

The status of *Catharus fumosus* Ridgway (Turdidae)

Author: Halley, Matthew R.

Source: Bulletin of the British Ornithologists' Club, 145(1) : 24-34

Published By: British Ornithologists' Club

URL: <https://doi.org/10.25226/bboc.v145i1.2025.a3>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The status of *Catharus fumosus* Ridgway (Turdidae)

by Matthew R. Halley 

Received 9 August 2024; revised 18 December 2024; published 5 March 2025

<http://zoobank.org/urn:lsid:zoobank.org:pub:EE502C3B-DFD8-4C6F-A60D-C278B7F5F8AD>

SUMMARY.—The name *Catharus fumosus* Ridgway, 1888 has traditionally been placed among the synonyms of Black-headed Nightingale-Thrush *C. mexicanus* (Bonaparte, 1856) and applied at subspecies rank to the population ranging from Nicaragua to Panama (*C. m. fumosus*). Recent data support species rank for *C. fumosus*, but the availability of the name is contested. Allan Phillips claimed that the *C. fumosus* holotype (USNM 101765) was a hybrid with '*C. fuscater*' (= *C. [f.] hellmayri* von Berlepsch, 1902, recently elevated to species), then re-described the Central American taxon under the name *C. m. carrikeri* A. R. Phillips, 1991. World checklists are now in conflict. Here, I review the relevant history and compare USNM 101765 to a geographically widespread sample of study skins of the putative parental forms, yielding little support for the hybrid hypothesis. This is the fourth in a series of papers concerning historical aspects of *Catharus* taxonomy and nomenclature.

Black-headed Nightingale-Thrush *Catharus mexicanus* (Bonaparte, 1856) is a polytypic species, with several disjunct populations ranging from Mexico to Panama, in need of a taxonomic revision. A recent phylogenetic study of nuclear DNA sequences obtained via ultraconserved elements (UCEs) found 100% support for two reciprocally monophyletic primary clades in the *C. [mexicanus]* complex (Halley 2021): (1) a southern clade formed by samples from Costa Rica (Alajuela, Cartago), Nicaragua (Matagalpa) and Honduras (Copán), encompassing the type localities of *C. fumosus* Ridgway, 1888 (Costa Rica), *C. m. carrikeri* A. R. Phillips, 1991 (Costa Rica) and *C. m. yaegeri* A. R. Phillips, 1991 (Honduras); and (2) a northern clade that comprised all other *C. [mexicanus]* samples, ranging from western Guatemala (Huehuetenango, c.210 km west of the type locality of *C. m. cantator* Griscom, 1930) to the Sierra Madre Oriental in eastern Mexico, c.245 km north-west of Xalapa, Veracruz, the type locality of *C. mexicanus* (Bonaparte, 1856). The range of the northern clade presumably extends north to Tamaulipas, the type locality of *C. m. smithi* Nelson, 1909, which was not sampled by Halley (2021); and the southern clade presumably extends to Panama (see Phillips 1991: 111).

In a recent revision of the polytypic Slaty-backed Nightingale-Thrush *Catharus [fuscater]* Lafresnaye, 1845, complex, Halley *et al.* (2023) treated populations at species rank when they were genetically diagnosable (monophyletic) and either morphologically or vocally diagnosable. In the *C. [mexicanus]* complex, southern specimens (i.e., from the range of the southern UCE clade) are said to be 'Darker gray below than [northern specimens], particularly on the sides [and] Dorsally ruddier (brownier, warmer) and darker than [*C. m. cantator* of Guatemala], particularly on the rump and upper tail-coverts, and darker than [more northern] races' (Phillips 1991: 111). Vocal studies are not yet available (Collar 2020). The geographic boundary between the clades is apparently located near the Guatemala/Honduras border, but more collecting and genetic sampling across the Río Motagua will be needed to confirm this hypothesis. Although a more formal analysis of phenotypic variation in this complex is unavailable at the present time (e.g., Halley *et al.* 2017, 2023), irrespective of whether the southern taxon is treated at species or subspecies rank, the nomenclatural

conflict needs to be resolved. Here, for simplicity, I recognise two phylogenetic species in the *C. [mexicanus]* complex, which correspond to the northern and southern UCE clades (see Appendix; Halley 2021).

The oldest available name for the northern clade is *C. mexicanus* (Bonaparte, 1856), and the oldest available name for the southern clade is *C. fumosus* Ridgway, 1888 (here referred to by the English name 'Black-capped Nightingale-Thrush'), which is contested. Phillips (1991: 111) claimed that the *C. fumosus* holotype (USNM 101765) was a hybrid between '*C. mexicanus*' and '*C. fuscater*', the latter taxon referring to 'Talamanca Nightingale-Thrush' *C. [f.] hellmayri* von Berlepsch, 1902, which was elevated to species rank by Halley *et al.* (2023) and is treated as such here. Phillips (1991) then re-described the southern taxon under the name *C. m. carrikeri* A. R. Phillips, 1991, setting up nomenclatural conflict. The holotype of *C. fumosus* is currently identified as '*Catharus fuscater* × *mexicanus*' in the USNM online database (<https://collections.nmnh.si.edu/search/birds/>, accessed 17 February 2025) and Collar (2020), Gill *et al.* (2024) and HBW & BirdLife International (HBW 2024) have adopted the name *C. m. carrikeri* for the southern taxon at subspecies rank. However, Clement (2000), Halley (2021) and Clements *et al.* (2022, 2024) continue to recognise the priority of *C. [m.] fumosus*. To resolve this conflict, in the following sections, I review the taxonomic history of *C. fumosus* and compare the phenotypic characters of its holotype (USNM 101765) to a larger sample of adult male study skins.

