the western Andes, on one hand, and the eastern side of the Abra de Porculla in the Huancabamba (LSUMZ 170103) and upper Chunchuca valleys (LSUMZ 170104) on the other, we hypothesize that *C. berlepschi* crossed the Abra de Porculla, from the west, sometime after the LGM.

Despite its monophyly in both genetic datasets, we treat the taxon from the eastern Andes as a subspecies of *C. berlepschi*, instead of its sister-species, because additional sampling is needed to assess the degree of vocal and morphological divergence. We note that *C. b. nebulus* ssp. nov. is apparently divergent from *C. b. berlepschi* in juvenile plumage and punctuation call structure, but this may be an artefact of low sample size. Study skins of *C. b. nebulus* ssp. nov. also exhibit subtle sexual dichromatism, unlike the sexually monochromatic (but clinally variable) *C. b. berlepschi* + *C. b. caniceps* clade. Males of *C. b. nebulus* ssp. nov. (e.g. FMNH 474413, LSUMZ 129006) were darker and less brown on the dorsal surface than adult females, including on the crown, and some adult males of *C. b. nebulus* ssp. nov. approached the brownish plumage of the adult female (e.g. LSUMZ 106496, with enlarged testes: 9 × 15 mm). This suggests that *C. b. nebulus* ssp. nov. may exhibit polychromatic plumage 'types' like *C.* [*f.*]

mentalis (see below). Notably, the strongest colour differences between *C. b. nebulus* ssp. nov. and the *C. b. berlepschi* + *C. b. caniceps* clade occur where their ranges approach each other in northern Peru, which may be indicative of character displacement.

The plumage of a juvenile from central Peru (LSUMZ 174204), identified as *C. b. nebulus* ssp. nov., was boldly marked relative to a juvenile *C. b. berlepschi* (ANSP 181216). LSUMZ 174204 has tawny streaks on the mantle, tawny spots on the breast, a whitish throat and abdomen, and a pale mandible (Fig. 19). At first glance, this specimen resembles the juvenile of *C. maculatus*, but there are multiple reasons to doubt that identification. CM 85107, a genuine *C. maculatus* juvenile from Cochabamba, Bolivia, has a dark mandible (vs. pale with dusky tip in LSUMZ 174204), a darker and more heavily marked belly (vs. white), and a brown 'collar' across the upper breast (vs. no collar). LSU 174204 was also collected at 2300 m, at the same site as an adult female *C. b. nebulus* ssp. nov. (LSUMZ 174203), and about 500 m upslope of the known upper range limit of *C. maculatus* in central Peru (Schulenberg *et al.* 2007). As noted by Ridgely and Tudor (1989: 110), *C. maculatus* and *C.* [*fuscater*] populations in South America 'seem rarely if ever actually to occur together, rather, replacing each other in an as yet not understood way'.

Freeman *et al.* (2022) played recordings of *C. b. nebulus* ssp. nov. in 'territories' of *C. b. berlepschi* and recorded the response of the 'territorial bird' (i.e. how closely the playback target approached the speaker, and whether and how much it vocalized). In each of eight different experiments, one recording was played in the vicinity of a singing individual, and three different stimuli were used overall (XC 175873 for two experiments, XC 30494 for three experiments, XC 144268 for three experiments). We reiterate that interpreting the results of these experiments (and 'sympatric' experiments using audio playback of *C. b. berlepschi* recordings in the range of *C. b. berlepschi*) is not straightforward, because the function of song (and, therefore, any response to it) is not clearly defined in species that exhibit cooperative parental care and/or facultative territoriality (e.g. Goetz *et al.* 2003, Halley 2014, Greeney *et al.* 2015, Halley *et al.* 2016).

Catharus opertaneus Wetmore 1955

Antioquia nightingale-thrush

(Figs 15, 16 19)

Catharus fuscater opertaneus Wetmore 1955: 46; Deignan 1961: 430; Meyer de Schauensee 1964: 317; Hilty and Brown 1986: 543; Fjeldså and Krabbe 1990: 554; Clement 2000: 299; Collar 2005: 700; Acevedo-Charry 2014; Halley 2020; Halley 2021.

Catharus fuscater Meyer de Schauensee 1966: 412 (in part); Meyer de Schauensee 1970: 342 (in part); Hilty and Brown 1986 (in part); Ridgley and Tudor 1989: 110 (in part); Beltrán and Kattan 2001; Krabbe *et al.* 2006; Cuervo *et al.* 2008; Molina Martinez 2014; Greeney *et al.* 2015; Dyrcz *et al.* 2015; Remsen *et al.* 2023 (in part).

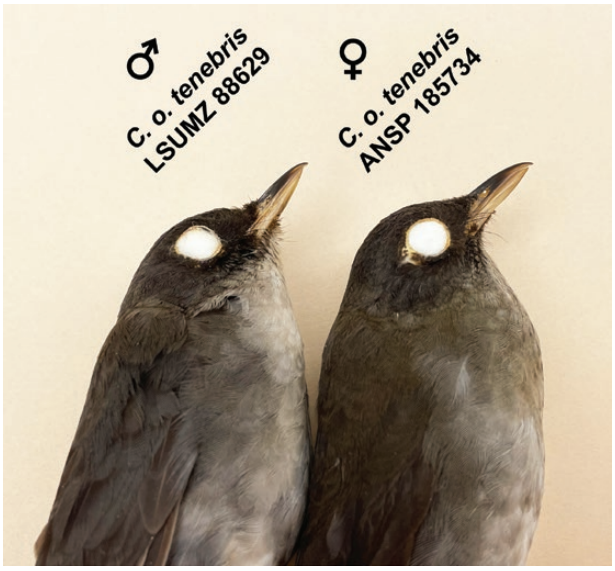

Figure 19. Side view of adult plumages in *C. o. tenebris* ssp. nov. Photograph by M.R.H.

Catharus fuscater fuscater Ridgley and Greenfield 2001: 660 (in part); LeCroy 2005: 38.

***Catharus opertaneus tenebris* ssp. nov.** (formerly Undescribed 2).

urn:lsid:zoobank.org:act:B1F7F134-2EB8-4FB9-A1EB-31E2CC7AB4D7.

Catharus fuscater Parker *et al.* 1985: 192 196; Rasmussen *et al.* 1996: 40.

Catharus fuscater fuscater Clement 2000: 299.

Catharus fuscater caniceps M.B. Robbins in Ridgley and Greenfield 2001: 660.

'Unnamed-2' Halley 2021: 133.

Type material

Catharus o. opertaneus: USNM 427029 (holotype), study skin, adult male, collected by M.A. Carriker Jr. at 'Haciendo Potreros' (1981 m elev.), 'on the Río Herradura, 15 miles south-west of Frontino', Antioquia, Colombia (approximately 6.39°, –76.09°; see: Paynter 1997: 190) on 10 June 1950 (Wetmore 1955, Deignan 1961: 430). USNM 436771 (paratype), study skin, collected by Carriker on the Río Urrao, Antioquia, on 14 September 1951. Both specimens were examined by M.R.H. on 23 October 2013.

