AOS Classification Committee – North and Middle America

Proposal Set 2026-A

6 January 2026

Treat *Formicarius destructus* as a separate species from *F. nigricapillus*

Note: This is the same proposal as 2025-D-2, which was postponed to allow SACC to consider the proposed split and to provide input on English names.

Effect on NACC:

If passed, this proposal will result in the elevation of extralimital taxon *destructus* to species status, resulting in a monotypic *Formicarius nigricapillus* and a monotypic *F. destructus*. This will require changes to the English name, distributional statement, and Notes for *F. nigricapillus*.

Background information:

The current SACC note reads " 1c. Areta & Benítez Saldívar (2025) provided vocal evidence for treating South American *destructus* as separate species. SACC proposal needed."

Areta & Benítez Saldívar (2025) summarized the situation as follows:

The Black-headed Antthrush (*Formicarius nigricapillus*) includes two allopatric subspecies: nominotypic *nigricapillus* in Costa Rica and Panama, and *destructus* in Colombia and Ecuador (Ridgway 1893; Hartert 1898; Wetmore 1972; Krabbe and Schulenberg 2003, 2020). Although the taxon *nigricapillus* was originally described as a species by Ridgway (1893) and treated as such by some authors (Chapman 1917, Cory & Hellmayr 1924), it was often considered to be a subspecies of the Black-faced Antthrush (*F. analis*) (Hartert 1902, Ridgway 1911). Conversely, the taxon *destructus* was originally described as a subspecies of *F. analis* by Hartert (1898), and was subsequently either considered as such (Hartert 1902), rarely afforded species-level status (Salvadori and Festa 1899; Howell and Dyer 2022), or most often considered to be a subspecies of *F. nigricapillus* (Chapman 1917, Cory & Hellmayr 1924, Wetmore 1972, Krabbe & Schulenberg 2003).

New information:

In Areta & Benítez Saldívar (2025), we assessed species limits in *F. nigricapillus* using vocal, plumage, and morphometric data, concluding that *nigricapillus* and *destructus* are better treated as two separate biological and recognition species (Paterson 1985). For more detailed explanations and discussions stemming from historical taxonomic references, please refer to the publication. What follows is a blend of selected copied and reorganized text and images from Areta & Benítez Saldívar (2025) with some minor adjustments to facilitate reading.

Songs: After discarding duplicates, Areta & Benítez Saldívar (2025) compiled a total of 57 songs of *nigricapillus* and 129 songs of *destructus* that were assessed aurally and through examination of spectrograms. The song of *nigricapillus* is a rapid series of around 25 clear, pulsated whistled notes that begins with a few more spaced notes that become mostly evenly paced with a slight rise in pitch halfway through the song and a relatively monotonous ending (sigmoid-like spectrographic contour; Fig. 1). The song of *destructus* is a very rapid, eerie series of around 40 ventriloquial notes that fall and rise in pitch and decrease markedly in pace in the second half (smile-like spectrographic contour; Fig. 1). The vocalizations of *nigricapillus* and *destructus* have been described accurately in field guides, but the importance of their differences has not been fully realized. The song of *nigricapillus* was described as "a rapid, pulsating series of ca. 20 deep, resonant, whistled notes, the first 2-3 slower, more staccato, the next 6-8 rising in pitch, the last 10-12 on the same pitch, with the final 2 notes slower, the entire series lasting 4-5 sec" (Stiles and Skutch 1989, p. 287), whereas that of *destructus* "resembles that of Rufous-capped Antthrush, but shorter, an eerie, quavering glissando of about 30 notes in 3 sec, sliding upscale and slowing noticeably at the end; ventriloquial" (Hilty and Brown 1986, p. 417). The song of *nigricapillus* has been aptly likened to the shorter song of Thicket Antpitta *Myrmothera dives* (Garrigues and Dean 2007; Vallely and Dyer 2018), a comparison that does not apply to the song of *destructus*.

The quantitative acoustic characterization showed that songs of both taxa are 100% diagnosable (n=21 *nigricapillus*, n=38 *destructus*). Acoustic data showed that 13 out of 15 variables differed significantly between *nigricapillus* and *destructus*, the differences in 10 of these 13 variables were very marked with non-overlapping mean±SD, automatically indicating that they belong to statistically different populations. Taxon *nigricapillus* showed lower song peak frequency, longer mean note duration and mean interval between notes, fewer notes per song, slower pace, relatively even pace in the first and second halves of the song, lower peak frequencies of first, median, and final note, and longer duration of first, median, and final note. In contrast, *destructus* had higher song peak frequency, shorter mean note duration and mean interval between notes, more notes per song, faster pace, a marked deceleration in the second half of the song, higher peak frequencies of first, median, and final note, and shorter duration of first, median, and final note (Table 1). The songs of both taxa were clearly separated in multivariate space (Fig. 2A) and a cluster analysis also revealed two distinct groups, unambiguously including all *destructus* samples clustered separately from all *nigricapillus* recordings (Fig. 2B).

The song of *nigricapillus* remains essentially identical through ca. 490km across Costa Rica and into C Panama in our sample, whereas the song of *destructus* remains basically the same through ca. 1130 km extending from NC Colombia to SW Ecuador. The diagnostic song types are separated by a gap of ca. 190 km between NW Colombia (Jardín Botánico del Pacífico, Chocó) and E Panamá (Nusagandi, Guna Yala), and exhibit no sign of intermediacy closer to their respective limits (Fig. 1). Further documented records are needed to properly understand the actual distributional gap between *nigricapillus* and *destructus.* The width of the gap is at least 190km as shown by our song-recordings dataset, but possibly much smaller: birds seen, heard, and tape recorded at Cuchilla del Lago on the Colombian side of of the Serranía de Darién in the Cerro Tacarcuna (Renjifo et al. 2017) most likely represent the taxon *nigricapillus*. This would reduce the gap between *nigricapillus* (Cuchilla del Lago; see question mark in Figure 1) and *destructus* (Reserva La Bonga) to 100 km within Colombia. Unfortunately, the sound recordings were not available at the time of our writing and could not be assessed (J. Avendaño in litt.). Further fieldwork should clarify the extent of their allopatry, and assess whether the Río Atrato and its formidable swamps act as a biogeographic barrier for these taxa (Haffer 1970, 1975, Renjifo et al. 2017). The Cerro Tacarcuna records, if confirmed to be *nigricapillus* (which seems very likely), would indicate that both taxa (*nigricapillus* and *destructus*) occur in South America.

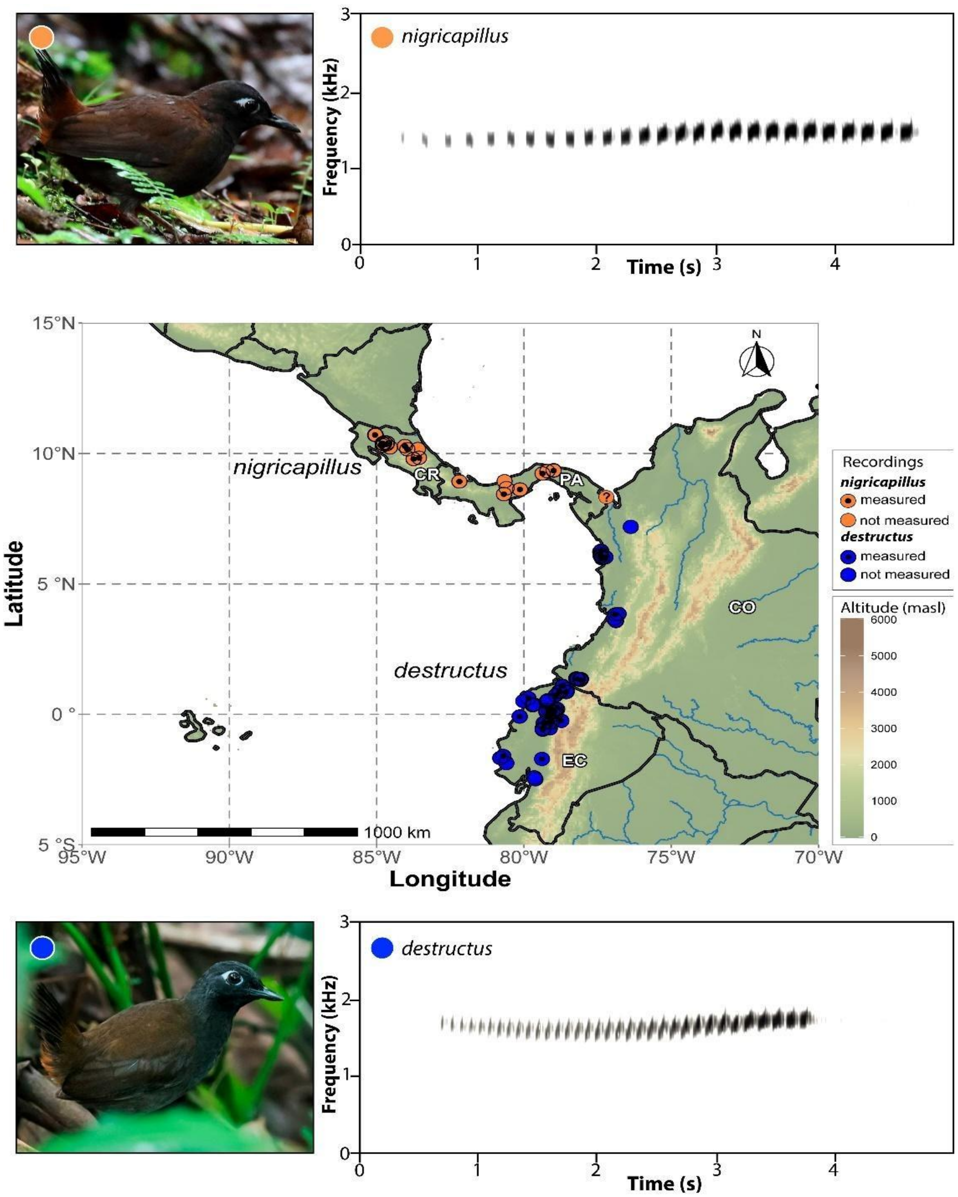


Fig. 1. Plumage aspect, songs, and geographic distribution of songs of Black-capped Antthrush (*Formicarius nigricapillus*), and Black-hooded Antthrush (*F. destructus*) analysed in this study. Orange circles: *F. nigricapillus* (photo: ML-452131711, San Gerardo Biological Station, Costa Rica, by Mark Hebblewhite; song: ML-220516, Reserva Biológica Bosque Nuboso Monteverde, Costa Rica by D. L. Ross). Blue circles: *F. destructus* (photo: ML-121617911, Rio Silanche Bird Sanctuary, Ecuador by Nick Athanas; song: JIA-10, Reserva de Bosque Seco Lalo Loor, Ecuador by J. I. Areta). Circles with a central dot denote songs measured quantitatively; plain circles denote songs studied aurally (see Appendices 1 and S1); question mark (?) indicates unconfirmed sound recording of *nigricapillus* from Cerro Tacarcuna in Colombia. The differences in plumage (chestnut nape in *nigricapillus*, black nape in *destructus*), song, and morphometrics collectively support the recognition of *nigricapillus* and *destructus* as separate species.

Table 1. Acoustic parameters of songs of Black-capped Antthrush (*Formicarius nigricapillus*), and Black-hooded Antthrush (*F. destructus*). Values shown are mean ± SD [range], n= sample size. Asterisk denotes significant statistical differences in the Mann-Whitney non-parametric test (α<0.05), and plus symbol denotes non overlapping mean±SD. See Appendix 1 for measured sound recordings.

Variable	***F. nigricapillus* (n=21)**	***F. destructus* (n=38)**
Bandwidth 90% (Hz)	205.35±56.37 [93.8-281.2]	207.93±38.45 [140.6-281.2]
Duration 90% (s)*	2.38±0.33 [1.74-3.00]	2.64±0.44 [1.92-3.88]
Peak frequency (Hz)* $^{+}$	1484.37±61.75 [1406.2-1593.8]	1689.91±61.7 [1546.9-1781.2]
Mean note duration (s)* $^{+}$	0.06±0.01 [0.05-0.09]	0.04±0.01 [0.02-0.07]
Mean interval between notes (s)* $^{+}$	0.08±0.01 [0.05-0.10]	0.04±0.01 [0.03-0.06]
Number of notes* $^{+}$	24.95±1.69 [22-29]	37.62±5.57 [28-52]
Sound density	0.56±0.06 [0.46-0.67]	0.6±0.08 [0.47 - 0.79]
Pace* $^{+}$	5.98±0.42 [5.44-6.96]	9.61±1.09 [7.76-11.81]
Pace change (second/first half)* $^{+}$	1.04±0.09 [0.88-1.19] (8.63±1.2/11.37± 1.08) [5.61-6.67/5.25-7.58]	0.76±0.07 [0.63-0.93] (6.18±0.32/5.99±0.66) [6.82-11.46/9.02-12.82]
Peak frequency first note (Hz)* $^{+}$	1345.97±68.13 [1218.8-1500]	1650.24±93.23 [1406.2-1781.2]
Peak frequency median note (Hz)* $^{+}$	1412.91±47.54 [1312.5-1500]	1617.82±58.76 [1453.1-1781.2]
Peak frequency final note (Hz)* $^{+}$	1477.67±60.46 [1406.2-1593.8]	1703.12±69.11 [1546.9-1875]
Duration first note (s)*	0.04±0.02 [0.01-0.06]	0.02±0.01 [0.01-0.03]
Duration median note (s)* $^{+}$	0.09±0.02 [0.04-0.14]	0.12±0.03 [0.04-0.10]
Duration final note (s)*	0.14±0.04 [0.10-0.26]	0.11±0.03 [0.06-0.21]

*=non-parametric Mann-Whitney test P-value <.05

$^{+}$=non-overlapping mean±SD

Plumage: To characterize the external appearance of *nigricapillus* and *destructus*, Areta & Benítez Saldívar (2025) examined photographs of 37 museum specimens, including the holotypes of both taxa, and vetted 40 good quality photographs on the citizen science platforms eBird (ebird.org) and iNaturalist (inaturalist.org). They found that *nigricapillus* exhibits chestnut-brown hindneck (sometimes extending to neck sides in a handkerchief or semicollar; Figure 1), and typically more chestnut-brown back (Fig. 1), whilst *destructus* exhibits all black hindneck and neck sides (Fig. 1), and typically browner back. There is some variation in back colour of specimens (but not in the back-neck contrast that distinguishes taxa), with some *nigricapillus* being seemingly identical in colour to typical *destructus* (Chapman 1917, USNM specimens). In some *nigricapillus* individuals, the chestnut-brown hindneck is extensive and expands onto the sides of the neck creating a semicollar, which gives these individuals a capped aspect, that is less prominent in birds with less extensive chestnut-brown hindneck. On the other hand, all individuals of *destructus* show a hooded aspect, caused by its wholly black head, hind neck and neck sides (Fig. 1).

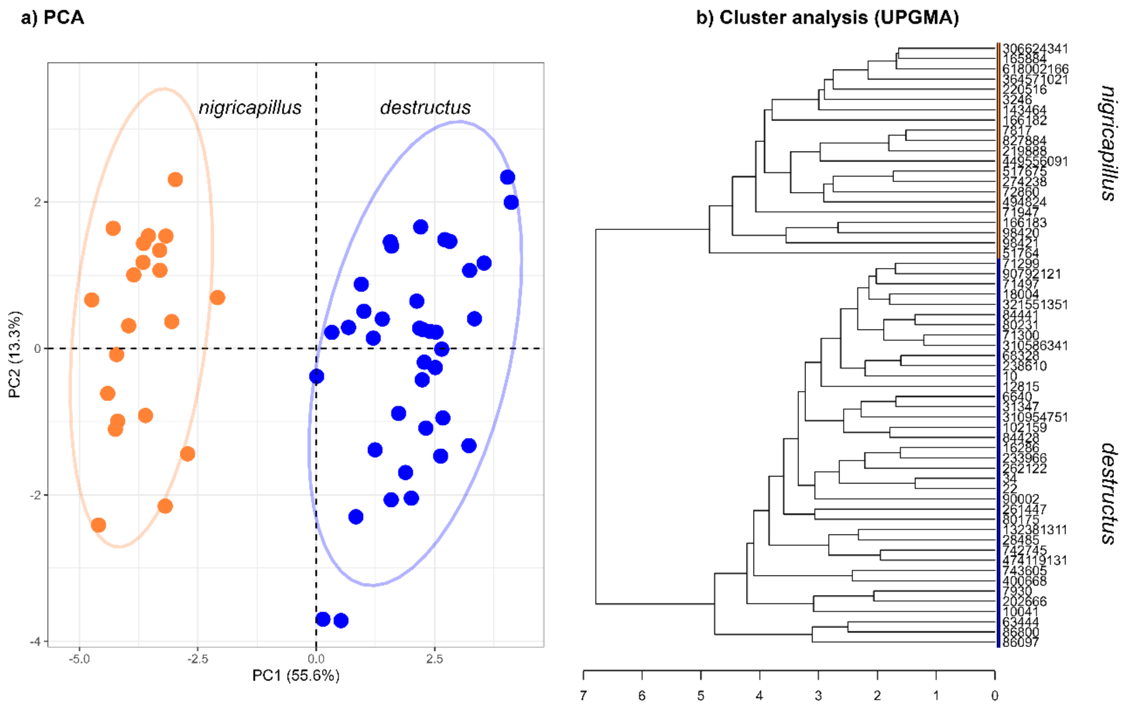


Fig. 2. Quantitative analyses of songs of Black-capped Antthrush (*Formicarius nigricapillus*), and Black-hooded Antthrush (*F. destructus*). (A) Plot of the first two principal components (PC1 vs. PC2) of the Principal Component Analysis. Ellipses depict 95% confidence intervals. (B) Dendrogram from the agglomerative hierarchical cluster analysis (UPGMA). Both methods consistently show that *nigricapillus* and *destructus* differ markedly in songs supporting their treatment as separate species. See Appendix 1 and S1 for songs measured.

Morphometry: based on a limited dataset (n=6 *nigricapillus*, n=9 *destructus*), Areta & Benítez Saldívar (2025) concluded that 1) bill length (exposed culmen) showed no overlap between taxa, with all individuals of *nigricapillus* having a longer bill than *destructus*, and therefore no overlap in mean ± SD values (Fig. 3a), 2) *nigricapillus* was longer winged than *destructus*, with exact overlap only in their extreme values, and no overlap in mean ± SD values (Fig. 3b), and 3) tail length was longer in *nigricapillus* than in *destructus*, but the difference was not statistically significant (two tailed t-test p=0.17) (Fig. 3c).

The differences in songs and plumage herein described can be readily appreciated in videos of free-ranging singing birds:
nigricapillus: https://macaulaylibrary.org/asset/608419951
destructus: https://macaulaylibrary.org/asset/316228641

Genetics: The coincidental break in plumage and vocalizations between *F. moniliger* and *F. analis umbrosus* (a representative of the *hoffmanni* group) were used as arguments to support the elevation of *moniliger* to species status (Howell 1994). More recently, phylogenetic data have shown that *F. moniliger* is sister to a clade including *F. destructus* as more closely related to *F. analis* (including representatives of the *hoffmanni* and *analis* subspecies groups) (Harvey et al. 2020). This distant relationship between *moniliger* and *analis* further reinforces the species-level split of *F. moniliger* and lends support to vocal differences as a useful tool to

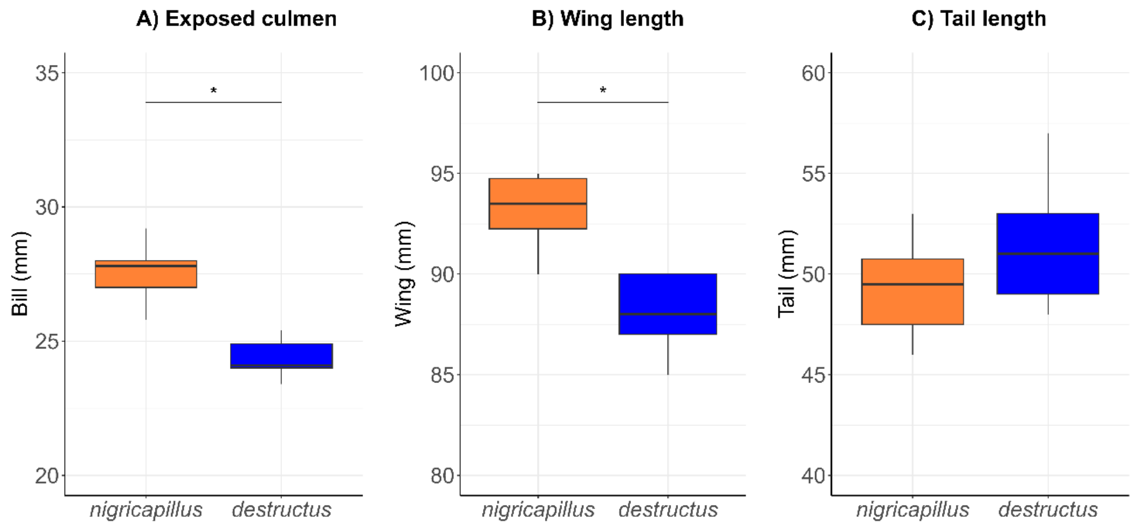
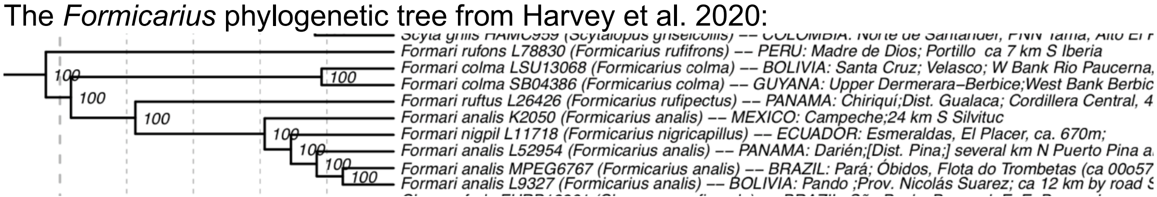


Fig. 3. Morphological measurements of Black-capped Antthrush (*Formicarius nigricapillus*), and Black-hooded Antthrush (*F. destructus*). Figure depicts median and quartiles on box plots. Asterisk denotes significant statistical differences in one-way ANOVA (α<0.05). The morphological differences in bill and wing length coupled to plumage differences give support to the treatment of *nigricapillus* and *destructus* as separate species. See Table 2 for sample sizes and data, and Appendix 2 and S2 for specimens measured and studied.

establish species limits in *Formicarius*. Although there are no available genetic data for nominotypic *nigricapillus*, the vocal distinctions between *nigricapillus* and *destructus* seem as or more marked than those between *F. moniliger* and *F. analis* of the *analis* and *hoffmanni* subspecies groups. In our paper we predicted that *nigricapillus* and *destructus* will exhibit levels of genetic differentiation tantamount to their vocal and morphological distinctions.

The *Formicarius* phylogenetic tree from Harvey et al. 2020:



Taxonomic assessment:

The marked differences in vocalizations and morphology, and moderate but consistent plumage differences strongly supports the elevation of the taxon *destructus* to species-level, leading to the recognition of two allopatric and monotypic species, *F. nigricapillus* and *F. destructus*. Areta & Benítez Saldivar (2025) based their taxonomic conclusions on the recognition concept of species (Paterson 1985), whilst the same species would be recognized by applying the biological species concept (Mayr 1963; “isolation concept” fide Paterson 1985). The inferred level of discontinuity between *nigricapillus* and *destructus* is of such a magnitude that presumably any other modern species concept would recognise them as separate species, whether based on mating or other important attributes, phenotypic distinctiveness, presence of autapomorphies, or phylogenetic independence (Cracraft 1983, Mishler & Brandon 1987, Gill 2014, Areta et al. 2019, Winker 2021). Howell & Dyer (2022:27) wrote that "Differences in plumage and song indicate that Central American *nigricapillus* and South American *destructus* (Choco Antthrush) are best treated as separate species." A view that is amply supported by Areta & Benítez Saldivar (2025).

In terms of plumage, the differences between *nigricapillus* and *destructus* (Fig. 1) would be among the least conspicuous for two *Formicarius* species-level taxa, and comparable to (although less obvious than) those between *F. moniliger* and *F. analis*. They differ most notably by the presence of a rufous-chestnut fore-collar below the black throat in *moniliger*, while the black throat contacts the grey chest directly in the two subspecies groups of *F. analis* (Howell 1994, Vallely and Dyer 2018). However, less obvious plumage differences exist between the *analis* and *hoffmanni* subspecies groups within *F. analis* despite their noticeable vocal differences (Howell 1994) which are compatible with species-level differences in the genus (Krabbe and Schulenberg 2003, van Dort et al. 2023, Benítez Saldívar & Areta in prep.).

English names:

Most species in the genus *Formicarius* carry common English names that refer to plumage features. We propose to adopt the name Black-capped Antthrush for *F. nigricapillus* and Black-hooded Antthrush for *F. destructus*, which focus on one of the main plumage differences between them, and retain a connection to the former Black-headed Antthrush used for the composite species. We find the proposed use of Black-hooded Antthrush for *F. nigricapillus* by Howell and Dyer (2022) to be misleading, as this taxon is capped rather than hooded. The smaller bill of *destructus* is difficult to appreciate in field conditions, and bill features do not seem useful to coin common names here. Finally, Choco Antthrush has been proposed for *destructus* (Howell and Dyer 2022); while a good name, there are other antthrushes in the Choco, and it loses the connection to the former Black-headed Antthrush name.

Recommendation:

(A) We recommend a YES vote to split *F. destructus* from *F. nigricapillus*.

(B) We recommend a YES vote to adopt the English name Black-capped Antthrush for *F. nigricapillus* and Black-hooded Antthrush for *F. destructus*

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Links to supplementary information

https://static-content.springer.com/esm/art%3A10.1007%2Fs10336-025-02265-5/MediaObjects/10336_2025_2265_MOESM1_ESM.xlsx

https://static-content.springer.com/esm/art%3A10.1007%2Fs10336-025-02265-5/MediaObjects/10336_2025_2265_MOESM2_ESM.xlsx

Submitted by; Juan I. Areta and M. Juliana Benítez Saldívar

Date of Proposal: 11 April 2025

Treat *Turdus ardosiaceus* as a separate species from Red-legged Thrush *T. plumbeus*

Background:

The Red-legged Thrush (*Turdus plumbeus*) occurs in the Greater Antilles area (Cuba, Hispaniola, the Cayman Islands, and Puerto Rico), the Bahamas, and Dominica in the Lesser Antilles. Seven subspecies are recognized, of which six are extant, including nominate *plumbeus* of the Bahamas, *rubripes* of western Cuba, *schistaceus* of eastern Cuba, *coryi* of Cayman Brac in the Cayman Islands, *ardosiaceus* of Hispaniola and Puerto Rico, and *albiventris* of Dominica; the extinct subspecies *perditus* occurred on the Swan Islands (Kirwan and Collar 2023).

The seven subspecies have been divided into two or three differentiated groups. Most authorities, in agreement with Ripley (1964) have traditionally treated the complex as one species with three groups, including the AOS (formerly AOU) Checklist (AOU 1983, 1998), Howard and Moore (Dickinson and Christidis 2014), Clements (Clements et al. 2024), and IOC (Gill et al. 2024). The groups are easily distinguished by differences in plumage and bare part coloration. These three groups also match the three species recognized by Ridgway (1907). Birds from the Bahamas (*plumbeus*) can also be grouped with the birds of Cuba and the Cayman Islands based on their solid black throat patch (versus streaked throat in *ardosiaceus* and *albiventris*), and the black or deep red bill and brighter red legs (versus more red-orange in *ardosiaceus* and *albiventris*). The two-species approach aligns with the treatment of Hellmayr (1934), who placed the *plumbeus* group with the *rubripes* group.

BirdLife International (HBW, 2024) currently treats the complex as three separate species: the “Northern Red-legged Thrush (*Turdus plumbeus*)” of the Bahamas, the “Western Red-legged Thrush (*Turdus rubripes*)” of Cuba, the Cayman Islands, and the Swan Islands, and the “Eastern Red-legged Thrush (*Turdus ardosiaceus*)” of Hispaniola, Puerto Rico, and Dominica. The justification for this treatment is as follows (del Hoyo and Collar 2016):

> [*Turdus ardosiaceus*] hitherto treated as conspecific with *T. plumbeus* and *T. rubripes*, but differs from former in characters given under that species. Differs from latter (comparing geographically and morphologically closest form *schistaceus*) in its black-and-white-striped vs black streaky throat (3); paler grey breast and flanks (1); white vs pale tan belly (2); narrower frequency range for lower-pitched notes in song, making these notes melodious rather than squeaky (1) (1). Two subspecies recognized.
>
> [*T. plumbeus*] … hitherto treated as conspecific with *T. rubripes* and *T. ardosiaceus*, but differs from both in its all-black vs deep red, bright red or yellow bill (2); all-grey vs pale rufous or white belly and vent (3); reduced white around base of bill and on throat, so that latter is all black or virtually so and with no sign of black streaks as in blacker-throated T. rubripes (2). Monotypic.

WGAC considered this issue in 2021 and voted to adopt the two-species treatment, splitting *ardosiaceus* from the *rubripes-plumbeus* group based on differences in phenotype, vocalizations, and genetics, but rejecting a split of *rubripes* from *plumbeus*.

In 2022, the North American Classification and Nomenclature Committee (NACC) of the AOS considered a proposal to split the Red-legged Thrush into either two or three species (see https://americanornithology.org/wp-content/uploads/2022/04/2022-A-final.pdf). The proposal to split into two species was rejected by a vote of 3 in favor and 7 against, whereas the option to split into three species did not receive any votes in favor (Chesser et al. 2022). Most of the rejecting voters stated that it was a difficult decision but ultimately felt that there was insufficient evidence for the split, with most committee members advocating for an analysis of vocal data. We briefly summarize the contents of the previous proposal in the remainder of the Background section:

Genetic data for the group are limited, but there is a relatively deep divergence between the western *plumbeus*/*rubripes* group and the eastern *ardosiaceus* group. Using mitochondrial DNA sequence data, Ricklefs and Bermingham (2008) found that the *plumbeus*/*rubripes* group was about 2.1% divergent from the *ardosiaceus* group (Fig. 1). Other studies have included samples of the Red-legged Thrush (e.g., Batista et al. 2020, Nylander et al. 2008), but none have offered much insight into the question of species status for either group, although branch lengths between the sample of *schistaceus* and *ardosiaceus* included in Batista et al. (2020) are at a similar level to branch lengths between other sister species in their phylogeny (Fig. 2).

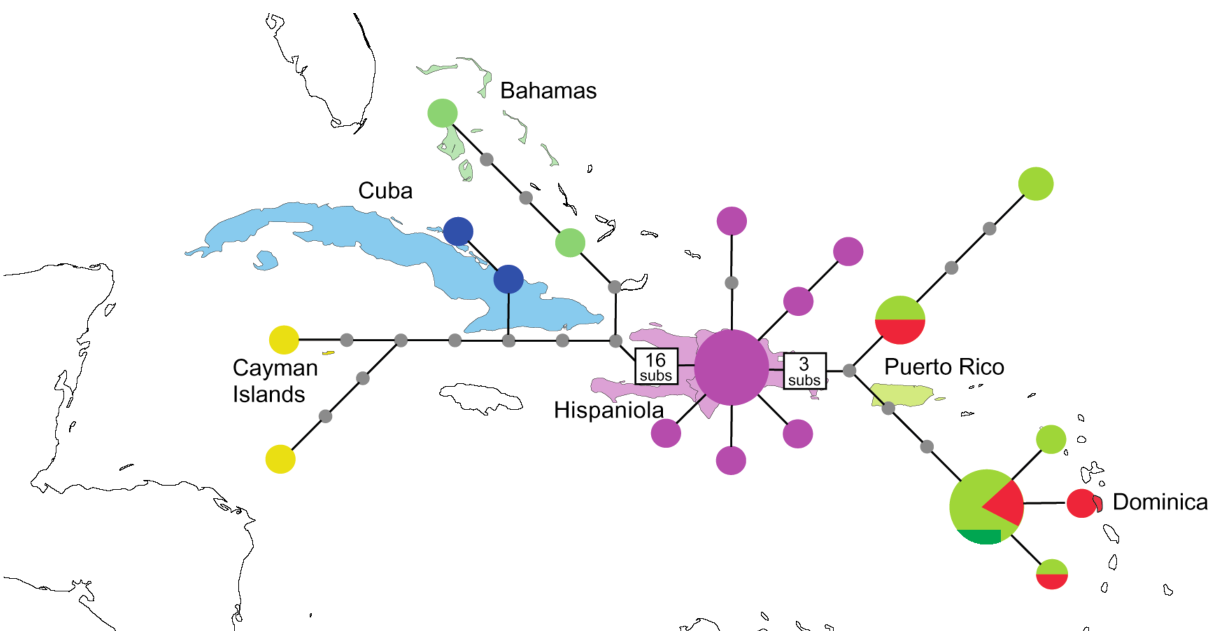

Figure 1. Figure from Ricklefs and Bermingham (2008) showing the haplotype network from ATPase 6 and 8 genes. Note the relatively deep divergence between the birds from Cuba, the Bahamas, and the Cayman Islands with the birds from Hispaniola, Puerto Rico, and Dominica. Also note the extensive haplotype sharing between birds from Puerto Rico and Dominica.

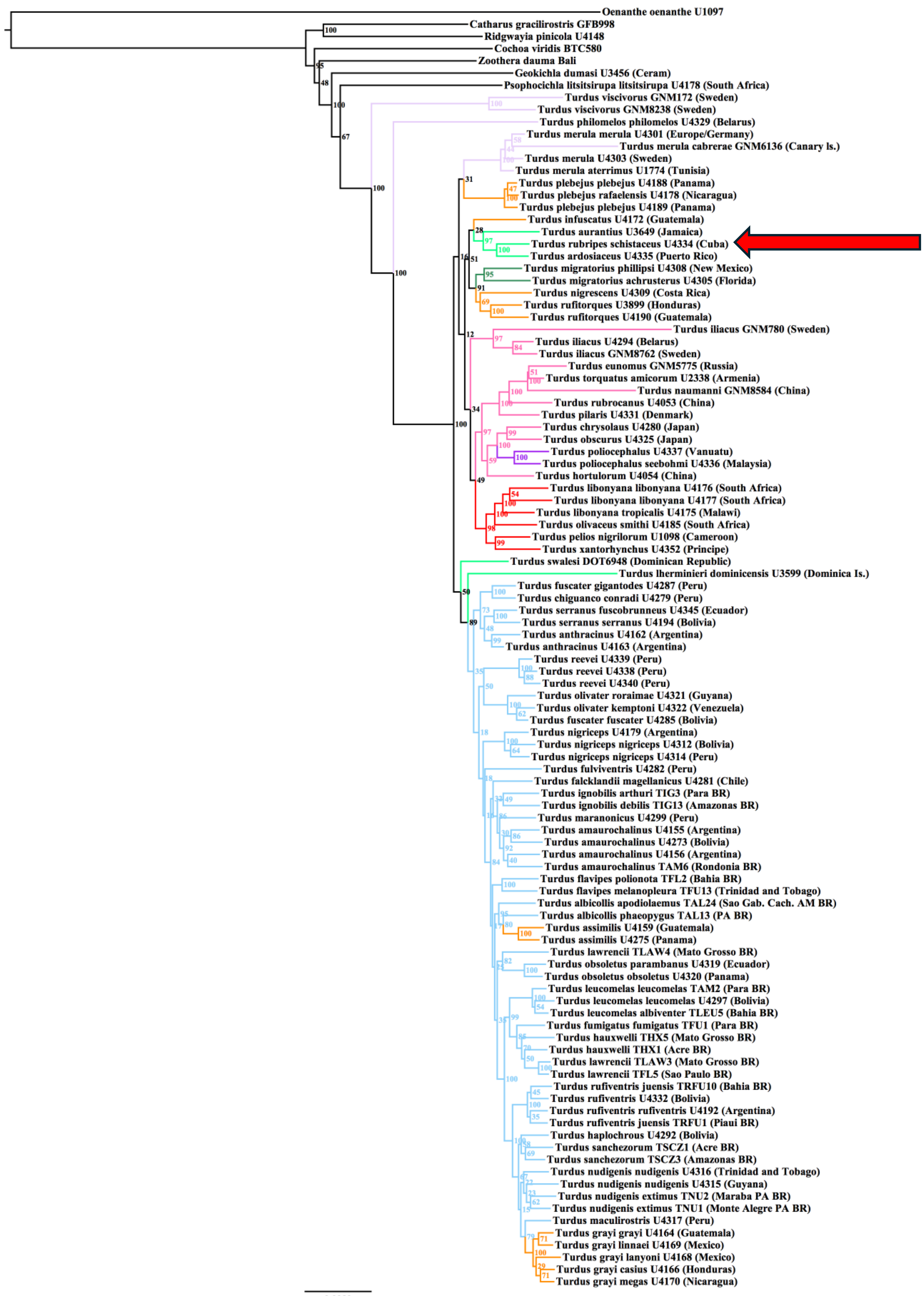

Figure 2. Supplemental Figure 4 from Batista et al. (2020) showing a maximum likelihood analysis of the 49 additional (non UCE) loci from the main paper. Red-legged Thrush (represented by subspecies *schistaceus* and *ardosiaceus*) taxa are here indicated by a red arrow.

In Boesman's (2016) assessment of the vocalizations, he noted that *T. p. ardosiaceus* differs from the birds of Cuba and the Bahamas in having their lower-pitched notes more melodious than the lower-pitched notes in the songs of *T. p. plumbeus*, *T. p. rubripes*, and *T. p. schistaceus*. This can be heard on recordings from Macaulay Library, some examples of which are presented below:

T. p. ardosiaceus (Hispaniola, Puerto Rico and Dominica)

- https://macaulaylibrary.org/asset/188091
- https://macaulaylibrary.org/asset/188070
- https://macaulaylibrary.org/asset/619377916

T. p. plumbeus (Bahamas)

- https://macaulaylibrary.org/asset/152734881
- https://macaulaylibrary.org/asset/14107
- https://macaulaylibrary.org/asset/14105

T. p. rubripes/schistaceus (Cuba)

- https://macaulaylibrary.org/asset/133259
- https://macaulaylibrary.org/asset/631020033
- https://macaulaylibrary.org/asset/183525
- https://macaulaylibrary.org/asset/133264
- https://macaulaylibrary.org/asset/161367321

T. p. coryi (Cayman I.)

- https://macaulaylibrary.org/asset/618578684

New Information:

There is no truly "new" information to present here, although we provide an alternative analysis of the genetic data presented in Ricklefs and Bermingham (2008; Fig. 1) using sequence data downloaded from Genbank (Fig. 3). In addition, we provide an assessment of phenotypic diagnoses with coloration traits, as well as a reassessment of the vocal data.