Taxonomic history

José Castulo Zeledón (1846–1923) collected USNM 101765 at an unknown locality in Costa Rica, on 20 October 1884, then deposited the specimen at the National Museum of Natural History, Smithsonian Institution, Washington (USNM), in January 1885, where Robert Ridgway (1850–1929) catalogued it under the name '*Catharus mexicanus*' (Fig. 1).



Figure 1. Three views of USNM 101765, the holotype of Black-capped Nightingale-Thrush *Catharus fumosus* Ridgway, 1888, and its two labels (courtesy of USNM Division of Birds, Smithsonian Institution)

Later that year, Zeledón (1885: 104) listed ‘*Catharus mexicanus* (Bonap.)’ in his catalogue of the Costa Rican avifauna, with an asterisk drawing attention to the USNM specimen. It was the first evidence of the species in Central America, and the first *C. mexicanus* specimen in the USNM collection (note the geographic range given by Baird 1874: 11). Ridgway and Zeledón apparently identified USNM 101765 by consulting published descriptions because no other specimens were immediately available for comparison (see Ridgway 1888). Bonaparte’s (1856) type had been collected by Auguste Sallé (1820–96) in ‘Jalappa’ (= Xalapa, Veracruz, Mexico) but its whereabouts are uncertain.¹

Three years later, Ridgway (1888: 505) described USNM 101765 as the holotype of a new species, *Catharus fumosus* Ridgway, 1888, after comparing it to a study skin from Guatemala in the private collection of George N. Lawrence (1806–95): ‘Although I have only one specimen of each for comparison, there cannot, I think, be any question of the propriety of separating this bird from true *C. mexicanus* ... [because the Guatemalan specimen] agrees very closely with descriptions of Mexican specimens, I have no doubt it belongs to the same form.’ Lawrence’s skin was probably AMNH 39095 (apparently the only Guatemalan skin of *C. mexicanus* in his large collection), which was catalogued at the American Museum of Natural History, New York, on 23 May 1889, and which Ridgway (1907: 23) later listed in his *C. m. mexicanus* sample.

However, after two decades of collecting efforts, the size of Ridgway’s (1907: 24) sample had barely improved. Now, in addition to USNM 101765, he had five or six adults from Costa Rica,² but this series was more similar in colour to two northern specimens (one each from Mexico and Guatemala) than to the aberrant USNM 101765. Ridgway (1907: 24) wrote:

‘The series of specimens of this species at my command is much too small to admit of any clear understanding of the extent of individual and geographical variation, especially the latter; but I believe there are three forms [i.e., not including *fumosus*], represented, respectively, by the birds of southern Mexico, Guatemala, and Costa Rica. Unfortunately I have only one each from the two first-named localities and five from the last ... The Costa Rican specimens are small, like the Guatemalan example, but besides differing in the blackish maxilla [vs. yellow], are deep brownish olive above (about intermediate in color between the Jalapa and Guatemala specimens), and have the chest, sides, and flanks mostly gray, instead of olive.’

However, unwilling to concede that the dark ventral plumage of USNM 101765 was merely an extreme example of individual variation in the Costa Rican sample, Ridgway (1907: 24) recognised both *C. m. mexicanus* (Mexico to Costa Rica) and *C. m. fumosus* (Costa Rica). The latter taxon, he proposed, was endemic to the ‘highlands of Costa Rica (precise locality unknown)’ and only one specimen was known.³ However, Carriker (1910: 749), who collected that specimen, dissented:

¹ Hellmayr (1934: 462) failed to locate the specimen among the remnants of Bonaparte’s collection at the Muséum national d’Histoire naturelle, Paris (MNHN). An extant Bonaparte mount (MNHN-ZO-MO-1858-1974, original no. = 8556) may be the type, but there are contradictory locality data given on the base of the pedestal (‘Guatemala’) and in the MNHN ledger (‘Mexique’), no collector data, and the original label is missing (P. Bousès *in litt.* 2025).

² Ridgway’s (1907: 23) table included measurement data from two males (CM P11127, P13539) and one female (CM P13557) in the Carnegie Museum of Natural History, Pittsburgh (CM). The female was later designated as the holotype of *C. m. carrikeri* A. R. Phillips, 1991. I examined these specimens in February 2023.

³ Wetmore’s (1944: 68) assertion that the *C. fumosus* holotype ‘came from one of the mountains near San José’ was apparently based on speculation, not original data. Deignan’s (1961: 430) claim that it was collected at Jiménez, Limón, was also unfounded (see Wetmore *et al.* 1984: 153).

'The name *Catharus fumosus* Ridgway was applied to a slightly immature specimen of an otherwise normal bird of the Costa Rican type of *C. mexicanus* ... all Costa Rican birds are very different from true *C. mexicanus* of Vera Cruz [Mexico], which fact was overlooked by Mr. Ridgway, and they must therefore be known under the name *Catharus mexicanus fumosus* (Ridgway), which name, although not really meant for the birds in question, must nevertheless be used for them.'