Catharus o. tenebris ssp. nov.: ANSP 185734 (holotype), study skin, adult female, collected and prepared by T.J. Davis in humid montane forest on the eastern slope of Cordillera de las Lagunillas, north bank of Río Isimanchi, about 6 km north-west of San Andrés, Zamora-Chinchipe, Ecuador (–4.7833°, –79.3333°, elev. 2250 m), on 6 November 1992. When it was prepared, the holotype weighed 35 g with no bursa and an ovary that measured 8 × 4 mm. Neither the ova nor the oviduct were enlarged, the skull was 50% pneumatized, and there were insect remains in the stomach. In 2022, the crown of ANSP 185734 was slightly darker than Sepia (219), transitioning to a darker version of Hair Brown (119A) on the back and rump. The

undertail coverts were Dark Drab (119B) and the flanks were darker and cooler than Vandyke Brown (121). The breast was Greyish Horn Colour (91) with faint vertical striations. The throat was Drab-Grey (119D), contrasting with the breast, and a dark brown line connected the malar regions across the chin. No moult was noted. Iris colour was recorded as 'grey' and there is a pencilled note by M.B. Robbins (MBR): '*Catharus fuscater caniceps*? 2 other adults at this locality [KU 186025 and ANSP 186025, both males] had greyish irides; M.B.R. '93. [and] 1 in MECN [Museo Ecuatoriano de Ciencias Naturales], Quito'. The maxilla was 'black' when the specimen was prepared, and it remains so (Table 4). The mandible and gape were 'dull orange' in life, the eye-ring was 'orange', and the feet were 'yellowish brown'.

Geographic range

Catharus o. opertaneus: In Colombia, occurs on the western slope of the Western Andes near Frontino and Urrao (Antioquia), at 1980 and 2730 m, respectively (Wetmore 1955), in the Central Andes near the cities of Pereira (Risaralda) and Manizales (Caldas) between 2400 and 2600 m (Beltrán and Kattan 2001), and at several other sites in Antioquia and Caldas (Cuervo *et al.* 2008) and Tolima (Molina Martinez 2014). In Ecuador, occurs at Yanyacu Biological Station near Cosanga, Napo province (Dyrcz *et al.* 2015, Greeney *et al.* 2015). If intervening populations between north-eastern Ecuador (Sucumbios) and northern Colombia (Antioquia) are of the same species, as we hypothesize, then two specimens collected by Carriker near Popayán, Cauca, Colombia, in 1959 and 1960 are probably *C. opertaneus* (WFVZ 16446, 16447).

Catharus o. tenebris ssp. nov.: Restricted to the Río Chinchipe watershed of northern Peru and south-eastern Ecuador, south of the Río Zamora.

Adult specimens examined

Catharus o. opertaneus (*N* = 2): Colombia (*N* = 2): Antioquia (one male, one female): Heda Potreros, 15 miles south-west of Frontino: USNM 427029 (male); Heda la Ilusion, Río Urrao: USNM 436771 (female).

Catharus o. tenebris ssp. nov. (*N* = 4): Ecuador (*N* = 1): Zamora-Chinchipe (one female): Cordillera de las Lagunillas, 6 km north of San Andrés: ANSP 185734 (female). Peru (*N* = 3): Piura (two males, one female): Playón: LSUMZ 88629 (male); 'Machete', on the Zapalache-Carmen Trail: LSUMZ 97810 (male); 'Batán', on the Zapalache-Carmen Trail: LSUMZ 97809 (female).

Immature specimens examined

Catharus o. opertaneus (*N* = 1): Ecuador (*N* = 1): Napo (1 male): Puente del Rio Quijos: AMNH 180631 (male).

Catharus o. tenebris ssp. nov. (*N* = 0).

Audio recordings examined

Catharus o. opertaneus (*N* = 12): Colombia (*N* = 7): Antioquia: Reserva Natural Cañón Del Río Claro: ML 101421201; Caldas: Reserva Ecológica Río Blanco: ML 101421201, 177887161, XC 440235; Risaralda: Santuario de Fauna y Flora Otún Quimbaya: ML 127271981, XC 102252; Tolima: La Plata, Cañón del Combeima: ML 345974171. Ecuador (*N* = 5): Napo: Cabañas San Isidro: ML 133453931; Cordillera Guacamayos: ML 142031581; Unknown locality: XC 255039; Volcán Sumaco: XC 443582; Sucumbíos: Lumbaquí, Gonzalo Pizarro: XC 529000.

Catharus o. tenebris ssp. nov. (*N* = 4): Ecuador (*N* = 4): Zamora-Chinchipe: Old Loja-Zamora Rd.: ML 318532061; Parque Nacional Podocarpus: XC 460029; Reserva Tapichalaca: XC 250592, 250647.

Diagnosis

Genetics: In the UCE tree, samples from the ranges of *C. o. opertaneus* and *C. o. tenebris* ssp. nov. formed reciprocally monophyletic clades, and together they formed a clade that was sister to the clade consisting of *C. b. berlepschi* + *C. b. nebulus* ssp. nov.. In the *ND2* tree, *C. o. opertaneus* was sister to the Darién clade (*C. mirabilis* + *C. arcanus* sp. nov.), with an estimated divergence of 2.5 Mya (95% HPD = 1.9–3.0), and *C. o. tenebris* ssp. nov. was sister to *C. b. berlepschi*, with a divergence estimate of 0.4 Mya (95% HPD = 0.2–0.5). ABGD and ASAP analyses of *ND2* data both identified *C. o. opertaneus* and *C. o. tenebris* spp. nov. as unique genetic clusters (uncorrected *p*-distance = 0.07), supporting the formal taxonomic recognition of both.

Morphology: Catharus opertaneus is sexually monochromatic with dark 'olive brown' dorsal plumage, unlike any other taxon in the complex (Wetmore 1955; photos in: Beltrán and Kattan 2001, Dyrcz *et al.* 2015). It was the only taxon with no difference between the sexes in the colour of the maxilla (i.e. both completely black). M.R.H. examined the *C. o. opertaneus* type in 2015, but lacked specimens for the standardized colour comparison. In comparisons between *C. o. tenebris* ssp. nov. and the rest of the complex, the closest match in colour was the *C.* [*f.*] *mentalis* adult female, which nevertheless had a darker throat than *C. o. tenebris* ssp. nov. (Figs 15–17; Table 3). We were unable to determine whether *C. o. opertaneus* and *C. o. tenebris* ssp. nov. differ in plumage colour (Table 3), but note that skins of *C. o. tenebris* ssp. nov. had paler irides (e.g. 'grey' ANSP 185734 female, 'grey brown' LSUMZ 97809 female, 'olive-brown' LSUMZ 88629 male) and 'orange' orbital skin (ANSP 185734, LSUMZ 88629, 97809), whereas *C. o. opertaneus* is said to have 'dark, cinnamon-brown' irides and yellow orbital skin, in both northern (Colombian) and southern (Ecuadorean) populations (see photos in: Beltrán and Kattan 2001, Dyrcz *et al.* 2015).