We reconstructed phylogenetic trees to assess the relationships across *T. plumbeus* populations plus *T. rufiventris*, *T. hortulum*, and *T. merula*, rooted at the *T. hortulum* + *T. merula* node. We generated Maximum Likelihood (ML) phylograms using IQ-TREE v1.6 (Nguyen et al., 2015) from the concatenated dataset of ATPase 6 and 8 gene sequences. We determined the best-fit substitution model of the dataset via ModelFinder, implemented within IQ-TREE (Kalyaanamoorthy et al., 2017) and performed a partitioned analysis by partitioning according to codon position. We calculated branch support with 10,000 replicates for the Ultrafast Bootstrapping algorithm (Hoang et al., 2018). We used the data from Ricklefs and Bermingham (2008), as well as sequences from *T. hortulorum*, *T. merula*, and *T. rufiventris* (NCBI accession numbers: NC_024552.1, NC_028188.1, NC_028179.1, respectively).

The Maximum Likelihood phylogeny revealed well-supported relationships among *T. plumbeus* populations across the Caribbean (Fig. 3). The consensus tree recovered two main clades).

One clade is composed of the so-called western group (Figs. 3-4), and includes reciprocally monophyletic Bahamian, Cuban, and Cayman Island populations, with Cuba and Cayman Islands taxa as sister (Figs. 3, 5). The second clade is composed of the so-called eastern group, and includes Puerto Rican, Hispaniolan, and Dominican populations. This topology, consistent with biogeographical isolation of the groups, supports a hypothesis that both groups represent distinct species.

All major island groups formed distinct clades with moderate to high bootstrap support (≥85), suggesting substantial phylogeographic structuring within *T. plumbeus*. Populations from Cuba, the Cayman Islands, and the Bahamas (western group) formed a strongly supported clade (UFBoot = 99), indicating a close evolutionary relationship among these islands.

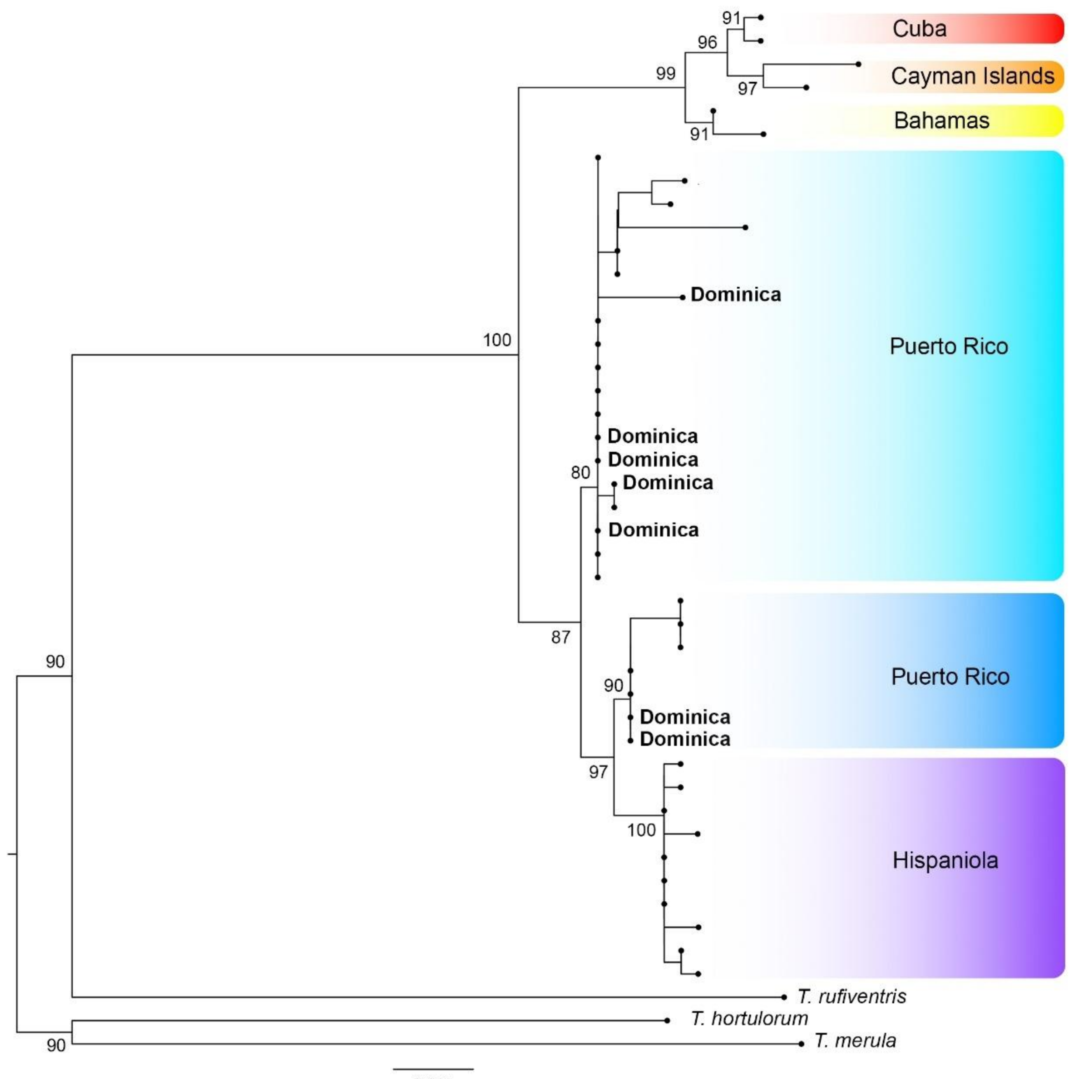

Figure 3. Maximum Likelihood consensus tree based on concatenated mitochondrial ATP6 and ATP8 gene sequences from *Turdus plumbeus* (sensu lato) populations across the Caribbean.

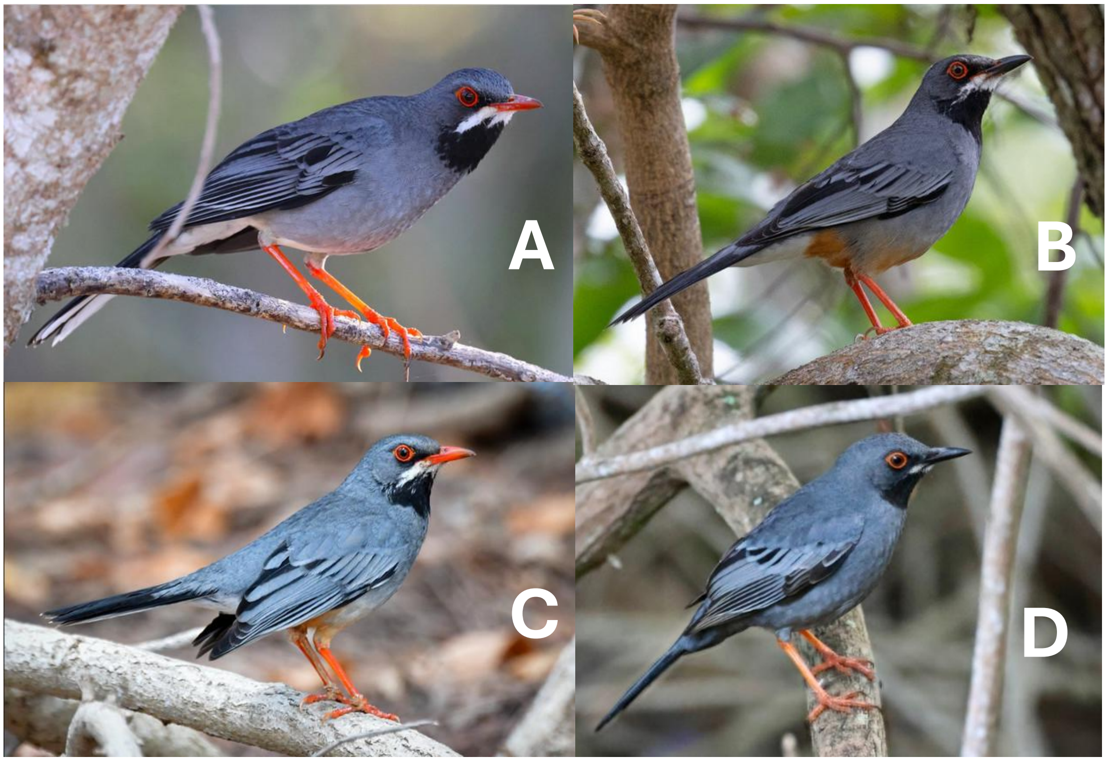

Figure 4. Western Red-legged Thrush (above), *credits at the end of the proposal*
Figure 5. Eastern Red-legged Thrush (below), *credits at the end of the proposal*

Populations from Puerto Rico (eastern group) were paraphyletic for two reasons: first, the two main clades included multiple individuals from Dominica, suggesting shared ancestry or possible gene flow between Puerto Rico and Dominica. Dominica samples were recovered in the two Puerto Rican clades, indicating that individuals from this island are not monophyletic and may represent multiple introductions from divergent lineages as suggested by Ricklefs and Bermingham (2008).

Second, one of the Puerto Rican clades was sister to a monophyletic Dominican Republic clade and not to the other Puerto Rican clade. The Hispaniola clade was also well supported (UFBoot = 100), and distinct from other *T. plumbeus* populations.

This phylogenetic clustering is also consistent with the grouping based on morphological and vocal similarities. Although each island population has its own vocal dialect, structural similarities can be identified among birds of the western and the eastern groups, respectively. In the western populations, these vocalizations are more elaborate and complex in terms of notes:

Western Red-legged Thrush (*plumbeus*, *schistaceus*, *rubripes*, *coryi*, and *perditus†*) (Fig. 4): Easily diagnosable due to its black throat patch, thick malar stripe and white chin patch (more restricted in the Bahamian populations), reduced black loral and supramalar mask (Fig. 6A), uniformly gray underparts with cinnamon belly patches in some cases, bare skin of deep red color, bill varying from black to reddish-brown (sometimes more red in populations from Cayman Island and eastern Cuba), and much richer and more varied vocalizations in terms of notes and harmonics.

Eastern Red-legged Thrush (*ardosiaceus*, *albiventris*) (Fig. 5): Easily diagnosable due to the presence of a white throat patch with black flecking-like streaking, white malar stripe absent, more extensive black loral and supramalar mask (Fig. 6B), ventral color that is lighter gray than the back, bare skin of bright reddish-orange in color, bill of the same color, and much less complex vocalizations with less variation in tone and high notes, and less elaborated notes, giving a more monotonous and more melodious impression.

It is important to note that the degree of differentiation found for these forms of *T. plumbeus* (*sensu lato*) is similar to—or even more pronounced and more easily diagnosable than—that observed in other populations of closely related groups that have previously been split and validated and now treated at the species level (Clements et al., 2024), such as: White-fronted Quail-Dove (*Geotrygon leucometopia*) vs. Gray-fronted Quail-Dove (*G. caniceps*); Stolid Flycatcher (*Myiarchus stolidus*) vs. La Sagra's Flycatcher (*Myiarchus sagrae*); the Greater Antillean Oriole complex (*Icterus melanopsis–northropi–dominicensis–portorricensis*), wherein *I. northropi* from the Bahamas has a call similar to that of the Cuban Oriole (*I. melanopsis*); Red-winged Blackbird (*Agelaius phoeniceus*) vs. Red-shouldered Blackbird (*A. assimilis*); Cuban Bullfinch (*Melopyrrha nigra*) vs. Grand Cayman Bullfinch (*M. taylori*); Cuban Nightjar (*Antrostomus cubanensis*) vs. Hispaniolan Nightjar (*A. ekmani*); and Cuban Palm Crow (*Corvus minutus*) vs. Hispaniolan Palm Crow (*C. palmarum*).

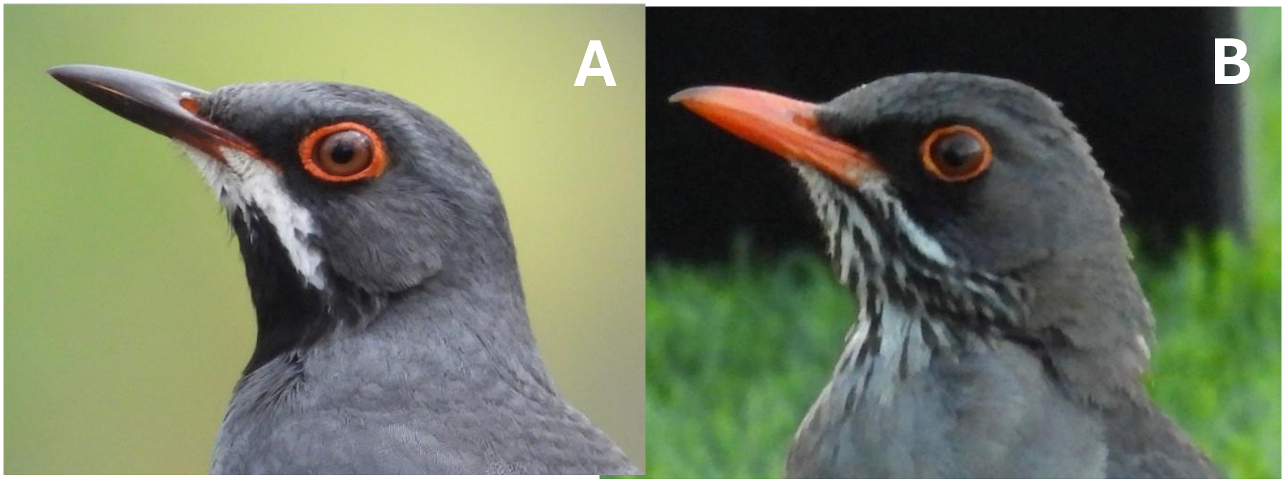

Figure 6. Comparison of the dark (black) loral and supramalar masked pattern in both proposed forms for separation: **A**: *Turdus plumbeus* and **B**: *T. ardosiaceus*. Note that in the latter, this dark area is much more extensive. Differences in bill structure and coloration, as well as in the bare skin areas, can also be observed.

A- Photo Dana Sterner, eBird. https://macaulaylibrary.org/asset/633608612

B- Photo Eliecer Nieves-Rodríguez, eBird. https://macaulaylibrary.org/asset/626992972

Recommendation:

Based on the reciprocal monophyly of the eastern and western groups, moderate levels of genetic divergence that is on par with levels of genetic divergence seen between other sister species in the Caribbean, substantial phenotypic diagnosability in both coloration and song patterns, we recommend splitting the Red-legged Thrush into two species: the Western Red-legged Thrush (*Turdus plumbeus*) occurring on Cuba, Bahamas, Cayman Islands, and Swan Island, and the Eastern Red-legged Thrush (*Turdus ardosiaceus*), occurring on Hispaniola, Puerto Rico, and Dominica

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Submitted by: Shawn M. Billerman (Cornell Lab of Ornithology), Nils Navarro Pacheco (APRM Archipiélago de los Colorados), and Javier Torres López (School of Biological Sciences, University of Nebraska-Lincoln

Date of Proposal: 13 May-2025

eBird Photo reference and credits for Figs. 4-5:

Western Red-legged Thrush
A- *Turdus plumbeus shistaceus*: Guantánamo Cuba: Photo Tammy Elizabeth, eBird
https://macaulaylibrary.org/asset/629740605
B- *T. plumbeus rubripes* (*sensu stricto*) Pinar del Río, Cuba: Photo Matthew Skalla, eBird
https://macaulaylibrary.org/asset/633764409
C- *T. plumbeus coryi*: Cayman Brac: Photo Nicole Martin, eBird
https://macaulaylibrary.org/asset/222304131
D- *T. p. plumbeus*: New Providence Bahamas, Photo Michael Perry, eBird
https://macaulaylibrary.org/asset/629376625

Eastern Red-legged Thrush
E- *T. p. ardosiaceus*: República Dominicana: Photo Jeffrey Gammon, eBird
https://macaulaylibrary.org/asset/626812676
F- *T. p. ardosiaceus*: Puerto Rico: Photo Sheila Rowe, eBird
https://macaulaylibrary.org/asset/620241081
G- *T. p. albiventris*: Dominica: Photo Jim Tietz, eBird
https://macaulaylibrary.org/asset/130362171
H- *T. p. ardosiaceus*: Puerto Rico: Photo Pranav Kumar, eBird
https://macaulaylibrary.org/asset/628002870

Treat Willet *Tringa semipalmata* as two species

This is an updated proposal based on, and adding to, NACC proposal 2017-A-10. If approved, the Willet (*Tringa semipalmata*) would be split into 'Eastern' Willet (*Tringa semipalmata*) and 'Western' Willet (*Tringa inornata*).

Background:

The Willet (*Tringa semipalmata*) includes two broadly allopatric subspecies that exhibit morphological, ecological, vocal, and genetic differentiation. O'Brien (2006) provided an excellent earlier identification-based treatment of the two that is highly recommended reading as background for this proposal. The eastern subspecies, *T. s. semipalmata* (Gmelin, 1789) breeds almost exclusively in saltmarshes and brackish coastline habitat along the Atlantic Coast, the Gulf of Mexico, and certain localities in the Caribbean (Lowther et al. 2020; O'Brien et al. 2006). In contrast, the western subspecies *T. s. inornata* (Brewster, 1887) breeds in brackish and freshwater wetlands in the Great Basin as well as prairies in the northwestern United States and southern Canada (Lowther et al. 2020, O'Brien et al. 2006). The winter range of the Eastern nominate is primarily the northern and eastern coasts of South America, but also to some extent coastal Pacific Central America. Western *inornata* winters on the Pacific coast from the northwestern United States south to Chile, as well as the Atlantic and Gulf coasts south through coastal Central America and the Caribbean, and to some extent on the Atlantic coast of South America. Both subspecies winter in rocky coastal habitat, estuaries, and sand flats, although *semipalmata* may generally prefer muddy tidal creeks. While the two taxa may co-occur during migration and on certain wintering grounds, pair bonding occurs on the breeding grounds (Howe 1982), which are entirely allopatric between the two taxa.

New or expanded information:

Differences in morphology exist between the two subspecies, as follows:

Size: Western *T. s. inornata* is larger overall with a longer wing and tarsus, and typically has a longer bill that is slimmer throughout its length, whereas the bill of the nominate typically appears deeper throughout. Females are larger and longer-billed than males in both taxa, such that there is overlap between larger female *semipalmata* and smaller male *inornata* (Lowther et al. 2020). In addition, the Gulf Coast population of *semipalmata* averages slightly larger than East Coast birds, although they are still smaller than most *inornata* (Lowther et al. 2020). The typically stark difference in size between *semipalmata* and *inornata* can readily be appreciated by numerous ML photos of the two together, mostly on the Atlantic Coast (https://tinyurl.com/yc3af5by). Even in a few cases in this gallery [which was derived from a search for ML images of Willet (Eastern) with background species Willet (Western)] in which the size differences are not that obvious, other clues (see below) help distinguish the two taxa. Non-breeding adults are best distinguished when direct size comparisons are possible with other shorebirds, especially the other form of Willet, but identification in this plumage may not always be possible.

Proportions and shape: O'Brien (2006) and others have pointed out that, in addition to size, there are subtle shape differences that may help to distinguish the two taxa, including the steeper angle of the crown in *inornata*, the typically proportionately deeper bill of *semipalmata* throughout its length than that of *inornata*, and the longer body behind the legs of *inornata*, creating a lankier appearance when compared to the more compact shape of *semipalmata*. However, none of these except bill shape can be relied upon in identification of photos of many isolated non-breeding adults. And, despite the typically shorter tarsi of *semipalmata*, differences in body proportions (longer rear body in *inornata*) mean that leg extension beyond tail appears about the same in both.

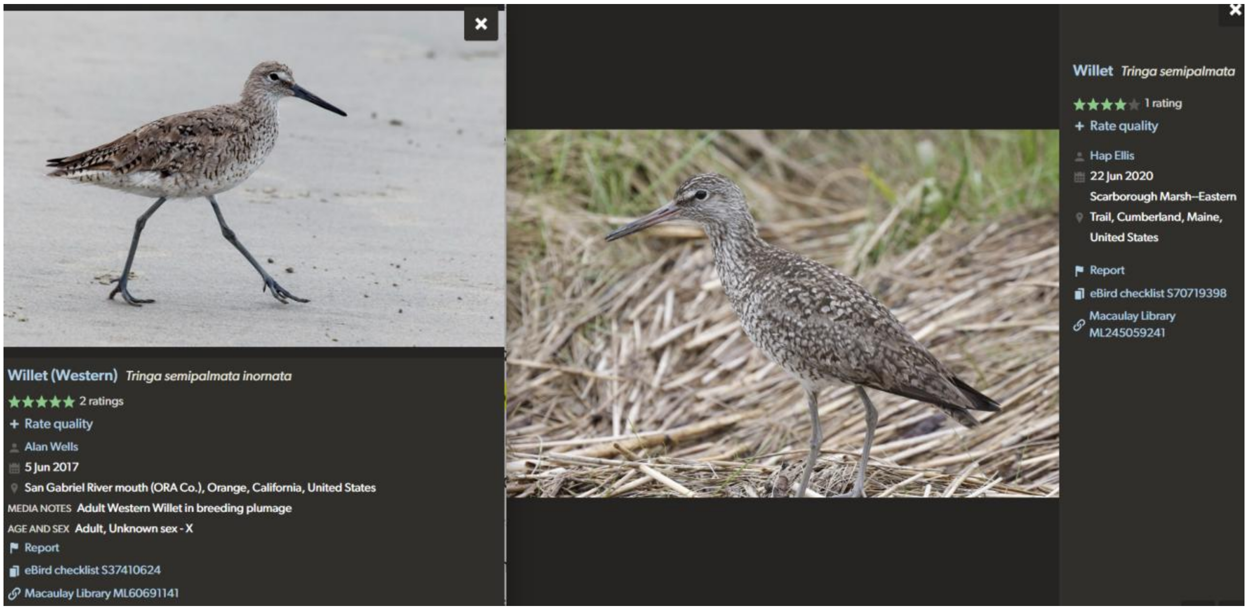
Soft-part colors: The basal half of the bill of *semipalmata*, but usually not *inornata*, typically becomes quite pink in the breeding season, but this difference is not absolute; for example, this *inornata* photographed in Oregon in May 2025 by PCR shows an extensively and notably bright pink bill base (ML636980784). However, 'Westerns' with distinctly pink-based bills do not seem to occur where the two overlap in the non-breeding season. In addition, 'Western' has more extensive black on the bill, and in some breeding birds the bill can look almost entirely black, unlike any 'Eastern' birds.

Plumage: Most breeding adult *semipalmata*, especially East Coast breeders, appear noticeably darker and browner due to the larger dark markings on the upperparts and flanks than in *inornata*, though the latter especially is notably variable. In addition, Gulf Coast 'Easterns' are somewhat paler than those on the East Coast, and West Coast 'Westerns' darker than prairie-breeding 'Westerns'. Thus, although overall darkness is generally helpful, there is overlap in this between darker 'Western' and paler 'Eastern'.

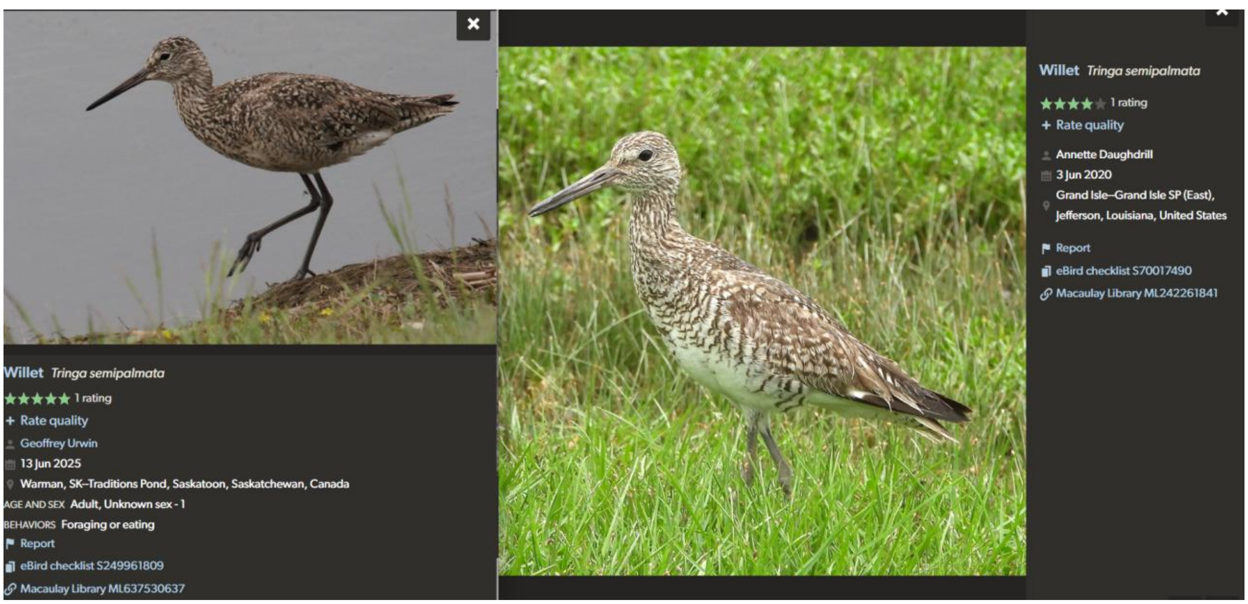
Here is a gallery of adult *semipalmata*, which includes adults in obvious saltmarsh habitat during June and July (thus avoiding inclusion of oversummering or newly arrived *inornata*): https://tinyurl.com/23rhc5b3

And here is a gallery of adult *inornata* from June (selected by filtering Jun-Jul birds tagged as adults and Best Quality; includes duplicates and vagrants in Canada and USA, except East and Gulf coast states and provinces): https://tinyurl.com/5c5aueca

Here's a comparison of breeding-plumaged adults of each form (*inornata* left, still molting from winter plumage, *semipalmata* right) that shows many of the usual differences:

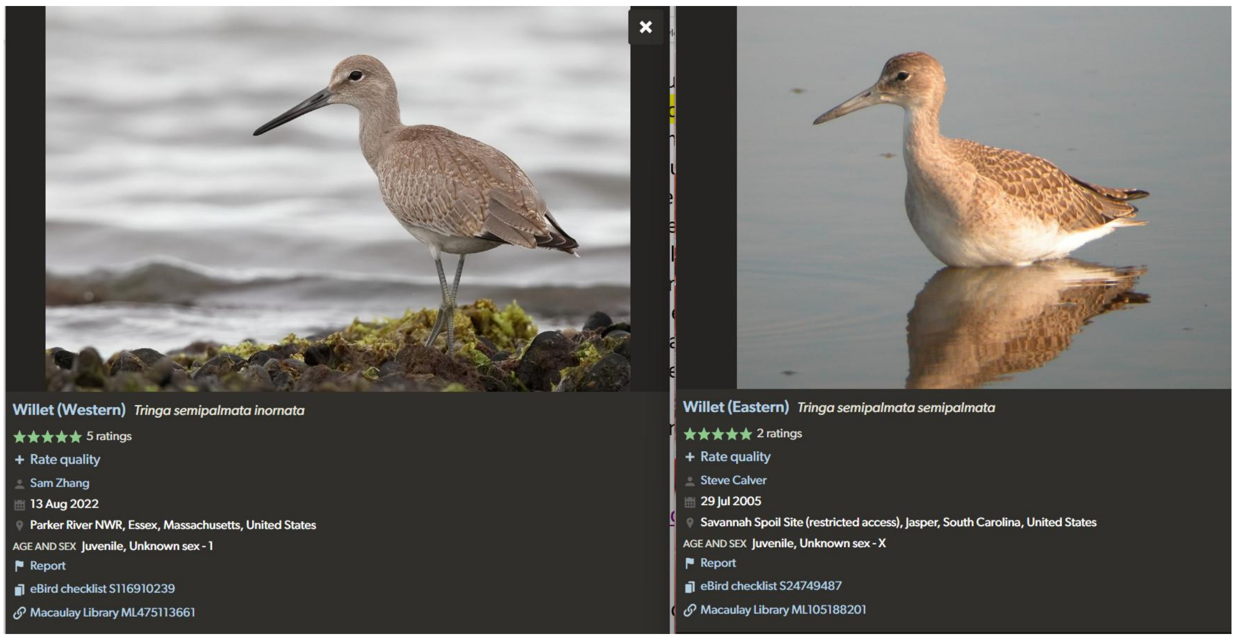


Here's a very heavily marked *inornata* (left) with a typical *semipalmata*:



Points of difference in breeding plumage include the more spotted (usually with obvious small dark spots) breast in *inornata* vs. heavily barred breast in *semipalmata*, the usually more finely barred flanks in *inornata* vs. heavily barred in *semipalmata*; the usually darker basal half of the bill in *inornata*, and the usually overall darker and browner upperparts plumage of *semipalmata*.

The juvenile plumage of *semipalmata* is usually obviously different than that of *inornata*, with 'Eastern' typically having the ground color of the scapulars and tertials darker, creating a more contrasting pattern with the light markings, and more contrast with the paler wing covert panel. The crown is darker on 'Eastern' as well. Commonly, 'Eastern' has larger dark blotches in the dorsal feathers and darker flanks relative to 'Western', which typically has thin dark subterminal crescents in the dorsal feathers. Often, *semipalmata* has complete transverse dark bars and broad buffy notching along the edges of the tertials, with less near the tip, while most *inornata* have pale markings concentrated toward the tip of the tertials (sometimes across the feather). There is considerable variation, however, in these features. This checklist (https://ebird.org/checklist/S116910239#willet1), especially image ML475113511, has a great comparison. And these two (*inornata* left, *semipalmata* right) show many of the typical differences well:



Both taxa only retain breeding and juvenile plumages for a short time, so the temporal window for easy identification is narrow. Full-sized, independent juvenile *inornata* are in fresh plumage in July, soon becoming worn, and by later August and September many are in molt, although some retain essentially full juvenile plumage into October.

The following galleries are of ML images of fully-grown or nearly full-grown birds tagged as juvenile or immature, and confirmed as such by inspection (non-juveniles or heavily molting immatures were removed, as were distant or otherwise unusable images). Western and interior birds were all presumed to be *inornata*, but East and Gulf coastal birds all had to be inspected. Many were identified to form by the photographer (and in general these were retained), and most were readily assigned to form (if the images were adequate).

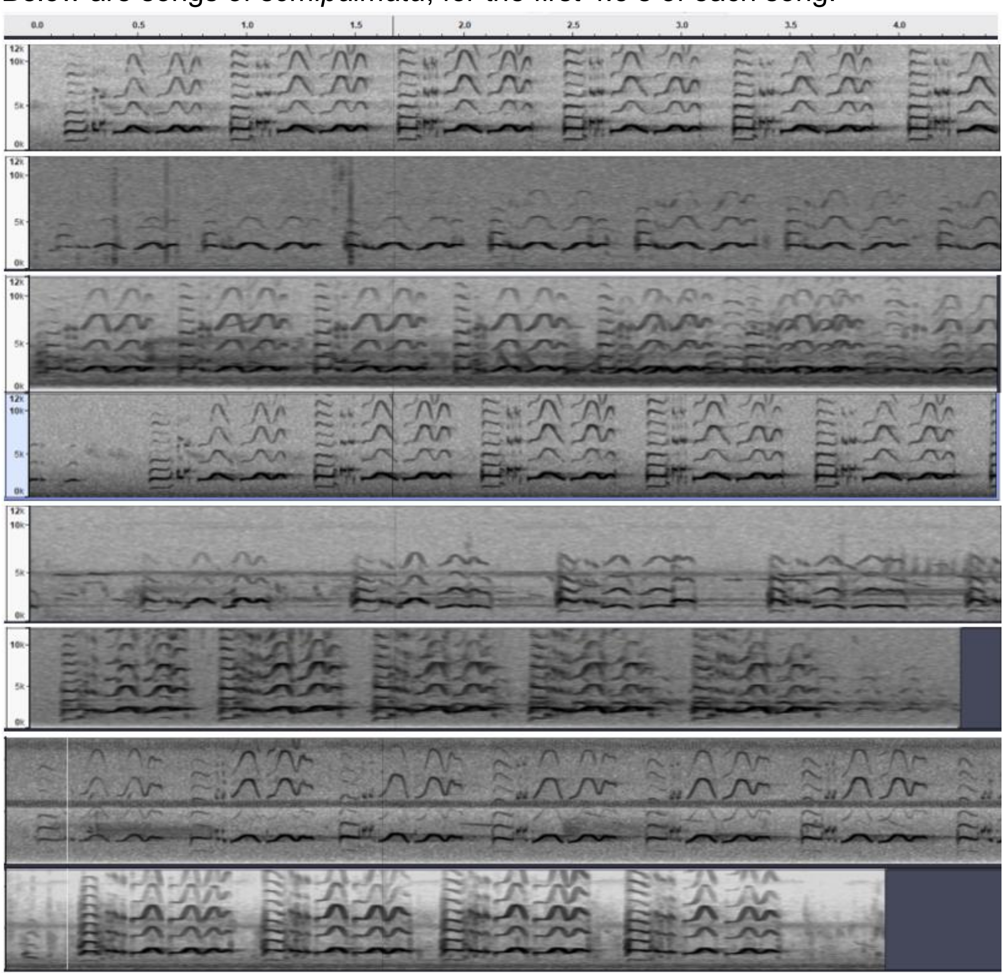
Juvenile *inornata*: https://tinyurl.com/46ujkjeu (note: where two or more birds are present, one may be a *semipalmata*)

Juvenile *semipalmata*: https://tinyurl.com/2k95ydth

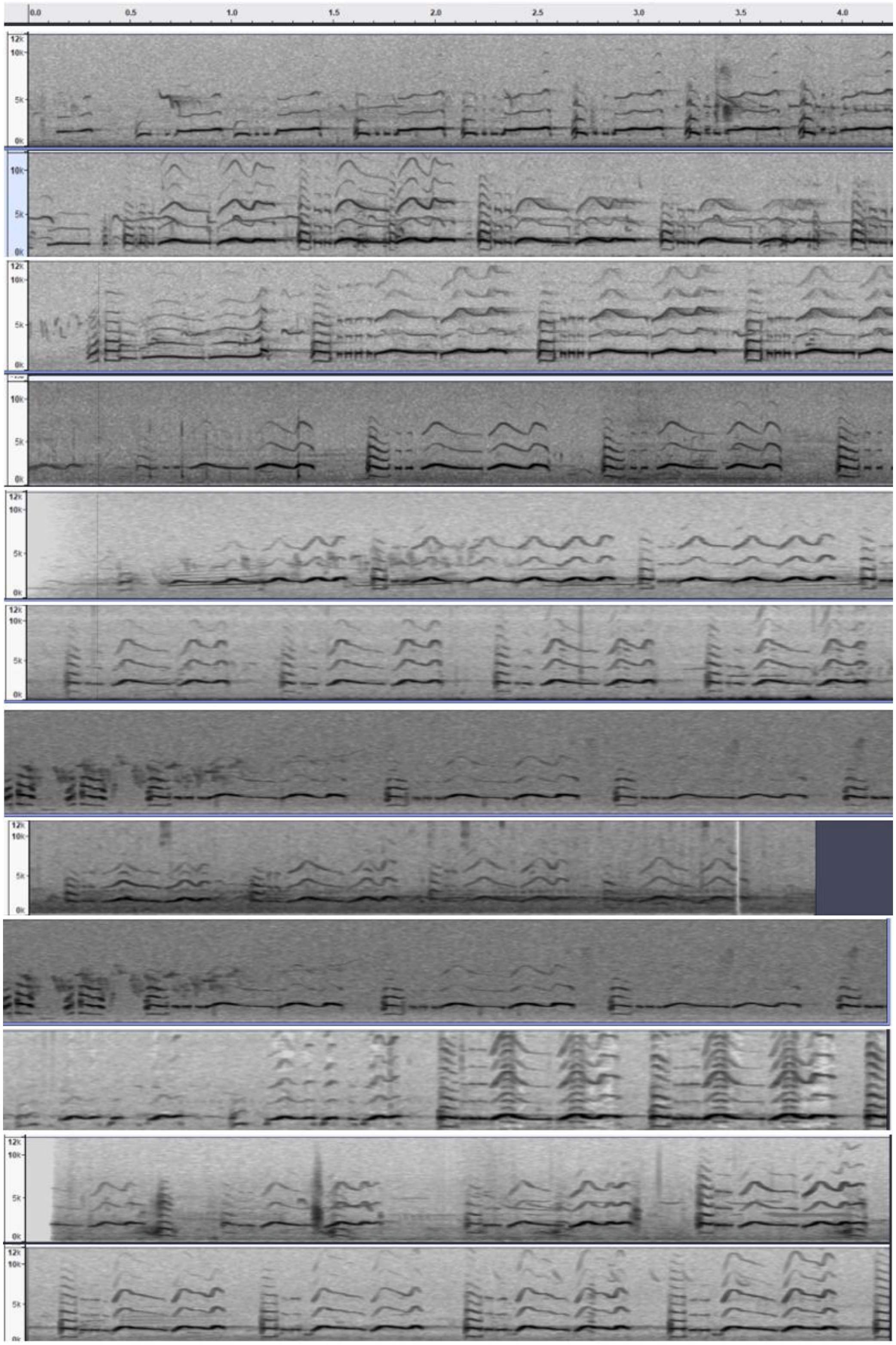
Potential geographic variation within Willet taxa: As has long been known, Gulf Coast Willets are somewhat larger than those on the Atlantic coast of North America, and with tracking data (see below) showing that at least some of them winter on the Pacific coast of Central and northern South America, it seems likely that they may be best recognized as a subspecies in the nominate *semipalmata* group (or within the *semipalmata* species, if split). Additionally, juveniles photographed on the Pacific coast of North America, which according to the tracking data originate from the western USA breeding population, often appear notably darker above, with larger dark feather centers, than those presumably from the mainly Canadian interior breeding population that turn up farther east in migration and winter. This apparent geographic variation may be best recognized at the subspecies level within the *inornata* group (or species, if split). This is a matter for further study, but in our opinion does not change the larger picture, given that they do not intergrade due to their wide allopatry, and that the darkest birds are also the most widely separated geographically.