Griscom (1930) eventually restricted *C. m. mexicanus* to Mexico, and *C. m. fumosus* to Costa Rica and western Panama, while describing Guatemalan specimens from the mountains north-west of the Río Motagua under the novel name *C. m. cantator* Griscom, 1930. Hellmayr (1934: 464) expressed doubts about *C. m. cantator* but nonetheless recognised all three subspecies and extended the range of *C. m. fumosus* to north-western Nicaragua. Ripley (1952: 40) inexplicably synonymised *C. mexicanus* with *C. dryas* (Gould, 1855), but later followed Hellmayr (1934) in applying *C. m. fumosus* to populations ranging from Nicaragua to Panama (Ripley 1964: 169). This was the status quo until the late 20th century, when Phillips (1991) re-examined the *C. fumosus* holotype and proposed that it was a hybrid.

The hybrid hypothesis

The origins of the 'hybrid hypothesis' are found in draft copies of Phillips's manuscript, now at the Delaware Museum of Nature & Science (DMNH, formerly Delaware Museum of Natural History), Greenville. In the earliest draft, Phillips stated that USNM 101765 'appears to me to be a hybrid', then edited the sentence to read, '[it] is evidently a hybrid' (Fig. 2). Finally, he removed all semblance of doubt in his final (published) draft, stating that '[it] is a hybrid' (Phillips 1991: 111):

'The puzzling type of *fumosus* approaches *C. fuscater* in its dark colors, long wing (88.5 mm), rather heavy bill, intermediate tail-graduation (4.5 mm), and perhaps somewhat shorter "crest". It resembles *mexicanus* in most ways, except ventrally ... Ridgway (1907: 24) considered it a distinct race of *mexicanus* from an unknown locality, differing from all other Costa Rican specimens. Carriker, finding no such race anywhere, assigned the name to all Costa Rican *mexicanus*, thinking the type somewhat abnormal as above. Each was right, in his way: Costa Rican *mexicanus* are unlike either

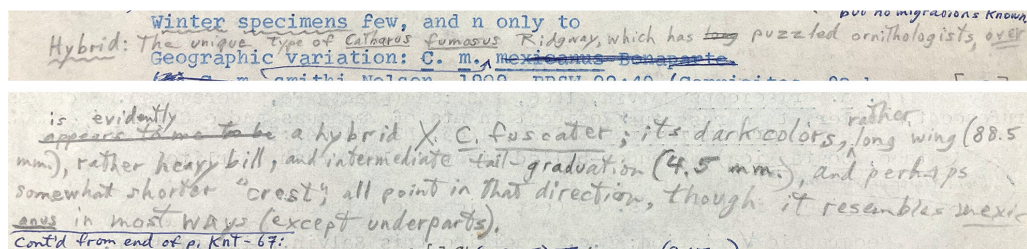


Figure 2. Early draft of Phillips's (1991) comments on the type of Black-capped Nightingale-Thrush *Catharus fumosus*, written in pencil: 'Hybrid: The unique type of *Catharus fumosus* Ridgway, which has long puzzled ornithologists ... appears to me to be a hybrid \times *C. fuscater*; its dark colors, rather long wing (88.5 mm), rather heavy bill, and intermediate tail-graduation (4.5 mm), and perhaps [a] somewhat shorter "crest", all point in that direction, though it resembles *mexicanus* in most ways (except underparts).' Reproduced courtesy of the Delaware Museum of Nature & Science (DMNH).

Mexican birds or the type of *fumosus*, which is a hybrid.'

Art. 23 of the Code, then in its third edition, stipulated that 'A species-group name established for an animal later found to be a hybrid [Art. 17(1)] must not be used as the valid name of either of the parental species' (ICZN 1985: 23). This rule was essentially unchanged in the fourth edition, despite some light editing (ICZN 1999, Art. 23.8). Therefore, after proposing the hybrid hypothesis, Phillips (1991) declared that Ridgway's (1888) description was invalid and re-described the Costa Rican taxon under the name *C. m. carrikeri* A. R. Phillips, 1991, based on CM P13557, the Costa Rican female examined by Ridgway (1907). At that time, there had been no credible reports of hybridisation between any *Catharus* species (McCarthy 2006); and even now, 36 years later, the only reports of early generation hybrids come from three closely related migratory species (FitzGerald *et al.* 2017, Martinsen *et al.* 2017, Termignoni-Garcia *et al.* 2022). No reports of hybridisation have been confirmed in any of the Neotropical resident *Catharus* lineages, to my knowledge, despite genetic evidence of prehistoric introgression (Everson *et al.* 2019).

Phillips (1991) offered scant evidence in support of the hybrid hypothesis. With respect to the dark ventral plumage, he merely implied, as Ridgway (1907) had done, that all *C. [mexicanus]* specimens from Costa Rica are uniformly bright in their ventral plumage, and therefore the 'dark' underparts of USNM 101765 needed an explanation. He contended that the 'long wing' and 'rather heavy bill' were evidence of hybrid origin but presented no evidence that his measurements were statistical outliers, or that they were intermediate between the putative parental species. Here, to resolve nomenclature, I compared the phenotypic characters (plumage colour and quantitative morphometrics) of USNM 101765 to a large and geographically representative sample of adult male study skins.