Voice: Catharus opertaneus (*sensu lato*) was distinguished from all taxa, except *C. b. nebulus* ssp. nov. and *C.* [*f.*] *mentalis*, by its Type 3 ('short/simple') punctuation calls (Fig. 9). Too few recordings of song were available to assess the divergence of *C. opertaneus* from other taxa in the complex. Of the four triadic contours detected in *C. o. opertaneus* (ABC, ACB, CAB, CBA), only one (ABC) was shared with *C. o. tenebris* ssp. nov.. Of the four tetradic contours detected in *C. o. opertaneus* (ABCD, CDAB, CDBA, DCBA), only one (CDAB) was shared with *C. o. tenebris* ssp. nov.. An aberrant recording of *C. o. opertaneus* from Sucumbios, Ecuador (XC 529000) contained a unique triadic song type in which the upper two notes were rapidly trilled before descending to a lower note (i.e. a combination of contours BCA and CBA), unlike any other song in our dataset.

Comments

Based on geography, we inferred that intervening populations in the Central Andes, between Sucumbios (ZMUC 119587) and Antioquia (ZMUC 134855), belong to the same clade (*C. opertaneus*). We hypothesize that the placement of *C. opertaneus* in the *ND2* tree, as sister to the Darién clade with relatively low support, may be evidence of ancient episodes of hybridization and mitochondrial capture between those taxa (see: Toews and Brelsford 2012). Greeney *et al.* (2015) documented cooperative breeding in *C. o. opertaneus* in the Ecuadorean population (i.e. five adults provisioning young in a single nest), the first report of this behaviour in a resident Neotropical *Catharus* species. Previously, this rare behaviour was known only in Bicknell's thrush (*C. bicknelli*, Goetz *et al.* 2003) and Veery (*C. fuscescens*, Halley and Heckscher 2012, Halley 2014, Halley *et al.* 2016).

Etymology

The proposed English name references Antioquia, Colombia, where the types were collected. The scientific name *C. o. tenebris* ssp. nov. is derived from the feminine Latin noun *tenebrae* (darkness), referring to the dark forest habitat of the taxon.

Catharus mentalis Sclater and Salvin 1879

Cochabamba nightingale-thrush

(Figs. 15, 16)

Catharus mentalis Sclater and Salvin 1876: 352, 1879: 591; Seebohm 1881: 285; Sharpe 1902: 182; Warren and Harrison 1971: 346.

Catharus fuscater mentalis Berlepsch 1902, Hellmayr 1934: 467; Bond and Meyer de Schauensee 1942, Bond 1956: 242; Ridgley and Tudor 1989: 109; Fjeldså and Krabbe 1990: 554; Clement 2000: 299; Collar 2005: 700 (in part); Halley 2020, Halley 2021.

Catharus fuscater Meyer de Schauensee 1966: 412 (in part); Meyer de Schauensee 1970: 342 (in part); Schulenberg *et al.* 2007(in part); Vidoz 2009, Remsen *et al.* 2023 (in part).

Type material

Monotypic species. NHMUK 1885.3.2.35 (syntype), study skin, from the Salvin–Godman Collection, collected by C. Buckley at 'Suape' in 'prov. Yungas, Bolivia' (=Suapi, La Paz, approximately –15.30°, –67.31°; see: Paynter 1992: 141), in 1876 (Warren and Harrison 1971: 346); NHMUK 1885.3.2.36 (syntype), collected by C. Buckley in 'Yungas' (presumably at Suapi, La Paz) in 1876; NHMUK 1886.8.2.20 (syntype), collected by C. Buckley at 'Suapi', Bolivia. These specimens were not examined in this study. Label data were provided by A.L. Bond (*in litt.*).

Geographic range

Occurs in southern Peru, east of the Río Apurímac, east to Santa Cruz, Bolivia (Vidoz 2009).

Adult specimens examined

Bolivia (N = 12): La Paz (five males, three females): Laguna Zongo: DMNH 67204, 67207 (males), DMNH 67201, 67206 (females); unspecified locality on the Río Aceramarca: AMNH 229261 (male); Sandillani: AMNH 138743 (male); Nequejahuruira: AMNH 229258 (male), AMNH 229257 (female); Cochabamba (two males, one female): Cerro Incachaca: CM 120346, FMNH 181675 (males), CM 120345 (female).

Peru (N = 9): Cusco (five males, two females): La Esperanza, Paucartambo: FMNH 433742, 433738 (males), FMNH 433740 (female); Pillahuatta, Puacartambo: FMNH 430057 (male); Bosque San Luis: FMNH 299706 (female); Limacpunco: FMNH 222381 (male); San Pedro Village: FMNH 364458 (male); Puno (one male): Oconeque: ANSP 102367 (male).

Immature specimens examined

Bolivia (N = 6): La Paz (five males, two females): Laguna Zongo: DMNH 67200, 67202, 67203, 67205 (males), DMNH 67198, 67199 (females); Acara: AMNH 229260 (male).

Peru (N = 3): Cusco (one male, two females): Occobauiba Valley, Tocopoquen: USNM 273314 (female); Bosque San Luis: FMNH 299705 (male); Pensión Suecia, km 138.5 on Cusco-Shintuya Highway, Cosnipata Valley: FMNH 398318 (female).

Audio recordings examined

Bolivia (N = 3): La Paz: Fuertecillo: XC 123041; Río Milluni near Titi Amaya, Inquisivi: XC 1998; Muñamachay: XC 73252.

Peru (N = 4): Junín: Cordillera Vilcabamba, headwaters of Río Poyeni: ML 92162; Puno: Sina: ML 148105, 148129, 148130.

Diagnosis

Genetics: In the UCE tree, samples of *C. mentalis* formed a clade that was sister to a large South American clade composed of samples of *C. o. opertaneus*, *C. o. tenebris* ssp. nov., *C. b. berlepschi*, and *C. b. nebulus* ssp. nov.. In the *ND2* tree, samples of *C. mentalis* also formed a clade, but its placement in the broader phylogeny of the complex was unresolved. The divergence of *C. mentalis* from *C. f. fuscater* was estimated at 2.4 Mya (95% HPD = 1.9–3.0), and *C. mentalis* was also highly divergent from *C. b. nebulus* ssp. nov., its northern geographic neighbour and the only population likely to establish secondary contact with it during glacial maxima (mean uncorrected p-distance = 0.07 ± <0.01). ABGD and ASAP analyses both identified *C. mentalis* as an independent genetic cluster.