Vocalizations: The two taxa also exhibit vocal differences, in which the western *T. s. inornata* produces vocal displays that are lower in frequency and slower than the eastern *T. s. semipalmata*. *Tringa s. semipalmata* preferentially responds to playback of *T. s. semipalmata* rather than *T. s. inornata* vocalizations, which might suggest some level of premating reproductive isolation (Douglas 1998). Lowther et al. (2020) summarized in considerable detail the varied vocalizations that are known from both taxa, much of it based on Sordahl (1979). However, few explicit comparisons between the two taxa are made therein; hence we offer comparisons of publicly available media from the ML library:

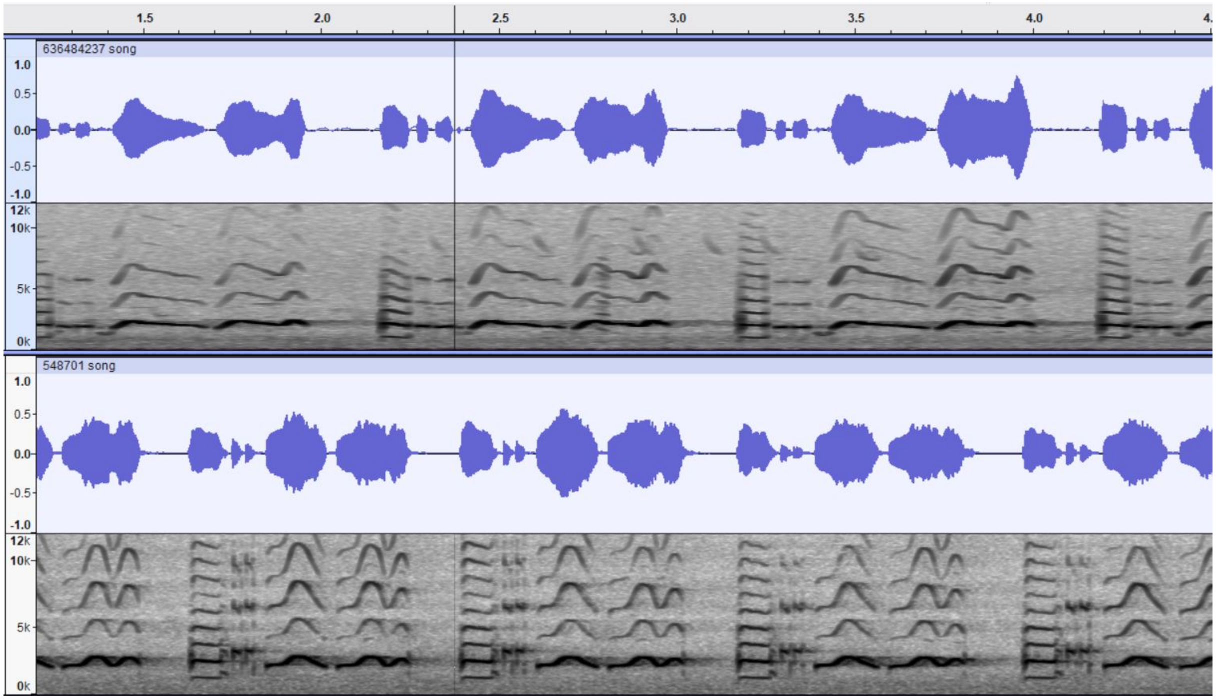
Below are songs of *semipalmata*, for the first 4.5 s of each song:



Below are songs of *inornata*, for the first 4.5 s of each song:

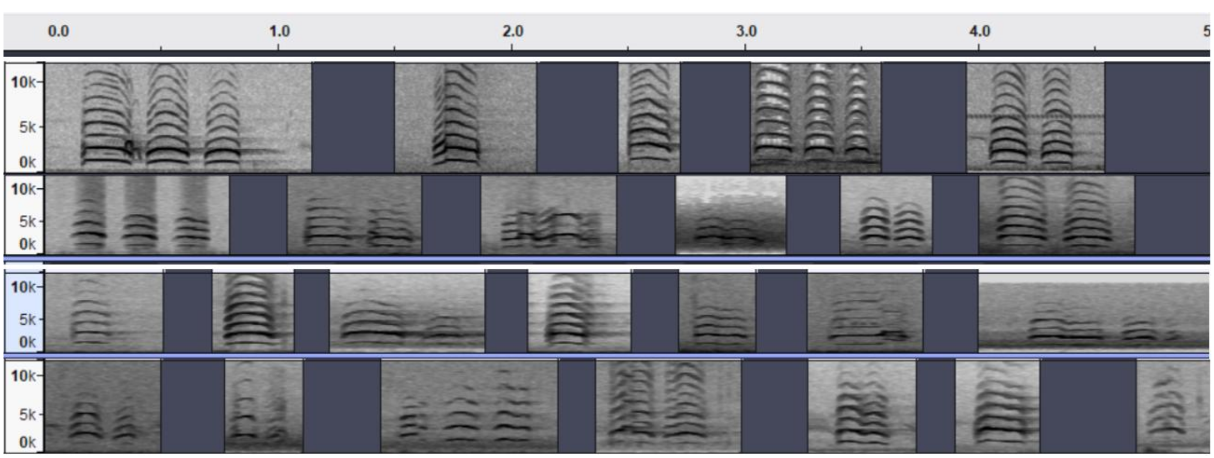


And below are the initial 4.5 s of randomly selected, and quite typical, songs, one for each (*inornata* top, *semipalmata* below):

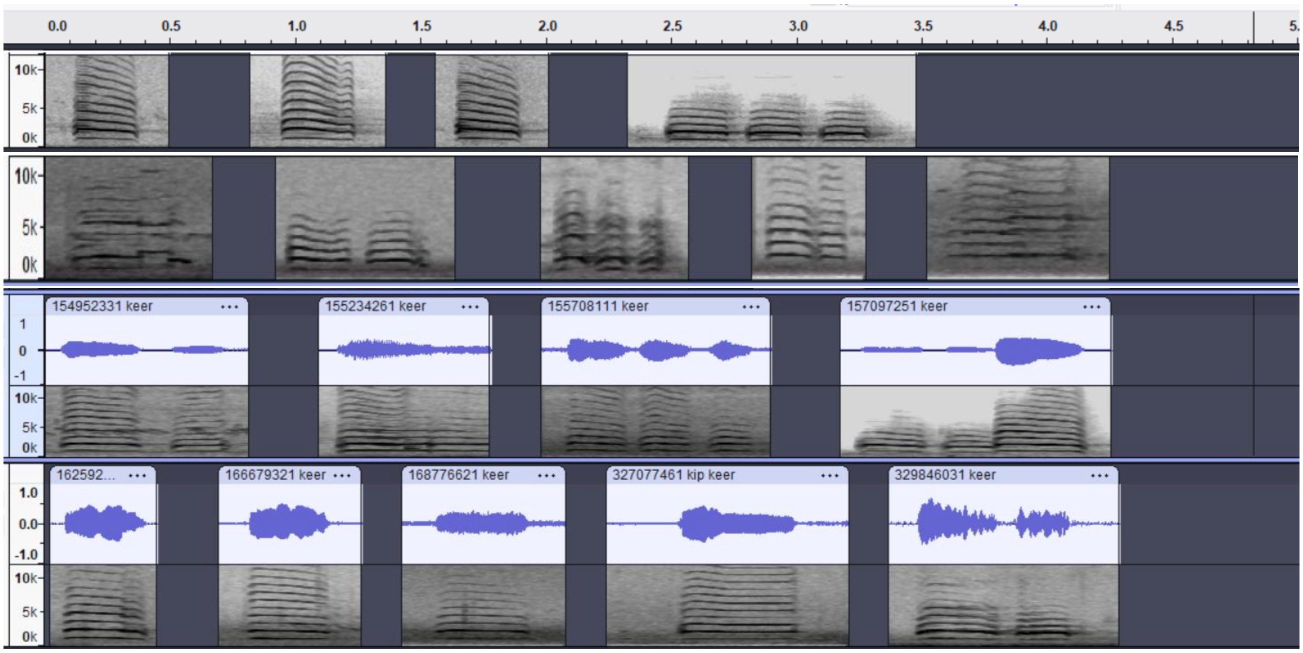


As can be seen by comparisons of the songs, there are multiple differences between the taxa in pattern, frequency, speed of delivery, modulation, and note shape. A quick listen to any of these should convince anyone of the difference in tone, which can be summarized as shrill and frantic-sounding in *semipalmata*, and much mellower and more leisurely in *inornata*. In the sample used here, length of song bouts was highly variable, with most *semipalmata* being less than 10 s long, some much shorter, whereas *inornata* also gave short songs but several much longer ones, up to 45 s. Note also that the second note in the *inornata* song tends to be longer and more drawn out.

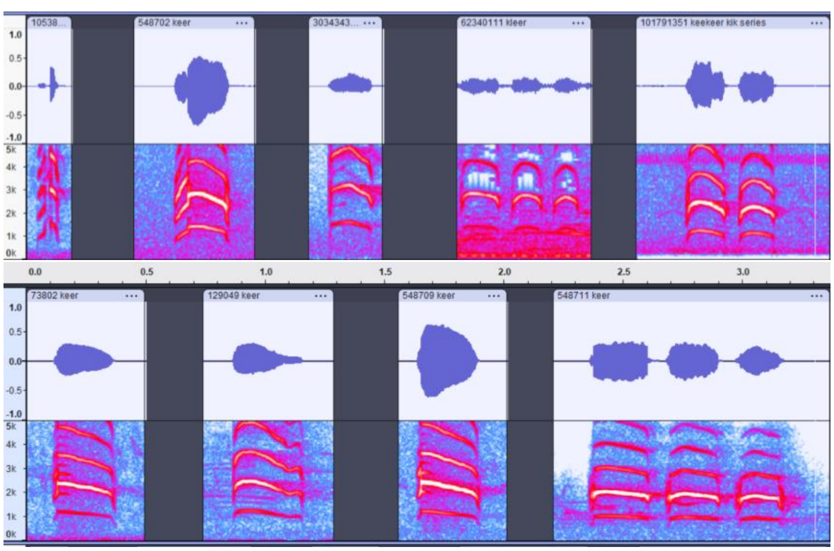
In addition to differences in song, there are differences in at least some calls as well. Below are ‘keer’ calls of *semipalmata* (longest in a series selected):



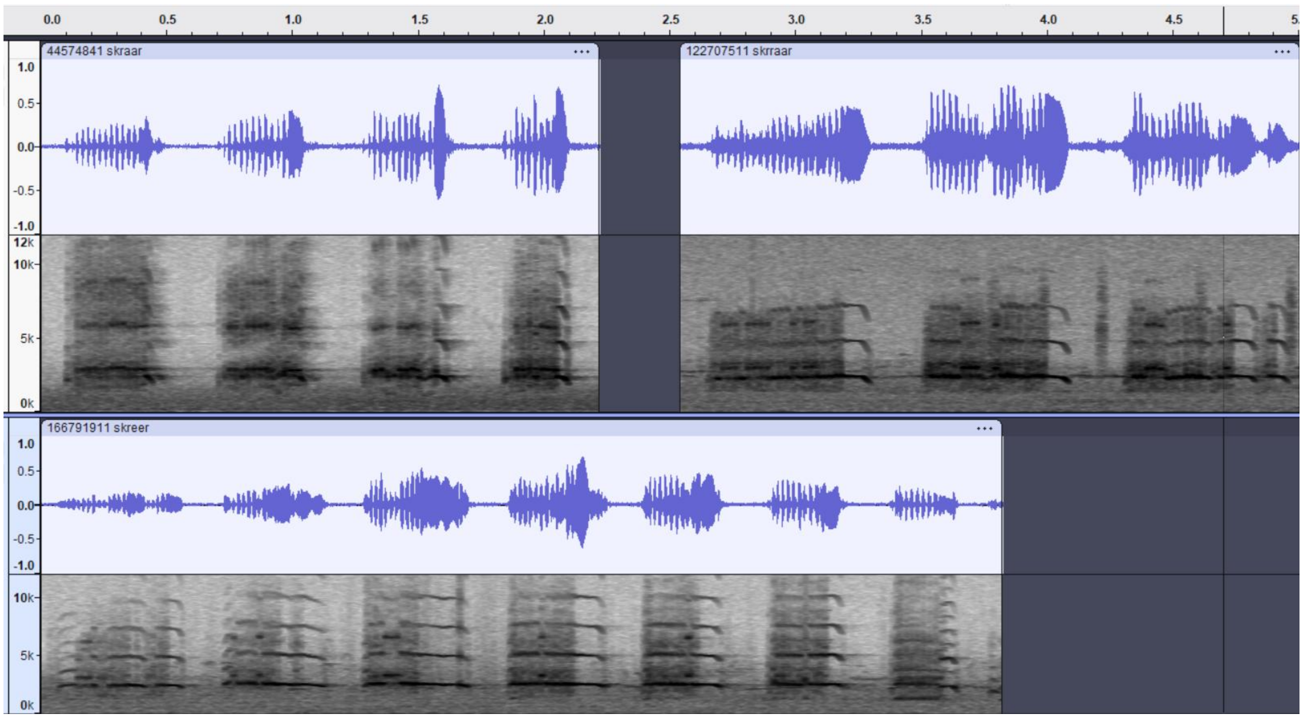
compared to ‘keer’ calls of *inornata* (longest in a series selected):



And below are a few randomly selected, and quite typical, ‘keer’ calls (*semipalmata* top, *inornata* below), in color to show where the maximum amplitude is (the broadest yellow band in each). These calls are somewhat variable in both, but maximum amplitude is closer to 2 kHz in *inornata* and closer to 3 kHz in most *semipalmata,* and most of the *semipalmata* ‘keer’ calls are shorter and more modulated than are most of the *inornata* ‘keer’ calls.



Of the other call types, one stands out as being seemingly unique to and commonly given by *inornata*, without an obvious homolog in *semipalmata*, and it may be the “scream flee” call from the sonagram in Sordahl (1979), the most thorough study thus far of *inornata* vocalizations. It does not perfectly match the description in Sordahl (1979), however, which states that it comprises a single narrow-band note that breaks up in rapid modulation. This does not square well with the below three randomly chosen examples of the call type in question (which tend to resemble a trilobite in the waveform). Of these, ML 44574841, for example, was made in January, so is clearly an adult vocalization. This call type may be that referred to by O'Brien (2006) as follows: "the year-round alarm is a more drawn-out, screaming *klaayii* and variations, often with a distinctly curlew-like quality, particularly in Western". Further study may locate a homologous vocalization in 'Eastern', but if so, it must be much less common and obvious than in 'Western'.

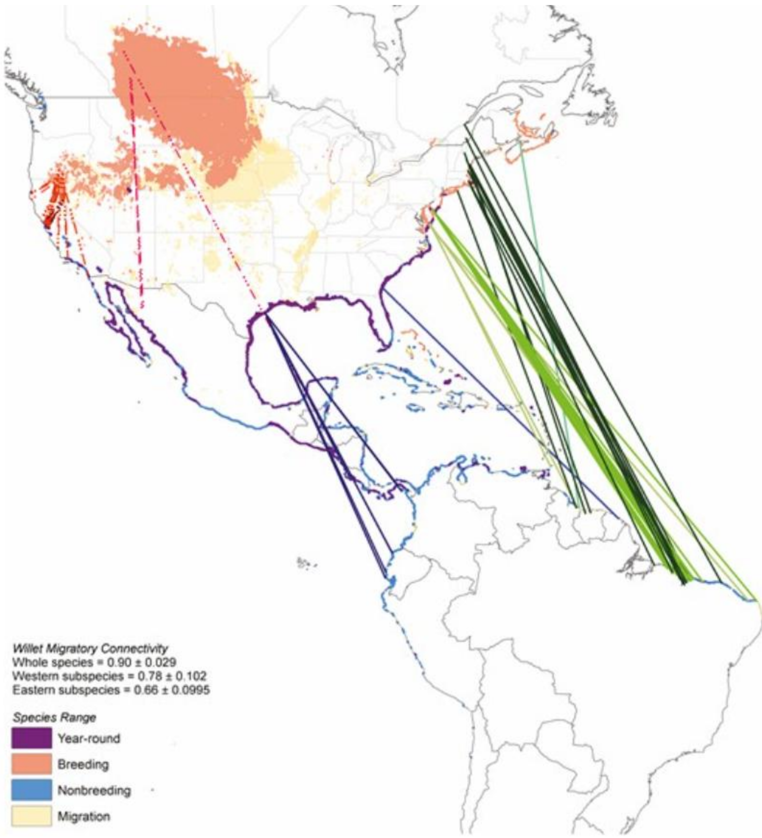


In summary with respect to vocalizations, as already known, songs differ rather markedly between the two, despite their obvious similarities. In addition, at least some calls differ, a common call in 'Western' perhaps lacking a homolog in 'Eastern'.

Molt: As summarized by O'Brien (2006), *inornata* wintering on North American coasts undergo a complete molt there, whereas nominate *semipalmata* only begins its flight feather molt after leaving North America, and body feather molt is limited, mostly occurring farther south. Therefore, Willets in primary molt in July and August are invariably *inornata*; however, since both winter in South America, either species may molt flight feathers there. In the spring, *semipalmata* typically molts into breeding plumage much earlier than *inornata*.

Migration and wintering:

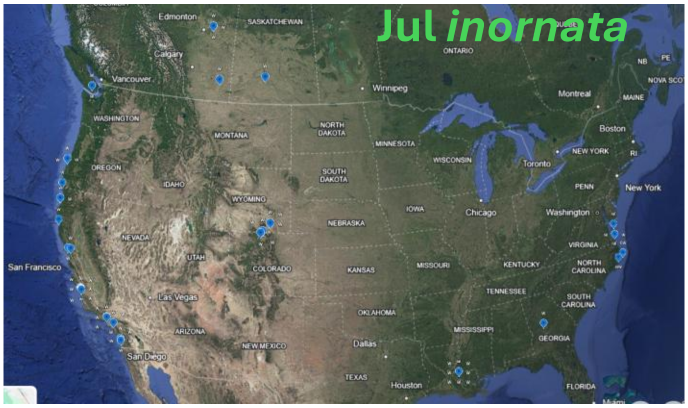
Huysman et al. (2022) compiled tracking and eBird data to map the distribution and migration routes of the two taxa. Although unfortunately the figure captions in their paper appear to be mismatched to the figures, this one clearly summarizes the overall picture:

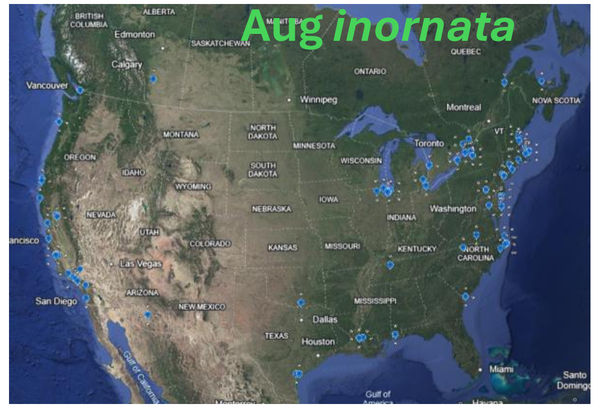


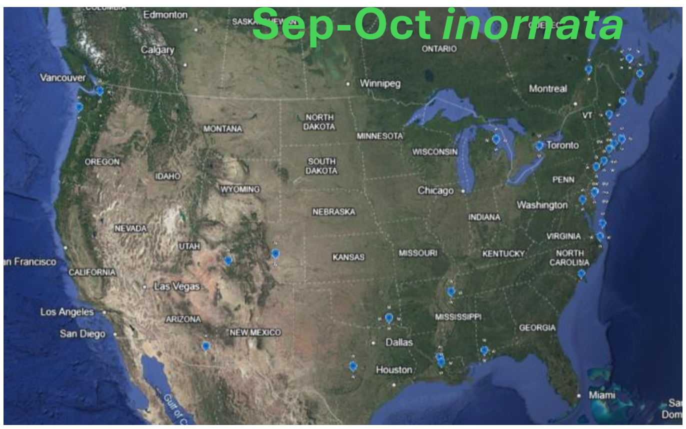
Note that Antillean breeders from the Bahamas through Greater Antilles and Cayman Islands are thought to be resident (Raffaele et al. 1998), but their breeding distribution and migratory status are not well-documented. Certainly, the breeding population in the West Indies is considerably augmented in the non-breeding season (Raffaele et al. 1998). Huysman et al. (2022) did not break down age categories further, and we have done so here for a more limited subset of individuals based on ML photos.

Juveniles: The following maps are generated from the URLs given above for juveniles (note that these are by no means all the juvenile Willet photos in ML, but they are the confirmed ones tagged as such for which photos are useful, plus a few others found incidentally). They confirm that a few juveniles are still present on or near the breeding grounds during July, but that many are already on the West Coast, and some already on the southeastern coasts. They are much more widespread by August, especially concentrating around the Great Lakes and Maritime provinces and northeastern USA (they also reach Florida in at least partial juvenile plumage but Florida photos were not included in this sample by happenstance). Juvenile *semipalmata*, on the other hand, do not normally scatter (and none of the inland photos tagged as juvenile appear to be of this taxon, even in eastern seaboard states and provinces), but some remain on the breeding grounds as far north as Nova Scotia through mid-September, although many juveniles depart much earlier.

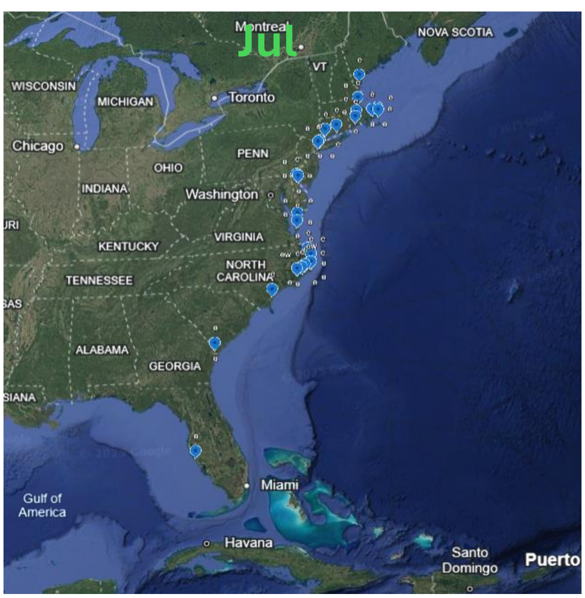
inornata tagged as juvenile, Canada-US ML photos (July, left upper; August, right upper; September-October below left):

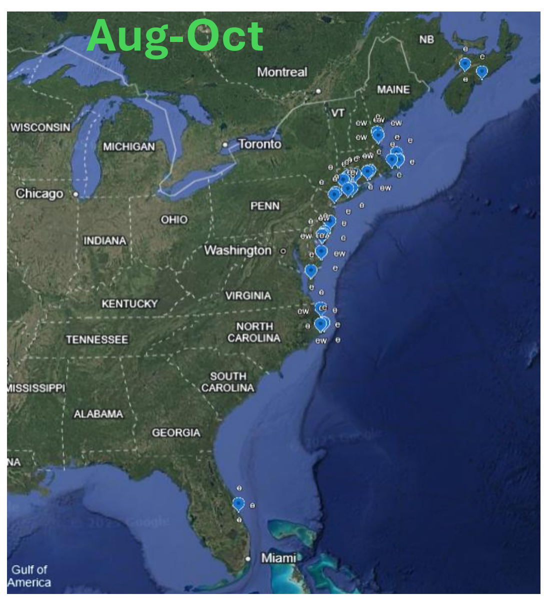




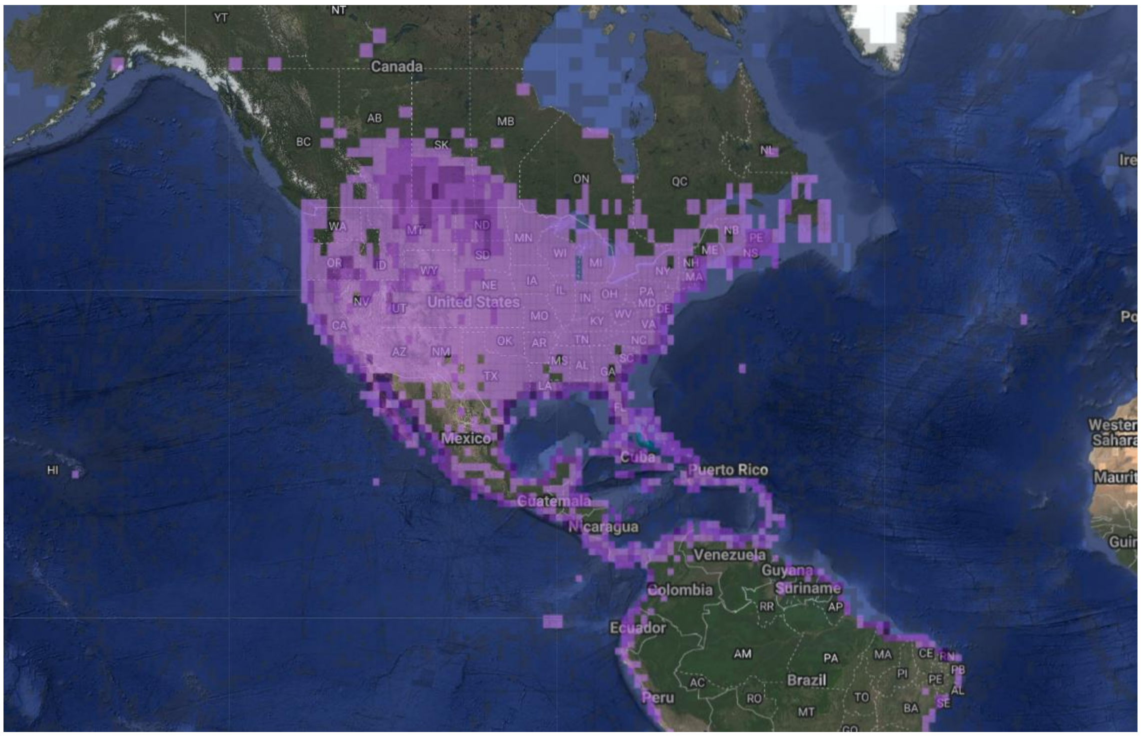


semipalmata tagged as juvenile, Canada-US ML photos (July, left; August-October below):*semipalmata* tagged as juvenile, Canada-US ML photos (July, left; August-October



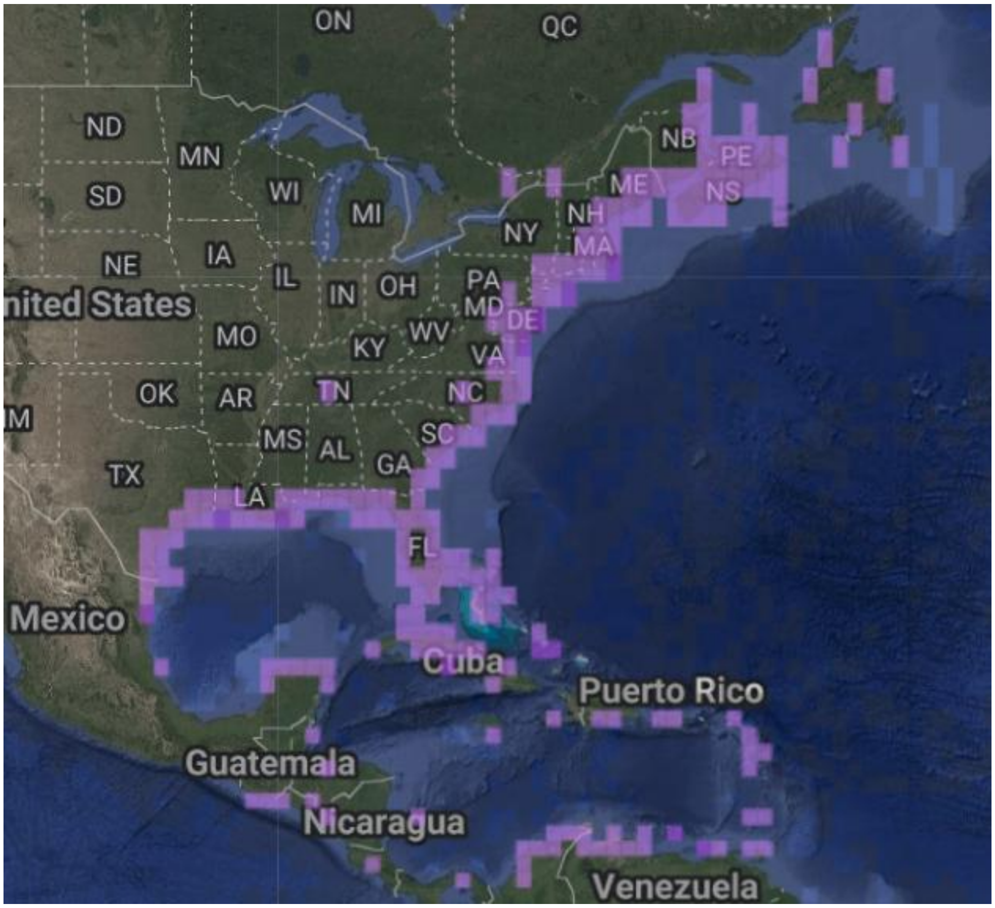


Vagrancy: Although there are many interior North American records assigned to or assumed to be *inornata* east and south of the breeding grounds, including in Mexico (Howell and Webb 1995), there are fewer inland in Central America and very few in South America (eBird data). Although breeding widely in Alberta, *inornata* is scarce in adjacent British Columbia (Campbell 2015). It has also been recorded in southern Alaska (https://ebird.org/checklist/S17925035), on Isla Clarion (https://ebird.org/checklist/S216537234), Cocos Island, Costa Rica (Garrigues et al. 2017, Blanco and Sandoval 2019), Hawaii, and Bermuda, at least.



The only accepted eBird reports of nominate *semipalmata* with photo vouchers from far inland North America are as follows (see also eBird map below):

1) A breeding-plumaged adult on 5 May from Tennessee (https://ebird.org/checklist/S136213793), very obvious in comparison to the flock of *inornata* it was with, all of which are still in heavy molt, whereas the *semipalmata* appears to be in complete, fresh breeding plumage (consistent with known differences in timing of molt; see e.g. Antonucci and Corso 2008).
2) A breeding-plumaged adult on 27 May from Ontario (https://ebird.org/checklist/S243684714), also apparently in full, fresh breeding plumage, with Short-billed Dowitchers but no other Willets.
3) Two breeding-plumaged adults on 17 Jun in Vermont (https://ebird.org/checklist/S37659936 and https://ebird.org/checklist/S37653495), with a Killdeer.
4) A breeding-plumaged adult 10 May 2024 from inland Pennsylvania (photos of this individual in this gallery).
5) A few inland in eastern seaboard states.



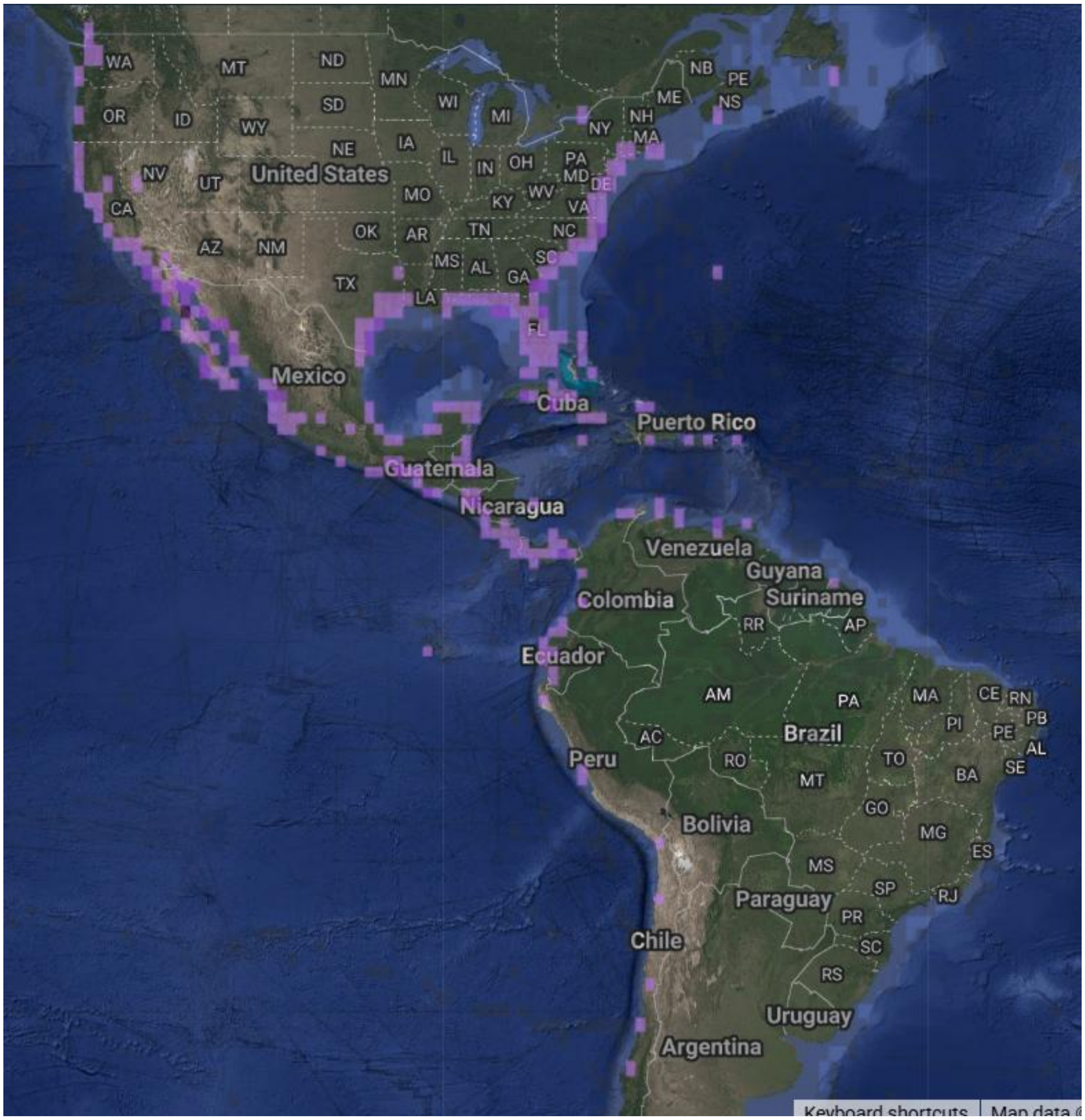
However, *semipalmata* is quite common in Bermuda, even in flocks, which makes sense given their overwater migration (summarized in Lowther et al. 2020). Of course, these are long-distance overwater migratory shorebirds, so it would be shocking if *semipalmata* did not at least occasionally turn up as vagrants, but they are indeed pretty good at avoiding heading west in North America, in marked contrast to the easterly autumn flight paths of many *inornata*.

There are of course several records of Willets in the Western Palearctic, most of them *inornata*, as expected by their strong west-east migration in fall (Antonucci and Corso 2008, Haas 2017); however, even *inornata* is among the rarer strongly migratory Western Hemisphere shorebird vagrants to the Eastern Hemisphere. One from Norway, however, has been considered to be *semipalmata* (Haas 2017), though this may perhaps need revalidation.

Wintering grounds: The non-breeding grounds of nominate *semipalmata* have long been considered to be primarily coastal eastern South America (Morrison and Ross 1989, Sick 1993, O'Brien 2006, Martínez-Curci 2014). However, whereas this appears to be the case for Atlantic coast birds (Smith et al. 2020, Gutowsky et al. 2025), Heath et al. (2021) found from nine geolocators retrieved from Texas Gulf Coast birds that all these individuals had overwintered on the Pacific coast of Central and South America. The wintering grounds of *semipalmata* (those mapped below are December-February eBird records tagged as Eastern, not checked for this proposal) thus are primarily Caribbean northern South America and the Atlantic coast of South America, with a smaller number on the Pacific coast of Mesoamerica. It is rare southward along the Argentine coast, including one in Tierra del Fuego (Argerich et al. 2011, Vander Pluym and Sterling 2019, Pearman and Areta 2020). One specimen of *semipalmata* was taken on the Río Babahoyo, near Guayaquil, Ecuador, by the Olallas in 1931 (Ridgely and Greenfield 2001; see Wiley 2010, who considers that it confirms the reliability of the huge Olalla collections, after considerable doubt had earlier been sown).

Below are winter (Dec-Feb) eBird records of *semipalmata.* Note that eBird show no records of *semipalmata* along the Pacific coast of Colombia and Ecuador, although track data show that they winter there. The difficulty of identifying *semipalmata* in winter, presence of *inornata* in the same area, and confusion over what taxa to expect there probably have led to extremely conservative reporting and review, which will need to be reassessed by the eBird team:

The wintering grounds of *inornata* (those mapped below are December-February eBird records tagged as 'Western', not checked for this proposal) include both coasts of the contiguous USA, the Caribbean, including north coastal South America (though mapped only for the Pacific coast of Colombia in Hilty 2021), both coasts of Mexico and Central America (Blake 1977), and the Pacific coast of South America (including the Galapagos; Brinkhuizen and Nilsson 2020). One record from Argentina is recognized (Pearman and Areta 2020). (The much larger number of records from North America may be due at least partly to observer bias, including whether reports are tagged, but this remains to be confirmed.)



Habitat: As is well-known, the breeding habitats of the two taxa differ markedly in salinity but not in structure. 'Western' Willets breed in inland marshes and prairies, mostly freshwater but in some saline inland habitats, while 'Eastern' Willets breed in coastal saltmarsh habitat. However, both winter primarily on open coastal flats, often together, and both may occur in saltmarshes in winter (Restall et al. 2006). At least 'Western' is common at some shrimp farms (Navedo and Fernandez 2019). And, it is well-known that during the breeding season both forms co-occur in the same general areas, but oversummering, non-breeding 'Western' Willet is not usually found in the saltmarshes, being largely found on the nearby coastal flats, and to a lesser extent inland wetlands and littoral habitats. Smith et al. (2021) showed that springtime arrival and breeding of 'Eastern' Willets is timed to coincide with the "green flush" of *Spartina* growth and thus habitat productivity. During the breeding season, 'Eastern' Willets are highly conspicuous in the saltmarsh due to their habit of perching on signposts and other vantage points, singing loudly and often, and displaying their prominent wing patterns, while the nearby non-breeding ‘Western’ Willets rather quietly (for a Willet) go about feeding. In fact, Martínez and González (2021) state that Willets are “virtually silent in Chile, giving only weak calls…”.