Methods

I examined and measured adult male study skins of *C. mexicanus* ($n = 56$) and *C. fumosus* ($n = 72$, including USNM 101765), identified by their collecting localities north-west and south-east of the Río Motagua, respectively (i.e., corresponding to the UCE clades; see Appendix), and *C. hellmayri* ($n = 41$), in the collections of the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), AMNH, CM, DMNH, Field Museum of Natural History, Chicago (FMNH), Museum of Comparative Zoology, Cambridge, MA (MCZ), and USNM. I used an iPhone to capture images of specimens in the USNM collection, to illustrate relevant patterns of colour variation. I used a metric wing ruler to measure the flattened length of the right wing of each specimen, from the carpal joint to the tip of the longest primary remex (WG); and the length of the tail from the insertion point of the two central rectrices to the tip of the longest rectrix (TL); and digital callipers to measure the length of the right tarsometatarsus (or left if the right was broken), from the intertarsal joint to the end of the final leg scale (TR); the length of the bill, from the anterior edge of the right naris to the tip (BL); and the width of the bill at the anterior edge of the naris (BW). I excluded 'tail graduation' from the analysis, although it was given by Phillips (1991) as an intermediate character, because of uncertainty about his measurement technique. All statistics were performed with R-Studio (R Core Team 2020). To examine potential clinal variation in the *C. [mexicanus]* complex, I estimated the collecting latitude of each specimen from label data or with Google Earth Pro. I performed linear regression analyses to model the relationships between latitude and the five morphometric variables, and interpreted models with p -values less than 0.05 as statistically significant. I also used boxplots to compare the measurements of USNM 101765 to the *C. mexicanus*, *C. fumosus* and *C. hellmayri* samples.

Plumage colour variation

The dark ventral colour of USNM 101765 was emphasised by Ridgway (1888, 1907) in the original and secondary descriptions of *C. fumosus*, and later by Phillips (1991: 111), who concluded that it was a hybrid character. However, there are other *C. fumosus* study skins that are nearly as dark (especially those collected in Panama, as acknowledged by Phillips 1991: 111, e.g., MCZ 137397 and 137398), and the ventral plumage of USNM 101765 is actually darker than that of most *C. hellmayri* males, not lighter as one would expect from a bird with an intermediate (hybrid) phenotype (Fig. 3). It appears that the ‘dark’ ventral plumage of USNM 101765 merely reflects one end of a continuum of intrapopulation (individual) variation within *C. fumosus*. For example, USNM 198803, an adult male from Bonilla, Limón, Costa Rica, collected by A. Alfaro with Ridgway present (see Halley 2024: 124) on 30 March 1905, is nearly as dark as USNM 101765 (Fig. 3), and digital photos of wild birds in the Macaulay Library (ML), taken between Volcán Tenorio and San José, show a considerable range of individual variation. The underparts of some individuals are pale grey (e.g., ML 557487321, 393335501), whereas others have a bright (whitish) throat that contrasts with a dusky grey belt across the lower breast (e.g., ML 525014371, 496253471), and others still have a dark grey throat like USNM 101765 (e.g., ML 550113391, 417916291, 352993681). The evolutionary history of this variation and its adaptive function (if any)



Figure 3. Ventral and dorsal views of (A) a ‘dark’ adult male Black-capped Nightingale-Thrush *Catharus fumosus* (USNM 198803) collected in 1905 at Bonilla, Limón, Costa Rica; (B) the adult male holotype of *C. fumosus* Ridgway, 1888 (USNM 101765) collected at an unknown locality in Costa Rica; and (C) an adult male of Talamanca Nightingale-Thrush *C. hellmayri* von Berlepsch, 1902, collected near Dota, San José, Costa Rica (USNM 209929). The difference between these photos, and those of USNM 101765 in Fig. 1, provide a valuable demonstration of how variable light conditions may deceive taxonomists working with *Catharus* specimens; specimens should only be compared within the same photo, not between photos taken under different conditions (Matthew R. Halley; reproduced courtesy of the USNM Division of Birds, Smithsonian Institution)

are unknown, but subtle patterns of polychromatism (sometimes called ‘colour phases’ or gradients) have been demonstrated in the closely related *C. [fuscater]* complex (Halley *et al.* 2023) and in two migratory species, Grey-cheeked Thrush *C. minimus* (Lafresnaye, 1848) and Bicknell’s Thrush *C. bicknelli* (Ridgway, 1882), with the variation being evident among adults in the same breeding population (e.g., Wallace 1939, Burleigh & Peters 1948), as Phillips (1991: 95) acknowledged. Therefore, there is no reason to assume that the ventral gradient in *C. fumosus*, or the ‘dark’ colour of USNM 101765 (i.e., one endpoint of that gradient), are the consequence of hybridisation with *C. hellmayri* or any other species (*contra* Phillips 1991: 111).

Morphometric variation

In the *C. [mexicanus]* complex, I detected significant relationships with latitude in four of five morphometric variables (Table 1, Fig. 4). WG showed a decreasing trend from north to south, and the ‘long wing’ of USNM 101765 (Phillips 1991: 111) fell comfortably within the *C. fumosus* distribution (Fig. 5). TR also decreased from north to south, but the effect was weak ($\beta = 0.051$, $t = 2.948$, Table 1, Fig. 4). USNM 101765 had a shorter than average TR for the *C. fumosus* sample—not longer, as one would expect of a hybrid with a *C. hellmayri* parent (Fig. 5). TL also decreased from north to south, with a medium effect size ($\beta = 0.384$, $t = 8.175$, Table 1) and the tail of USNM 101765 (58 mm) was below average for *C. fumosus*, not above average as predicted by the hybrid hypothesis ($n = 35$, mean TL = 58.2 mm, Fig. 5). BL increased weakly with latitude ($\beta = 0.019$, $t = 2.686$) and this