Morphology: Specimens of *C. mentalis* exhibited polychromatic plumage colour, with two distinct colour phenotypes in males, unlike other taxa in the complex (Fig. 8), except possibly *C. f. fuscater* and *C. b. nebulus* ssp. nov. (see above). Male specimens were clearly separable into 'grey' (FMNH 222381, FMNH 430057) and 'brown' (ANSP 102367, FMNH 181675, FMNH 299705, FMNH 364458) phenotypes. 'Grey' males were similar to *C. f. sanctaemartae* males, but with slightly browner (and less dark) breasts and throats and reduced black on the chin. 'Brown' males resembled *C. mentalis* females in plumage colour, and in having a black maxilla (a retained juvenile character). Females of *C. mentalis* were similar in colour to *C. f. fuscater* females (Tables 3, 4).

Voice: Catharus mentalis was distinguished from all taxa except *C. o. tenebris* ssp. nov., *C. o. opertaneus*, and *C. b. nebulus* ssp. nov., by its Type 3 ('short/simple') punctuation call structure. Its 'ascending' blurred call was of higher frequency, simpler in structure, and shorter in duration than the 'check-shaped' blurred calls of *C. b. nebulus* ssp. nov. and *C. b. berlepschi* (Fig. 11). Among these taxa, the punctuation calls of *C. mentalis* were the simplest in structure (Fig. 9). No tetradic song contours were detected in *C. mentalis* (Fig. 12). Our classification system for song contours was unable to score a remarkably slow-paced song (BAC) followed by a rapid trill (XC 123041) and a six-note contour that featured a typical BA contour followed by an extremely rapid CDAB contour (XC 1998). Although our sample of recordings is small, these two songs were unique in our dataset, suggesting that *C. mentalis* is vocally divergent from the rest of the complex. Of the three triadic contours (ACB, BAC, CBA) detected in *C. mentalis*, two (ACB, BAC) were detected in its northern neighbour (*C. b. nebulus* ssp. nov.).

Comments

To our knowledge, the plumage polychromatism of *C. mentalis* is novel in the *C. fuscater* complex (except possibly in *C. f.* [*fuscater*] and *C. b. nebulus* ssp. nov., see above) and unprecedented in the genus *Catharus*. This pattern is illustrated by two specimens with enlarged testes (FMNH 433738, 433742), collected at the same site in November 2001, a 'mossy forest' at La Esperanza (2800 m. elevation), north-east of Paucartambo, Cusco, Peru (Fig. 8).

CONCLUSION

We have presented the first nuclear (UCE) phylogenetic hypothesis of the *C.* [*fuscater*] complex, the first molecular clock analyses of mitochondrial (*ND2*) sequence data, and a broad survey of geographic variation in phenotypic characters. These data have significantly advanced scientific knowledge of this poorly known Neotropical clade, setting the stage for an integrative taxonomic revision. Here, we recognized seven species and four subspecies in the complex, of which one species (*C. arcanus*) and two subspecies (*C. o. tenebris*, *C. b. nebulus*) were newly described. Future research, including additional collecting, will be needed to assess whether these new subspecies are sufficiently distinct to be considered species, as we suspect. We also anticipate that future studies of this complex will shed light on many different topics, including the evolution of white irides, sexual polychromatism, cooperative parental care, and the role of the Pleistocene glacial cycles as a driver of range expansion and isolation for Neotropical montane lineages.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

Table S1. Taxonomic variation in iris colour, scored with two levels (brown vs. white, see text) in a sample of *C.* [*fuscater*] study skins and digital photos ($N = 341$).

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DATA AVAILABILITY

Nuclear (UCE) sequences used in this study have been deposited in the NCBI Sequence Read Archive (SRA), bioproject number PRJNA972128, accession numbers SAMN35066547–SAMN35066569. Mitochondrial (ND2) sequences have been deposited in the NCBI GenBank, accession numbers OQ985968–OQ986002.

CONFLICT OF INTEREST

We have no conflicts of interests to declare.

REFERENCES

Acevedo-Charry OA. Aves de Quindicocha–Valle de Sibundoy, Putumayo–Colombia: Potencial àrea de conservación. *Universitas Scientiarum* 2014;**19**:29–41.

Allen JA. List of birds collected in the district of Santa Marta, Colombia, by Mr. Herbert H. Smith. *Bulletin of the American Museum of Natural History* 1900;**13**:117–84.

Allen JM, LaFrance R, Johnson KP, *et al.* aTRAM 2.0: An improved flexible locus assembler for NGS data. *Evolutionary Bioinformatics* 2018; **14**:1176934318774546. https://doi.org/10.1177/1176934318774546

Amaral FSR, Neves LG, Resende MFR Jr, *et al.* Ultraconserved elements sequencing as a low-cost source of complete mitochondrial genomes and microsatellite markers in non-model amniotes. *PLoS One* 2015;**10**:e0138446.

Angehr GR, Christian DG, Aparicio KM. A survey of the Serranía de Jungurudó, an isolated mountain range in eastern Panama. *Bulletin of the British Ornithologists' Club* 2004;**124**:51–62.

Astudillo PX, Tinoco BA, Siddons DC. The avifauna of Cajas National Park and Mazán Reserve, southern Ecuador, with notes on new records. *Cotinga* 2015;**37**:2–12.

Axelsson E, Willerslev E, Gilbert MTP, *et al.* The Effect of Ancient DNA Damage on Inferences of Demographic Histories. *Molecular Biology and Evolution* 2008;**25**:2181–7.

Bangs O. On some new or rare birds from the Sierra Nevada de Santa Marta, Colombia. *Proceedings of the Biological Society of Washington* 1899;**13**:91–108.

Bangs O. On a second collection of birds made in Chiriqui, by W. W. Brown, Jr. *Proceedings of the New England Zoological Club* 1902;**3**:15–70.

Bangs O. Types of birds now in the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology* 1930;**70**:145–426.

Bankevich A, Nurk S, Antipov D, *et al.* SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* 2012;**19**:455–77.

Beltrán W, Kattan G. First record of the Slaty-backed Nightingale-Thrush in the Central Andes of Colombia, with notes on its ecology and geographical variation. *Wilson Bulletin* 2001;**113**:134–9.

von Berlepsch HG, Taczanowski L. Deuxième liste des Oiseaux recueillis dans l'Ecuadeur occidental par MM. Stolzmann et Siemiradski. *Proceedings of the Zoological Society of London* 1884;**1884**:281–313.

von Berlepsch HG. Beschreibung zweier neuer Drosselformen aus Südamerika. *Ornithologische Monatsberichte* 1902;**5**:69–71.

Biancucci L, Martin TE. Can selection on nest size from nest predation explain the latitudinal gradient in clutch size? *Journal of Animal Ecology* 2010;**79**:1086–92.

Blotta I, Prestinaci F, Mirante S, *et al.* Quantitative assay of total dsDNA with PicoGreen reagent and real-time fluorescent detection. *Annali dell'Istituto Superiore di Sanità* 2005;**41**:119–23.

Bock W. Species: The concept, category and taxon. *Journal of Zoological Systematics and Evolutionary Research* 2004;**42**:178–90.

Bolger AM, Lohse M, Usadel B. Trimmomatic: A flexible trimmer for Illumina Sequence Data. *Bioinformatics* 2014;**30**:2114–20.