Genetics: Oswald et al. (2016) examined morphological and genetic differentiation using a large panel of nuclear and mitochondrial loci. Combined with previous evidence for ecological, morphological, and genetic differentiation, these new findings suggest that species limits within *Tringa semipalmata* should be revisited.

Oswald et al. (2016) investigated genetic and morphological differentiation within *T. semipalmata*, using genetic sampling of 19 individuals of *T. s. inornata* and 11 of *T. s. semipalmata*. For their *T. s. inornata* samples, the authors included six samples from a single breeding locality in Wyoming; the remaining *T. s. inornata* samples were from various wintering populations on the Pacific Coast. The *T. s. semipalmata* samples included representatives of breeding populations from the Atlantic and Gulf Coast, but did not include Caribbean individuals. Oswald et al. (2016) sequenced a panel of ultraconserved elements (UCEs) from all thirty individuals; the authors used a bioinformatics pipeline to extract SNPs from each UCE locus as well as full alignments for use in multiple downstream programs to examine population structure and the demographic history of the complex. The authors also sequenced the ND2 mitochondrial gene region for 8 *T. s. inornata* and 10 *T. s. semipalmata* samples.

Oswald et al. (2016) recovered 4352 variable UCE loci, which included 19,322 SNPs; the authors identified 42 loci containing 43 SNPs that were fixed for alternative alleles between *T. s. semipalmata* and *T. s. inornata*. Discriminant analyses of principal components (DAPC) recovered two distinct genetic clusters that correspond to *T. s. semipalmata* and *T. s. inornata* (Figure 1). This finding was further corroborated by Structure, which also inferred two distinct genetic clusters with no evidence of admixture between them (Figure 1).

Additional analyses based on species trees built from SNPs revealed strong support for a coalescent-based species delimitation scenario with *T. s. semipalmata* and *T. s. inornata* split into two species (Bayes Factor = 978 with Bayes factors > 10 usually considered ‘decisive’; Figure 2A). Furthermore, Oswald et al. (2016) found evidence for reciprocal monophyly in mitochondrial DNA with 0.85% mean sequence divergence, five base pairs separating the most similar haplotypes from the two subspecies, and an estimated divergence time of ~700,000 ya (Figure 2B).

The morphological dataset from Oswald et al. (2016) corroborated previous evidence that *T. s. inornata* is larger overall, but that there is overlap in morphospace between the two subspecies.

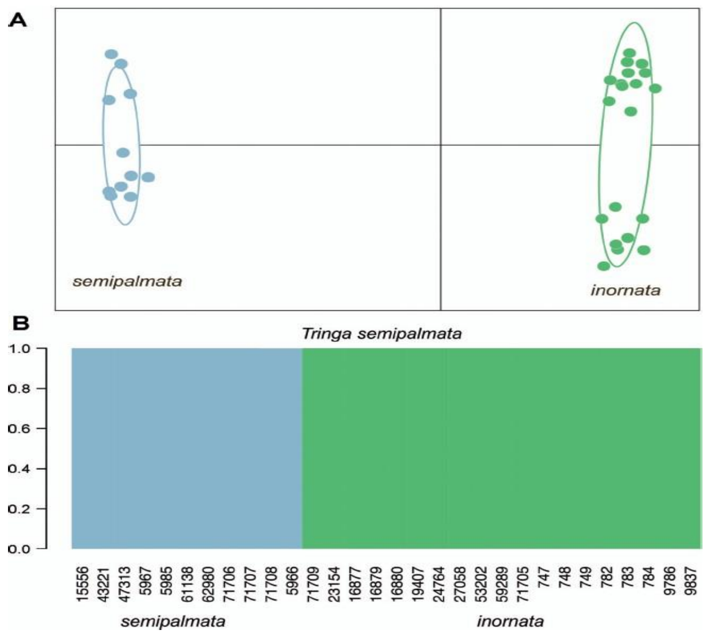


Figure 1: Panel A shows discriminant analyses of principal components with two distinct clusters corresponding to subspecies within the Willet. Panel B shows the output of Structure, which also supports the existence of two distinct population clusters within *T. semipalmata*.

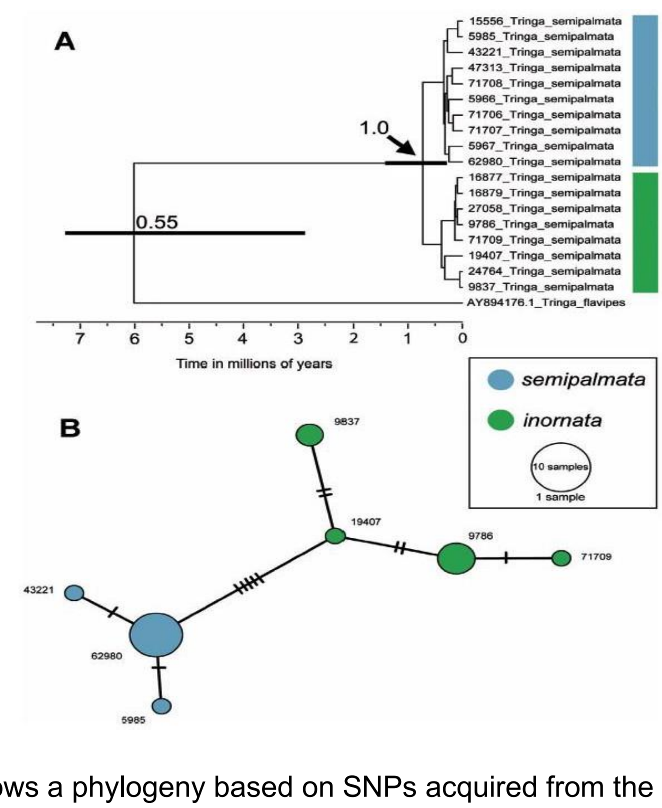


Figure 2: Panel A shows a phylogeny based on SNPs acquired from the ultraconserved element loci. Panel B shows a haplotype network based on ND2 sequences of mitochondrial DNA.

Taken together, Oswald et al. (2016) found strong evidence of genomic differentiation across thousands of loci and little to no gene flow between *T. s. semipalmata* and *T. s. inornata*. Although the amount of mitochondrial differentiation is somewhat low (0.85%), these findings suggest that *T. s. semipalmata* and *T. s. inornata* are independent evolutionary lineages that are not interbreeding and are on separate evolutionary trajectories.

Recommendation:

The extensive evidence that these two subspecies differ in ecology, vocalizations, and morphology, and genetics lead to the conclusion that *T. s. semipalmata* and *T. s. inornata* are most appropriately treated as separate species, despite their fairly recent divergence. Already, for example, the editors of *Dutch Birding* considered them two species as of 2017 (Redactie Dutch Birding 2017); Howell and Dyer (2023) and Dyer and Howell (2023) limbo-split *inornata*; and Kirwan et al. (2019) stated that Willet is probably best treated as two species. We strongly recommend the split of Willet (*Tringa semipalmata*) into two species, *Tringa semipalmata* and *Tringa inornata*.

English names:

The names 'Eastern Willet' and 'Western Willet' have become extremely well-entrenched, and the geographic names are largely appropriate even on much of the migration routes and wintering grounds. However, good numbers of *inornata* spend much time in the eastern US, right next to the saltmarsh-breeding *semipalmata*, and Texas *semipalmata* are now known from Pacific Mesoamerica and the northwestern South American coast. The names Prairie and Saltmarsh willets have been suggested, and although they are only relevant during the breeding season, they are evocative and could help to draw awareness to the need for conservation of these two endangered ecosystems for these endemic-breeding, large-bodied and *k*-selected shorebirds, both of which are declining and facing numerous conservation concerns (e.g. Correll et al. 2017, Klingbeil et al. 2018, Shaffer et al. 2019, Huysman et al. 2022, Muñoz-Salas et al. 2023, Sandercock and Gratto-Trevor 2023, Suthar et al. 2025).

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Submitted by: Pamela C. Rasmussen, Nicholas A. Mason, Michael O'Brien, Marshall Iliff, and Brian Sullivan

Date of Proposal: 18 August 2025

Change the linear sequence of species of *Sialia* (bluebirds)

Background:

In the current AOS checklist, *Sialia* are listed in the following sequence:

1. Eastern Bluebird *Sialia sialis*
2. Western Bluebird *Sialia mexicanus*
3. Mountain Bluebird *Sialia currucoides*

Historically, *S. sialis* and *S. mexicanus* have been considered closely related due to their similarities in plumage (Gowaty and Plissner 2020), with these species diverging *ca.* 2.5 mya (Klicka and Zink 1997).

New information:

Hybrids between *S. sialis* and *S. mexicanus* appear rare, but hybridization between *S. sialis* and *S. currucoides* has been widely documented in areas where the species are sympatric (Rounds and Munro 1982, Gowaty and Plissner 2020). For *S. sialis* and *S. currucoides* in the Canadian prairie provinces, "[d]ata show that hybrid males back-crossed equally to females of both species, but female hybrids have been observed back-crossed only to [*S. currucoides*] males" (Rounds and Munro 1982). Despite hybrid combinations showing comparable reproductive success rates to non-hybrid pairs, there appears to be a fitness penalty for backcrossing between hybrid males and female *S. sialis*, and birds in the area of overlap hybridize at low rates and hybridization does not occur every year (Rounds and Munro 1982), suggesting some prezygotic reproductive incompatibilities. These hybridization patterns suggest a close relationship between these taxa while also confirming that *S. sialis* and *S. currucoides* are separate biological species. Hybridization has also been repeatedly observed between *S. mexicanus* and *S. currucoides*, but this is apparently restricted to pairs where the male is *S. mexicanus* and the female *S. currucoides*, and only occurs in areas where *S. mexicanus* occurs at a much lower density than *S. currucoides* (Duckworth and Semenov 2017). We found only one reference to a hybrid between *S. sialis* and *S. mexicanus* from New Mexico, leading us to infer that hybridization between these species is rare, although more work in the mountains of western Mexico may be required to fully understand dynamics between these clades. Regardless, hybridization data suggest a closer relationship between *S. sialis* and *S. currucoides* than between *S. sialis* and *S. mexicanus*.

More recently, phylogenetic work with mitochondrial sequences found that *S. sialis* and *S. currucoides* are more closely related to each other than either is to *S. mexicanus*, further supporting this sister relationship (Fig. 1) (Klicka et al. 2005). This work was later contradicted by further work with the mitochondrial cytB and ND2 genes, where *S. sialis* was found to be sister to *S. mexicanus* (Voelker and Klicka 2008).

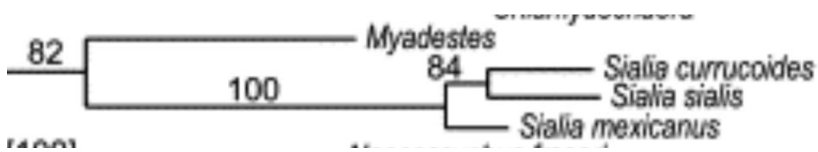

Figure 1. A portion of the tree derived from mitochondrial sequence data of the thrushes, showing 84% bootstrap support for the sister relationship between *S. sialis* and *S. currucoides* (Klicka et al. 2005).

In the 2020s, genome-wide research in the genus *Sialia* found evidence of historical gene flow throughout the genus, including evidence for incomplete lineage sorting and mito-nuclear discordance that could potentially explain previous disagreements in the species-level phylogenies (Veale 2023). In Veale (2023), sequences derived from nuclear DNA (via single nucleotide polymorphisms) and from the ND2 gene supported the sister relationship between *S. sialis* and *S. currucoides* (Fig. 2). Conversely, Veale (2023) found that trees constructed from cytB and COI, both mitochondrial genes, supported the relationship between *S. sialis* and *S. mexicanus*. Veale (2023) suggested that sex-biases in hybrid pair formation between *S. mexicanus* and *S. currucoides* may explain why these species were never placed as sister to one another despite showing evidence of hybridization in analyses of the nuclear DNA (Fig. 3) (Duckworth and Semenov 2017).

Figure 2. Single nucleotide polymorphism (SNP) tree of the three bluebird taxa, showing evidence for rapid diversification while also unequivocally showing a closer relationship for *S. sialis* ("EABL") and *S. currucoides* ("MOBL") (Veale 2023).

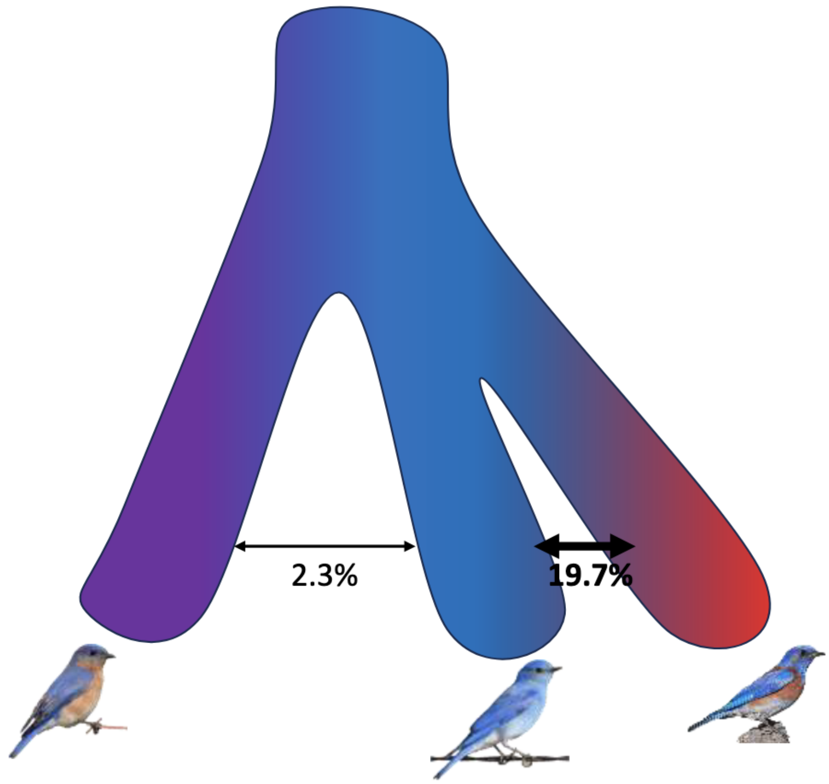

Figure 3.7 A graphical representation of the novel bluebird phylogeny based on the PCoA and SVD quartets with estimated gene flow percentages based on f_4-ratio.

Figure 3: Figure 3.7 from Veale (2023), showing gene flow in nuclear genomes between the three *Sialis* species. From left to right: *S. sialis, S. currucoides,* and *S. mexicanus*.

Recommendation:

Evidence from multiple studies on hybridization between these taxa and across multiple genes indicates that these species represent a rapid evolutionary radiation, and that hybridization has occurred repeatedly in their evolutionary past. Despite this, a clear pattern emerges: *S. sialis* and *S. currucoides* appear to be more closely related, as supported by genomic evidence and from the extent of hybridization occurring between these three taxa. Ongoing hybridization appears to have a greater genomic signature within the sympatric taxa, but the fact remains that hybridization is rarest between *S. sialis* and *S. mexicanus*, who are classically considered sister to one another. In light of this evidence, and following linear sequence conventions, we propose rearranging the genus *Sialia* as follows:

1. Western Bluebird *Sialia mexicanus*
2. Mountain Bluebird *Sialia currucoides*
3. Eastern Bluebird *Sialia sialis*
4.

This reshuffling does not require the editing of any species accounts, and more accurately reflects the relationships within the genus.

We recommend a “Yes” vote to reorder the genus *Sialis* to better reflect their evolutionary history.

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Submitted by: Jacob C. Cooper & Oscar Johnson

Date of Proposal: 20 October 2025

Treat *Myiopsitta luchsi* as a separate species from Monk Parakeet *M. monachus*

***Note*:** This is a modified version of SACC Proposal 1021, which incorporated elements from two previous proposals on the same subject (SACC 93 and SACC 503). SACC 1021 passed unanimously (7-0).

Effect on NACC:

Monk Parakeet *Myiopsitta monachus* is an introduced species in the NACC area. If this proposal passes, the split of *M. luchsi* from *M. monachus* would result solely in a modification of the distributional statement and Notes of *M. monachus.* The scientific and English names would remain the same.

Background:

Prior to passage of SACC 1021, the SACC note on *M. monachus* read:

21b. Collar (1997) treated Andean *luchsi* as a separate species from *Myiopsitta monachus* based on differences in plumage and nest site; this taxon was formerly (e.g., Cory 1918) treated as a separate species, but Peters (1937) considered them conspecific. SACC proposal to treat *luchsi* as a separate species did not pass because of insufficient published data. Russello et al. (2008) found that *luchsi* was genetically isolated from lowland populations. SACC proposal to treat *luchsi* as a separate species did not pass. Del Hoyo & Collar (2014) treated *luchsi* as a separate species ("Cliff Parakeet").

The basic set-up is that widespread *Myiopsitta monachus* is treated as consisting of 4 subspecies, 3 of which are from the lowlands of southern South America, and the fourth (*luchsi*) is found in the dry valleys of the Andes of central Bolivia. Lowland birds make stick nests in trees and telephone poles, whereas *luchsi* places these nests on cliff ledges or within bromeliads on cliffs. Vocalizations seem to differ but have not been quantitatively analyzed.

Information from SACC Proposal 503 by Dan Lane:

Molecular study: In their Figure 2 (reproduced here), Russello et al. (2008) provided a network of haplotypes of mtDNA (control region, 558 bp) from all named taxa within *Myiopsitta* (*monachus* N=38*, calita* N=9*, cotorra* N=16, and *luchsi* N=14; plus 64 birds from feral populations in US of unknown taxon) mostly from toe-pad sampling of AMNH specimens).

The network showed little uniqueness of haplotypes among the taxa within *Myiopsitta* with the strong exception of *luchsi*, which shared no haplotypes with any of the other named taxa (the localities from which specimens of *cotorra*, the closest geographic representative of lowland birds to *luchsi*, were taken were from Matto Grosso, Brazil, and central Paraguay). Russello et al. (2008) took this result to mean that *luchsi* is a monophyletic and diagnosable group that has been reproductively isolated from the rest of the members of *M. monachus*, despite being reported only 175 km away from the nearest population of *M. m. cotorra*, and proposed that it be accepted as a distinct Phylogenetic Species (and more subtly suggesting that the names *cotorra* and *calita* be synonymized with *monachus*, at least if one follows the PSC).

BMC Evolutionary Biology 2008, **8**:217 http://www.biomedcentral.com/1471-2148/8/217

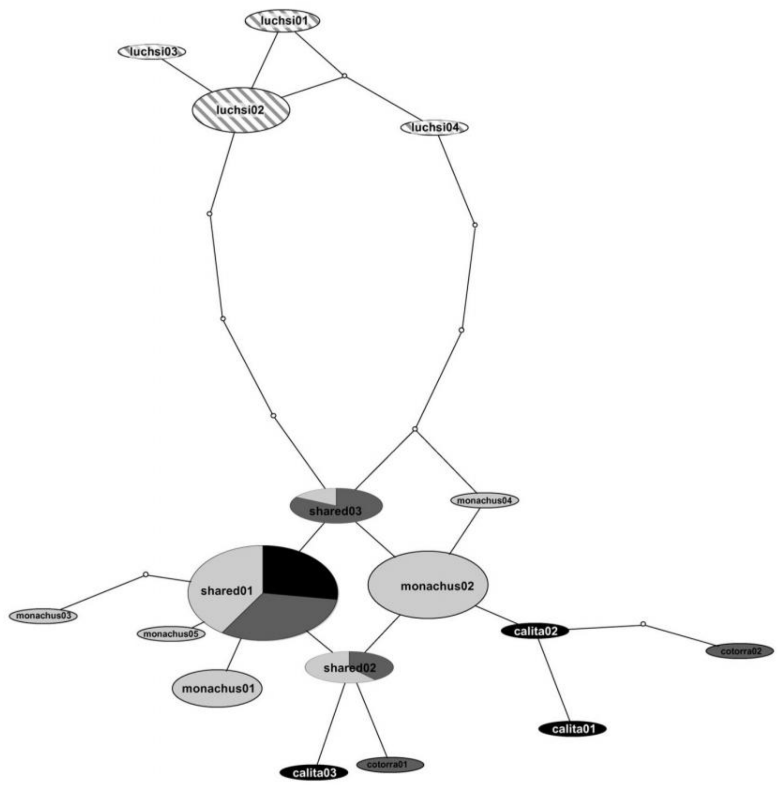

Figure 2
Network showing genealogical relationships among *Myiopsitta monachus* haplotypes sampled in the native range. Haplotypes are connected with a 95% confidence limit. The size of each oval is proportional to the frequency of the haplotype in the analysis. White dots represent mutational steps separating the observed haplotypes. Different shades represent the proportion of individuals of each subspecies exhibiting that particular haplotype (colors as in Figure 1).

Nesting: As the proposed English name ‘Cliff Parakeet’ suggests, this species does seem to be entirely restricted to breeding sites on cliffs, despite the presence of trees and telephone poles within its range that could allow it to nest in the same manner as its lowland counterparts. However, *luchsi*, based on my personal experience with it, is considerably rarer than lowland *monachus* within its range, and its nests are smaller affairs that cluster around bromeliads and other low plant growth along steep cliffs. I have only an experience of N=1 with nesting colonies, but the one I know has remained stable over a ten-year period, with only about 2-5 pairs nesting within a complex, and perhaps only 2-3 nest complexes comprising the colony. Photographs of nests are available here:

http://www.flickr.com/photos/8013969@N03/6202463428/

Voice: See the following:

http://www.xeno-canto.org/species/Myiopsitta-monachus

Listeners are likely to be impressed by the rather distinct vocalizations of *luchsi* in comparison to the lowland forms of *M. monachus*. The typical calls of cliff-nesting *luchsi* are consistently higher-pitched, less grating, and generally shorter in duration that those of the lowland birds.

To illustrate the plumage differences, here are some photographs from Macaulay. The top one is *monachus* from Buenos Aires by Adrian Grilli, and bottom one is *luchsi* from dpto. Cochabamba by Paul Bartlett. Note especially the differences in the chest-breast area in terms of scaliness and color.

New information:

Del Hoyo & Collar (2014) treated *luchsi* as a separate species based on the Tobias et al. point scheme as follows:

"Usually regarded as conspecific with *M. monachus*, but treated as separate species in HBW (and this is supported by recent genetic analysis (1)) on basis of characters now scored as follows: uniform (unbarred) and much paler grey breast and crown (also no bars on mantle) (3); pure buffy-mustard vs yellow-tinged grey mid-belly (2); stronger green in all areas (1); bluer tail and darker flight-feathers and wing-coverts (ns[1]); darkish mark on base of upper mandible (ns[1]); cliff-nesting vs tree-nesting habit (1) (which, incidentally, may be related to apparently longer claws). Monotypic."

Note that the "recent genetic analysis" was considered minor and insufficient evidence by SACC when considering proposal 503. Clearly, the expectation for an isolated population, one that also has plumage differences, is that it will also be differentiated at the neutral loci that could be sampled in 2008, regardless of taxonomic rank of the populations.

Peter Boesman and Shaun Peters simultaneously alerted me to the fact that after del Hoyo & Collar (2016), an analysis was published by Boesman (2017), who corroborated many of the differences noted by Dan, presented many sonograms, and concluded:

"I conclude that the voices of Monk Parakeet and Cliff Parakeet show some clear differences, further supporting their treatment as two species."

I have listened to all the recordings of *luchsi* on xeno-canto: https://xeno-canto.org/species/Myiopsitta-luchsi

I have also listened to about 20 of *monachus* on xeno-canto from Argentina and Brazil (skipping recordings from feral populations: https://xeno-canto.org/species/Myiopsitta-monachus?pg=1

I can hear what I would consider to be consistent differences between the two, precisely as described back in 2011 by Dan and further documented by Boesman (2017), so I am convinced that two species are involved. I recommend that everyone take a few minutes to listen to some recordings of each at the xeno-canto links above.

Discussion and Recommendation:

We now have a much larger N of "published" online recordings of *luchsi*, and we also have Boesmans' synopsis. Given that splitting them is not a novel taxonomic treatment, I think it is ok to relax our standards slightly in terms of requiring a formal quantified published analysis for a change in classification. Cory (1918) treated *luchsi* as a separate species, and Peters (1937), as was his practice, lumped them without any explicit rationale. Of course, Cory treated many taxa as species that we now consider subspecies, so that doesn't count for much. Nonetheless, all these recordings in my opinion trump Peters (1937) and place burden-of-proof on its treatment as a subspecies.

As for the other evidence, the plumage differences in my subjective opinion, now that we have good photos of *luchsi* to admire, are similar or greater in degree to those between many taxa of New World parrots treated as species. On the other hand, I think the difference in nest sites is overblown as far as its significance. A cliff ledge really isn't that different from a telephone pole or an isolated tree. Species with restricted availability of suitable nest sites can often be quite flexible within certain parameters. Within several parrot species, nest-site flexibility is well-documented, e.g. see Romero-Vidal et al. (2023), and so this has no demonstrable taxonomic importance. I regard the genetic data as inconclusive: the genetic distance between them could be argued as evidence for or against species rank.

Reasons to vote YES for the split could be that differences in vocalizations are strongly associated with, for better or worse, species rank in parrots, and that given those differences accompanied by plumage differences consistent with species rank within several genera of parrots, we have sufficient evidence to treat them as species.

Reasons to vote NO could be that all of the above may be true, but we still lack a peer-reviewed publication on the vocalizations, but we have softened our stance on that somewhat in recent years in that recordings themselves are available online (and in this and many other cases, Peter Boesman has provided some quantification.)

English names:

Del Hoyo & Collar (2014) and others have used "Cliff Parakeet" for *luchsi* and retained "Monk Parakeet" for the much more widely distributed and familiar species. This fits with our SACC Guidelines on English names, and Cliff Parakeet is a good name, so I suggest that no English proposal name is needed.

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Submitted by: Van Remsen

Date of Proposal: July 2024, modified for NACC by R. T. Chesser on 20 November 2025

SACC comments on Proposal 1021:

Comments from Areta: "YES. This is a tough case by which I am torn. The case is borderline and may be so forever. The two taxa differ in plumage, vocalizations (although no rigorous study has been performed), and nesting habits. Even though nesting habits can be seen as labile in parrots (e.g., *Psittacara mitrata* can nest in holes on cliffs or in trees in the same localities), the truth is that despite available cliffs in *monachus* habitat and available trees in *luchsi* habitat, I am not aware of *luchsi* nesting on a tree or *monachus* nesting on a cliff. There is also the communality of those nests: *monachus* nests are most of the time massive buildings with many pairs in a single nest (with separate entrances and breeding chambers), while those of *luchsi* are mostly single pairs that place their nests in relatively close association (or quite separately) on cliffs, but never have I encountered nests cluttered together in a single structure as in *monachus*.

"Turning into genetic data, they are evidently very recently diverged, and there is not a great comparative dataset to work on. Yet, the fact that *luchsi* is restricted to Dry Inter-Andean Valleys, add a bit more of evidence in favour of its recognition as a separate species.

"Confronted with the question of whether in the event of meeting these two would interbreed, to me the answer is yes. Yet, I cannot predict what would happen in terms of gene flow or breadth of a hybrid zone. In an unexpected plot twist, I will vote YES to the split, while recognising that the evidence is not perfect, while honouring the many differences in plumage, life-history and vocalizations known between *luchsi* and *monachus*."

Comments from Robbins: "YES. After listening to vocalizations on xeno-canto and confirming plumage differences via photos at Macaulay Library, I again (as I did in proposal 503) vote to recognize *luchsi* as a species."

Comments from Andrew Spencer (voting for Remsen): "YES - this is one of those cases where multiple lines of evidence all seem to support a split. I do think the nesting differences are quite important here - there are plenty of spots near where I've seen *luchsi* that would be great locations for *monachus* nests, and there are other locations with *monachus* that *luchsi* would probably be happy with too. So it's more than just sticking to the available nesting substrates -- there's a real preferential difference there. But foremost to me are the vocal differences, which over the wide range of *monachus*, both native and introduced, really don't seem to vary that much. And then you have these bizarre sounding birds in one part of Bolivia. That is, I believe, a situation unmatched in other parrot species (though happy to hear if that's not true!)"

Comments from Stiles: "YES. The evidence is definitely borderline, but now sufficient, in my view, to place the burden of proof on those who would maintain *luchsi* as a subspecies of *monachus."*

Comments from Lane: "YES. These two taxa are quite distinct, and my own observations (which I offered in Prop 503) agrees with Andrew's: that the substrates for tree or pole nesting are available in the immediate vicinity of *M. luchsi* nests, but they ignore them for cliffs. Voice and plumage additionally make this taxon quite distinct compared to the remaining taxa within *Myiopsitta*."

Comments from Claramunt: "YES. The combination of differences in plumage, nesting behavioral, vocalizations, and genetics make a compelling case for the species status of *luchsi*."

Comments from Ryan Terrill (voting for Del-Rio): "YES. I think Nacho's comment that *M. monachus* does not nest on cliffs where available is pertinent here - as this may represent a barrier to hybridization, and I think the lack of a clear hybrid zone helps with this one. Parrots seem to be pretty happy to hybridize as a taxon in general -- they aren't quite ducks but seem to have a slightly elevated rate of hybridization compared to most families - especially in anthropogenic secondary contact; and I don't know of any hybrids between *M. m. monachus* and *M. m. luchsi* in Bolivia. I don't have access to specimens right now, but did take a perusal through Macaulay and don't see any that are clearly intermediate. These two taxa do get pretty close to each other in Bolivia, especially for vagile birds like parrots. I think *Thamnophilus caerulescens*, as mentioned before, might be a good yardstick for this. They have similar distributions but probably move around quite a bit less, and have a clear zone of morphological integration that we don't see in *Myiopsitta*. Combined with the plumage and vocal differences, I think this all adds up to a pretty good case for split.

Treat Long-tailed Woodcreeper *Deconychura longicauda* as three species

***Note*:** This is a modified version of SACC Proposal 997, which passed 9-1. The three species now recognized are Piping Long-tailed Woodcreeper *Deconychura typica*, Whistling Long-tailed Woodcreeper *D. longicauda*, and Mournful Long-tailed Woodcreeper *D. pallida*.

Effect on NACC:

The only post-split species that occurs in our area is *D. typica*, so passage of this proposal would add *D. typica* to the Checklist and remove *D. longicauda*.

Background and New Information:

BirdLife International split *Deconychura* into three species based on the following rationale:

"Little Long-tailed Woodcreeper [*D. typica*, including also subspecies *darienensis* and *minor*; from Honduras through Central America to N. Colombia]: In past, sometimes considered a separate species from *D. longicauda* and *D. pallida*, and this arrangement restituted here, based on smaller size (male wing 91–99 mm, n=9, vs respectively 106–110, n=3, and 102–111, n=4; allow 2); spots vs streaks on breast (2); chestnut undertail-coverts (2); clearer buff-white chin and throat (1); song a long fast series of short piping notes, starting slowly and slowing at end, hence high number of notes (4) and very short note lengths (4) (1). Birds from NW Colombia (Córdoba) may be intergrades between darienensis and minor. Three subspecies recognized.

"Northern Long-tailed Woodcreeper [*D. longicauda*; the Guianas and Brazil N of the Amazon]: Usually considered conspecific with *D. typica* and *D. pallida* (see both). Monotypic.

"Southern Long-tailed Woodcreeper [*D. pallida*, including also subspecies *connectens*; W and S Amazonia]: Hitherto considered conspecific with *D. longicauda* and then usually also with *D. typica*, but differs from latter in characters given under that species and from former in its shorter tail (in male 92–105 mm, n=4, vs 107–109; at least 1); whitish vs strong buffish chin and streaks on throat to breast (1); and distinctive song, a series of c. 8 flat whistles vs a series of 6–10 long upslurred whistles (both gradually descending in pitch), hence having much shorter notes (3) with pitch of first note much higher (3) and note shape different (ns[2]) (1). Populations in Andean foothills of E Ecuador apparently belong to *connectens*, but adjacent lowland birds may be of race *pallida*; in these foothills, either *connectens* or an undescribed taxon sings a very different song, a series of c. 10–14 double notes, slightly descending in pitch, suggesting a species-rank difference; undescribed taxon, perhaps same, reported from foothills of NE & NC Peru (2). Recent analysis of whole genus using voice, morphology and genetics (3) proposed promotion to full species status of the three races currently included herein, as well the undescribed taxon from Andean foothills; however, differences appear slight, and vocal analysis based on very small samples, some of which may be unrepresentative.
Names *pallida* and *connectens* published simultaneously; former awarded priority by First Reviser (4). Three subspecies recognized.

Prior to the split, the SACC note for *D. longicauda* read as follows:

109. The subspecies *typica* was formerly (e.g., Ridgway 1911, Cory & Hellmayr 1925) treated (with *minor* and Panamanian *dariensis*) as a separate species from *Deconychura longicauda*, but Zimmer (1934) treated it as a subspecies of *D. longicauda* without comment, and this was followed by Peters (1951) and subsequent classifications. Marantz et al. (2003) indicated that vocal differences among populations suggest that more than one species might be involved, with the *typica* group possibly more closely related to *Certhiasomus stictolaema* than to Amazonian *longicauda* group. Barbosa (2010) found vocal evidence that *D. longicauda* consists of three of more species. Boesman's (2016f) analysis of vocalizations also supported recognizing at least three species, and this was done by del Hoyo & Collar (2016): *D. typica* of primarily Middle America, *D. longicauda* of the Guianan Shield, and *D. pallida* of Amazonia.

Here are LSUMNS specimens of the three proposed species, top to bottom: *typica* (represented by *darienensis*), *longicauda*, and *pallida*). Note that HBW/BLI awarded something like 7 points in the Tobias et al. scheme based on phenotypic characters such as throat color, undertail coverts color, and size (if I am interpreting the numbers above correctly); make your own call on whether what you see below would be sufficient for species rank. See also photos in Barbosa (2010), although some of those did not reproduce well.

The vocal data in the BLI account come from Boesman's (2016) brief synopsis, one of 457 he prepared to evaluate vocal differences in advance of del Hoyo & Collar (2016) for use in the Tobias et al.'s point system: once a total of 7 points is achieved using various morphological and vocal characters, a taxon is ranked as a species. The analysis of the *Deconychura* referred to as "(3)" in the accounts is an unpublished MS thesis (Barbosa 2010). The reference to treatment as separate species in the past likely refers to Cory & Hellmayr (1927), which treated the complex as two species, *D. typica* and *D. longicauda*; at that time no subspecies were described within *longicauda* and it thus including all Amazonian populations. Of interest is that the linear sequence of species in *Deconychura* in Cory & Hellmayr implies that they did not consider them sister species (*D. stictolaema* separating them), as is also implied in their discussion of similar species in the footnotes.

This situation in an increasingly familiar one in species limits in Neotropical birds: fragmentary and anecdotal information strongly suggest that more than one species is involved yet no peer-reviewed paper has been published that evaluates the evidence. The conundrum is whether to anticipate what a formal analysis would indicate or wait for the formal analysis to appear.

In this case, we do have an unpublished formal analysis, and so the conundrum also includes whether to treat an unpublished analysis, albeit available online, as sufficient evidence. (It's a solid thesis; Alex Aleixo was Barbosa's advisor, and John Bates and Jason Weckstein served on the committee.)

As for the Tobias et al. point system used by BLI/HBW, none of the phenotypic characters mentioned in the quoted accounts above is any more associated with species-level differences than with subspecies-level differences. In the dendrocolaptids, differences in all those features are routinely found between taxa treated as subspecies because of vocal similarities. So, it all boils down to vocal differences in my opinion.

Marantz et al. (2003) noted that the typica group had once been considered a separate species, possibly more closely related to then=*Deconychura,* now=*Certhiasomus stictolaema.* They also outlined the strong vocal differences between the *typica*, *pallida* and *longicauda* groups. At that time the Andean foothill taxon was not well known and was thought to be *D. p. connectens*.

Barbosa (2010) presented sonograms for each of the 8 well-supported clades found in the genetic analysis; those 8 clades include the 3 recognized as species by BLI/HBW plus the undescribed foothill taxon plus and additional 3 clades within the Amazonian *pallida* group.

They all appear qualitatively different, but as noted by Boesman (2016), there are problems with taking each sonogram as representative of the clades because of small N, differences in "motivation" (as emphasized by Marantz et al. 2003 for interpreting woodcreeper vocalizations in general). Further, although *longicauda* and *typica* appear distinctive, so to varying degrees do some of the groups within *pallida*. I suspect this is in part due to non-homologous vocalizations, but it's hard to say. Barbosa's Discriminant Function Analysis of standard vocal characters shows that one of the *pallida* clades (5) is actually the most distinctive, and that clade 1 (*longicauda* sensu stricto) is actually more similar to some of the *pallida* group than are some *pallida* clades to each other, although this may be a consequence of the way characters are scored.