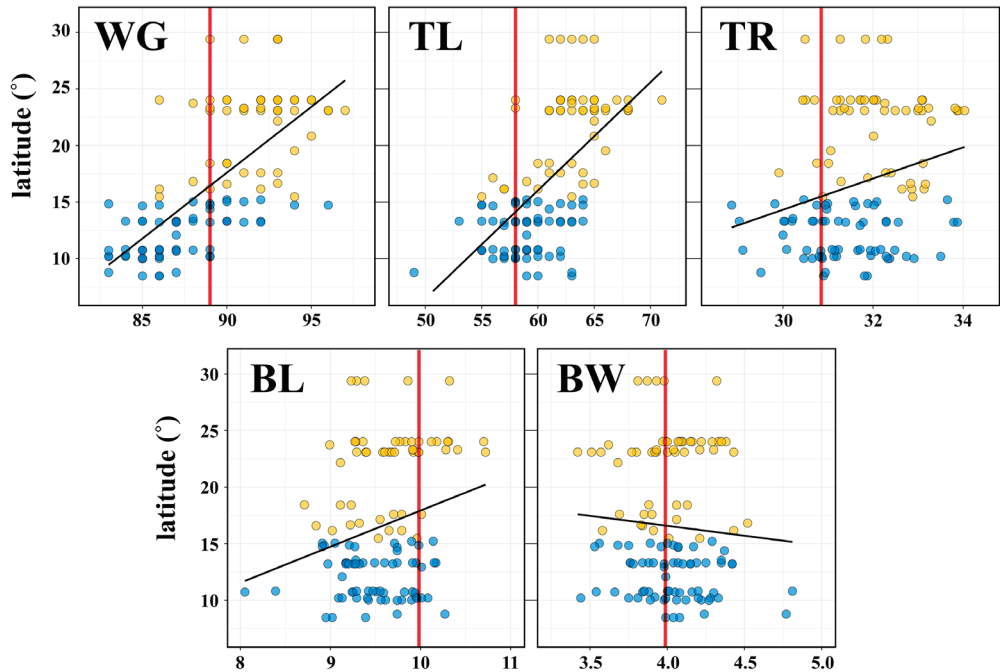


Figure 4. Relationships between latitude (predictor) and five morphometric variables in a sample of adult male study skins of Black-headed Nightingale-Thrush *Catharus mexicanus* (yellow dots: Mexico to Guatemala) and Black-capped Nightingale-Thrush *C. fumosus* (blue dots: Honduras to Panama): wing length (WG), tail length (TL), tarsometatarsus length (TR), bill length (BL) and bill width (BW). Latitude is shown on the y-axis for visualisation purposes. All variables have millimetres (mm) as units. Linear regression trendlines for the combined data are shown in black. Red vertical lines denote the measurements of the *C. fumosus* holotype (USNM 101765).

TABLE 1
Results of linear regression models of relationships between latitude (predictor) and five morphometric variables (WG, TL, TR, BL, BW) in a range-wide sample of adult male *Catharus [mexicanus]* study skins ($n = 128$).

Variable	R ²	df	β	t	p
WG	0.485	114	0.417	10.37	<0.002
TL	0.368	115	0.384	8.175	<0.001
TR	0.070	116	0.051	2.948	0.004
BL	0.060	114	0.019	2.686	0.008
BW	0.006	115	-0.003	-0.822	0.413