Bond J. Additional notes on Peruvian Birds II. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1956;**108**:227–47.

Bond J, Meyer de Schauensee R. *The Birds of Bolivia*. Philadelphia: Academy of Natural Sciences of Philadelphia, 1942.

Bright A, Waas JR. Effects of bill pigmentation and UV reflectance during territory establishment in blackbirds. *Animal Behaviour* 2002;**64**:207–13.

Bueter C, Weckstein JD, Johnson KP, *et al.* Comparative phylogenetic histories of two louse genera Found on *Catharus* thrushes and other birds. *The Journal of Parasitology* 2009;**95**:295–307.

Bush MB, Colinvaux PA. A pollen record of a complete glacial cycle from lowland Panama. *Journal of Vegetation Science* 1990;**1**:105–18.

Cadena CD, Pérez-Emán JL, Cuervo AM, *et al.* Extreme genetic structure and dynamic range evolution in a montane passerine bird: implications for tropical diversification. *Biological Journal of the Linnaean Society* 2019;**126**:487–506.

Cadena CD, Cuervo AM, Céspedes LN, *et al.* Systematics, biogeography, and diversification of *Scytalopus* tapaculos (Rhinocryptidae), an enigmatic radiation of Neotropical montane birds. *The Auk: Ornithological Advances* 2020;**137**:1–30.

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* 2009;**25**:1972–3.

Carriker MA Jr. An annotated list of the birds of Costa Rica including Cocos Island. *Annals of the Carnegie Museum* 1910;**6**:314–915.

Catanach TA, Hablley MR, Allen JM, *et al.* Systematics and conservation of an endemic radiation of Accipiter hawks in the Caribbean islands. *Ornithology* 2021;**138**:ukab041.

Chapman FM. Descriptions of new birds from Ecuador, Colombia, Peru, and Bolivia. *American Museum Novitates* 1924;**138**:1–16.

Chesser RT, Isler ML, Cuervo AM, *et al.* Conservative plumage masks extraordinary phylogenetic diversity in the *Grallaria rufula* (Rufous Antpitta) complex of the humid Andes. *The Auk: Ornithological Advances* 2020;**137**:1–25.

Cicero C, Mason NA, Jimenez RA, *et al.* Integrative taxonomy and geographic sampling underlie successful species delimitation. *Ornithology* 2021;**138**:ukab009.

Clement P. *Thrushes*. Princeton: Princeton University Press 2000.

Clements JF, Shany N. *A Field Guide to the Birds of Peru*. Temecula, CA: Ibis Publishing Company, 2001.

Collar NJ. Family Turdidae (Thrushes). In del Hoyo J, Elliott A, Christie DA, (eds). *Handbook of the Birds of the World*. **Vol. 10**. *Cuckoo-shrikes to Thrushes*, pp. 514–807. Barcelona: Lynx Edicions 2005.

Cracraft J. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs* 1985;**36**:49–84.

Cracraft J. Species concepts and the ontology of evolution. *Biology and Philosophy* 1987;**2**:329–46.

Cuervo AM. *Evolutionary assembly of the Neotropical montane avifauna*. Ph.D. Thesis, Louisiana State University, ProQuest Dissertations Publishing. 2013.

Cuervo AM, Pulgarín PC, Calderón D. New distributional bird data from the Cordillera Central of the Colombian Andes, with implications for the biogeography of north-western South America. *The Condor* 2008;**110**:526–37.

Davis LI. *A Field Guide to the Birds of Mexico and Central America*. Austin and London: University of Texas Press, 1972.

Deignan HG. *Type Specimens of Birds in the United States National Museum*. Smithsonian Institution Bulletin 221. Washington, DC: United States Government Printing Office, 1961.

Del Fabbro C, Scalabrin S, Morgante M, *et al.* An extensive evaluation of read trimming effects on Illumina NGS data analysis. *PLoS One* 2013;**8**:e85024.

De Queiroz K. A unified concept of species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences* 2005;**56**:196–215.

De Queiroz K. Species concepts and species delimitation. *Systematic Biology* 2007;**56**:879–86.

Dilger WC. Hostile behaviour and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. *The Auk* 1956;**73**:313–53.

Dobzhansky T. *Genetics and the Origin of Species*. New York: Columbia University Press, 1937.

Drummond AJ, Rambaut A. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 2007;**7**:214.

Dyrcz A, Port J, Mikusek R, Greeney HF. Parental care of nestlings in the Slaty-backed Nightingale-Thrush (*Catharus fuscater*) in eastern Ecuador. *Ornitología Neotropical* 2015;**26**:117–23.

Edgar RC. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acid Research* 2004;**32**:1792–7.

Faircloth BC. *Illumiprocessor: A Trimmomatic Wrapper for Parallel Adapter and Quality Trimming*, 2013. http://dx.doi.org/10.6079/J9ILL.

Faircloth BC. PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* 2016;**32**:786–8.

Faircloth BC, McCormack JE, Crawford NG, *et al.* Ultraconserved elements anchor thousands of genetic markers for target enrichment