73

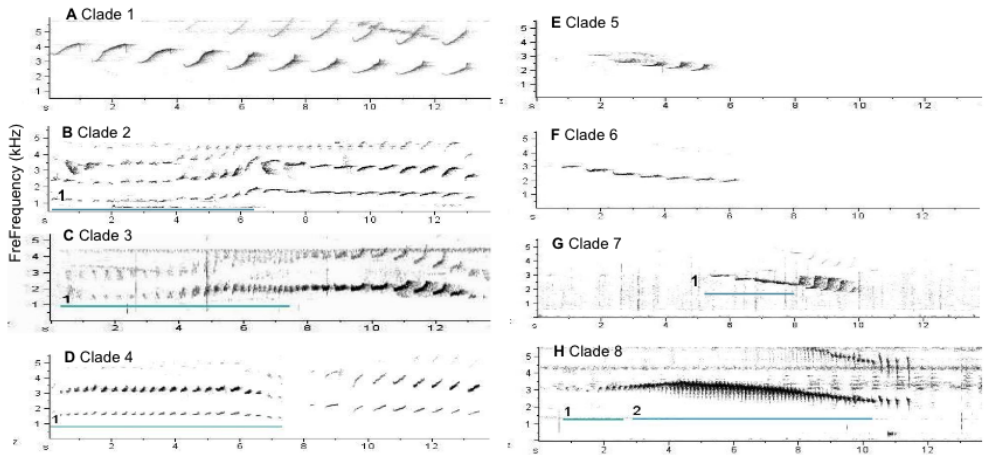

Figure 4. Loudsongs of natural populations of *Deconychura longicauda* (clades 1-8) recovered in a molecular phylogeny (Figure 2). (A) Clade 1: French Guiana, La Trinité (XC 22249); (B) Clade 2: Peru, Loreto: Tierra Blanca (XC20711); (C) Clade 3: Peru, Madre de Dios, Porto Maldonado (ML35539); (D) Clade 4: Brazil, Amazonas, Iranduba, Terra Verde Lodge (ML112796); (E) Clade 5: Brazil, Amazonas, Maués, Pau-Rosa National Forest (AP 1078); (F) Clade 6: Brazil, Pará, Santarém, Tapajós National Forest (BR

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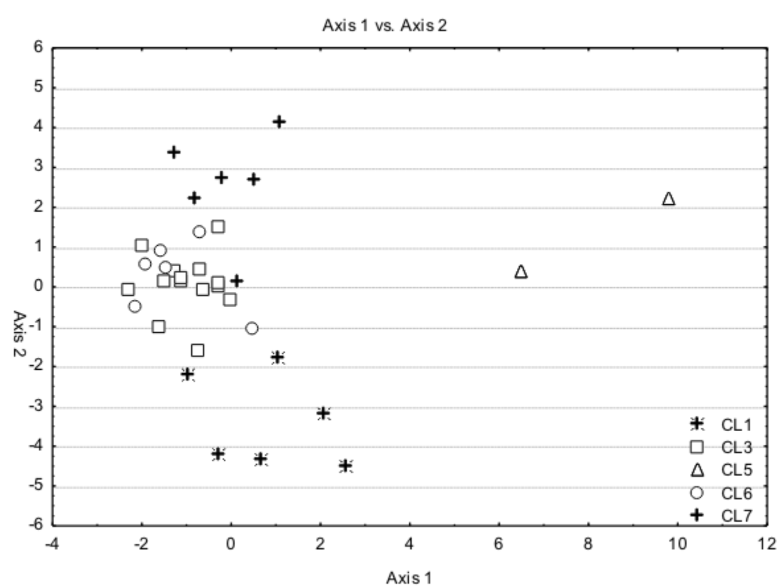


Figure 5. Stepwise DFA with the vocal characters that best discriminate the vocal groups. The clades were those defined by a molecular phylogeny (Figure 2), considering the five vocal groups with more than two recordings.

Barbosa's (2010) phylogenetic tree (based on cyt-b and ND2) is presented below:

71

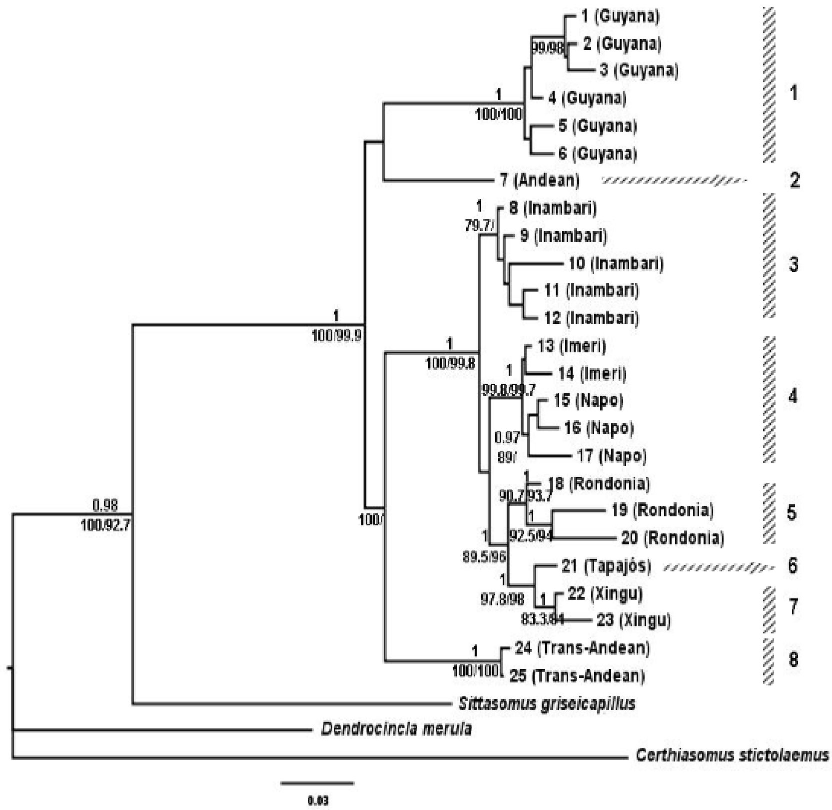


Figure 2. Bayesian phylogenetic tree of *Deconychura* populations based on partial mt DNA sequences (Cyt B and ND2). Numbers above the branches indicate posterior probabilities (BI) and numbers below indicate bootstrap values (MP/ML). Nodes with statistical support below 0.95 (BI) and 75% (MP and ML) are not shown. Numbers at the branch tips refer to tissue collecting localities shown in Figure 1 with names in parenthesis corresponding to Amazonian areas of endemism or major Neotropical regions where those sites are located (see Appendix 2 for detailed locality descriptions). Numbers next to bars represent clades 1-8 (see text).

Note that clade 1 represents *longicauda*, clade 2 the undescribed Andean foothill taxon, clades 3-7 *pallida*, and clade 8 *typica*. My personal view is that these data say nothing about taxon rank per se.

Recommendation:

I don't have a strong recommendation. When I listen to cherry-picked sample recordings, my subjective reaction is "have to be different species":

• *typica* from Puntarenas: https://xeno-canto.org/168203 (by Chris Benesh).
• *longicauda* from Sipaliwini: https://xeno-canto.org/519473 (by Rolf A. de By)
• what would become nominate *pallida* (type loc. rio Purus) from Rondônia: https://xeno-canto.org/427298 (by Caio Brito).

But there are dangers in that approach, and I can see the rationale for waiting for more detailed, published analyses, especially given the tricky nature of dendrocolaptid vocal analysis.

In support of a split, note that *typica* was formerly treated as a separate species (e.g., Ridgway 1911, Cory & Hellmayr 1925) and was subsequently treated as conspecific with *D. longicauda* without published rationale (as far as I can find).

English names:

SACC considered two proposals (SACC 1025.1 and 1025.2) for English names for this complex. After extensive and wide-ranging discussion (see https://www.museum.lsu.edu/~Remsen/SACCprop1025.htm), the following English names were adopted:

D. typica: Piping Long-tailed Woodcreeper
D. longicauda: Whistling Long-tailed Woodcreeper
D. pallida: Mournful Long-tailed Woodcreeper

References:

Barbosa, I. 2010. Revisão sistemática e filogeografia de *Deconychura longicauda* (Aves - Dendrocolaptidae). MSc Thesis. Universidade Federal de Pará, Belem.

Boesman, P. 2016. Notes on the vocalizations of the Long-tailed Woodcreeper (*Deconychura longicauda*). HBW Alive Ornithological Note 78, In: Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona.

Cory, C. B., and C. E. Hellmayr. 1925. Catalogue of birds of the Americas. Field Museum Nat. History Publ., Zool. Ser., vol. 13, pt. 4.

Del Hoyo, J., and N. J. Collar. 2016. HBW and BirdLife International Illustrated Checklist of the Birds of the World. Vol. 2: Passerines. Lynx Edicions, Barcelona.

Marantz, C. A., A. Aleixo, L. R. Bevier, and M. A. Patten. 2003. Family Dendrocolaptidae (woodcreepers). Pp. 358-447 *in* "Handbook of the Birds of the World, Vol. 8. Broadbills to tapaculos." (J. del Hoyo et al., eds.). Lynx Edicions, Barcelona.

Peters, J. L. 1951. Check-list of Birds of the World, vol. 7. Museum of Comparative Zoology, Cambridge, Massachusetts.

Ridgway, R. 1911. The birds of North and Middle America. Bulletin U.S. National Museum, no. 50, pt. 5.

Zimmer, J. T. 1934e. Studies of Peruvian birds, No. 16. Notes on the genera *Glyphorhynchus, Sittasomus, Deconychura, Margarornis Premnornis, Premnoplex,* and *Sclerurus. Ameri*can Museum Novitates 757: 1-22.

Submitted by: Van Remsen

Date of Proposal: May 2024, modified for NACC by R. T. Chesser on 20 November 2025

SACC comments:

Comments from Lane: "This is a topic that has been on my mind a long time, and I reviewed Barbosa's dissertation work with many comments and suggestions while it was still in the works, but it appears he incorporated few of them, which makes me reluctant to accept his results at face value. Among my concerns were: 1) he had a few specimens that he misidentified to taxon through a misunderstanding of localities. 2) he made little to no effort to control for vocal variation due to agitation to playback versus "calmer" emotional state, and given the small sample sizes of recordings he used in his comparisons, this resulted in magnifying differences that are probably not real, and 3) he completely ignored *minor* Todd, 1917 (type loc. El Tambor, Santander; recognized by Peters 1951) as a taxon worth investigating, simply lumping it in with *typica* and *darienensis*, without much rationale.

"That said, his phylogenetic tree does show that it is necessary to split *Deconychura* up into several species, and there is strong voice distinction that correlates with this. The present 3-way split (plus the undescribed Andean taxon that Jonas Nilsson and I and others have a manuscript in the works to describe) seems to be the best move with current phylogenetic and voice information available to us. I think *minor*, presently nearly unknown in life, may be another taxon to keep an eye on, and I believe Andres Cuervo has re-encountered it recently, so I am interested to see how that shakes out.

"So at present, between Barbosa's dissertation and my own experience with several of the forms, I would say YES to splitting *Deconychura* up into three named species as listed in the proposal, with the Andean taxon yet to be described as a fourth:

D. *typica* (including *darienensis*, but with the caveat that minor probably doesn't belong here)
D. *longicauda* (monotypic)
D. *pallida* (including all other Amazonian lowland forms for now).

"A more in-depth study may require more fine-tuned splitting of the pallida complex, and *minor*, but for now, this is the best option."

Comments from Claramunt: "YES. Songs and genetic data suggest the presence of fairly divergent lineages. In particular, the separation of typica from the Amazonian taxa seems supported by both. Phenotypic differences are subtle, some claimed to be diagnostic but with no formal analysis. But subtle differences in the shape of the light spots or the extension of spotting across the plumage should not be disregarded as insignificant, as woodcreepers are very conservative in plumage and such differences are associated with species-level taxa in other genera. At the very minimum, we have to accept that the historical lumping of *typica* into *longicauda* was done without presenting any evidence, and we don't have any evidence today. On the contrary, songs and mtDNA suggest a clear divergence between the two. For the separation of *pallida* from *longicauda*, the vocal and genetic evidence also show similar levels of divergence and I don't see any evidence of gene flow or admixture between the nominate form and the other Amazonian forms. Therefore, having similar evidence, the conclusion should be the same: separate species. Once the situation of the Andean clade is clarified we can revisit this problem."

<u>Comments from Stiles</u>: "YES to the 3-way split of *Deconychura longirostris*. I note that the species epithet *longirostris* was proposed in Natterer's (unpublished?) catalogue in the genus *Dendrocolaptes*, but was apparently first published by Pelzeln (1868) in the genus *Dendrocincla*. The genus *Deconychura* was named by Cherrie (1891) with the species epithet *typica* as its type species. Again, I presume that a proposal pending regarding E-names will be forthcoming. As an aside, I recall seeing a recommendation (but I unfortunately can't recall where) to discourage use of the name *typica* for proposed type species because with generic transfers, this could result in messy homonyms."

<u>Comments from Robbins</u>: "NO. Given the widely recognized limitations of using cyt B and ND2 for discerning species limits coupled with concerns of comparing appropriate primary vocalizations, I lean for waiting until there is a more complete assessment of this complex before making changes. Clearly, plumage morphology does not add insight into species limits within this complex. I look forward to Dan et al.'s upcoming paper that will address some of the issues that he brings up in his comments on this proposal. At that point, it may become clear just how many species should be recognized."

<u>Comments from Jaramillo</u>: "YES – Thanks Dan for your comments, they persuaded me at least. I suggest Short-tailed longtailed Woodcreeper as a name for one of the taxa."

<u>Comments from Curtis Marantz (voting for Remsen):</u> "YES. Based on my field experience with at least several of the Amazonian taxa, the work that we did putting together the HBW account, and the genetic work done subsequently by Barbosa, my feeling is that the split of this complex into three species is well supported. I know nothing about the recent Andean taxon, and therefore cannot comment on it, but it appears that this one can be dealt with following the publication of a description.

"We knew even before the HBW accounts were published that there were multiple vocal groups, with the Central American ones being especially distinct, and both looking and sounding much like what is now recognized as *Certhiasomus*, which the genetics appear to show as being quite different. The genetic, morphological, and vocal datasets all support recognition of this complex as a full species, especially given that there appears to be no real justification for lumping it with the Amazonian taxa in the first place.

"The Amazonian populations present a more complex situation. Despite their morphological similarity, *D. longicauda* is moderately different vocally from the members with which I am familiar in the *pallida*-group. I will nevertheless note that, in my opinion, the vocal differences between these groups represent more a case of moderate variation on a theme rather than totally different themes, as is true for the Amazonian versus Central American groups. Moreover, within "Southern" Long-tailed Woodcreeper group, which I might add is poorly named because it occurs almost as far north as does the "Northern" Long-tailed Woodcreeper, I find minimal variation in the songs. Looking at the sound spectrograms shown in Figure 4 of the proposal taken from Barbosa, I would have to argue that the representative examples were either based on a very small sample of unrepresentative recordings, or instead, they were "cherry picked" to show differences that are unlikely to be real. For comparison, check out the songs in the four recordings at the links below taken from widely separated locations within the range of the *pallida*-group, and clearly representing both *D. l. pallida* and *D. l. connectens* as the ranges of each are described.

Ucayali, Peru - ML127031131 - Long-tailed Woodcreeper - Macaulay Library

Para, Brazil - ML115073 - Long-tailed Woodcreeper (Southern) - Macaulay Library

Napo, Ecuador - ML343373841 - Long-tailed Woodcreeper - Macaulay Library

Amazonas, Venezuela - ML65714 - Long-tailed Woodcreeper (Southern) - Macaulay Library

“Having just looked superficially at the spectrograms and listened to a song or two from each recording, I will not deny that there could be subtle differences in the songs included in each of these recordings, but to me, they sound pretty much the same. Moreover, almost more so than any woodcreepers that I know, *Deconychura* can get really worked up after playback, and they can emit a wide variety of sounds, so one must be careful t compare songs given under similar motivational states, this being most easily done by looking at natural songs that were not recorded during a territorial dispute.

“This said, I do think the song differences between nominate *D. longicauda* and the *pallida*-group are consistent, and when used in combination with the genetic data, probably sufficient to treat these two groups as separate species.

“Given the morphological, vocal, and genetic variation presented in our HBW accounts, Barbosa's thesis, and the proposal, I do feel that treating *Deconychura* as three species is warranted. The decision about whether to split these populations up now, or instead, wait until more information is available for the new Andean population and those in the zone between the Amazonian and Central American forms in Colombia is another issue. I suppose I fall more in the camp of waiting until the whole picture is clear before making changes, which is why we treated these populations as one species for HBW even though we knew that more than one species was almost certainly involved. Given my experience with at least several of the Amazonian populations, s exemplified by the recordings above, I do not see support at this point for further subdividing the *pallida*-group into multiple species.

“Given their scientific names, I might suggest naming the *typica*-group the Little Woodcreeper, keeping Long-tailed Woodcreeper for *D. longicauda*, and maybe Pallid Woodcreeper for *D. pallida*, though admittedly, it is not overly "pallid" as far as woodcreepers go... “

Additional comments from Remsen: "Curtis, inspired by Alvaro and clearly trying to audition for a voting position on SACC for English names, further made the following, logical suggestion, perhaps implicit in Alvaro's:

Little Long-tailed Woodcreeper
Long-tailed Long-tailed Woodcreeper
Short-tailed Long-tailed Woodcreeper"

Comments from Areta: "YES. I am not enthusiastic about this kind of splits. I would really like to see the paper describing the new taxon and assessing the species limits in *Deconychura* as a whole, which will surely provide solid nomenclatural and taxonomic assessments. I admit that it is difficult, at this point in time, to recognize a single species when the information is screaming that there are multiple species. I do not see the need for rapid assessments when there is people working in good, detailed studies that will shed light on this. This being said, I support the 3-way split that has been around for a long time."

Comments from Bonaccorso: "NO. The song differences are compelling, but the vocal analysis is based on a handful of recordings. The plumage differences don´t seem to add much; I think they are far from diagnostic, although that seems to be the case for many good species in this group of birds. I think more genetic information (nuclear loci) based on more specimens, especially at potential contact zones, are needed."

Comments from Andrew Spencer (voting for Del-Rio): "YES - There's not much I can say here that hasn't already been said by previous votes for the split, but to reiterate: the vocalizations of these groups are so drastically different, especially in *typica,* that I think the burden of proof is squarely on those who want to keep them together. I personally feel that in the age of enormous sound collections that are continually vetted by experts from all over the world, that requiring the perfect rigorous analysis in cases of obviously very divergent vocalizations is overkill. Yes, I'd love to see that analysis. But I don't think we need it to state the obvious that has already been thoroughly vetted. Also, and this is purely circumstantial and minor evidence, I have played the songs of southern birds to individuals in Costa Rica and Panama and was completely ignored. Both before and after playback of typical *typica* (ha that was fun to write). And I have also played *typica* to a bird at Cristalino, Mato Grosso, with the same lack of response."

Comments from Zimmer: "YES to the proposed three-way split. Even given some of the problems with the vocal analyses of Barbosa (as highlighted by Dan and Curtis), the vocal differences between the *typica*-group and both *longicauda* and the *pallida*-group are not even in the same ballpark in my opinion, and the distinctiveness of the *typica*-group is further supported by morphometric and (to a lesser extent) plumage differences, as well as by the genetic data from Barbosa (2010). That the Central American birds were described as a species separate from *longicauda*, and subsequently lumped without justification, is all the more reason to split them in my opinion. I would also add, that like Andrew Spencer, I have conducted informal playback trials by presenting individuals of *typica,* encountered on the Pacific Slope of Costa Rica (specifically, in Carara NP, and the Wilson Botanic Gardens), with playback of songs of various subspecies in the *pallida*-group that I had personally recorded in Brazil, and had zero response. I have performed similar trials, using playback of recordings of *typica* from Costa Rica to *pallida*-types at various spots south of the Solimões/Amazon in Brazil, and had identical zero response, and this, from birds that were highly responsive to geographically appropriate, taxon-specific vocalizations. So, in sum, the split of the *typica*-group from the others is a slam-dunk in my opinion.

”I also feel that N bank *longicauda* is vocally distinct from everything I’ve encountered on the S bank of the Solimões/Amazon, and although these vocal distinctions are not as striking as those of Central American versus Amazonian populations, they are, to my ears, both significant and consistent, and the genetic data of Barbosa (2010) further support treating nominate *longicauda* as distinct from the *pallida*-group. That’s as far as I’m willing to take it at this point. I know nothing about the Andean population that Dan is working on, nor do I know anything of *minor*, so I have nothing to add there. As regards the 3 additional clades that Barbosa recovered within the *pallida*-group, I remain unconvinced regarding the purported vocal distinctions. Echoing the concerns of others regarding the problems of small sample sizes, lack of proof that homologous vocalizations are being compared, and lack of accounting for the motivational state of the audio-recorded individuals involved, I’m reluctant to give the qualitative distinctions evident in Barbosa’s spectrographs too much weight. The importance of the motivational state of the recorded birds cannot, in my opinion, be emphasized enough. As Curtis states in his comments, woodcreepers in general, but particularly these pallida-types, can get really wound-up by playback. One thing that I’ve noted in particular among *pallida*, is that when presented with playback, they have a decided tendency to modulate the frequency of each note, often dramatically so, which can change the entire quality of the song, in addition to changes in pace, and total number of notes. This tendency, when coupled with small sample sizes, could result in spectrographs that seriously inflate perceived differences in songs. In summation, I would vote YES to the suggested 3-way split, but hold off on any further action until Dan & co-authors sort out some of these remaining issues.”

Treat *Onychorhynchus swainsoni* as a separate species from Royal Flycatcher *O. coronatus*

***Note*:** This is a modified version of SACC Proposal 1055, which presented four options for revising the taxonomy of Royal Flycatcher *Onychorhynchus coronatus*. Option B, to treat *O. swainsoni* as a separate species while maintaining the other five subspecies as part of *O. coronatus*, passed by an 8-1 vote. The English name adopted for *O. swainsoni* Atlantic Royal-Flycatcher, and the English name of *O. coronatus* was changed to Tropical Royal-Flycatcher.

Effect on NACC:

If this proposal passes, the split of *O. swainsoni* from *O. coronatus* would result in a modification of the English name, distributional statement, and Notes for *O. coronatus.* The scientific name would remain the same.

Background:

Prior to passage of SACC 1055, the SACC Note on *O. coronatus* read:

2. Ridgway (1907), Cory & Hellmayr (1927), and Pinto (1944) considered the four subspecies groups in *Onychorhynchus coronatus* as separate species: *mexicanus* of Middle America and northwestern Colombia, *occidentalis* of western Ecuador and northwestern Peru, *coronatus* of Amazonia, and *swainsoni* of southeastern Brazil. Meyer de Schauensee (1966, 1970) treated them all as conspecific without providing justification, and this was followed by Traylor (1977<?>, 1979b), AOU (1998), Sibley & Monroe (1990), Fitzpatrick (2004), Ridgely & Tudor (1994), who provided rationale for their continued treatment as conspecific, and Dickinson & Christidis (2014), but this was not followed by Wetmore (1972), who considered the evidence insufficient for the broad treatment. Ridgely & Greenfield (2001) and Hilty (2003) returned to the classification of Cory & Hellmayr (1927). Collar et al. (1992) considered *occidentalis* as a separate species. See Whittingham & Williams (2000) for analysis and discussion of morphological characters. Del Hoyo & Collar (2016) recognized four species: *O. mexicanus* of Middle America and n. South America; *O. occidentalis* of the Tumbesian region; *O. coronatus* of Amazonia; and *O. swainsoni* of the Atlantic Forest. Reyes et al. (2023) presented data relevant to recognition of as many as six separate species based mainly on deep divergence in mtDNA. SACC proposal badly needed.

Birds of the World/Clements has instituted a 2-way split: https://ebird.org/species/royfly1

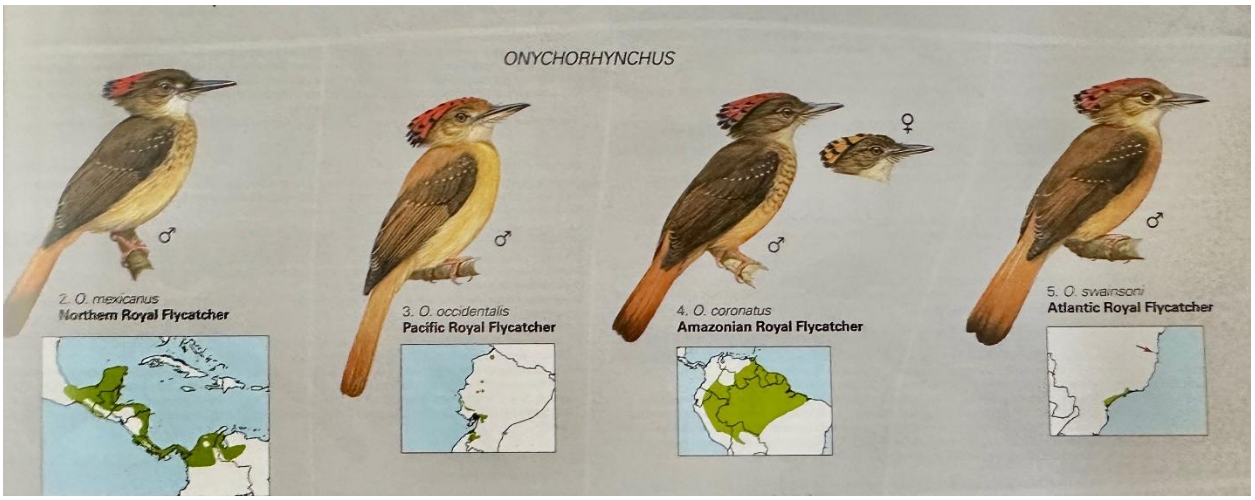
Ridgely & Tudor (1994) thought that perhaps four species could be recognized, but that treating them all as conspecific was the best course given similarities I behavior and voice, as far as was known at the time. (They mistakenly cited AOU 1983 as having recognized two species.)

Six taxa are recognized in the complex (Dickinson & Christidis 2014):

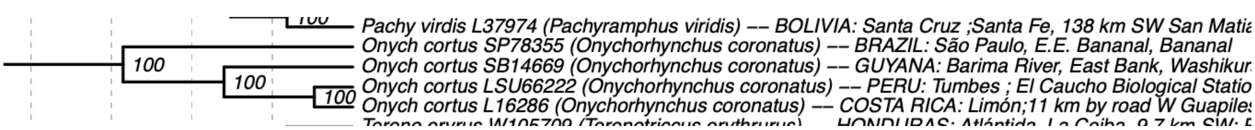
• *mexicanus* (s. Mexico to Panama)

• *fraterculus* (n. Colombia and nw. Venezuela
• *occidentalis* (Tumbesian region)
• *coronatus* (Guianan Shield and n. and e. Amazonian Brazil)
• *castelnaui* (w. Amazonia)
• *swainsoni* (se. Brazil)

Here are Hilary Burn's illustrations from del Hoyo and Collar (2016), which illustrate the differences in plumage, primarily in degree of markings on breast and general plumage tone. Note that swainsoni and geographically distant *occidentalis* are the palest and least spotted of the group, and I suspect this is what influenced Meyer de Schauensee's reasoning for treating them all as conspecific.



In Harvey et al.'s (2020) massive phylogenetic analysis of the suboscines using genomic (UCE) data, 4 subspecies were included. *Swainsoni* was "basal" to the other taxa, with an estimated divergence time of ca. 6 MYA; nominate *coronatus* was the sister to *mexicanus* + *occidentalis*, with divergence estimate of ca. 3 and ca. 1 MYA, respectively:



Just eye-balling node depth in adjacent clades in the Harvey et al. tree indicates that 6 MYA divergence is more typical for taxa treated at the species level, whereas 3 and 1 MYA are more typical for taxa traditionally treated as conspecific. This is no substitute for a formal analysis but is meant only to provide a crude comparison of node depths. Feel free to make your own comparisons, of course.

New information:

Reyes et al. (2023; see figures on the next page) produced the first genetic analysis of the complex. They used a single mtDNA marker: NADH. They sampled 40 individuals, including individuals of all taxa in the complex. They had only 1 *swainsoni* but had at least 5 for the other 5 taxa.

The topology of the tree was consistent with that of Harvey et al. (2020), including the placement of the taxon with arguably the most divergent plumage, *occidentalis*, within the northern *mexicanus* group. Their geographic sampling was reasonably thorough except for the absence of specimens from the populations attributed to *coronatus* from Brazil south of the Amazon and e. Bolivia.

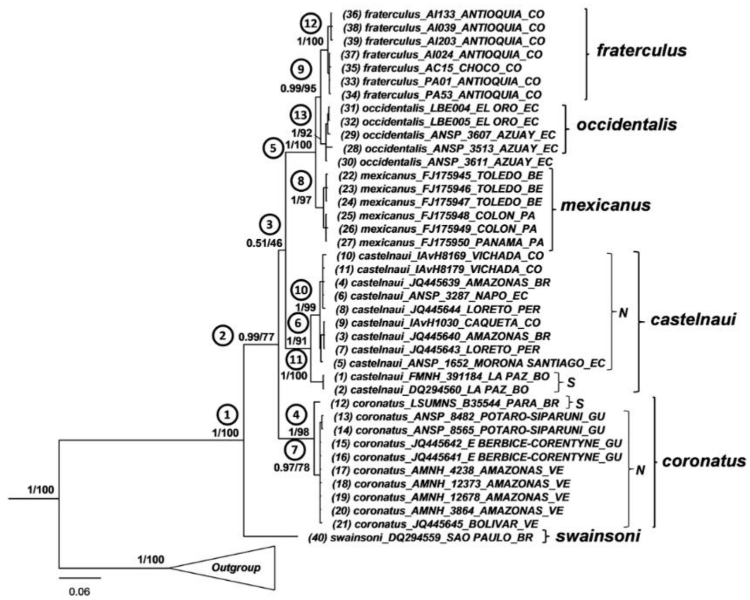


Figure 2. Bayesian majority-rule consensus tree of *Onychorhynchus* from the three-partition model analysis (−lnL = −4328.31). Support values correspond to Bayesian posterior probabilities and bootstrap values of the three-partition model ML tree (−lnL = −4309.04). Nodes that recovered ingroup relationships are numbered 1–13. Numbers in parentheses refer to each unique specimen ID (Fig. 1, Supporting information).

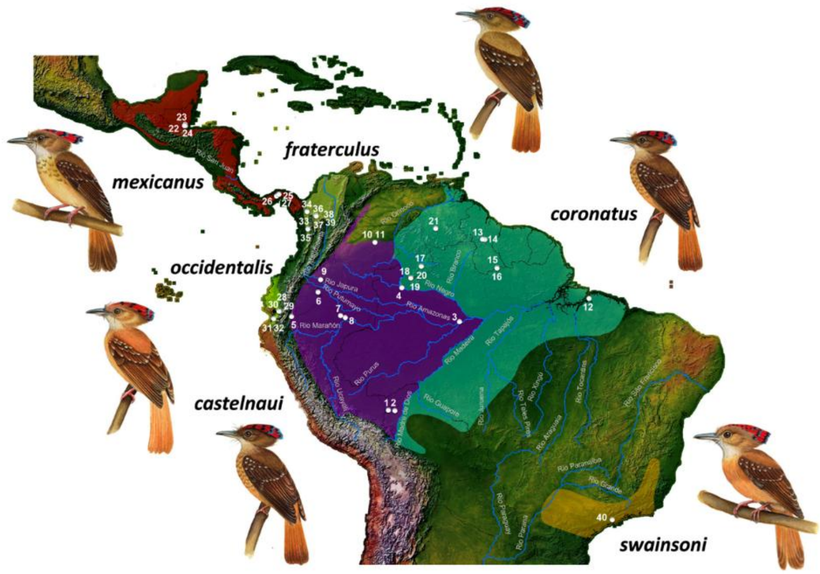


Figure 1. Distribution of *Onychorhynchus*, including collecting localities for the specimens that were used in this study. Points indicate sample collection localities and numbers refer to unique specimen IDs, which are also referenced in Fig. 2, 3 , and Supporting information. Illustrations of *Onychorhynchus* lineages showing plumage coloration differences. Illustrations by Francy Tamayo.

The mean estimate of the divergence time between *swainsoni* and the rest was 6.1 MYA, remarkably similar to that of Harvey et al. (2020). The focus of the paper was on historical biogeography, not taxonomy, so the paper did not produce any firm taxonomic recommendations. Nevertheless, their analysis produced evidence for 6 independently evolving mtDNA lineages that they suggested could be treated as species. Caution is required because the geographic and numerical sampling is possibly insufficient to be certain that the lineages are monophyletic, at least in southwestern Amazonia, where large areas of *coronatus* distribution in potential contact with *castelnaui* have not been sampled. Their concluding paragraph is as follows:

“Furthermore, this study helped to reveal independently evolving lineages that might have to be treated as separate species with different conservation concerns. Complementary studies that include nuclear DNA, morphology, niche differentiation, and vocalizations with thorough sampling throughout the *Onychorhynchus* distribution are needed to fully resolve the evolutionary relationships and delimit species within this genus.”

Potential changes in species limits are also implied in the section titled Cryptic Diversity. I have to point out that the diversity cannot be described as “cryptic” if it has been known for more than a century with at least 4 taxa treated as separate species for the first half of the 20th century, and the only taxon not described before 1860 was *fraterculus* Bangs 1902. In fact, Reyes et al. make this very point in that same section.

As for vocalizations in this group, analyses are handicapped by how few samples there are. Royal Flycatchers vocalize infrequently, and dawn songs are poorly known. Thus, It is no surprise to me that Peter Boesman did not include this species as one of his 400+

“Ornithological Notes” (for HBW/BLI) despite this complex being a prime candidate for a preliminary analysis.

Kirwan et al. (2024a, b) summarized what is known about vocalizations in this group, with links to recordings. In Birds of the World, they are treated as two species: *O. swainsoni* for se. Brazil and *O. coronatus* for everything else. Kirwan et al. (2024b) outlined the differences used by del Hoyo & Collar’s (2016) adoption of the Tobias et al. scoring system and said this about voice: “Also distinctive in call, which is significantly shorter (effect size 4.9; score 2) and higher-pitched (effect size also 4.9; score 2) than that of other taxa.” [It sounds lower-pitched to me.] Here are the recordings cited by Kirwan et al. (2024b):

https://search.macaulaylibrary.org/catalog?taxonCode=royfly5&mediaType=audio&sort=rating_rank_desc

Kirwan et al. (2024a) described the vocalizations of the *coronatus* group as follows:

“Song. A rarely heard series of whistles, which apparently varies geographically. There are however hardly any recordings available, thus the following are merely examples of specific cases:

· **Northern group**: audio 2 In Costa Rica and Panama, a series of rather sharp downslurred whistles preceded by a short introductory note, *whit..eeeuw...eeeuw...eeeuw ...*, uttered at a rate of about one whistle per second. In the literature, Song in this region is described as a long series of higher, sharper notes with a most peculiar intonation (8) or (in Mexico) a descending, slowing series of plaintive whistles, usually 5–8, *whi' peeu peeu peeu peeu peeu* ..., or *wh' wheeu wheeu ...* (65).
· **Amazonian group**: In Brazil, a series of long melodious whistles, starting with a loud flat-pitched introductory note and followed by a series of lower-pitched disyllabic mellow whistles *wheeee-pihuuw-pihuuuw-pihuuw*. Another variant is structurally similar, but disyllabic whistles are more modulated *wheeeee-priririuuw-priririuuw...* audio Also described as a squeaky *PEE'u* occasionally followed by a lower, musical *PEE'u-brrrr* (66).
· **Pacific group**: Possibly a homologous vocalizations is described as a squeaky *whi-CHEW* in a series in a display (66). No recordings of Song are available.

“**Primary call**. audio 3 A short disyllabic nasal *keeeyup*, repeated many times at intervals of ca. 2 seconds. On sonogram, note has a characteristic shape, initially reaching a flat-pitched top around 3 kHz, after which frequency drops sharply with a hiccup around 2 kHz, for a total duration of about 0.20–0.25 second. Also described as a low-pitched *sur-líp*, sometimes [repeated] over and over (67); a loud, mellow, hollow-sounding whistle, usually two-syllabled: *keeeyup* or *keee-yew* (8); a squeaky to hollow, plaintive *whee-uk* or *see-yuk* (65); and as a loud, plaintive squeak: *PEE'yuk* (42).”

Three recordings of the primary call are presented here, one from *mexicanus*, one from *castelnaui*, one from *coronatus*: https://birdsoftheworld.org/bow/species/royfly1/cur/sounds#vocal. These indeed sound very different from *swainsoni*, and sound very similar to each other. No primary call of *occidentalis* was presented.

Discussion and Recommendation:

This complex has been on everyone's radar "forever" in terms of species limits, especially because classifications in the early 1900s treated them as four species, and Meyer de Schauensee provided no rationale for the lump. One could argue on that basis alone that a return to the taxonomy of Ridgway-Cory-Hellmayr-Pinto is warranted, and thus place burden-of-proof on treatment as a single species.

Based on qualitative perusal of sonograms of what is called the primary call, one could easily justify treating *swainsoni* as a separate species, as done by Birds of the World. Based on that same qualitative perusal of N=1 primary calls of *mexicanus*, *coronatus*, and *castelnaui*, the primary calls sound similar to me, and their sonograms have that distinctive appearance noted by Kirwan et al. Calls of *occidentalis* and *fraterculus* were not presented, but perusal of xeno-canto suggests that *occidentalis* (N=1; https://xeno-canto.org/264700) and *fraterculus* (N=1; https://xeno-canto.org/664102) are also qualitatively similar. However, none of this is a substitute for a quantitative analysis, so that concerns me.

It is not the job of SACC members to do original quantitative analyses, and this is what would be ideal for a decision on species limits in *Onychorhynchus*. The qualitative difference between *swainsoni* and the others could be considered sufficient, in my opinion, for placing burden-of-proof on a single species treatment. This is also consistent with the genetic data of Harvey et al. (2020) and Reyes et al. (2023). However, in my opinion, further splits would require quantitative analyses of the vocalizations. Studies of contact zones would be the best of all, but *occidentalis* is isolated, and I'm not sure if contact zones exist between *mexicanus* and *fraterculus*, *fraterculus* and *coronatus*, *fraterculus* and *castelnaui*, or *coronatus* and *castelnaui*.

For voting purposes let's break this down as follows, with YES/NO votes on the following

A. Retain traditionally defined broad *O. coronatus*. If YES, then B, C, and D are automatically NO.

B. Recognize two species (as in HBW and Birds of the World): *O. swainsoni* and *O. coronatus*, which would include all other taxa.

C. Recognize four species: *O. mexicanus*, *O. occidentalis*, *O. swainsoni*, and *O. coronatus* (return to the classification of Cory & Hellmayr and others, following del Hoyo and Collar 2016):

D. Recognize six species (*O. mexicanus*, *O. occidentalis*, *O. fraterculus*, *O. castelnaui*, *O. coronatus*, and *O. swainsoni*) for each of the lineages elucidated by Reyes et al. (2023).

Pending input from those more knowledgeable than I, my recommendations are as follows: A. No – the original lump was never justified; B- Yes – based on published sonograms of primary call note and a genetic distance more consistent with species rank in related lineages; C. No – this would require additional, qualitative research on vocalizations in my opinion; D. No –

likewise, and I oppose using mtDNA lineages for taxonomy, particularly because of the well-known potential problem of gene trees conflicting with species trees; this point was implicit in Reyes et al.

Note on English names:

BOW uses "Atlantic Royal Flycatcher" for *swainsoni* and "Tropical Royal Flycatcher" for everything else. If Option B passes, then I think we can save ourselves plenty of work and simply adopt the current BOW names Tropical Royal-Flycatcher and Atlantic Royal-Flycatcher. If you object and would like a separate proposal, and are also willing to write that proposal, speak out. "Tropical" may only be a temporary name pending more data on future splits. There will be the usual howls concerning use of names of oceans as names of terrestrial species, but I think it is widely understood what the implication of such names are for land birds. If Option C or D passes, then we will have to do a separate SACC proposal on English names depending on which taxonomy we adopt. See the illustration above for names used by BLI for a 4-way split.