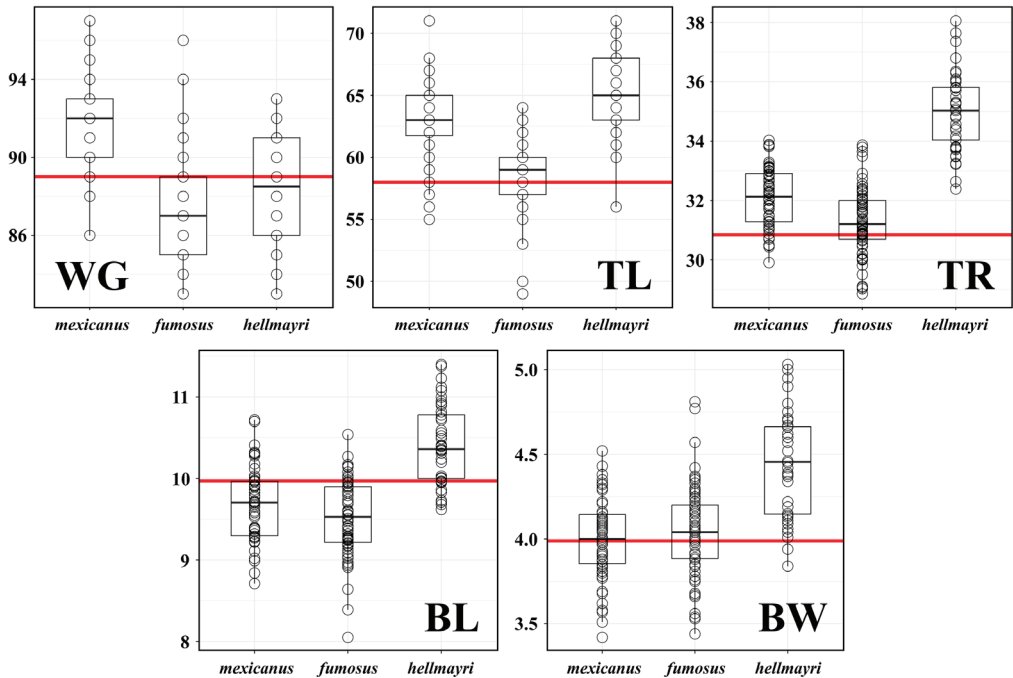


Figure 5. Geographic variation in five morphometric variables in a sample of adult male study skins of Black-headed Nightingale-Thrush *Catharus mexicanus* (Mexico to Guatemala), Black-capped Nightingale-Thrush *C. fumosus* (Honduras to Panama) and Talamanca Nightingale-Thrush *C. hellmayri* (Costa Rica to Panama): wing length (WG), tail length (TL), tarsometatarsus length (TR), bill length (BL) and bill width (BW). All variables have millimetres (mm) as units. Red horizontal lines denote the measurements of the *C. fumosus* holotype (USNM 101765).

relationship was not significant (Table 1, Fig. 4). The BW of USNM 101765 was slightly below average for the *C. fumosus* sample (Fig. 5), not above average as predicted by the hybrid hypothesis.

Taxonomy and nomenclature

The supposedly hybrid characters of USNM 101765, the adult male holotype of *C. fumosus* Ridgway, 1888, fall within the normal range of phenotypic variation of the southern clade of the *C. [mexicanus]* complex, for which the name *C. fumosus* has priority (Halley 2021). With respect to its ‘darker’ ventral plumage, Phillips (1991) was evidently misled (like Ridgway 1888, 1907) by individual (intrapopulation) variation, reminiscent of polychromatic patterns in the *C. [fuscater]* complex (Halley *et al.* 2023).

Specimens and photographed individuals of *C. fumosus* exhibit a range of brightness in the ventral plumage, perhaps but not necessarily related to age or sex. Therefore, the most parsimonious explanation is that USNM 101765 merely represents one extreme of a plumage brightness gradient. The 'long wing' and 'rather heavy bill' of USNM 101765, which Phillips (1991) emphasised as potentially hybrid characters, also fall within the normal range of variation in *C. fumosus*. Analysis of three other morphometric characters (TL, TR, BL), which were not mentioned by Phillips (1991), similarly failed to produce support for the hybrid hypothesis. Therefore, I recommend that the name *C. fumosus* Ridgway, 1888 be retained for the southern clade of the *C. [mexicanus]* complex, irrespective of its taxonomic rank. The taxon *C. m. carrikeri* A. R. Phillips, 1991, is its junior synonym (see Appendix). If additional research finds support for the hybrid hypothesis, in the interest of nomenclatural stability, I recommend that a neotype be designated to preserve the long-standing nomenclature (ICZN 1999, Art. 75).

Acknowledgements

I am grateful to Jason D. Weckstein, Nathan H. Rice, Gary Rosenberg, Richard M. McCourt, Jacob A. Russell, Guy M. Kirwan, and one anonymous reviewer for commenting on early versions of the manuscript. For assistance with study skins, I thank Christopher M. Milensky and Brian K. Schmidt (USNM), Paul R. Sweet (AMNH), Serina S. Brady (CM), Nathan H. Rice (ANSP), Ben D. Marks (FMNH) and Jeremiah Trimble (MCZ).

References:

- Baird, S. F. 1874. Review of American birds in the museum of the Smithsonian Institution. Part 1. *Smiths. Misc. Coll.* 12: 1–484.
- von Berlepsch, H. G. 1902. Beschreibung zweier neuer Drosselformen aus Südamerika. *Orn. Monatsb.* 5: 69–71.
- Bonaparte, C. L. 1856. Additions et corrections aux tableaux paralléliques de l'ordre des hérons et des pélagiens ou gavies, et à la partie correspondante, déjà publiée, du Conspectus Avium de S. A. Monseigneur le Prince Charles-L. Bonaparte. *Compt. Rend. Acad. Sci., Paris* 43: 990–999.
- Burleigh, T. D. & Peters, H. S. 1948. Geographic variation in Newfoundland birds. *Proc. Biol. Soc. Wash.* 61: 111–126.
- Carriker, M. A. 1910. An annotated list of the birds of Costa Rica including Cocos Island. *Ann. Carnegie Mus.* 6: 314–915.
- Clement, P. 2000. *Thrushes*. Princeton Univ. Press.
- Clements, J. F., Schulenberg, T. S., Iliff, M. J., Fredericks, T. A., Gerbracht, J. A., Lepage, D., Billerman, S. M., Sullivan, B. L. & Wood, C. L. 2022. The eBird/Clements checklist of birds of the world: v2022. <https://www.birds.cornell.edu/clementschecklist/download/>.
- Clements, J. F., Rasmussen, P. C., Schulenberg, T. S., Iliff, M. J., Fredericks, T. A., Gerbracht, J. A., Lepage, D., Spencer, A., Billerman, S. M., Sullivan, B. L., Smith, M. & Wood, C. L. 2024. The eBird/Clements checklist of birds of the world: v2024. <https://www.birds.cornell.edu/clementschecklist/download/>.
- Collar, N. 2020. Black-headed Nightingale-Thrush (*Catharus mexicanus*), version 1.0. In del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & de Juana, E. (eds.) *Birds of the world*. Cornell Lab of Ornithology, Ithaca, NY. <https://doi.org/10.2173/bow.bhnthrl.01> (accessed 5 April 2024).
- Deignan, H. G. 1961. Type specimens of birds in the United States National Museum. *Bull. US Natl. Mus.* 221: 1–718.
- Dickerman, R. W. & Parkes, K. C. 1997. Taxa described by Allan R. Phillips, 1939–1994: a critical list. Pp. 211–234 in Dickerman, R. W. (ed.) *The era of Allan R. Phillips: a Festschrift*. Horizon Communications, Albuquerque, NM.
- Everson, K. V., McLaughlin, J. F., Cato, I. A., Evans, M. M., Gastaldi, A. R., Mills, K. K., Shink, K. G., Wilbur, S. M. & Winker, K. 2019. Speciation, gene flow, and seasonal migration in *Catharus* thrushes (Aves: Turdidae). *Mol. Phylo. & Evol.* 139: 106564.
- FitzGerald, A. M., Whitaker, D. M., Ralston, J., Kirchman, J. J. & Warkentin, I. G. 2017. Taxonomy and distribution of the imperilled Newfoundland Gray-cheeked Thrush, *Catharus minimus minimus*. *Avian Conserv. & Ecol.* 12: 10.
- Gill, F., Donsker, D. & Rasmussen, P. (eds.) 2024. IOC world bird list (v 14.1). doi:10.14344/IOC.ML.14.1. (accessed 5 April 2024).
- Gould, J. 1855. Description of a new bird from Guatemala, forming the type of a new genus. *Proc. Zool. Soc. Lond.* 22: 285.
- Griscom, L. 1930. Studies from the Dwight collection of Guatemala birds. III. *Amer. Mus. Novit.* 438: 1–18.