spanning multiple evolutionary timescales. *Systematic Biology* 2012;**61**:717–26.
Fjeldså J, Krabbe N. *Birds of the High Andes*. Svendborg, Denmark: Zoological Museum, University of Copenhagen, and Apollo Books, 1990.
von Frantzius A. Ueber die geographische Verbreitung der vogel Costaricas und deren Lebensweise. *Journal für Ornithologie*, Series 2, 1869;**101**: 289–318.
Freeman BG, Montgomery GA. Using song playback experiments to measure species recognition between geographically isolated populations: A comparison with acoustic trait analyses. *The Auk: Ornithological Advances* 2017;**134**:857–70.
Freeman BG, Rolland J, Montgomery GA, *et al.* Faster evolution of a premating reproductive barrier is not associated with faster speciation rates in New World passerine birds. *Proceedings of the Royal Society B* 2022;**289**:20211514.
Gill FB. Species taxonomy of birds: Which null hypothesis? *The Auk: Ornithological Advances* 2014;**131**:150–61.
Ginés H, Aveledo H. R, Pons A, Yépez G, Muñoz Tebar R. Lista y comentario de las aves colectadas en la región. In: Sociedad de Ciencias Naturales La Salle, (eds). *La Región de Perijá y sus Habitantes.* Caracas: Sociedad de Ciencias Naturalcs La Salle, 1953.
Goetz JE, McFarland KP, Rimmer CC. Multiple paternity and multiple male feeders in Bicknell's Thrush (*Catharus bicknelli*). *The Auk* 2003;**120**:1044–53.
Goodfellow W. Results of an ornithological journey through Colombia and Ecuador. *Ibis* 1901;**43**:300–19.
Greeney HF, Dyrcz A, Mikusek R, *et al.* Cooperative breeding at a nest of Slaty-backed Nightingale-Thrushes (*Catharus fuscater*). *Wilson Journal of Ornithology* 2015;**127**:323–5.
Guoy M, Guindon S, Gascuel O. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 2010;**27**:221–4.
Halley MR. *Kin structure and mating system of the Veery (Catharus fuscescens) in the Mid-Atlantic Piedmont*. M.S. Thesis, Delaware State University 2014. https://doi.org/10.13140/2.1.1775.9369
Halley MR. Slaty-backed Nightingale-Thrush (*Catharus fuscater*), version 1.0. In: Schulenberg TS, ed. *Birds of the World*. Ithaca: Cornell Lab of Ornithology, 2020. https://doi.org/10.2173/bow.sbnthr1.01
Halley MR. *Integrative systematics and evolution of seasonal migration in the nightingale-thrushes (Aves: Turdidae: Catharus)*. Ph.D. Thesis, Drexel University, ProQuest Dissertations Publishing. 2021.
Halley MR. Taxonomic status of the Western Hemispingus *Sphenopsis ochracea* (Passeriformes: Thraupidae) and a review of species limits in the genus *Sphenopsis* P. L. Sclater 1861. *Bulletin of the British Ornithologists' Club* 2022;**142**:211–25.
Halley MR, Heckscher CM. Multiple male feeders at nests of the Veery. *Wilson Journal of Ornithology* 2012;**124**:396–9.
Halley MR, Heckscher CM, Kalavacharla V. Multi-generational kinship, multiple mating, and flexible modes of parental care in a breeding population of the Veery (*Catharus fuscescens*), a trans-hemispheric migratory songbird. *PLoS One* 2016;**11**:e0157051.
Halley MR, Klicka J, Sesink Clee P, *et al.* Restoring the species status of *Catharus maculatus* (Aves: Turdidae), a secretive Andean thrush, with a critique of the yardstick approach to species delimitation. *Zootaxa* 2017;**4276**:387–404.
Hausberger M, Henry L, Rethoré B, *et al.* When perceptual laterality vanishes with curiosity: A study in dolphins and starlings. *Laterality: Asymmetries of Brain, Behaviour, and Cognition*, 2021;**26**:238–259. https://doi.org/10.1080/1357650X.2021.1890758
Hazzi NA, Moreno JS, Ortiz-Movliav C, *et al.* Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America* 2018;**115**:7985–90.
Heckscher CM. *Use of the Veery (Catharus fuscescens) call repertoire in vocal communication*. Ph.D. Thesis, University of Delaware, ProQuest Dissertations Publishing, 2007.
Heckscher CM. The seasonal pattern of Veery calls and song in relation to reproductive contexts. *Northeastern Naturalist* 2018;**25**:291–307.
Helbig AJ, Knox AG, Parkin DT, *et al.* Guidelines for assigning species rank. *Ibis* 2002;**144**:518–25.
Hellmayr CE. Catalogue of birds of the Americas and the adjacent islands in Field Museum of Natural History, including all species and subspecies known to occur in North America, Mexico, Central America, the West Indies, and islands of the Caribbean Sea, the Galapagos Archipelago and other islands which may be included on account of their faunal affinities. *Field Museum of Natural History, Zoological Series 13* 1934;**7**:1–531.
Hilty SL. *Birds of Venezuela*, 2nd edn. Princeton and Oxford: Princeton University Press, 2003.
Hilty SL, Brown WL. *A Guide to the Birds of Colombia*. Princeton: Princeton University Press, 1986.
Huxley J (ed.) *The New Systematics*. New York: Oxford University Press, 1940.
Isler ML, Isler PR, Whitney BM. Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *The Auk* 1998;**115**:577–90.
Jackman SD, Vandervalk BP, Mohamadi H, Chu J, Yeo S, Hammond SA, Jahesh G, Khan H, Coombe L, Warren RL, Birol I. ABySS 2.0: Resource-efficient assembly of large genomes using a Bloom filter. *Genome Research* 2017;**27**:768–777.
Jankowski JE, Robinson SK, Levey DJ. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* 2010;**91**:1877–84.
Katoh S. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 2013;**30**:772–80.
Kikuchi DW. Terrestrial and understorey insectivorous birds of a Peruvian cloud forest: species richness, abundance, density, territory size and biomass. *Journal of Tropical Ecology* 2009;**25**:523–9.
Kounek F, Sychra O, Capek M, *et al.* Chewing lice of genus *Myrsidea* (Phthiraptera: Menoponidae) from Turdidae (Passeriformes) of Costa Rica, with descriptions of seven new species. *Zootaxa* 2013;**3620**:201–22.
Krabbe N, Flórez P, Suárez G, *et al.* The birds of Páramo de Frontino, western Andes of Colombia. *Ornitología Colombiana* 2006;**4**:39–50.
Kroodsma DE. Leaning and the ontogeny of sound signals in birds. In: Kroodsma DE, Miller EH (eds). *Acoustic Communication in Birds*. New York: Academic Press, 1982.
de Lafresnaye MF. Description de quelques oiseaux nouveaux. *Revue Zoologique par la Société Cuvierienne* 1845;**8**:337–42.
Lanfear R, Calcott B, Ho SY, *et al.* PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 2012;**29**:1695–701.
Lanfear R, Frandsen PB, Wright AM, *et al.* PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 2017;**34**:772–3.
Lanyon WE. Development of song in the Wood Thrush (*Hylocichla mustelina*), with notes on a technique for hand-rearing passerines from the egg. *American Museum Novitates* 1979;**2666**:1–27.
Lawrence GN. A catalogue of the birds found in Costa Rica. *Annals of the Lyceum of Natural History of New York* 1868;**9**:86–149.
Lawrence GN. Description of a new species of bird of the genus *Catharus*, from Ecuador. *Proceedings of the United States National Museum* '1887' (=1888);[**1887**]:503.
LeCroy M. Type specimens of birds in the American Museum of Natural History. Part 6, Passeriformes: Prunellidae, Turdidae, Orthonychidae, Timaliidae, Paradoxornithidae, Picathartidae, and Polioptilidae. *Bulletin of the American Museum of Natural History* 2005;**292**:1–132.
Lerner HR, Meyer M, James HF, *et al.* Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Current Biology* 2011;**21**:1838–44.
Lohse M, Bolger AM, Nagel A, *et al.* RobiNA: a user-friendly, integrated software solution for RNA-Seq-based transcriptomics. *Nucleic Acids Research* 2012;**40**:W622–7.
Loiselle BA, Blake JG. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 1991;**72**:180–93.