Literature Cited:

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Kirwan, G. M., R. Sample, B. Shackelford, R. Kannan, and P. F. D. Boesman. 2024b. Atlantic Royal Flycatcher (*Onychorhynchus swainsoni*), version 1.1. In Birds of the World (T. S. Schulenberg and B. K. Keeney, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.royfly5.01.1

Reyes, P., J. M. Bates, L. N. Naka, M. J. Miller, I. Caballero, C. Gonzalez-Quevedo, J. L. Parra, H. F. Rivera-Gutierrez, E. Bonaccorso, and J. G. Tello. 2023. Phylogenetic relationships and biogeography of the ancient genus *Onychorhynchus* (Aves: Onychorhynchidae) suggest cryptic Amazonian diversity. J. Avian Biology 2023: e03159.

Whittingham, M. J., and R. S. R. Williams. 2000. Notes on morphological differences exhibited by Royal Flycatcher *Onychorhynchus coronatus* taxa. Cotinga 13: 14-16.

Submitted by: Van Remsen

Date of Proposal: May 2025, modified for NACC by R. T. Chesser on 20 November 2025

Comments from SACC:

Comments from Robbins: "Van has done an excellent job of distilling the issues with species limits within *coronatus*. I agree with his concluding assessment that more complete genetic

sampling (it is unfortunate that the Harvey et al. UCE data lacked two of the taxa) is needed, especially from western Amazonia. For reasons that fieldworkers have known for a long time and was reiterated by Van, relevant vocal data with sufficient sample sizes may be a long time in coming. Although there are certainly more than two species involved, to be conservative at this point, I follow Van's recommendations:
"A. NO
B. YES
C. NO
D. NO"

Comments by Lane: "YES to B and NO to the other options until a better case is built for additional splits. I have uploaded my recordings of *occidentalis* with the "whi-chew" vocalization (ML637382910... cut off, unfortunately), suggesting it to be similar to other members of the overall "tropical" group. I can't argue that the evidence to split this group up more is convincing at this time, and thus vote for a 2-species taxonomy largely based on vocal differences."

Comments from Areta: "First of all, Reyes et al. (2023) indicated the need of further sampling and the integration of more lines of evidence in order to sort the taxonomy of *O. coronatus*. Thus, any taxonomic decision taken at this point will not be the most informed one.

"Secondly, I see the phylogenetic tree of Harvey et al. (2020) as being consistent with that in Reyes et al. (2023), except that it lacks samples from some key taxa.

"Third, my vote for AviList/WGAC on this issue before the publication of Reyes et al. (2023) was 'Initially, assuming the topology and divergences shown in Harvey et al 2020 are representative of this complex, I was leaning towards a 3-way split (Atlantic Forest, "Amazon", and Central America/Pacific South America). But after listening to the relatively good sampling of calls across the range, I agree with the 2-way split: Atlantic Forest vs rest of the World. I hope someone undertakes a deeper analysis on *Onychorhynchus*!"

A. Retain traditionally defined broad *O. coronatus*. NO
B. Recognize two species (as in HBW and Birds of the World): *O. swainsoni* and *O. coronatus*, which would include all other taxa. Maybe (see below)
C. Recognize four species: *O. mexicanus*, *O. occidentalis*, *O. swainsoni*, and *O. coronatus* (return to the classification of Cory & Hellmayr and others, following del Hoyo and Collar 2016). NO, this is untenable in light of the phylogenetic results: how can we split *occidentalis* (with *fraterculus*) from *mexicanus* without also splitting *castelnaui* from *coronatus*?
D. Recognize six species (*O. mexicanus*, *O. occidentalis*, *O. fraterculus*, *O. castelnaui*, *O. coronatus*, and *O. swainsoni*) for each of the lineages elucidated by Reyes et al. (2023). NO, this seems to be over-splitting the *mexicanus* group, which has shallow divergences. The biogeographic pattern linking birds from NW South America and the Pacific of Ecuador and Peru to birds from Central America-Mexico is not unusual. Sometimes the taxa have speciated, sometimes they have not. In this case, I don´t think the level of divergence justifies splitting them as biological (or recognition) species.

“To me the dilemma is whether we should recognize 2 species (*swainsoni* and a polytypic *coronatus*; Van´s Option B) or 4 species (*swainsoni*, *castelnaui*, *coronatus*, and a polytypic *mexicanus*; my new Option E). Both alternatives are compatible with phylogenetic data, and the genetic divergence between the W Amazonian *castelnaui* and the *mexicanus* group is nearly as deep as that between these two groups and *coronatus*. I examined the calls unsystematically again, and the vocalizations seem very similar. It could be that *coronatus* might have a slightly higher pitched and perhaps shorter call than *castelnaui*, but the vocalizations are overall quite similar, and a proper study is needed to increase our understanding of vocal variation in the phylogroups uncovered by Reyes et al. 2023. Given the (apparent!) vocal similarities and the not-so-deep (but also not-so-shallow) genetic differences between *castelnaui-coronatus-mexicanus*, I vote for option B for now. If new information appears, or someone with a deeper understanding of vocalizations of the group uncovers diagnostic differences in calls of these groups, I would be delighted to support my option E, but at present I think that the information is not there to show that this is the best option.”

Comments from Naka: “As you have guessed, there is a reason why we decided not to propose a complete taxonomic rearrangement of this species in the Reyes et al. article, mostly due to lack of i) nuclear data and ii) proper morphological and vocal assessment in the clade. Although I agree with the major finding of the article, that the six taxa involved likely represent six independent lineages, I would not encourage, nor vote for a 6-species split at this stage. As we all know, mDNA is great in reaching reciprocal monophyly, yet it represents a bad proxy for gene flow. Therefore, we lack that key piece of evidence to declare these taxa as fully independent lineages beyond a reasonable doubt (meaning, these can fall apart in the next genomic study).

“I personally like the idea of having three biogeographically-sound main lineages, including i) a similar sounding Middle American/trans-Andean taxon (*including mexicanus, occidentalis*, and *fraterculus*, although I wish the dry forest *occidentalis* would sound any different!); ii) a rather distinct Atlantic Forest taxon (*swainsoni*); and an Amazonian lineage (*O. coronatus* + *O. castelnaui*). However, this arrangement contrasts with the mtDNA results, which show that the two Amazonian forms are not sister taxa, as first found by our study back in 2018 (Naka and Brumfield, 2018). Therefore, the options here (if we are to follow the mtDNA tree), are to have 2, 4 or 6 lineages. At this stage, given the lack of better genetic resolution, and the poor vocal sampling available, I will vote for option B.
In short:

“A. NO, to Retain traditionally defined broad *O. coronatus*.
“B. YES, to Recognize two species (as in HBW and Birds of the World): *O. swainsoni* and *O. coronatus*, which would include all other taxa.”
“C. NO
“D. NO”

Comments from Stiles: “A. YES; B. NO - the evidence for further splits is weak and inconsistent as it stands: more data required: C. NO; D. NO.”

Comments from Zimmer:
“A. NO.

“B. YES.
“C. NO
“D. NO.

“Personally, the arrangement that makes the most sense to me intuitively, is the 4-way split (i.e. Return to the classification of Cory & Hellmayr), but I don’t think this option is rigorously defensible on current knowledge. I feel pretty confident from personal experience that *swainsoni* is worthy of being elevated to species rank, based upon noted vocal differences, genetic data, plumage, ecological differences and distribution and how those fit established biogeographic patterns. As an aside, I don’t think that the illustrations included in the Proposal adequately convey just how different *occidentalis* and *swainsoni* are in overall color from the much duller Amazonian taxa that occupy the intervening areas – both of those taxa, one occupying dry forest and the other Atlantic Forest are really richly ochraceous and very different from other taxa in the complex. Regardless, I think the best course of action for now, at least in terms of what is well supported by existing data, is the conservative two-way split of *swainsoni* versus everything else. In that case, Van’s suggestion that we adopt the existing BOW names of Atlantic Royal-Flycatcher for *swainsoni*, and Tropical Royal-Flycatcher for everything else makes the most sense, with the latter name being easily changed to adapt to any further splits.”

<u>Comments from Bonaccorso</u>: “
“A. NO. As several SACC members have already acknowledged, there is preliminary evidence suggesting that maintaining the traditionally defined *O. coronatus* may overlook the complexity of the group.

“Still, obtaining complete vocal data for all populations could prove very difficult. Based on our experience with the western Ecuadorian population (*O. coronatus occidentalis*), gathering vocalizations from this taxon will be particularly challenging due to its rarity, highly localized distribution, and potential seasonal movements throughout the year.

“B. YES. For the time being, based on limited nuclear (UCE) and mitochondrial (ND2) data (both topology and distances), and qualitative vocal differences, it seems safe to call O. *swainsoni* a separate species from *O. coronatus*.

“C. NO. More data are needed.
“D. NO. More data are needed.”

<u>Comments from Glaucia Del-Rio (guest vote)</u>:

“A. NO
“B.YES
“C. NO
“D. NO

“I do not think the available data justify splitting beyond the two-species treatment. As mentioned before, mitochondrial DNA, while useful for revealing genealogical structure, is not sufficient to delimit species. For me, the consistent placement of *O. swainsoni* as the deepest lineage in both mtDNA and UCE studies, and its distinctive plumage and vocal differences, provide sufficient evidence to recognize it a different species from the *O. coronatus* complex.”

Treat Great Egret *Ardea alba* as two or more species

Background:

The Great Egret *Ardea alba* has long been considered a single cosmopolitan species, despite the fact that numerous authors have suggested otherwise, and have sometimes enacted different treatments, based largely on geographic variation in breeding soft-part colors, as well as apparent differences in display (Hancock 1984) and vocalizations. Genetic data, however, have thus far remained inadequate to help resolve this problem, and have led to the splitting of Eastern Great Egret *Ardea modesta* (by, e.g., Christidis and Boles 2008, Gill and Donsker 2010), later shown to be based on a misinterpretation of DNA-DNA hybridization data (Pratt 2011, Collar and Inskipp 2011). Thus, despite the striking and well-known differences in breeding colors, little serious consideration has been given to this issue.

That there are four well-defined subspecies of *Ardea alba* has long been non-controversial, though as usual there are several synonyms as well. These are, as far as known, entirely allopatric in breeding range, although the possibility that intergradation occurs between two of the Old World subspecies (*alba* and *modesta*) in Japan and elsewhere in northeastern Asia has been suggested (Amadon and Woolfenden 1952) but not well documented or confirmed. Nominate *alba* Linnaeus, 1758, occurs throughout much of the Western Palearctic and eastward to northeastern Asia (southern Ussuriland according to Vaurie 1964); *melanorhynchos* Wagler, 1827, occurs in sub-Saharan Africa and Madagascar; *modesta* Gray, 1831, occurs from Pakistan east through Japan and New Zealand, and *egretta* Gmelin, 1789, occurs almost throughout the more temperate and tropical parts of the Western Hemisphere.

The AOU (1886, 1895, 1910) treated *egretta* as a distinct species, the American Egret, but in the 4th Edition (1931) and in Peters (1931) it was treated as a subspecies of *Ardea alba*. However, this trend had started considerably earlier; Mathews (1911) already considered *syrmatophora* (Gould, 1846) and *neglecta* (Mathews, 1912), two subspecies now synonymized with *modesta*, as subspecies of *Ardea alba*. Hartert (1920) considered *Ardea alba* to have five subspecies, including *maoriana* (Mathews & Iredale, 1913) of New Zealand, now synonymized with *modesta*.

In all taxa, the bill is yellow during the non-breeding season and immature stages, when facial skin is yellowish to olive green, and tarsi are at least partly black. In the three Old World taxa, the bill of adults becomes completely black in the briefly held high breeding colors, with the black starting at the bill tip and progressing forward (Pratt 2011). Conversely, in New World *egretta*, the entire bill never becomes all-black: typically part or all of the culmen becomes black, while the lower mandible remains entirely yellow. In *melanorhynchos* and *egretta*, the entire tarsi remain black (occasionally partly grayish) year-round, whereas in *alba* and *modesta* the exposed tibiae show variable amounts of yellowish when non-breeding to reddish when breeding, when this color sometimes extends well onto the tarsi. In breeding plumage, the facial skin of all briefly turns bright bluish-green.

New information:

Non-breeding soft parts and head structure.—Reyt et al. (2025) presented a carefully documented study of soft-part colors and head structure of non-breeding plumaged birds (including immatures) based on study of 1031 high-quality images of birds that they called "winter plumage", though, as they discuss, ageing of these taxa is poorly understood and they thus included immatures along with non-breeding adults in this category (Figs. 1, 2, 3; Table 1). Several characteristics were quantified in the Reyt et al. (2025) study, and these elucidate heretofore unclear differences between the soft part colors of each taxon. They showed that in non-breeding condition, *melanorhynchos* is the most distinctive taxon due to the long, broad, obvious black or olive-green gape that extends beyond the rear eye and that clearly sets it apart from other taxa (although it is not always obvious). In the other three taxa, the gapes only extend to around the rear of the eye and are less obvious, lacking the strong black mark. Of these, *alba* is most distinctive in non-breeding condition in lacking a black "whisker" on the lower face, but in having a prominent dark splotch or moustache extending from the gape reaching or nearly reaching the tomium. Surprisingly, Reyt et al. (2025) show that *modesta* and *egretta* show a rather similar range of variation to each other in the non-breeding facial skin, in lacking the dark facial splotch of *alba* but having a blackish whisker.

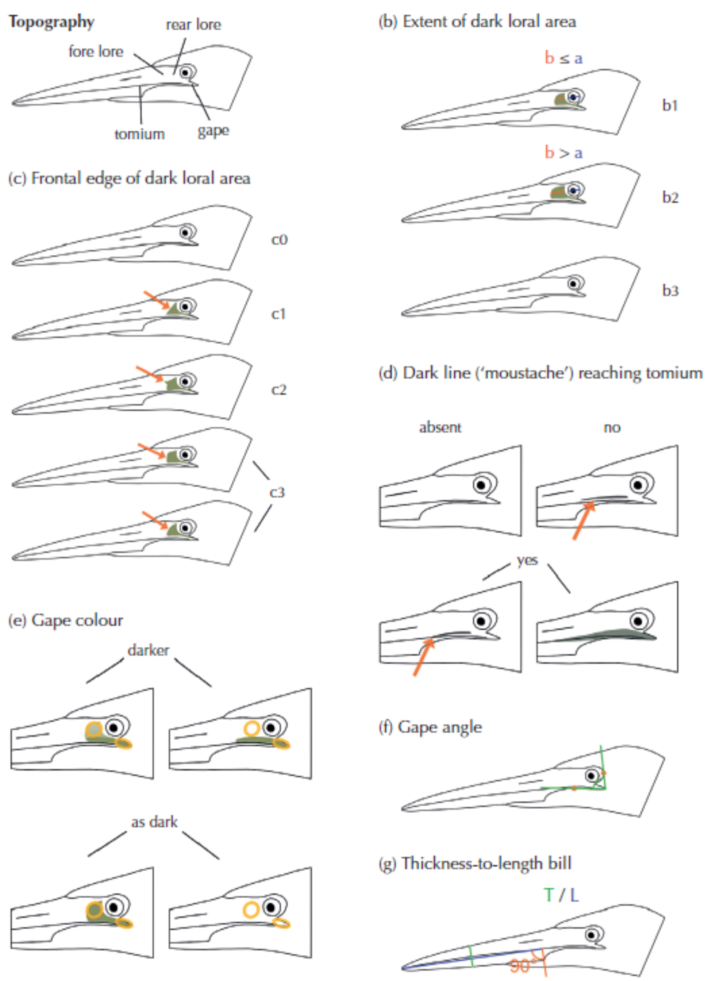


Fig. 1. Characteristics of non-breeding *Ardea alba* scored or measured by Reyt et al. (2025).

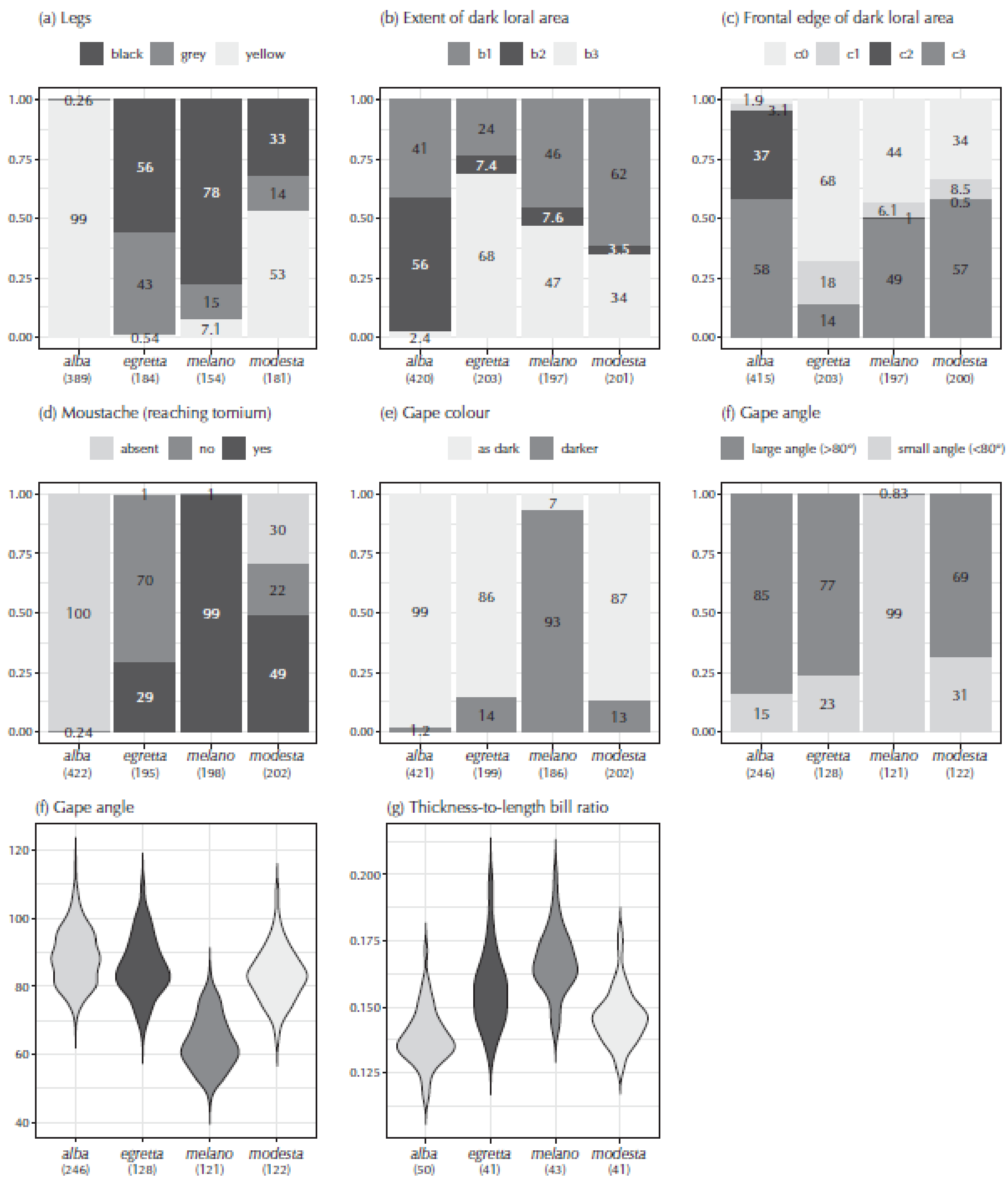


Fig. 2. Results of the analyses of Reyt et al. (2025).

Table 1. Summary of features of non-breeding *Ardea alba* from Reyt et al. (2025).

TABLE 1 Summary of features for distinguishing taxa in 'Great Egret' *Ardea alba* complex. Information about size of different taxa was collected from Cramp & Simmons (1977), Marchant & Higgins (1990) and McCrimmon et al (2020).

	alba	***melanorhynchos***	***modesta***	***egretta***
Size and structure	Largest and most elongated taxon (like Grey Heron *A cinerea* or slightly smaller), with long legs and neck	C 15% smaller than *alba*	Smallest taxon, c 17% smaller than *alba*	C 15% smaller than *alba*
Bill	Thin and spike like, with fairly straight culmen and gonys	Strong and dagger shaped, with distinctly curved culmen and gonys. Reminiscent of Grey Heron.	As in *alba* (slightly thicker on average)	As in *melanorhynchos*, but slightly thinner
Gape length	Extending little or not at all behind eye	Long gape, extending widely beyond eye	Extending little or not at all behind eye	Extending little or not at all behind eye
Gape colour (compared with rear lore colour)	Almost always as dark or paler than rear lore	Darker than rear lore with a few exceptions	Most often as dark or paler than rear lore	Most often as dark or paler than rear lore
Dark line on lore and bill side ('moustache')	Absent	Present. Typically broad and extending on gape. Almost always reaching tomium.	More often present. Variable aspect when present, sometimes being sharper on fore lore and more diffuse on rear. Generally reaching tomium.	Present. Typically thin and sharp, especially distinct on lore and bill base. Not reaching tomium in typical birds.
Dark area on rear lore (in front of eye)	Wider than eye in more than half of individuals, as wide or less wide in less than half of individuals. When present, dark area often having rounded or abrupt frontal edge, or sometimes forming typical pointed tip.	Absent or as wide or less wide than eye in most. When present, dark area generally having rounded/abrupt frontal edge.	As wide or less wide than eye in more than half of individuals and absent in quarter of individuals. When present, dark area generally having rounded/abrupt frontal edge.	Absent in c two thirds of individuals and as wide or less wide than eye in quarter of individuals. When present, dark area having either strictly diagonal or rounded/abrupt frontal edge.
Leg	Almost always with yellow on upper parts	Most often all black, sometimes with grey, rarely with yellow	Variable: often with yellow (typically less extended than in *alba*), sometimes all black or with grey on upper parts	Almost always all black or with some grey on upper parts

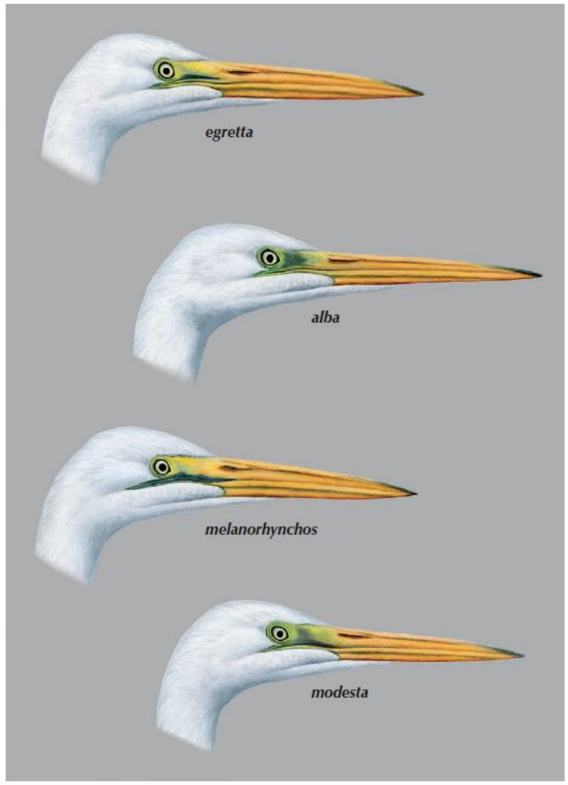


FIGURE 4 Typical heads of of 'Great Egret' *Ardea alba* taxa *(Sébastien Reeber)*. From top to bottom: American Great Egret / Amerikaanse Grote Zilverreiger *A egretta;* Western Great Egret / Grote Zilverreiger *A a alba*; African Great Egret / Afrikaanse Grote Zilverreiger *A* a *melanorhynchos*; and Eastern Great Egret / Aziatische Grote Zilverreiger *A a modesta*.

Fig. 3. Typical non-breeding heads of all four taxa of *A. alba s.l.*, from Reyt et al. (2025)

Identification.—Given that all taxa of *Ardea alba s.l.* have all-white plumage, the number of potential morphological differences between them are limited. In addition, it should be borne in mind that there is strong tendency for people to misidentify white egrets to species, especially in Asia, between *Ardea intermedia* and *modesta* Great Egret. and that distant or poor white egret photos probably can often not be confidently identified to species. With many thousands of ML egret photos, and new ones coming in all the time from all over the world, from people with a wide variety of experience and interest, it is no surprise that great care is needed with species identification when evaluating any given photograph. Thus we provide in an Appendix a brief summary of egret identification features to ensure that no one compares photos of other taxa with those of *Ardea alba sensu lato.* Those already well-familiar with such matters can simply skip the Appendix, but be aware that there are some tricky, region-specific issues that may not be well-covered in field guides.

Morphology

Plumes.—All four taxa have nuptial plumes that are restricted to the upper back, and partly due to the short duration for which they remain relatively intact, they are difficult to compare. However, it is notable that a high percentage of photos show well-developed, very long plumes in *egretta* and *modesta* compared to the other taxa, *alba* and *melanorhynchos*. In addition, in the relatively fewer photos of *alba* and *melanorhynchos* showing obvious plumes, these appear relatively droopy, wispy, and filmy compared to those of *egretta* and *modesta*, and they can be bushy, long, and full (e.g., for *alba*, https://tinyurl.com/4c3kxp63 and for *melanorhynchos*, https://shorturl.at/gk6DA, compared to those of *egretta* (https://tinyurl.com/3yb4e34h) and *modesta*, https://tinyurl.com/u9xruphx). From photos it seems that the plume shafts are stronger and the barbs seem more widely spaced in the latter two taxa. Indeed, this is borne out in a sample of specimens bearing reasonably fresh plumes at the Field Museum of Natural History: 5 *melanorhynchos*; 3 *modesta*; and 4 *egretta*, but no nominate *alba* (Figs. 4, 5). Of these three taxa, the *egretta* clearly had stiffer, larger diameter plume shafts than the others, with *modesta* seemingly intermediate between the heavy-shafted *egretta* and the thinner-shafted *melanorhynchos*. Larger samples and measurements will be needed, obviously, but these differences seem striking and likely have some bearing on display and mate choice.

Fig. 4. Five plume-bearing FMNH specimens of *melanorhynchos*: left to right, FMNH 85818, 85819, 214718, 269078, 369241.

Fig. 5. Left panel: Three plume-bearing FMNH specimens of *modesta*: left to right, FMNH 228250, 226229, 228254. Right panel: Four plume-bearing FMNH specimens of *egretta*: left to right, FMNH 128725, 351458, 128725, 128726.

Thus, it seems likely (but remains to be confirmed) that there is both a difference in timing of plume-bearing (probably a longer period in *modesta* and *egretta*) and in plume structure as well. The attainment of high breeding colors and maximal development of plumes can be somewhat out-of-synch in any of these taxa. This can be seen in the following gallery of *egretta* that show to some degree at least one feature of breeding plumage: https://tinyurl.com/mum6htzn.

High breeding facial coloration: Although facial coloration is highly variable in all four taxa, apparently depending largely on stage of the breeding cycle, it is evident that *egretta* does not seem to achieve the dark bluish-green facial coloration typical of the other three at the height of breeding coloration, although some have pale blue-green facial skin, such as these individuals (ML590686521, ML631773889, ML432999521).

High breeding bill coloration: As with facial coloration, there is variability in bill coloration in high breeding condition, but as far as we can determine the bill always becomes entirely black in the three Old World subspecies, and almost never does so in New World *egretta* (but see ML191008561 and ML629270579 for birds with anomalous bill coloration for *egretta*). In North America, *egretta* often attains a considerable amount of blackish along the culmen, with approximately the maximum extent of black for *egretta* exemplified by ML590686521 and ML631773889.

There does appear to be a largely or entirely unrecognized difference between North and South American populations of *egretta* in breeding bill coloration, in that South American birds evidently almost never achieve a mostly dark culmen (the two examples in the previous paragraph are South American, and are very different from the typical bill pattern). This gallery (https://tinyurl.com/5bhfdw67) features those images of South American birds with the largest amounts of black or dusky on the bill; as can be seen, except in the two anomalous birds it is just the tip of the culmen ridge with a short black mark, and the vast majority of South American birds have even less than those in the gallery. The name *Ardea leuce* Lichtenstein, 1823, with type locality "Brasil", appears to be available for this population, should it be recognized subspecifically, although it is possible that an earlier applicable name may exist.

Recall that the recent split of Cattle Egret into *Ardea ibis* and *Ardea coromanda* was based largely on differences in breeding plume coloration, distribution, and texture, as well as proportions, while that of Intermediate Egret into *Ardea brachyrhyncha, intermedia*, and *plumifera* was based largely on differences in breeding soft part coloration, and to a lesser extent plume development. Thus, even without genetic or vocal support, such differences as exhibited by Great Egret taxa have widely been considered to be of species-level importance.

Genetics.—Sasikala et al. (2012) found substantial genetic divergence in COI between

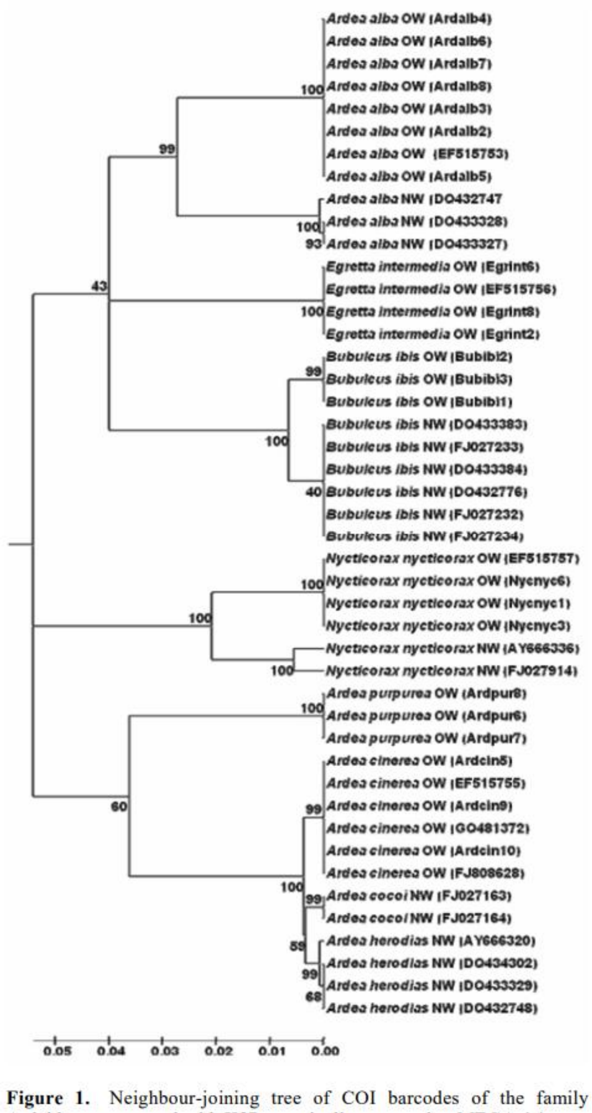
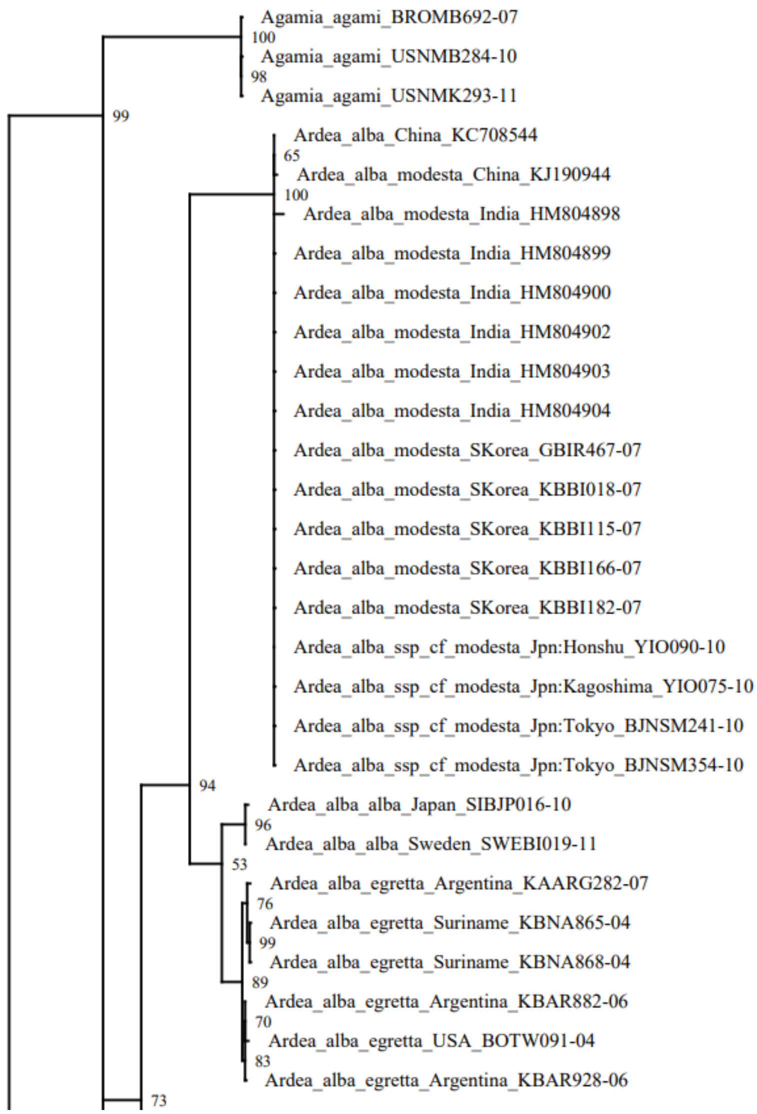


Fig. 6. Neighbor-joining tree based on sequences of COI from Sasikala et al. (2012).

samples of *modesta* from India and South Korea vs. *egretta* from Louisiana, Florida, and Suriname. These distances were considerably more than between species in the *Ardea herodias/cinerea/cocoi* clade, though only slightly more than between New World and Old World subspecies of Black-crowned Night-Heron *Nycticorax nycticorax*, which are morphological almost inseparable.

Raty (2014, https://www.birdforum.net/threads/lynx-birdlife-taxonomic-checklist.242240/page-24) prepared a tree (partially reproduced below) based on COX1 barcodes, in which (with low support), *modesta* was sister to a clade comprised of *egretta* and *alba* (note that *alba* breeds in northern Japan). African *melanorhynchos* does not appear to have been genetically sampled yet.

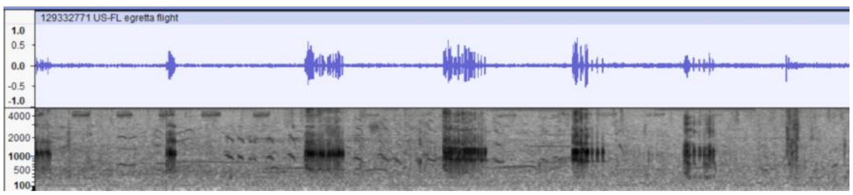


Vocalizations.---Boesman (2016) showed that *egretta* differs strongly in at least two common call types from all other taxa. He also suspected that *modesta* gives a lower-pitched flight call than nominate *alba*, and that the small sample then available for *melanorhynchos* was intermediate in this respect.

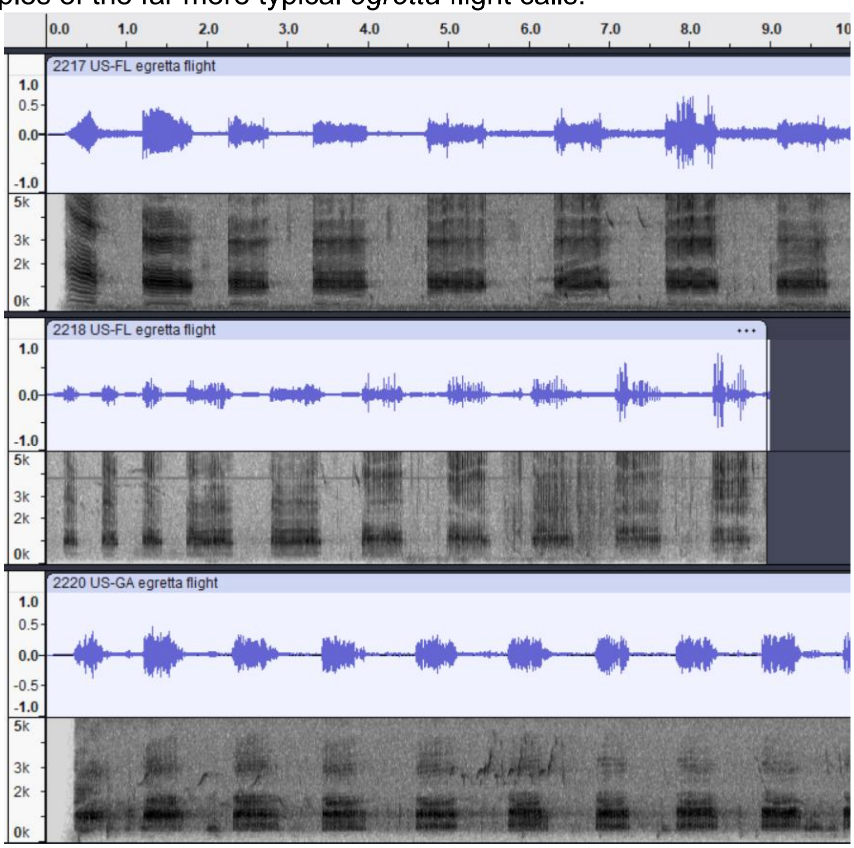
As noted by Boesman (2016), the flight call is commonly given by all taxa mainly upon takeoff and in flight as a series of drawn-out notes. In all Old World taxa, it is usually rattled (see below for discussion of "nasal" calls), while in *egretta* it does not sound like a rattle, but rather a croak. Boesman (2016) thus considered that the rattle call of all Old World taxa was lacking a homolog in New World *egretta*. However, we consider that the equivalent context establishes the croak of *egretta* and the rattles of the other taxa as homologous.