- Halley, M. R. 2021. Integrative systematics and evolution of seasonal migration in the nightingale-thrushes (Aves: Turdidae: *Catharus*). Ph.D. thesis. Drexel University, Philadelphia.
- Halley, M. R. 2024. Remarks on the Costa Rican expeditions of Ridgway and Zeledón in 1905 and 1908, with a focus on three type localities. *Bull. Brit. Orn. Cl.* 144: 121–131.
- Halley, M. R., Klicka, J., Sesink Clee, P. & Weckstein, J. D. 2017. Restoring the species status of *Catharus maculatus* (Aves: Turdidae), a secretive Andean thrush, with a critique of the yardstick approach to species delimitation. *Zootaxa* 4276: 387–404.
- Halley, M. R., Catanach, T. A., Klicka, J. & Weckstein, J. D. 2023. Integrative taxonomy reveals hidden diversity in the *Catharus fuscater* (Passeriformes: Turdidae) complex in Central and South America. *Zool. J. Linn. Soc.* 199: 228–262.
- HBW & BirdLife International (HBW). 2024. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. v9. http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v9_Oct24.zip.
- Hellmayr, C. E. 1934. Catalogue of birds of the Americas and the adjacent islands, pt. 7. *Publ. Field Mus. Nat. Hist., Zool. Ser.* 13(7): 1–531.
- International Commission on Zoological Nomenclature (ICZN). 1985. *International code of zoological nomenclature*. Third edn. International Trust for Zoological Nomenclature, London.
- International Commission on Zoological Nomenclature (ICZN). 1999. *International code of zoological nomenclature*. Fourth edn. International Trust for Zoological Nomenclature, London.
- Lafresnaye, M. F. 1845. Description de quelques oiseaux nouveaux. *Rev. Zool. Soc. Cuvierienne* 8: 337–342.
- Lafresnaye, M. F. 1848. Description de quelques oiseaux nouveaux de Caracas (province de Venezuela) et de Bogota. *Rev. Zool. Soc. Cuvierienne* 11: 2–12.
- LeCroy, M. 2005. Type specimens of birds in the American Museum of Natural History. Part 6. Passeriformes: Prunellidae, Turdidae, Orthonychidae, Timaliidae, Paradoxornithidae, Picathartidae, and Polioptilidae. *Bull. Amer. Mus. Nat. Hist.* 292: 1–127.
- Martinsen, E. S., McFarland, K. P. & Rimmer, C. C. 2017. Documentation of a hybrid Bicknell's Thrush (*Catharus bicknelli*) × Veery (*C. fuscescens*) using vocalization and genetic data. *Wilson J. Orn.* 130: 70–80.
- McCarthy, E. M. 2006. *Handbook of avian hybrids of the world*. Oxford Univ. Press, New York.
- Phillips, A. R. 1991. *The known birds of North and Middle America*, pt. 2. Privately published.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.r-project.org/index.html> (accessed 14 March 2023).
- Ridgway, R. 1882. Descriptions of two new thrushes from the United States. *Proc. US Natl. Mus.* 4: 374–379.
- Ridgway, R. 1888 (= 1887). Descriptions of some new species and subspecies of birds from Middle America. *Proc. US Natl. Mus.* 10: 505–510.
- Ridgway, R. 1907. The birds of North and Middle America, pt. 4. *Bull. US Natl. Mus.* 50: 1–973.
- Ripley, S. D. 1952. The thrushes. *Postilla* 13: 1–48.
- Ripley, S. D. 1964. Subfamily Turdinae, thrushes. Pp. 13–227 in Mayr, E. & Paynter, R. A. (eds.) *Check-list of birds of the world*, vol. 10. Mus. Comp. Zool., Cambridge, MA.
- Salvin, O. & Godman, F. D. 1879. *Biologia Centrali-Americana. Aves*, vol. 1. R. H. Porter, London.
- Slater, P. L. 1859a. List of the first collection of birds made by Mr. Louis Fraser at Pallatanga, Ecuador, with notes and descriptions of new species. *Proc. Zool. Soc. Lond.* 1859: 135–147.
- Slater, P. L. 1859b. A synopsis of the thrushes (Turdidae) of the New World. *Proc. Zool. Soc. Lond.* 1859: 321–347.
- Termignoni-Garcia, F., Kirchman, J. J. & Clark, J. 2022. Comparative population genomics of cryptic speciation and adaptive divergence in Bicknell's and Gray-cheeked Thrushes (Aves: *Catharus bicknelli* and *Catharus minimus*). *Genome Biol. & Evol.* 14: evab255.
- Wallace, G. J. 1939. Bicknell's thrush, its taxonomy, distribution, and life history. *Proc. Boston Soc. Nat. Hist.* 41: 211–402.
- Wetmore, A. 1944. A collection of birds from northern Guanacaste, Costa Rica. *Proc. US Natl. Mus.* 95: 25–80.
- Wetmore, A., Pasquier, R. F. & Olson, S. L. 1984. *The birds of the Republic of Panamá*, pt. 4. Smithsonian Institution Press, Washington, DC.
- Zeledón, J. C. 1885. Catalogue of the birds of Costa Rica, indicating those species of which the United States National Museum possesses specimens from that country. *Proc. US Natl. Mus.* 8: 104–118.