López-O JP, Avendaño JE, Gutiérrez-Pinto N, *et al*. The birds of the Serranía de Perijá: The northernmost avifauna of the Andes. *Ornitología Colombiana* 2014;**14**:62–93.
Martin T. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London B* 2002;**269**:309–16.
Mayr E. Speciation phenomena in birds. *American Naturalist* 1940;**74**:249–78.
Mayr E. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. Cambridge, MA: Harvard University Press, 1942.
Mayr E, Linsley EG, Usinger RL. *Methods and Principles of Systematic Zoology*. New York: McGraw-Hill Book Company, Inc., 1953.
McCormack JE, Tsai WLE, Faircloth BC. Sequence capture of ultraconserved 838 elements from bird museum specimens. *Molecular Ecology Research* 2016;**16**:1189–120.
McCullough JM, Oliveros CH, Benz BW, *et al*. Wallacean and Melanesian Islands promote higher rates of diversification within the global passerine radiation Corvides. *Systematic Biology* 2022;**2022**:syac044. doi: 10.1093/sysbio/syac044
Meyer de Schauensee R. The birds of the Republic of Colombia: Order Passeriformes. *Caldasia* 1950;**5**:645–871.
Meyer de Schauensee R. *The Birds of Colombia and Adjacent Areas of South and Central America*. Narberth, Pennsylvania: Livingston Publishing Company, 1964.
Meyer de Schauensee R. *The Species of Birds of South America with their Distribution*. Narberth, Pennsylvania: Livingston Publishing Company, 1966.
Meyer de Schauensee R. *A Guide to the Birds of South America*. Wynnewood, Pennsylvania: Livingston Publishing Company, 1970.
Miller MA, Pfeiffer W, Schwartz T. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, pp. 1–8. Institute of Electrical and Electronics Engineers, New Orleans, LA, 2010.
Molak M, Ho SYW. Evaluating the impact of post-mortem damage in ancient 843 DNA: A theoretical approach. *Journal of Molecular Evolution* 2011;**73**:244–55.
Molina Martinez YG. Birds of the Totare River Basin, Colombia. *Check List* 2014;**10**:269–86.
Naveda-Rodríguez A, Bisbal F. Avifauna of Dinira National Park, Venezuela. *Check List* 2008;**4**:373–81.
Nelson EW. Descriptions of new genera, species and subspecies of birds from Panama, Colombia and Ecuador. *Smithsonian Miscellaneous Collections* 1912;**60**:1–25.
Parker TA III, Schulenberg TS, Graves GR, *et al*. The avifauna of the Huancabamba region, northern Peru. *Ornithological Monographs* 1985;**36**:167–97.
Payne RB. Bird songs and avian systematics. In Johnston RF, (ed.) *Current Ornithology*, Vol. **3**. New York, NY: Plenum Press, 1986, pp. 87–126.
Paynter RA, Jr. *Ornithological gazetteer of Bolivia*, 2nd edn. Cambridge, MA: Printed by the President and Fellows of Harvard College, 1992.
Paynter RA, Jr. *Ornithological Gazetteer of Ecuador*, 2nd edn. Cambridge, MA: Printed by the President and Fellows of Harvard College, 1993.
Paynter RA, Jr. *Ornithological Gazetteer of Colombia*, 2nd edn. Cambridge, MA: Printed by the President and Fellows of Harvard College, 1997.
Peterson AT, Navarro-Sigüenza AG. Consistency of taxonomic treatments: A response to Remsen (2005). *The Auk* 2006;**123**:885–7.
Phillips AR. An ornithological comedy of errors: *Catharus occidentalis* and *C. frantzii*. *The Auk* 1969;**86**:605–23.
Phillips AR. *Known Birds of North and Middle America, Part 2*. Denver: Self-published, 1991.
Powell GVN. Structure and dynamics of interspecific flocks in a Neotropical mid-elevation forest. *The Auk* 1979;**96**:375–90.
Price T. *Speciation in Birds*. Greenwood Village, Colorado: Roberts and Company Publishers, 2008.
Puillandre N, Lambert A, Brouillet S, *et al*. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* 2012;**21**:1864–77.
Puillandre N, Brouillet S, Achaz G. ASAP: Assemble species by automatic partitioning. *Molecular Ecology Resources* 2019;**21**:609–20.
Raposo MA, Höfling E. Overestimation of vocal characters in Suboscine taxonomy (Aves: Passeriformes: Tyranni): causes and implications. *Lundiana* 2003;**4**:35–42.
Rasmussen JF, Rahbek C, Poulsen BO, *et al*. Distributional records and natural history notes on threatened and little known birds of southern Ecuador. *Bulletin of the British Ornithologists' Club* 1996;**116**:26–46.
Remsen JV Jr. High incidence of 'leapfrog' pattern of geographic variation in Andean birds: Implications for the speciation process. *Science* 1984;**224**:171–3.
Remsen JV Jr. Pattern, process, and rigor meet classification. *The Auk* 2005;**122**:403–13.
Remsen JV Jr, Cadena CD, Jaramillo A, Nores M, Pacheco JF, Robbins MB, Schulenberg TS, Stiles FG, Stotz DF, Zimmer KJ. *A Classification of the Bird Species of South America*. Washington DC: American Ornithologists' Union, 2023. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm>, Version 24 February 2023, accessed 1 March 2023.
Renjifo LM, Repizo A, Ruiz-Ovalle JM, *et al*. New bird distributional data from Cerro Tacarcuna, with implications for conservation in the Darién highlands of Colombia. *Bulletin of the British Ornithologists' Club* 2017;**137**:46–66.
Ridgley RS, Greenfield PJ. *The Birds of Ecuador: Status, Distribution, and Taxonomy*. Ithaca, NY: Comstock Publishing Associates, Cornell University Press, 2001.
Ridgley RS, Gwynne JA. *A guide to the birds of Panama*. Second edition. Princeton: Princeton University Press, 1989.
Ridgley RS, Tudor G. *The Birds of South America* Vol. **1**: The Oscine Passerines. Austin: University of Texas Press, 1989.
Ridgway R. Remarks on some Costa Rican birds. *Proceedings of the United States National Museum* 1881;**4**:333–7.
Ridgway R. Remarks on *Catharus berlepschi* Lawr. *Proceedings of the United States National Museum* '1887' (=1888);[**1887**]:504.
Ridgway R. Descriptions of seven new species and subspecies of birds from tropical America. *Smithsonian Miscellaneous Collections* 1904;**47**:112–3.
Ridgway R. The birds of North and Middle America, pt. 4. *Bulletin of the United States National Museum* 1907;**50**:1–973.
Robbins MB, Parker TA, Allen SA. The avifauna of Cerro Pirre, Darién, Panama. *Ornithological Monographs* 1985;**36**:198–232.
Salvin O. On some collections of birds from Veragua. Part 1. *Proceedings of the Zoological Society of London* 1867;**1867**:129–61.
Salvin O. On some collections of birds from Veragua. Part 2. *Proceedings of the Zoological Society of London* 1870;**1870**:175–219.
Salvin O. On birds collected in Peru by Mr. O. T. Barron. *Novitates Zoologicae* 1895;**2**:1–22.
Salvin O, Godman FD. *Biologia Centrali-Americana. Aves*, **Vol. 1**. London: R.H. Porter, 1879.
Saunders AA. The songs and calls of the Wood Thrush. *The Auk* 1961;**78**:595–606.
Schmitt CJ, Schmitt DC, Tiravanti CJ, *et al*. Avifauna of a relict *Podocarpus* forest in the Cachil Valley, north-west Peru. *Cotinga* 2013;**35**:15–23.
Schulenberg TS, Stotz DF, Lane DF, O'Neill JP, Parker, TA, III. *Birds of Peru*. Princeton: Princeton University Press, 2007.
Sclater PL. List of the first collection of birds made by Mr. Louis Fraser at Pallatanga, Ecuador, with notes and descriptions of new species. *Proceedings of the Zoological Society of London* 1859a;[**1859**]:135–47.
Sclater PL. A synopsis of the thrushes (Turdidae) of the New World. *Proceedings of the Zoological Society of London* 1859b;[**1859**]:321–47.
Sclater PL, Salvin O. On new species of Bolivian birds. *Proceedings of the Zoological Society of London* 1876;[**1876**]:352–8.
Sclater PL, Salvin O. On the birds collected in Bolivia by Mr. C. Buckley. *Proceedings of the Zoological Society of London* 1879;[**1879**]:588–645.
Seebohm H. *Catalogue of the Passeriformes or Perching Birds in the Collection of the British Museum*, **Vol. 5**. London: Printed by the order of the trustees, 1881.