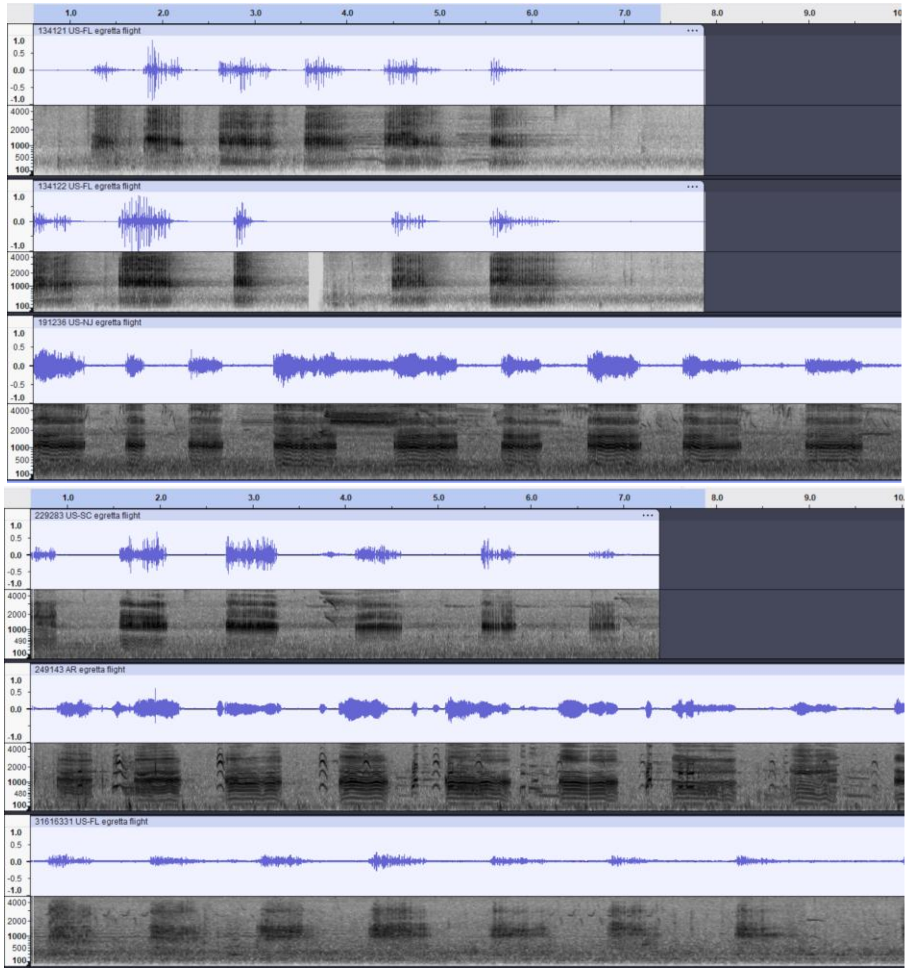
For the below comparisons, only ML recordings tagged as flight calls were used, except in the case of *melanorhynchos*, for which only a small sample of tagged calls was available, so numerous other recordings clearly of this type were also used. From the samples compared, a random sample of composites of each are shown below. It should also be borne in mind when comparing vocalizations that many photos of egrets are misidentified, and the same is likely true of recordings, but that does not apply to the rattle call which does not appear to be similar to the calls of likely co-occurring species, and so we have high confidence in the identification of the examined recordings.

A very few calls of *egretta* (e.g. ML129332771, below) have a slight rattle, though they still sound creaky rather than rattled.



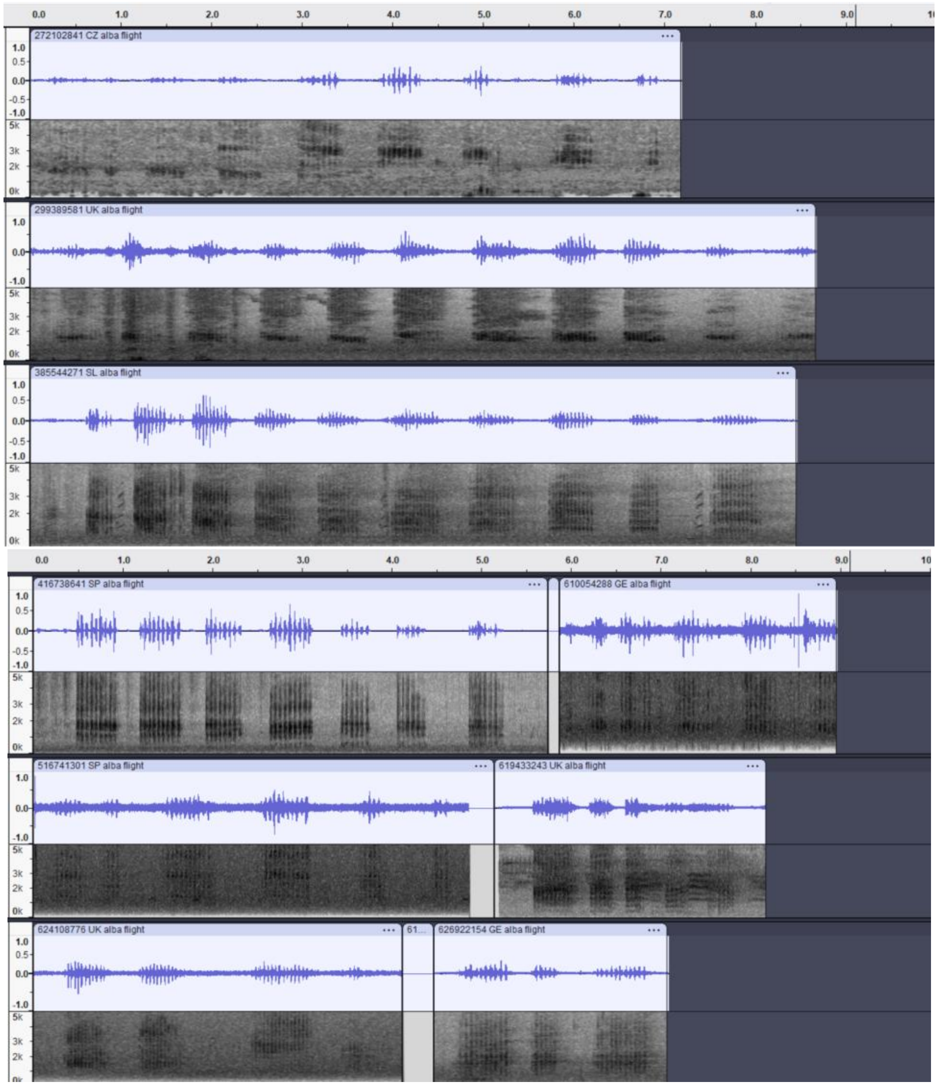
Here are examples of the far more typical *egretta* flight calls:



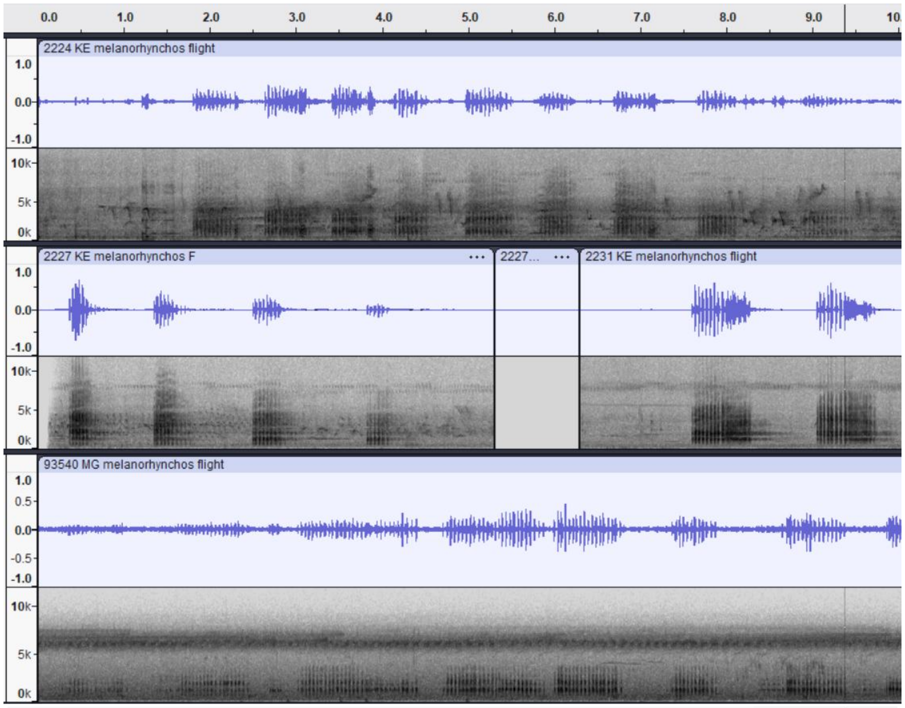


And there are many more, and none from *egretta* that give a true rattle. As projected on a 10 s window, the waveforms are essentially continuous.

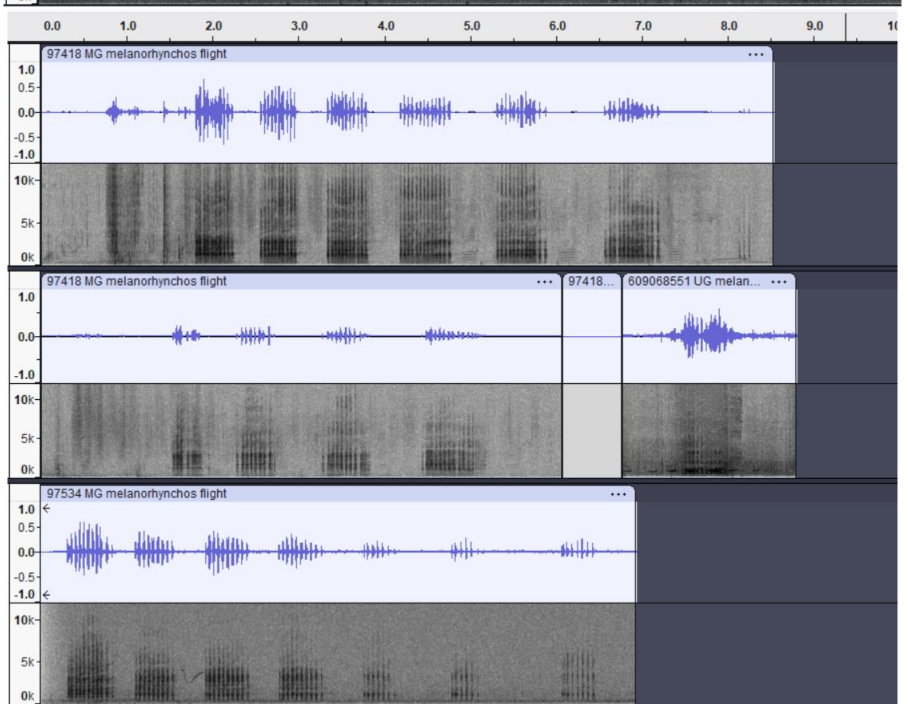
Below are typical examples of *alba* flight rattles:



The rattled flight call of Palearctic *alba* are thus typically comprised of short, rapidly rattled strophes, and as projected on a 10-s window they show as distinct pulses on the waveform. The rattled flight calls of African *melanorhynchos* (below) are similar to those of nominate *alba*:

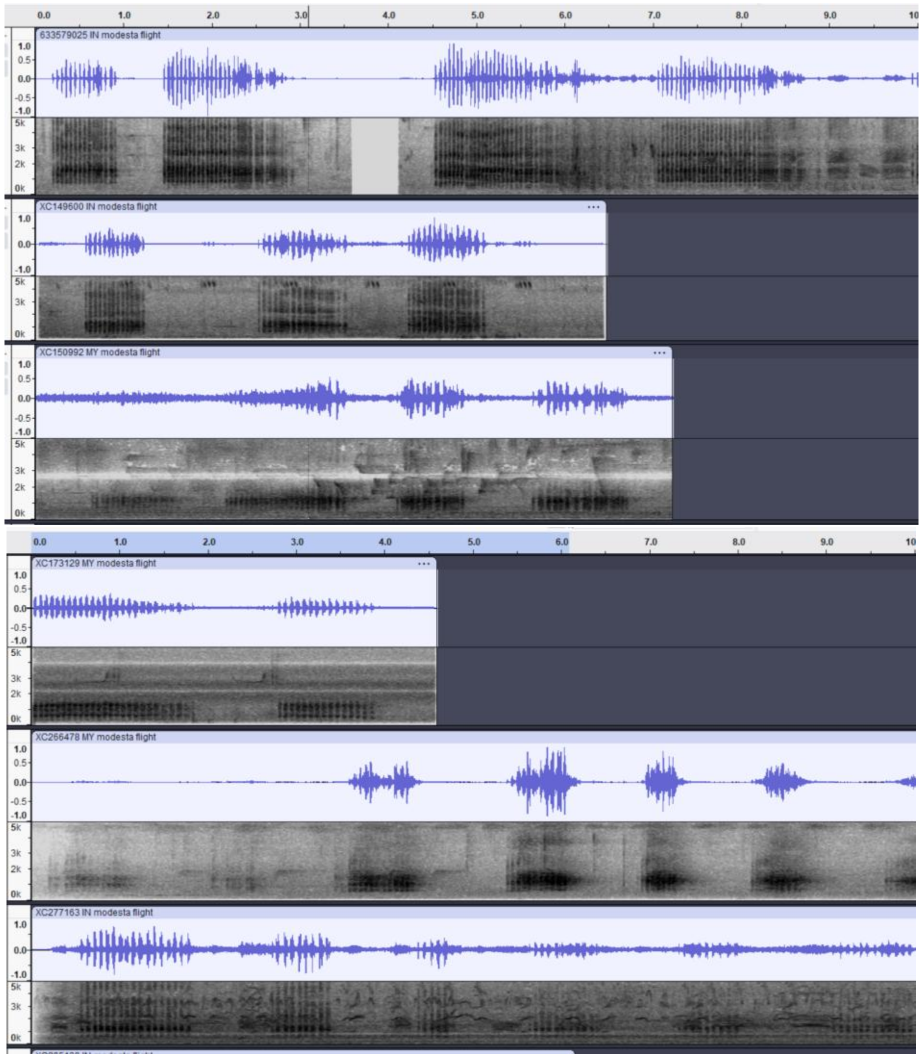


2224 KE melanorhynchos flight
2227 KE melanorhynchos F
2227...
2231 KE melanorhynchos flight
93540 MG melanorhynchos flight



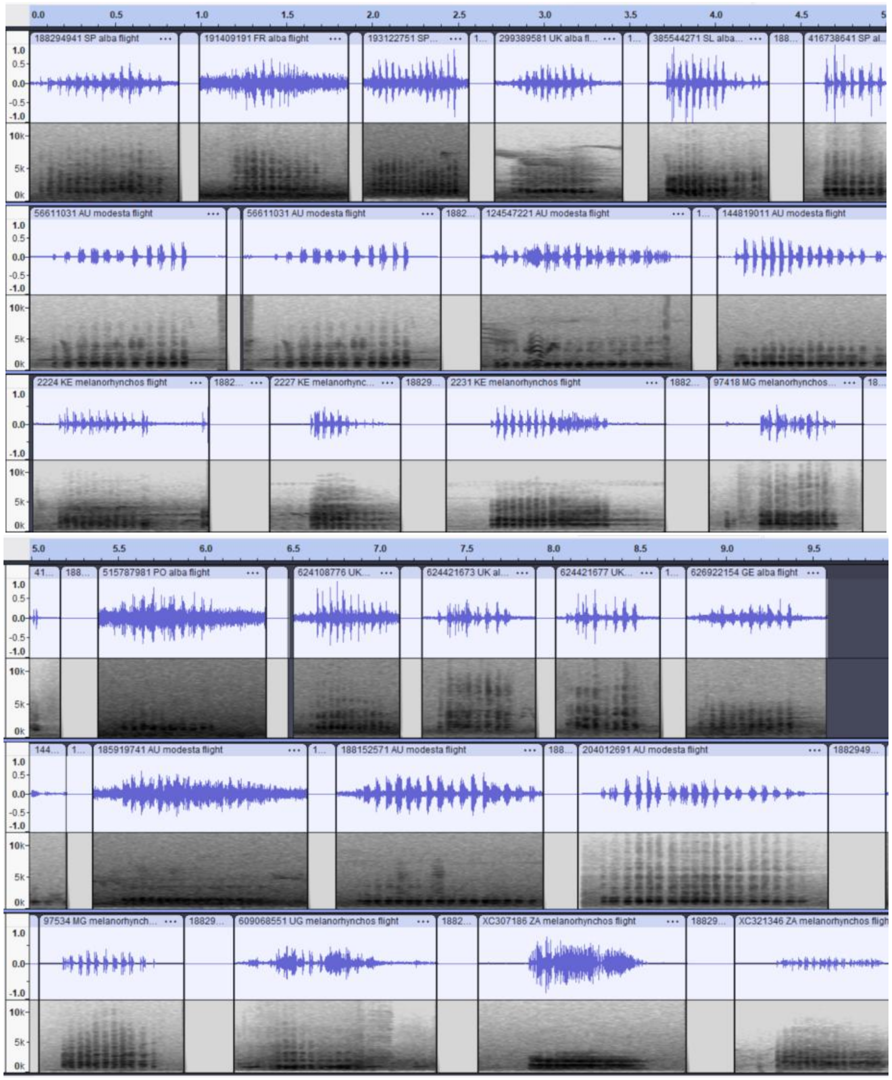
97418 MG melanorhynchos flight
97418 MG melanorhynchos flight
97418...
609068551 UG melan...
97534 MG melanorhynchos flight

The rattle flight calls of Asian *modesta*, however (below), are typically even more distinctly rattled than in *alba* and *melanorhynchos*, with each note in the rattle longer and more spaced apart, although there is variation in this. In addition, as Boesman (2016) suspected based on a small number of samples, larger samples than he had available confirm that the dominant frequencies are distinctly lower in *modesta*, despite its considerably smaller size than in nominate *alba.*

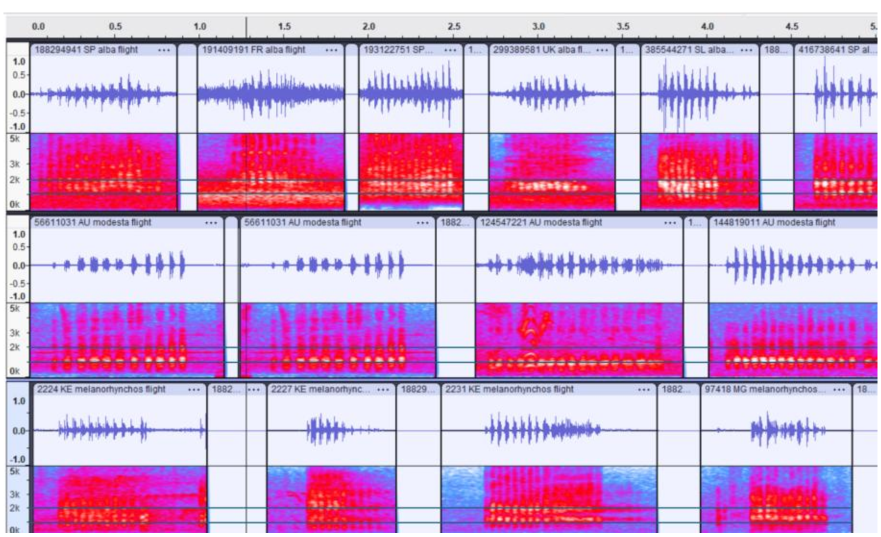


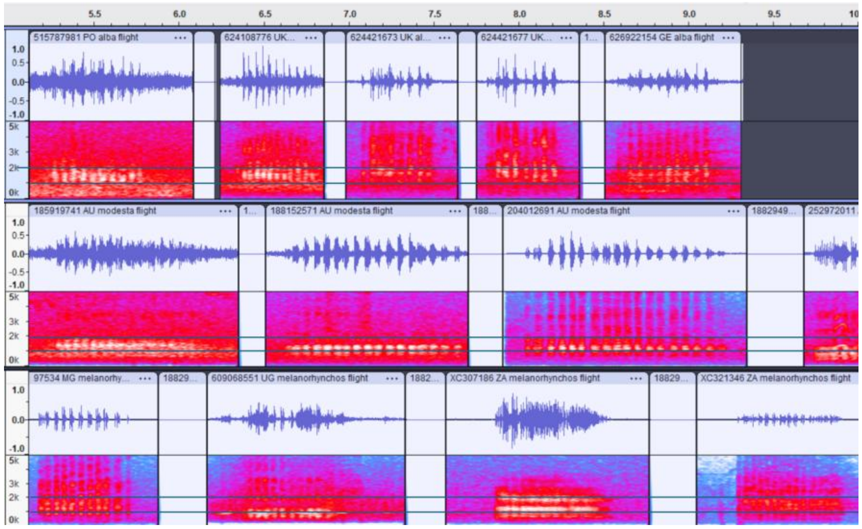
On the NACC Google Drive are two versions of a composite file in which several recordings of *alba* are first, followed by a long pause, then several recordings of *modesta* from Australia, and then after another long pause several recordings of *melanorhynchos*. The typically lower dominant frequencies of modesta compared to the others are obvious, despite variation in all three taxa. The .aup version can be viewed and listened to in Audacity (a free download), or the .wav version in other applications.

Here are the sonagrams for this comparison, with *alba* first, *modesta* second, and *melanorhynchos* third in each set:



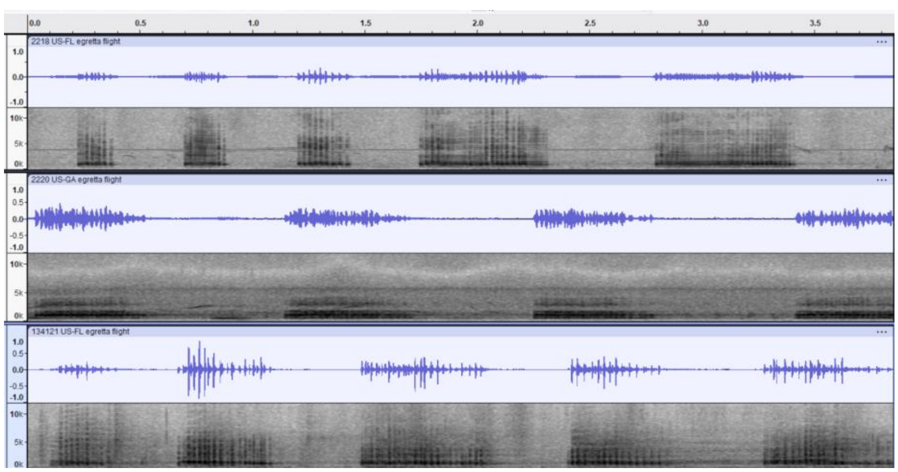
And to better allow visualization of frequencies, here are the same comparisons, in color (yellow being maximum power) and with the window set to 5000 kHz, and with lines indicating 1 and 2 kHz:





In this view, the frequency difference between *alba* + *melanorhynchos* (mostly between 1-2 kHz, sometimes exceeding 2 kHz) vs. *modesta* (centered on 1 kHz) becomes obvious.

Returning to *egretta* vs. the others, although the former sounds like a croak and the latter like rattles, when projected on an expanded timescale (as below, for 4 s), it is obvious that many of the croaked flight calls of *egretta* are comprised of very closely spaced elements, in agreement with their being homologous to the flight calls of the other three taxa, despite how different they sound.



Nasal call: As Boesman (2016) noted, *egretta* also commonly gives a much more nasal call type, with more widely spaced harmonics, than do the Old World forms.

Behavior: Hancock (1984) and Hancock and Kushlan (1984) mentioned a putative courtship breeding behavior difference between *modesta* and other subspecies. Because courtship behavior in Ardeidae is stereotyped (McCrimmon et al. 2020 and references therein), such a difference would likely have significance for species limits. However, Pratt (2011) disputed the uniqueness of this display, stating that "Brown et al. (1982) described a somewhat similar and possibly homologous flight display in *melanorhyncha* without naming it". In fact, however, Brown et al. (1982) simply summarized two studies, one on *melanorhynchos* (Tomlinson 1976) and the other on *egretta* (Mock 1978), both of which described a "Circle Flight" (see below). Pratt (2011) also quoted M. Bartosik (pers. comm.) who “believes it may be the same as an aggressive flight display he has observed repeatedly in Europe” (with a URL to an image that does not now seem to exist at that site).

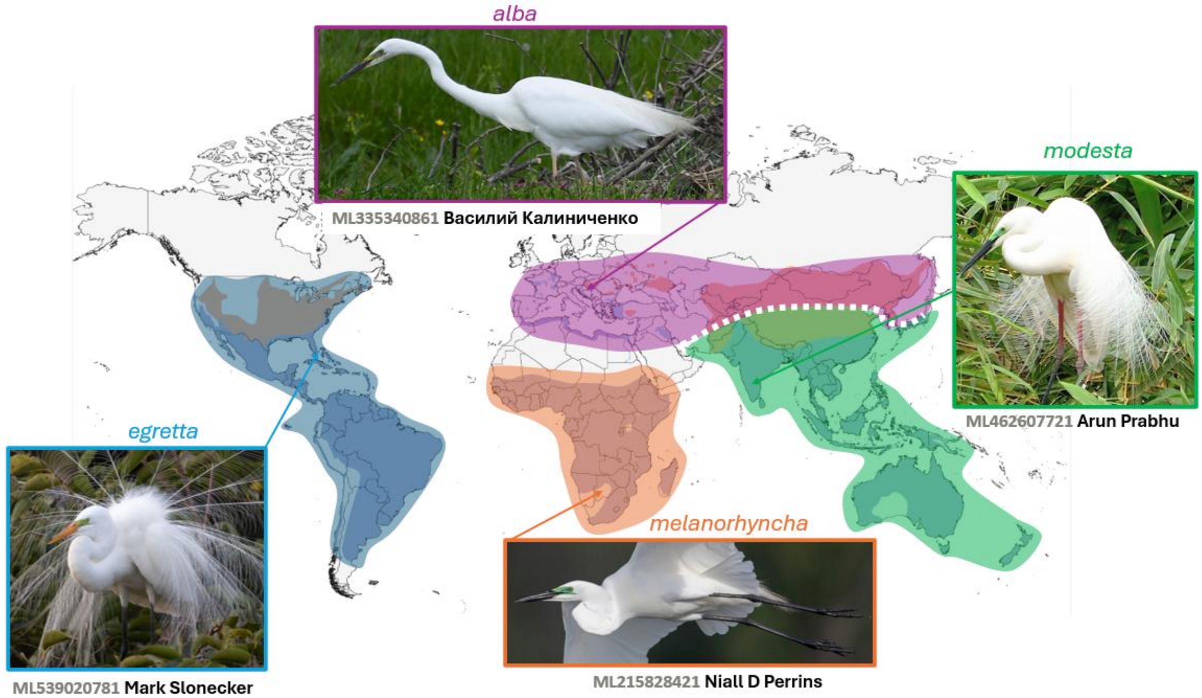
At first glance, it seems unclear how this display, the “Aerial Stretch Display” documented by Hancock (1984) for *modesta* differs from the “Extended Neck Flight” described for *egretta* by Mock (1978), described thus: “[an] egret takes off with its bill pointing 45-60° above horizontal and usually flies with the neck recurved and almost fully outstretched… it may retract the head against the shoulders and continue flying … [i]n landing, the egret extends its neck and points the bill upwards as it brakes to perch” (Mock 1978).

However, Hancock (1984) described the “Aerial Stretch Display” of *modesta* thus: “The bird took up a position on a bush at some height above its nest and some 500 m from it. It stood erect, stretched its neck forward, dropped its wings, and uttered a harsh croak. It then launched itself into the air, and descended to the nest in a direct line. Its flight was undulating, occasioned by the backwards and forwards movement of the neck and legs. The arching backwards and forwards of the neck during this spectacular flight was done quickly but gracefully, and the final outstretching of the legs brought it close to the edge of the nest.” Thus it seems likely that the “Aerial Stretch Display” of *modesta* differs from the “Extended Neck Flight” of *egretta* (Mock 1978) in the former repeatedly arching neck and legs during the flight, as well as by its taking off from a higher perch than the nest site. It furthermore differs from the “Circle Flight” described by Mock (1978) for *egretta* in not following a circular path. Despite the careful documentation of other displays of *melanorhynchos* by Tomlinson (1976), no mention was made of an “Extended Neck Flight”.

No ML videos were found that clearly show the “Aerial Stretch Display” of *modesta*. What might be part of or related to this display is seen in a video (ML 201351061) of *modesta* from Cambodia, between 9–10 s from the beginning, in which the bird dramatically stretches its neck when approaching the colony, before semi-retracting it again when about to land. We did not find any useful video material with respect to this display for *melanorhynchos*. Those few videos we found that show nest-site displays for taxa other than *egretta* seem to show a less intense type of display than is commonly observed for *egretta*.
In summary, it seems likely but far from well-established that display differences exist between some of the taxa now united in *Egretta alba*. It would seem to be a relatively straightforward matter with modern video equipment for observers to document these stereotyped behaviors in a manner that would allow comparisons to be made for these conspicuous, colonial breeders. To be maximally useful, these would need to be carefully documented with contextual information as well.

Distributions and extralimital records

The graphic below shows an approximation of the usual distributions of each taxon superimposed on the *Ardea alba s.l.* map from BOW, with breeding-plumaged individuals selected. Although the situation with vagrants is not very well understood yet, should one or more splits be enacted that will likely change. Records from the western and central Aleutians are, as far as known, *modesta*, of which two specimens that were identified as such on



measurements are held at University of Alaska Museum, while New World *egretta* is casual to southeastern and south-central Alaska (Gibson and Withrow 2015). A black-billed bird was recorded in Chincoteague, Virginia, in May-June 2008. The form on Bermuda is *egretta* (Amos 1991, many eBird images). In Barbados, only *alba* is recorded (Buckley et al. 2009), however, only *egretta* is mentioned for the West Indies by Kirwan et al. (2019).

Summary.---To recap, the four recognized subspecies of *Egretta alba* differ from each other in ways that are not typical of single species. However, the ways in which they differ seem kaleidoscopic, making determination of species limits less than straightforward.

First, *egretta* differs conspicuously in breeding soft part colors: from the three other taxa in bill coloration, and to a lesser extent facial skin coloration, and from *alba* and *modesta* but not *melanorhynchos* in tarsal coloration. However, in non-breeding colors its facial pattern is quite similar to that of *modesta*. It also evidently differs from *alba* and *melanorhynchos*, but not *modesta*, in the heavier-shafted plumes that seem likely to be held over a longer period. The very different croak flight calls (vs. rattled flight calls of the other taxa) and the commonly delivered very nasal calls (vs. harsher nasal calls of the others) immediately set *egretta* apart. In addition, most other heron species differ specifically between the New and Old World, with the exception of the near-cosmopolitan Black-crowned Night Heron *Nycticorax nycticorax* (when *Butorides* is split, as in AviList and followed by Clements v2025; and indeed new data strongly support the hemispheric *Butorides* split; PCR ms). Although the limited and poorly supported mtDNA tree presented by Raty (2014) can be interpreted as contradicting the picture of an *Ardea alba* split along strictly hemispheric lines, the Sasikala et al. (2012) study strongly suggests that *egretta* and *modesta* are non-conspecific, based on the greater divergence between them and other heron species pairs or clusters.

Among Old World taxa, *alba* is the largest taxon, with a subtly distinctive slim bill shape and non-breeding facial colors (the dark greenish facial patch) that usually enable its identification, but it has been said to perhaps intergrade with *modesta* in northeastern Asia. This however does not appear to have actually been documented anywhere that we are aware of, and side-by-side the two taxa are quite strikingly distinct in size. It is quite easy to distinguish most or all nominate *alba* from African *melanorhynchos*, given a reasonable view/photo, especially on the basis of the gape, but also bill shape and non-breeding facial soft part colors, as well as the color of the upper tarsi (pale to reddish in alba, black in *melanorhynchos*). (For example, if one filters *Ardea alba* by major region: Africa, photos of nominate *alba* from the Canary Islands and North Africa are easy to pick out from the sub-Saharan *melanorhynchos*.) The difference in gape prominence between *alba* and *melanorhynchos* also does not seem typical of a subspecific character. However, *melanorhynchos* does not appear to have been molecularly sampled, is very similar to nominate *alba* at least in the rattle call, and bears similar plumes, both seemingly for a relatively short period.

On the other hand, whereas *alba* and *modesta* are very similar in breeding soft-part colors, they are evidently not as similar to each other in plume type and periodicity, and in body size (and a size cline does not appear to have been substantiated but cannot be ruled out without further study). They also differ strikingly in the rattle call, with that of *modesta* noticeably slower and lower-pitched compared to *alba* and *melanorhynchos*, a difference exactly the opposite of the usual pattern of smaller-bodied birds giving higher-pitched calls. Furthermore, the limited molecular data seem to indicate that *modesta* is the most genetically distant of all three sampled taxa.

Ardea alba is now considered to comprise four species in the online resource "Taxonomy in Flux" (http://jboyd.net/Taxo/List8a.html#ardeiformes, accessed 28 July 2025). It is currently considered two species by the CSNA (Redactie Dutch Birding 2014), and this is the taxonomy followed by Reyt et al. (2025), though they also pointed out the incongruence of the apparently high genetic distinctness of *modesta* with this treatment.

Recommendation:

We strongly recommend the recognition of New World *egretta* as a separate species. The available data, however, are more equivocal for the other three taxa, at least two of which (*alba* and *modesta*) have been recorded in North America. Nevertheless, despite their similarity in breeding soft-part colors, *alba* and *modesta* differ in a number of other ways, including their possible greater genetic divergence. PCR and AJS thus consider that *modesta* should also be considered a separate species, while JLD is unconvinced of this and considers that this is beyond the purview of NACC. While we suspect that ultimately four species will be recognized in the complex, and *melanorhynchos* and *alba* do differ in a number of ways, including the long dark gape of *melanorhynchos*, we all agree that it seems premature to take the step of further splitting *melanorhynchos* from *alba*, given their similar vocalizations and plumes, and the lack of genetic data for the former.

English names:

Should one or more splits be adopted, we recommend use of the English names that have gained great traction, and that highlight that these are members of a species complex. These are American Great Egret *Ardea egretta*, Eastern Great Egret *Ardea modesta*, and Western Great Egret *Ardea alba* (including *melanorhynchos*). Should *melanorhynchos* be split, African Great Egret is also fairly well-established; however, the use of Western Great Egret for just these two taxa may be a cause for concern.

If only *Ardea egretta* were to be split, American Great Egret would still apply, but an English name encompassing all the Old World taxa would need to be found. Old World Great Egret, contrasting with American, would be appropriate and may be the only geographical name that fits. Another appropriate name would be Rattling Great Egret, which is descriptive of the calls of the Old World taxa but perhaps not likely to garner support.

Acknowledgments*:* We thank especially Dan Gibson for providing information on the Aleutian specimens, and Marshall Iliff for discussion. We are grateful for the many recordists and photographers who have made their media publicly available, without which much of this proposal would not have been possible.

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Submitted by: Pamela C. Rasmussen, Jon Dunn, and Andrew Spencer

Date of Proposal: 10 December 2025

Appendix. Region-specific identification of white ardeids often confused with Great Egret.

In the Western Palearctic, if an egret is very lanky, with a notably thin, long bill and legs, and lacks any head or chest plumes, it may be a Great Egret (s.l.). If it is very much larger than other egrets in the same photo, the same pertains. In the Western Palearctic, the main confusion species with nominate *alba* are non-breeding Little Egret *Egretta garzetta*, which has a longer, mostly black bill with a pale lower base, and yellow feet (never found in *alba*), typically yellower to redder lores, and often remnants of thin head and chest plumes); and non-breeding Western Cattle-Egret *Ardea ibis* (which has a shorter, more curved culmen and much shorter neck and legs).

In Africa, there are additional confusion species as well as the above. These include Western Reef-Heron *Egretta gularis*. which is mostly coastal, with a white morph much like Little Egret but with a thicker, paler or yellower bill and legs, especially along the rear edge and toes. More troublesome for ID is non-breeding Yellow-billed Egret *Ardea brachyrhyncha* (formerly the African form of Intermediate Egret), which often shows chest plumes and has a shorter bill, rounder head, relatively larger eye, shorter neck and legs, and much shorter, less conspicuous gape than African *melanorhynchos.* Typically, *melanorhynchos* can be readily distinguished from any other sympatric white egret on this character alone, since it has a black or dark olive gape that is very extensive beyond the eye (although sometimes even this is hard to discern). Also, the upper tarsi of *melanorhynchos* are normally all-black, almost never yellowish, and probably never reddish (as in breeding Yellow-billed). In addition, the taxonomy of the Dimorphic Egret *Egretta dimorpha* is unsettled, but the white morph looks much like a Little Egret, of which it is currently considered a subspecies in AviList v2025 (https://www.avilist.org/about/).

In Asia, the confusion species with subspecies *modesta* (and *alba* across northern Asia) include, first, non-breeding Eastern Cattle-Egret *Ardea coromanda* (and Western eastward to Iran and Central Asia), which is somewhat lankier than Western and thus invites confusion, but shares with Western a more arched bill and still relatively compact proportions. Next, white morph Western Reef-Heron (as described under Africa) occurs eastward to India, and white morph Pacific Reef-Heron *Egretta sacra*, occurring coastally eastward from Myanmar and the Andamans, has a robust shape, especially the deep bill and thick, short legs. The Chinese Egret *Egretta eulophotes,* mainly of the eastern seaboard and insular Asia, is in non-breeding plumage surprisingly similar to white-morph Pacific Reef-Heron (see, e.g., Poole et al. 1999; https://www.orientalbirdclub.org/chinese-egret), though more elegant and with other subtle differences. But the most problematic species for identification of *modesta* is by far Medium Egret *Ardea intermedia* (formerly the Asian subspecies of Intermediate Egret). The latter is very often confused with *modesta*, and even has very similar soft-part colors in high-breeding plumage, with green facial skin and an all-black bill, although the lores tend to be more olive (not blue-green), and the upper tarsi of *intermedia* are all-black, never attaining the reddish tinge of breeding *modesta* (the opposite of the situation with *brachyrhyncha* and *melanorhynchos* in Africa!). In addition, non-breeding Medium Egrets share their more compact proportions, round-headed, large-eyed, and short-gaped shape with Yellow-billed Egret, as well as often showing remnants of the chest plumes that are entirely lacking in *modesta*.

In Australasia, the same basic set of confusion species for *modesta* occur as in Asia, with the exception of Western Reef-Heron (which does not occur) and the occurrence of Plumed Egret *Ardea plumifera* rather than Medium Egret. In non-breeding plumage Plumed Egret differs from *modesta* in the same basic ways as does Medium Egret, although in breeding plumage it closely resembles in soft-part colors the Yellow-billed Egret of Africa, but appears somewhat lankier. Thus, Plumed can share reddish upper tarsi with *modesta*, but not the black bill of the latter.