Address: Delaware Museum of Nature & Science, Wilmington, Delaware 19807, USA; and Academy of Natural Sciences of Drexel University, Dept. of Biodiversity, Earth & Environmental Science, Drexel Univ., Philadelphia, Pennsylvania 19104, USA, e-mail: matthewhalley@gmail.com

Appendix

Synonyms and taxonomic combinations of *C. mexicanus* (Bonaparte) and *C. fumosus* Ridgway, and their principal citations. In this treatment, the sister species have allopatric ranges occurring north-west and south-east, respectively, of the Río Motagua in eastern Guatemala (see above, Halley 2021).

***Catharus mexicanus* (Bonaparte)**
Black-headed Nightingale-Thrush

Malacocychla mexicana (not *Catharus mexicanus*) Bonaparte, 1856.

Holotype: not located; missing from Bonaparte's collection at the Muséum national d'Histoire naturelle, Paris (MNHN), see footnote 1.

Catharus mexicanus Sclater 1859a: 136; Sclater 1859b: 324; Salvin & Godman 1879: 6–7 (in part).

Catharus mexicanus mexicanus Ridgway 1907: 22; Griscom 1930: 4; Hellmayr 1934: 462–463; Phillips 1991: 110; Clement 2000: 303; Halley 2021: 202; Clements *et al.* 2024; Gill *et al.* 2024; HBW 2024.

Catharus mexicanus smithi Nelson 1909; Phillips 1991: 109.

Holotype: USNM 204801, in National Museum of Natural History, Smithsonian Institution, Washington, DC: 'Carricitos pueblo (5,500–6,000 ft.) in Sierra Madre about 40 miles west & 20 miles north of [Ciudad] Victoria ... in a deep barranca', Tamaulipas, Mexico (see Deignan 1961: 429).

Catharus mexicanus cantator Griscom 1930: 4; Hellmayr 1934: 463 (in part); Phillips 1991: 110 (in part); Clement 2000: 303 (in part); Clements *et al.* 2024 (in part); Gill *et al.* 2024; HBW 2024 (in part).

Holotype: AMNH 396410, in American Museum of Natural History, New York: Finca Sepacuité, Alta Verapaz, Guatemala (see LeCroy 2005: 39).

Catharus dryas mexicanus Ripley 1952: 40.

Catharus dryas cantator Ripley 1952: 40.

***Catharus fumosus* Ridgway**
Black-capped Nightingale-Thrush

Catharus mexicanus Salvin & Godman 1879: 6–7 (in part).

Catharus fumosus Ridgway 1888: 505.

Holotype: USNM 101765, in National Museum of Natural History, Smithsonian Institution, Washington, DC: 'Costa Rica' (see Deignan 1961: 429–430).

Catharus mexicanus fumosus Ridgway 1907: 24; Carriker 1910: 748; Griscom 1930: 4; Wetmore 1944: 68; Hellmayr 1934: 464; Clement 2000: 303; Halley 2021: 202; Clements *et al.* 2024.

Catharus mexicanus cantator Hellmayr 1934: 463 (in part); Clement 2000: 303 (in part); Phillips 1991: 110 (in part); Clements *et al.* 2024 (in part); HBW 2024 (in part).

Catharus dryas fumosus Ripley 1952: 40.

Catharus mexicanus yaegeri Phillips 1991: 110; Gill *et al.* 2024; HBW 2024.

Holotype: not located: 'Las Penitas, N.W. Honduras' (see Dickerman & Parkes 1997: 222).

Catharus mexicanus carrikeri Phillips 1991: 111; Gill *et al.* 2024; HBW 2024.

Holotype: CM P13557, in Carnegie Museum of Natural History, Pittsburgh: 'in lower foothills N of Volcán Turrialba, Costa Rica (see Dickerman & Parkes 1997: 222).

Catharus mexicanus subsp.? Phillips 1991: 111.