Sharpe RB. *A Hand-list of the Genera and Species of Birds* **Vol. IV**. London: Printed by the order of the trustees, British Museum (Natural History), 1902.
Slud P. The birds of Costa Rica: Distribution and ecology. *Bulletin of the American Museum of Natural History* 1964;**128**:1–430.
Smithe FB. *Naturalist's Colour Guide*. New York: American Museum of Natural History, 1975.
Solano-Ugalde A, Arcos-Torres A, Greeney HF. Additional breeding records for selected avian species in north-west Ecuador. *Boletín SAO* 2007;**17**:17–25.
Stamatakis A. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 2014;**30**:1312–3.
Stevens L, Traylor MA. *Ornithological Gazetteer of Peru*. Cambridge, MA: Printed by the President and Fellows of Harvard College, 1983.
Stiles FG, Skutch AF. *A Guide to the Birds of Costa Rica*. Ithaca, NY: Comstock Publishing Associates, Cornell University Press, 1989.
Strewe R, Navarro C. New distributional records and conservation importance of the San Salvador Valley, Sierra Nevada de Santa Marta, Colombia. *Ornitología Colombiana* 2003;**1**:29–41.
Stutchbury BJM, Morton ES. *Behavioural Ecology of Tropical Birds*. London & San Diego: Academic Press, 2001.
Swofford DL. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), 4.0*. Sunderland, MA: Sinauer Associates, 2002.
Taczanowski L. Liste des Oiseaux recueillis par M. Constantin Jelski dans la partie centrale du Pérou occidental. *Proceedings of the Zoological Society of London* 1874;[**1874**]:501–64.
Taczanowski L. Liste des Oiseaux recueillis au Nord du Pérou par MM. Stolzmann et Jelski en 1878. *Proceedings of the Zoological Society of London* 1879;[**1879**]:220–45.
Taczanowski L. Liste des Oiseaux recueillis par M. Stolzmann au Pérou nord-oriental. *Proceedings of the Zoological Society of London* 1882;[**1882**]:2–49.
Taczanowski L. *Ornithologie du Pérou*. Berlin: R. Friedländer & Sohn, 1884.
Tenorio EA, Londoño GA. Nesting biology of the Spotted Nightingale-Thrush (*Catharus dryas*) and comparison of life histories in the genus *Catharus*. *Journal of Natural History* 2019;**53**:2563–78.
Tobias JA, Seddon N, Spottiswoode CN, *et al*. Quantitative criteria for species delimitation. *Ibis* 2010;**152**:724–46.
Tobias JA, Donald PF, Martin RW, *et al*. Performance of a points-based scoring system for assessing species limits in birds. *Ornithology* 2021;**138**:ukab016.
Todd WEC, Carriker MA **Jr**. The birds of the Santa Marta region of Colombia: A study in altitudinal distribution. *Annals of the Carnegie Museum* 1922;**14**:1–582.
Toews DPL, Brelsford A. The biogeography of mitochondrial and nuclear discordance in animals. *Molecular Ecology* 2012;**21**:3907–30.
Tsai WLE, Schedl ME, Maley JM, *et al*. More than skin and bones: Comparing extraction methods and alternative sources of DNA from avian museum specimens. *Molecular Ecology Resources* 2019;**20**:1220–7.
Vidoz JQ. Nuevos registros departamentales de aves en Bolivia. *Kempffiana* 2009;**5**:72–7.
Voelker G, Bowie RCK, Klicka J. Gene trees, species trees and Earth history combine to shed light on the evolution of migration in a model avian system. *Molecular Ecology* 2013;**22**:3333–44.
Warren RLM, Harrison CJO. *Type-specimens of Birds in the British Museum (Natural History)*. Vol. **2**, Passerines. London: Trustees of the British Museum (Natural History), 1971.
Weir JT, Bermingham E, Miller MJ, *et al*. Phylogeography of a morphologically diverse Neotropical montane species, the Common Bush-Tanager (*Chlorospingus ophthalmicus*). *Molecular Phylogenetics and Evolution* 2008;**47**:650–64.
Wetmore A. Further additions to the avifauna of Colombia. *Novedades Colombianas* 1955;**2**:45–7.
Wetmore A, Pasquier RF, Olson SL. *The birds of the Republic of Panamá, Part 4*. Washington DC: Smithsonian Institution Press, 1984.
Whitney CL. Temporal stability of song in a local population of Wood Thrushes. *Wilson Bulletin* 1992;**104**:516–20.
Whitney CL, Miller J. Song learning in the Wood Thrush. *Canadian Journal of Zoology* 1987;**65**:1038–42.
Wiley EO. The evolutionary species concept reconsidered. *Systematic Zoology* 1978;**27**:17–26.
Winger BM, Bates JM. The tempo of trait divergence in geographic isolation: avian speciation across the Marañón Valley of Peru. *Evolution* 2015;**69**:772–87.
Winker K, Rocque DA, Braile TM, *et al*. Vainly beating the air: Species concept debates need not impede progress in science or conservation. *Ornithological Monographs* 2007;**63**:30–44.
Wolfe JD, Chandler RB, King DI. Molt patterns, age, and sex criteria for selected highland Costa Rican resident landbirds. *Ornitologia Neotropical* 2009;**20**:451–9.
Young BE, Garvin MC, McDonald DB. Blood parasites in birds from Monteverde, Costa Rica. *Journal of Wildlife Diseases* 1993;**29**:555–60.
Zeledon JC. Catalogue of the birds of Costa Rica, indicating those species of which the United States National Museum possesses specimens from that country. *Proceedings of the United States National Museum* 1885;**8**:104–18.
Zink RM. Species concepts, speciation, and sexual selection. *Journal of Avian Biology* 1996;**27**:1–6.
Zink RM. Rigor and species concepts. *The Auk* 2006;**123**:887–91.
Zink RM, Barrowclough G. Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology* 2008;**17**:2107–21.