Finally, in the New World, especially in the Caribbean region, there are multiple confusion species, well summarized in Armistead and Sullivan (2015), and thus not repeated here.

Recognize Whimbrel *Numenius phaeopus* as two species

Effect on NACC:

This would elevate the New World subspecies of Whimbrel (*Numenius phaeopus hudsonicus*) to species level; as both daughter species have occurred in North America, the North American avifauna would gain one species.

Background:

Numenius hudsonicus Latham, 1790, was described initially as a species distinct from *Numenius phaeopus* Linnaeus, 1758, and this treatment was followed by most or all authorities, including the AOU (e.g., AOU 1886, AOU 1931), until Peters (1934) reduced *hudsonicus* to a subspecies of *N. phaeopus*. This change in species limits was followed by the 19th AOU supplement (AOU 1944) and subsequent editions of the AOU Checklist (e.g., AOU 1957). The current edition of the Checklist (AOU 1998) treats the taxa as subspecies groups, stating:

> Notes–Groups: *N. hudsonicus* Latham, 1790 [Hudsonian Curlew] and *N. phaeopus* [Whimbrel]. The two groups are genetically strongly differentiated (Zink et al. 1995) and may constitute two different species.

Although no rationale for the change to subspecies was published at the time it was made, most major taxonomic authorities followed Peters in treating Whimbrel as one species — though with increasing numbers of recent exceptions (e.g., Sangster et al. 2011) — until 2025, when AviList and its parties restored Hudsonian Whimbrel to species status (Rheindt et al. 2025). This complex was last considered by the NACC in 2022, when a proposal to split was rejected due in part to concerns about no known vocal differentiation and the fact that other major taxonomic authorities all considered Whimbrel to be a single species.

The Whimbrel complex includes ca. five subspecies in two groups under the status quo, with the *hudsonicus* group containing only *N. p. hudsonicus* (proposed subspecies *N. p. rufiventris* is generally treated as a junior synonym of *N. p. hudsonicus*) and the *phaeopus* group including *N. p. phaeopus, N. p. alboaxillaris, N. p. rogachevae, N. p. variegatus*, and in some treatments other subspecies like *N. p. islandicus*, although *N. p. islandicus* is now frequently synonymized with the nominate subspecies.

All breeding populations in the Nearctic are referable to *N. p. hudsonicus* (though, when *N. p. rufiventris* is recognized, birds from Alaska and northwest Canada are assigned to that subspecies and *hudsonicus* is restricted to the largely disjunct population breeding in the Hudson Bay region); *hudsonicus* winters mainly on coastlines through much of the rest of the New World south of Canada (Fig. 1). The nominate subspecies breeds in northwestern Eurasia, with populations in Iceland and southeastern Greenland sometimes split as *N. p. islandicus*; *phaeopus* breeds east to west-central Siberia but apparently does not come into contact with the breeding distributions of *alboaxillaris* or *rogachevae*. The eastern limits of the winter range of *phaeopus* are unclear due mainly to confusion with *rogachevae*, which was not described until 2008; earlier reports of *phaeopus* from, e.g., southeast Asia are likely referable to *rogachevae* instead. Subspecies *phaeopus* winters principally in Africa and the western Indian Ocean basin and is likely rare or absent east of the Indian subcontinent. Subspecies *alboaxillaris* breeds on the steppes of Kazakhstan and southwestern Siberia (thus sometimes referred to as Steppe Whimbrel), although occasional birds intermediate between *phaeopus* and *alboaxillaris* have occurred as migrants in western Europe and elsewhere (Cramp and Simmons 1983); these may be intergrades, but their geographic origin is unknown. Similarly, the winter range of *alboaxillaris* is poorly known, although winterers have been recorded from Maputo Bay, Mozambique (Allport et al. 2018). *Rogachevae* breeds in an isolated area of central Siberia and winters in Southeast Asia and western Australia; *variegatus* evidently breeds in several disjunct populations in eastern Siberia and the Russian Far East, wintering in southern Asia and widely in Australasia. Two records exist of radio-tracked birds summering in an area between the breeding distributions of *rogachevae* and *variegatus*, but whether they bred is unknown (Kuang et al. 2022). Atlases of status and distribution (e.g., Cramp and Simmons 1983, Smith et al. 2025) and monographs (e.g., Hayman et al. 1986) are generally consistent in reporting that *phaeopus*, the populations now recognized as *rogachevae* (formerly inconsistently attributed to *variegatus* and/or *phaeopus*), and *variegatus* do not overlap with one another in breeding distribution and suggest that *phaeopus* and *variegatus* do not likely come into contact with one another on the wintering grounds or during migration, though works such as Tan et al. (2019) use distribution maps to suggest that *rogachevae* and *phaeopus* may overlap without providing rationale; additional work characterizing the distributions of the Old World subspecies in greater detail would be useful.

Fig. 1. Map showing the distribution of the subspecies of *Numenius phaeopus* (yellow = breeding range, green = passage migration, blue = wintering range). Map from datazone.birdlife.org, using map data from openstreetmap.org

Whimbrels of various subspecies have extensive and well-documented patterns of vagrancy, with *hudsonicus* occurring fairly regularly in the United Kingdom and on the Azores and exceptionally elsewhere in the western Palearctic (e.g., records from Israel, the Cape Verde islands, etc.); there are also records from Australia, New Zealand, the Chatham Islands, and perhaps Taiwan, whereas *phaeopus* has reached the Atlantic coasts of North and South America many times and *variegatus* is a fairly regular vagrant to Alaska and has occurred elsewhere on the Pacific coast of North America (see Skeel et al. 2025 and Smith et al. 2025 for more detailed overviews and additional references). Records of vagrancy within the Old World by subspecies of the *phaeopus* group are few, likely due in part to identification issues and uncertainty relating to the ordinary distributions of Old World subspecies.

The *hudsonicus* and *phaeopus* groups are readily differentiated on the basis of plumage. The most widely-cited difference is the pattern of the rump and lower back, which are concolorous with the remainder of the dorsum in *hudsonicus* (i.e., dark brown with pale buff fringing or spotting) and contrastingly white in the *phaeopus* group, with limited dark barring varying somewhat in extent among the subspecies in that group: the westernmost subspecies (*phaeopus*) shows the least dark marking in the white patch and the easternmost subspecies (*variegatus*) shows the most, although even *variegatus* does not approach *hudsonicus* in this regard.

There are other substantial differences also, including:

- The base color of the axillaries and underwing coverts is buffy in *hudsonicus* and white in the *phaeopus* group; there is variation in the density of the dark barring within the subspecies of the *phaeopus* group (again with *phaeopus* being least marked and with the density of marking increasing in more easterly subspecies), but all *phaeopus*-group subspecies are white in base color and *hudsonicus* is always buffy.

- The supercilium and sides of the face are largely whitish with sparse, thin dark streaking in *hudsonicus*, whereas these areas are often much more densely and coarsely streaked in the *phaeopus* group. This creates the impression of a neat facial pattern with the dark transocular and sides of the crown contrasting strongly with the very pale supercilium and sides of the head in *hudsonicus* and the impression of a less strongly marked face in the *phaeopus* group, with the dark transocular and sides of the crown contrasting more weakly against the moderately pale supercilium and sides of the face, whereas the white eye-arcs stand out more strongly in the *phaeopus* group due to the darker background.

- In *hudsonicus*, the underparts (in particular the foreneck, chest, and flanks) average darker and buffier than in any member of the *phaeopus* group. Zink et al. (1995), comparing *hudsonicus* to *variegatus*, observed that “their differences in background coloration gives [*sic*] *variegatus* a strikingly whiter or grayer overall appearance.” Cramp and Simmons (1983) attributed this difference mainly to the greater extent of dark brownish coloration in the bases of the contour feathers in these regions in *hudsonicus*.

- In juvenile plumage, Smith et al. (2025) and Skeel et al. (2025) proposed that *hudsonicus* may average buffier below and also warmer brown above than the *phaeopus* group. Differences in back and underwing pattern are present in juvenile plumage, but differences in head pattern are less pronounced.

- In various morphometrics *hudsonicus* shows mean differences from the *phaeopus* group, being, e. g., longer-billed and marginally shorter-legged and longer-winged than *variegatus* on average (Cramp and Simmons 1983 and references therein; Hayman et al. 1986; Engelmoer and Roselaar 1998).

It is notable that the striking white rump of the *phaeopus* group features in displays given both in the context of courtship and in the context of agonistic interactions on the non-breeding grounds. Cramp and Simmons (1983) began their discussion of breeding behavior by stating that "tail-fanning and exposure of white rump [is] a feature of courtship (at least in nominate *phaeopus*)." It is also a feature of agonistic displays, as documented, e. g., in eBird (S119699748).

In contrast, during the analogous displays of *hudsonicus*, presentation of the rump—which lacks a contrasting white patch—is less common. Skeel et al. (2025), describing the behaviors of *hudsonicus*, observed "When extremely excited, a displaying bird droops its wings downward and spreads its tail to form a 110° angle; usually the tail is lowered, but occasionally the fanned tail is twisted to face the intruder." When the tail is lowered, as is usually the case, the rump is not presented; conversely, the norm in the *phaeopus* group is for the tail to be elevated, displaying the bright white rump (Williamson 1946, Cramp and Simmons 1983).

Many authors, using a range of methodologies, have demonstrated wide genetic differentiation between *hudsonicus* and the *phaeopus* group and a much more limited degree of variation among the four subspecies within the *phaeopus* group. Examinations of mitochondrial DNA (mtDNA) in this complex include Zink et al. (1995), who found a degree of difference in mtDNA restriction fragment profiles between *variegatus* and *hudsonicus* that they considered consistent with distinctness at the species level; Kerr et al. (2009), who reported 3.57% divergence between *variegatus* and *hudsonicus* and flagged Whimbrel for a potential species-level split; Johnsen et al. (2010), who found 3.62% divergence between the nominate subspecies and *hudsonicus* and likewise flagged the complex for a potential split; and Humphries and Winker (2011), who similarly found support for strong mtDNA divergence between these groups, though they also examined nuclear DNA (amplified fragment length polymorphisms, or AFLPs) and did not find robust differentiation using that approach, perhaps (as a co-author of that paper, Kevin Winker, suggests) due to limited sample sizes. These studies spanned multiple mitochondrial loci. A meta-analysis of these works plus others comparing *variegatus* with *phaeopus* (samples being harder to come by for other *phaeopus* group subspecies) presented by Sangster et al. (2011) likewise called for the separation of *hudsonicus* from the *phaeopus* group at the species level.

Zink et al. (1995) identified degrees of divergence in the mitogenome consistent with distinctness at the species level in populations separated by the Bering Strait of (*sensu lato* in all cases) Marbled Murrelet (*Brachyramphus marmoratus*), Three-toed Woodpecker (*Picoides tridactylus*), Whimbrel (*Numenius phaeopus*), Mew Gull (*Larus canus*), Black-billed Magpie (*Pica pica*), American Pipit (*Anthus rubescens*), and Rosy Finch (*Leucosticte arctoa*). All these complexes have now been split by the AOS and other authorities—in most cases, or perhaps all except for *L. arctoa*, based in part on the work of Zink et al.—except for Whimbrel. These splits resulted in the recognition of Long-billed Murrelet (*B. perdix*), American Three-toed Woodpecker (*P. dorsalis*), Short-billed Gull (*L. brachyrhynchus*), Black-billed Magpie (*P. hudsonia*), Siberian Pipit (*A. japonicus*), and the American rosy-finches (*Leucosticte* spp.).

Studies of nuclear DNA in this group — with the sole exception of Humphries and Winker (2011) as mentioned above — corroborate these conclusions. Tan et al. (2019) found strong and deep divergence between *hudsonicus* and the *phaeopus* group (including all four subspecies), along with evidence of extensive gene flow among highly allopatric breeding populations within the *phaeopus* group. McLaughlin et al. (2020) likewise found signals of strong and deep divergence between *hudsonicus* and *variegatus*, and estimated a rate of gene flow consistent with one hybridization event every 5–6 generations (0.08–0.18 individuals per generation), which is remarkably low. In this light, it may be unsurprising that there are no confirmed records of hybridization between the *hudsonicus* and *phaeopus* groups. These studies employed different methodologies, with Tan et al. using 6,653–8,421 (varying by mode of analysis) single nucleotide polymorphisms and McLaughlin et al. using 2,388 ultraconserved element (UCE) loci.

New Information:

A thorough treatment of Eurasian Whimbrel vocalizations is still needed. However, a preliminary treatment is presented here. Additionally, some new information on the biogeographic history and population genetics of this complex is now available (Tan et al. 2023)—and, lastly, AviList and its many parties have split Whimbrel, so NACC would no longer be the only taxonomic authority to recognize this split.

New Genetic Information. A challenge of interpreting previous genetic studies (e.g., Zink et al. 1995, McLaughlin et al. 2020) examining divergence between Hudsonian and Eurasian whimbrels is that, when they provide context relating to degrees of divergence in other pairs of taxa, those taxa are typically other trans-Beringian complexes (e.g., *Anas crecca crecca/carolinensis, Mareca penelope/americana, Pinicola enucleator kamschatkensis/ flammula*) that are vaguely similar in distribution to the *N. phaeopus* complex, but drastically different in life history and evolutionary history. Tan et al. (2023) provided the first examination of the systematics of the entire genus *Numenius*, contextualizing the divergence between *hudsonicus* and the *phaeopus* group with respect to congeners rather than distantly related fellow trans-Beringians. This adds a valuable perspective.

Tan et al. (2023) reported an estimated divergence date of just over 1 million years ago, similar to the estimated divergence date of Eurasian (*N. arquata*) and Slender-billed (*N. tenuirostris*) curlews and only slightly more recent than the estimated divergence of Far Eastern Curlew (*N. madagascariensis*) from the Eurasian+Slender-billed clade (Fig. 2). This Whimbrel divergence date is in accordance with that estimated by Humphries and Winker (2011) using mtDNA. So, in other words, it is not just in comparison to degrees of divergence in taxa like ducks (as in McLaughlin et al. 2020) that the divergence between *hudsonicus* and the *phaeopus* group appears consistent with species-level distinctness; the same is true in comparisons to other curlew species.

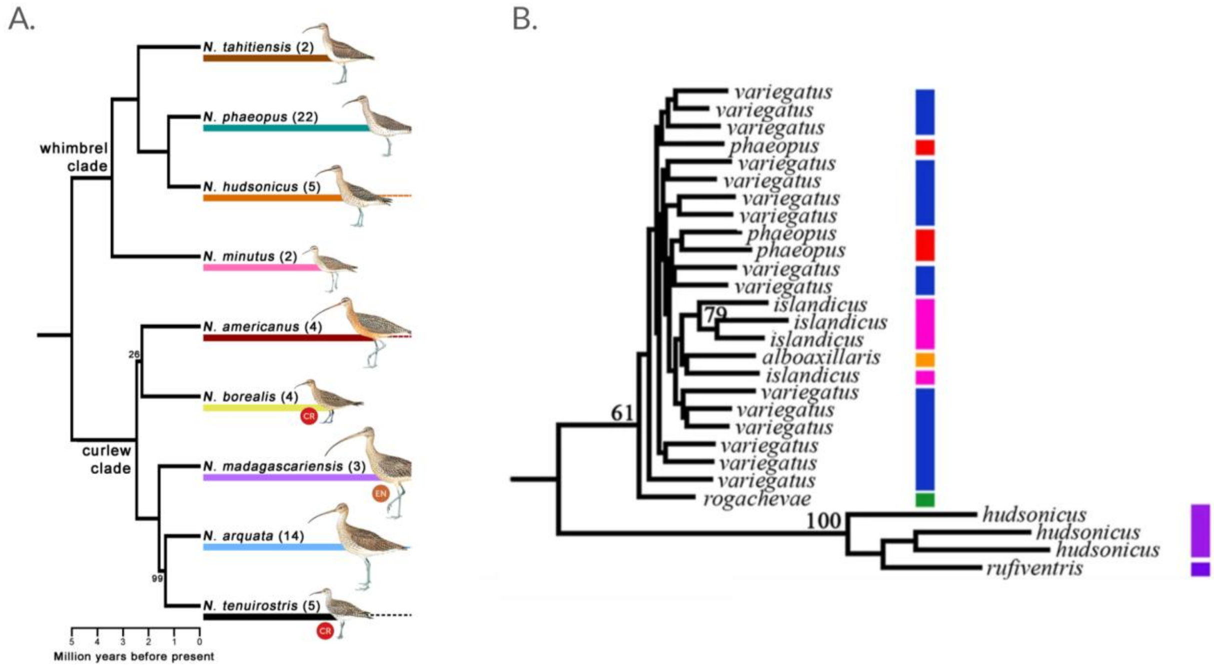

Fig. 2A. Reproduced from Figure 1B from Tan et al. (2023), showing a phylogeny of *Numenius* contextualizing the depth of the split between *hudsonicus* and the *phaeopus* group (which the authors treat as separate species). The phylogeny was built using 514,771 base pairs across 524 nuclear loci. The sample size for each taxon is given in parentheses and all bootstraps <100 are specified. **2B**. Reproduced from Figure 2B from Tan et al. (2019), demonstrating the paraphyly of subspecies within the *phaeopus* group and the distinctness of *hudsonicus* (into which *rufiventris* is typically subsumed). This phylogeny was constructed with 438,477 base pairs of sequence data.

Vocal Differentiation. An examination of whether vocal differences exist between these taxa is hampered by the remarkable lack of detailed descriptions of the vocal behavior of the *phaeopus* group. The work of Skeel (1978) documented the vocal behavior of *hudsonicus* on the breeding grounds, but there is nothing satisfactory on the *phaeopus* group for comparison.

The best available study is Williamson (1946), though it is quite old and is far less thorough than Skeel's work. However, Skeel (1978) and Skeel et al. (2025) reported that breeding Hudsonian Whimbrels in Manitoba are silent during the first phase of the aerial display ("In Manitoba, Canada, the male is silent during the climb"), while Williamson (1946) stated that the opposite is true of Eurasian Whimbrels in the Faeroe Islands ("Sometimes the climb is silent, but it is more often punctuated by the sweet and mournful 'koo' note at short intervals, the intervals becoming less and the recital more impassioned as the climactic trill is neared").

I used recordings from Xeno-canto and the Macaulay Library to compare the aerial display song, low trill call, and scolding trill call (all as described by Skeel 1978) across these taxa. However, the utility of this analysis was restricted by the limited number of high-quality recordings of most vocalizations available and by the extreme variability of most Whimbrel vocalizations. Some of this variation may also be introduced by inconsistency in recording equipment and circumstances, which is considerable in these repositories.

I confirmed that the scolding trill calls of the *phaeopus* group fall into the same categories that Skeel describes for *hudsonicus* (types I–III; see Skeel 1978). I was unable to perform other useful evaluations of the scolding trill call due to inadequate sample sizes of each type of trill. I found no consistent difference in any aspect of the aerial display song (n=34 for *phaeopus* group, n=25 for *hudsonicus*) that I examined: these aspects were peak frequency and frequency range for all low whistle elements and for low trill call components I–II (low whistles plus the three-phrase form of the low trill call forming the aerial display song), peak frequency and frequency range separately for the modulated and trilled portions of low trill component III, rate of modulation for the modulated portions of low trill component II and III, rate of delivery of trill elements for the trilled portion of low trill component III, and duration of low trill call components I–II. However, the variability shown even within multiple instances of a low trill call in the same recording of the same individual was extremely large, and it is most certainly possible that subtle but consistent differences exist that I was unable to detect.

I identified a potential difference—although it requires further study—in the structure of the low trill call part of the aerial display song. Skeel (1978) stated that the low trill call never contains more than three elements in the populations of *hudsonicus* that she examined, and Skeel et al. (2025) reiterated this; I also did not examine any recordings of *hudsonicus* seeming to give more than three elements. But several recordings of individuals of the *phaeopus* group (e.g., XC57912, XC832600, XC965553) appear to feature four elements of that call. The introductory element(s) of the low trill call can be differentiated from preceding low whistle calls by the slight upturn at the end of the note, generally absent from low whistle calls.

There are also several recordings of *phaeopus* group birds giving vocalizations that do not seem readily to fit into any of the categories identified by Skeel for *hudsonicus* (e.g., ML611229892, ML585198541), but the same can be said of some *hudsonicus* recordings (e.g., ML321836621). In general, these analyses are in no way an adequate substitute for a detailed examination of the vocal behavior of the *phaeopus* group and an examination comparable to that of Skeel (1978) should still be performed.

Discussion:

Additional study of the vocalizations of the *phaeopus* group in particular are needed, but it is clear enough that, should consistent vocal differences in fact exist, they must be fairly subtle. Relatively few shorebird species pairs are only subtly differentiated vocally, though there are examples, e.g., Rock (*Calidris ptilocnemis*) and Purple (*C. maritima*) sandpipers and the sand-plovers (Hayman et al. 1986, Hirschfeld et al. 2000, Mlodinow and Boesman 2025; but see Wei et al. 2022, who found some evidence for vocal differentiation in a PCA, albeit with no difference in specific vocal features that one can evaluate in a given recording).

However, that does not necessarily mean that vocal similarity should have veto power over shorebird splits, in general. There are evidently differences in courtship behavior (*hudsonicus* is silent during the ascent phase of the aerial display, while *phaeopus* is reportedly vocal during that phase; Williamson 1946, Skeel 1978) and agonistic behavior (*hudsonicus* reportedly does not present the rump as frequently in agonistic displays and courtship displays as do members of the *phaeopus* group; Williamson 1946, Skeel 1978, Cramp and Simmons 1983). It is not clear that such differences should be considered as less important than vocal differences.

The evolution of shorebird vocalizations is generally very slow (Miller 1996). The two principal lineages of Whimbrel, although they are genetically very well differentiated and some putative mechanisms for reproductive isolation in the event of contact (i.e., differences in displays and in morphology) may be identified, have only been separated for ca. 1 million years. Limited vocal differences may be a signature of the relative youth of this divergence, but that is not quite the same as a veto on the validity of the split.

Interestingly, there are many complexes of shorebird taxa in which the Eurasian member(s) feature contrasting white areas on the underwing (Common Snipe vs. Wilson's, European Golden-Plover vs. American and Pacific, Black-tailed Godwit vs. Hudsonian, etc.), on the rump or back (Green Sandpiper vs. Solitary, both redshanks and both greenshanks and Marsh Sandpiper vs. Willet and both yellowlegs), or both (Bar-tailed Godwit vs. Marbled, Eurasian Whimbrel vs. Hudsonian). The New World and Old World lineages in all these complexes—with the sole exception of Whimbrel—are recognized as separate species.

One could argue that Whimbrel should *not* be split because the two putative daughter species are more vocally similar to one another than are most other shorebird species pairs. Conversely, one could argue that Whimbrel *should* be split because the two putative daughter species are much more morphologically different from one another than many other shorebird species pairs are, including other pairs that show the same kind of interesting dichotomy in rump and/or underwing pattern. Both of these standards are somewhat subjective. The vocal similarity reflects that the divergence is not too old (about 1 million years, in fact), but the morphological difference seems to indicate that the *phaeopus* group has been sufficiently reproductively isolated from *hudsonicus* for long enough to develop the interesting shared plumage patterns characteristic of so many large Eurasian shorebirds and absent from their Nearctic counterparts, including Hudsonian Whimbrel.

The breeding ranges of some subspecies in the *phaeopus* group are widely allopatric: e.g., the nominate subspecies is widely separated from *variegatus* (both by intervening subspecies and, more importantly, by large areas of Siberia in which there are no breeding Whimbrels), in fact more widely than *variegatus* is separated from *hudsonicus*. The winter ranges of these two subspecies also appear not to overlap, with *phaeopus* evidently rare east of the Indian subcontinent and *variegatus* wintering in Southeast Asia and Australia. Despite this, Sangster et al. (2011) and Tan et al. (2019)—using mtDNA and nuclear DNA, respectively—both reported indications of extensive gene flow between *phaeopus* and *variegatus*. In both their phylogenies, these subspecies were not monophyletic with respect to one another, but instead thoroughly intermixed. Both studies, however, recovered *hudsonicus* as strongly and deeply separated. Using genetic differentiation to assess the species status of allopatric populations is fraught, but considering that *variegatus* and *phaeopus* manage to retain high levels of gene flow despite allopatry (or, generously, possibly parapatry) while *variegatus* and *hudsonicus* do not—though *variegatus* is a regular vagrant to the breeding range of *hudsonicus* in Alaska—is suggestive of the presence of some reproductive barrier other than geography capable of separating *hudsonicus* from the *phaeopus* group, but incapable of separating members of the *phaeopus* group from one another.

English Names:

Hudsonian Whimbrel and Eurasian Whimbrel are in common use for *hudsonicus* and the *phaeopus* group, respectively, including in the treatment of AviList/Clements. These names reflect their close relationship and are congruent with the usage adopted by other nomenclatural authorities.

An alternative possibility is to resurrect the name Hudsonian Curlew for *hudsonicus*, under which the taxon was first described, and restrict the name Whimbrel to the *phaeopus* group. The name Hudsonian Curlew predates Hudsonian Whimbrel, but it has been in much less frequent use than Hudsonian Whimbrel in recent decades and removing "whimbrel" from the name of the North American taxon, although it technically restores an older name, does not in fact represent nomenclatural stability from the perspective of most birders and ornithologists alive today. Doing so would also be inconsistent with NACC precedent for the naming of daughter species in cases, as here, where there is not a marked difference in range size.

Recommendation:

Few other complexes recently mooted for splits have such a robust body of literature supporting the split from a genetic standpoint. Together with the very marked, consistent morphological differentiation and some evidence for differences in displays—and the fact that the lump was evidently implemented with no published rationale and no very clear reasons—I think the balance of evidence is sufficient to outweigh the vocal similarity and warrant support of the split, bringing the AOS checklist into alignment with other major checklists. I recommend a YES vote. In the event of a split, I recommend adopting Hudsonian Whimbrel and Eurasian Whimbrel as common names.

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Submitted by: Martin Freeland, Stanford University

Date of Proposal: 18 December 2025

Treat Yucatan Vireo *Vireo magister* as two species

Background: The Yucatan Vireo was first described from Belize by Baird, as *Vireosylva magister* Baird, 1871 (also attributed to Lawrence, 1871). Shortly after having described 13 new species from Grand Cayman in 1886, Cory received another box of birds from "that most interesting island", and bestowed the name *Vireo caymanensis* Cory, 1887, on a specimen that he perceived to be a new species (Cory 1887). Cory provided a detailed description of *caymanensis*, but nevertheless failed to explicitly compare it with any other taxon. That same year, Ridgway (1887) likewise received a single specimen of this vireo from Grand Cayman, which he referred to by Cory's new name *caymanensis*.

At least until 1911, *caymanensis* was treated as a species (Lowe 1911). Ridgway (1904) referred to it as being most like *Vireo magister* of Cozumel (then treated as *Vireo magister cinerea*), but with "pileum, hindneck, and back pale drab-gray instead of deep smoke gray, and coloration in general much paler, especially sides of head and under parts".

Bangs (1916) considered *caymanensis* "very closely related to *V. magister* of the coast of British Honduras and unlike any West Indian form", and stated that it differs only by its paler coloration. He referred to it as *Vireosylva caymanensis* in the earlier sections of his paper, and then in the species accounts as *Vireosylva magister caymanensis*, in what seems likely to have been the first use of this trinomial. This was soon followed by Fisher and Wetmore (1931), with the statement "[t]he junior author agrees with Bangs[13] that this bird should be treated as a race of *Vireo magister*." Hellmayr (1935) then treated *caymanensis* as a subspecies of *magister*, with the footnote "merely differs from the typical race by its paler coloration and more whitish under parts". In Bond's West Indies checklist (Bond 1940), *caymanensis* was treated as a subspecies of *V. magister* without comment, and this treatment has been followed ever since (e.g., Hellmayr 1935, Bond 1947, Blake 1968, and many others). Paynter (1955) furthermore united both subspecies of *magister* under *V. altiloquus* (Vieillot, 1808) with the express justification that they are nowhere sympatric; however, this treatment was not widely taken up and was countered by, e.g., Phillips (1991), on the grounds of *altiloquus* and *caymanensis* co-occurring on the Cayman Islands.

In the intervening years there have been indications of the distinctiveness of *caymanensis* that seem to have gone largely unheeded. Bradley (1994: 395) stated that "Barlow (pers. comm. to Johnston 1971) suggested the Cayman race should be considered a distinct species on the basis of song (lack of response to a recording of *V. m. magister* from Honduras), size and iris color." Nevertheless, Johnston et al. (1971) simply followed the single-species treatment. Much later, in the notes accompanying his compilation tape of vireo recordings, Barlow (1995) merely stated that "[s]ong is also more complex in mainland populations than in those on islands, e.g., *V. m. magister* (cut 56), of circum-Caribbean, lowland Mexico and Belize, has a longer song than does the insular *V. m. caymanensis* (cut 57)". Further evidence of the subtle distinctiveness of *caymanensis* was provided by J. P. O'Neill, who was sent photos of a 1984 vagrant in Texas that he concluded was indeed *Vireo magister*, and furthermore that "[t]he form *V.m. caymannensis [sic]* is much paler and really not like the bird in the photos" (Morgan et al. 1985). Phillips (1991) stated that "[i]n its clear white throat and superciliary, and pale underparts, *caymanensis* agrees better with the *virescens* [*olivaceus*]-"*altiloqua*" group than with the other races of *magister*." Furthermore, Phillips (1991) described nominate *magister* as "heavier than *caymanensis*, less brownish above, and deeper below (dull buffy)."

Note that some checklists and other authorities (e.g., del Hoyo and Collar 2016, Kirwan et al. 2019, Brewer 2020, AviList 2025, Gill et al. 2025) recognize two additional insular subspecies described by A. R. Phillips: *decoloratus* Phillips, 1991, of islets off northern and central Belize (described as larger and duller above, and whiter below than the nominate), and *stilesi* Phillips, 1991, of islets off southern Belize and northern Honduras (described as brighter on wing and tail edgings and rump than nominate *magister*). del Hoyo and Collar (2016), however, considered these "doubtfully valid", and they were not recognized by Clements (1978) nor Clements et al. (2024). In any case, both *decoloratus* and *stilesi* are close to nominate *magister* and the question of their validity seems unlikely to be relevant to the discussion of the taxonomic status of *caymanensis*.

New information:

Now that massive amounts of media are available for the two taxa recognized by Clements et al. (2024) as subspecies of *Vireo magister*, we are in a position to reevaluate this biogeographically unparalleled situation within the Caymans avifauna. It seems that specimens do not tell the full story regarding the distinctiveness of *caymanensis*. In addition to evaluation of media for this proposal, PCR examined 18 specimens of *caymanensis* (including the type) and 6 of nominate *magister* at the Field Museum of Natural History.

Iris color: According to Bradley (1994), J. Barlow considered iris color as one of the reasons why *caymanensis* should be considered specifically distinct. We do not know what differences he may have perceived, however. In the many photographs of both forms viewed, we are unable to discern any difference in iris color. While this does not mean that no differences in iris color exist, if they do they must be subtle.

Size: Another reason given by Barlow (see Bradley 1994) for separate species status for *caymanensis* is size. According to Brewer (2020), male nominate weights range from 19·5–24·8 g, female nominate weights from 16·7–22·5 g, whereas *caymanensis* ranges in weight from 13·5–17 g. The single male *caymanensis* measured by Ridgway (1904) falls within the range of female nominates in most measures, although in bill depth it equaled the smallest-billed female nominate. Comparisons at FMNH between the type series of *caymanensis* and a series of six *magister*, however, do not suggest a marked difference in overall size that would likely be statistically significant, although all bill measurements, wing length, and tail length average slightly smaller in *caymanensis* than in *magister* (PCR measurements).

Structure: Although we have not been able to locate any remarks to this effect, the bill shape of *caymanensis* appears to differ from that of the nominate in being more slender and less deep, and this accords with the measurements in Ridgway (1904). While the nominate often looks quite front-heavy and bulky, *caymanensis* has a slighter, more well-proportioned appearance, somewhat like a warbling-vireo, and this could also account for the above-mentioned difference in weights.

Plumage and soft parts: Although earlier authors mostly dismissed plumage differences as a matter of *caymanensis* only being paler than nominate *magister*, we find that most individuals in good-quality photographs can rather easily be distinguished on a combination of characteristics:

- The lower mandible is typically more uniformly silver-gray in *caymanensis*, right to the base, lacking the pale (often pinkish) base to the mandible in most *magister*. In addition, many (but by no means all) individuals of *caymanensis* have paler cutting edges, not observed by PCR in photos of *magister*.

- The supercilium of *caymanensis* is not broadest at the front, but rather is typically broadest behind the eye, and the dark color of the forecrown rather broadly meets the bill in front, whereas in *magister* the pale supercilium flares out in front and nearly meets in the center, grading somewhat into the crown color. (This feature of the supercilium is very difficult to see in most specimens of the FMNH series due to preparation style, but the broader dark crown where it meets the bill is apparent in the better-prepared specimens.)

Frontal view of typical FMNH specimens of *caymanensis* (left) and *magister* (right).

- The eyeline is very dark and narrow in front of the eye in *caymanensis*, and notably paler behind the eye, whereas it is typically broader in front and more similar in both areas in *magister*. (This is apparent in the better-prepared FMNH specimens.)

- The sides of the face (e.g., auriculars) are typically paler, almost whitish, in *caymanensis*, vs. darker and grayer/browner for *magister*. (This is apparent in all FMNH specimens except one poorly prepared individual.)

Lateral view of typical FMNH individuals of *caymanensis* (above) and *magister* (below).

- The overall plumage of *caymanensis* often looks brown above and rather strongly contrastingly white below and on the supercilium, whereas this impression is not found among good photos of *magister*. (This is apparent in FMNH specimens except for one very worn individual.)

- The undertail coverts of *caymanensis* are washed ochraceous or yellowish, vs. usually whitish in *magister* (sometimes slightly yellowish).

- The wing and tail edgings of *caymanensis* (except when worn) often have a decidedly yellowish-olive cast, unlike those of *magister*.

- The feathers edging the bend of the wing in *caymanensis* can have a yellowish tinge that is lacking in *magister*.

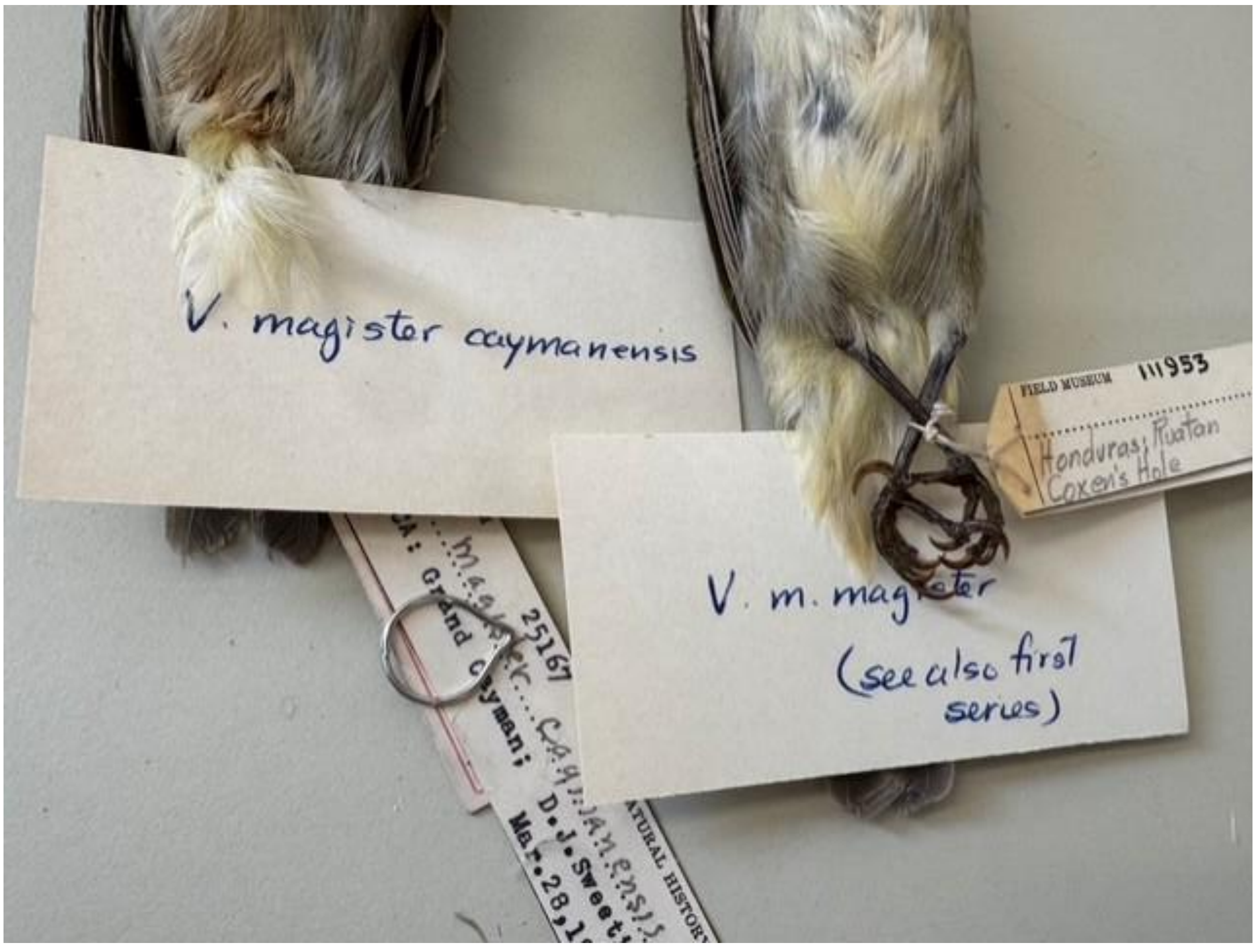
In addition, examination of specimens elucidates some additional differences that are less obvious and less reliably determined in photos.

- The FMNH specimen series confirms that *caymanensis* specimens are typically obviously paler above and below, though a few are only marginally so, than the nominate *magister* available there.

Ventral and dorsal views of FMNH *caymanensis* (left two rows); *magister* (right row).

- In *caymanensis*, the sides, from the sides of the face through the flanks, are dull grayish-white, differing little from the dull whitish central underparts, whereas these areas are fairly dark gray-brown in nominate *magister*, contrasting rather markedly with the whitish central underparts (see ventral photo of series, above).

- The undertail coverts of *caymanensis* are unmarked very pale yellowish, whereas those of nominate *magister* are typically whiter, but with faint to moderately prominent dark mottling to streaking (probably only noticeable in specimens).



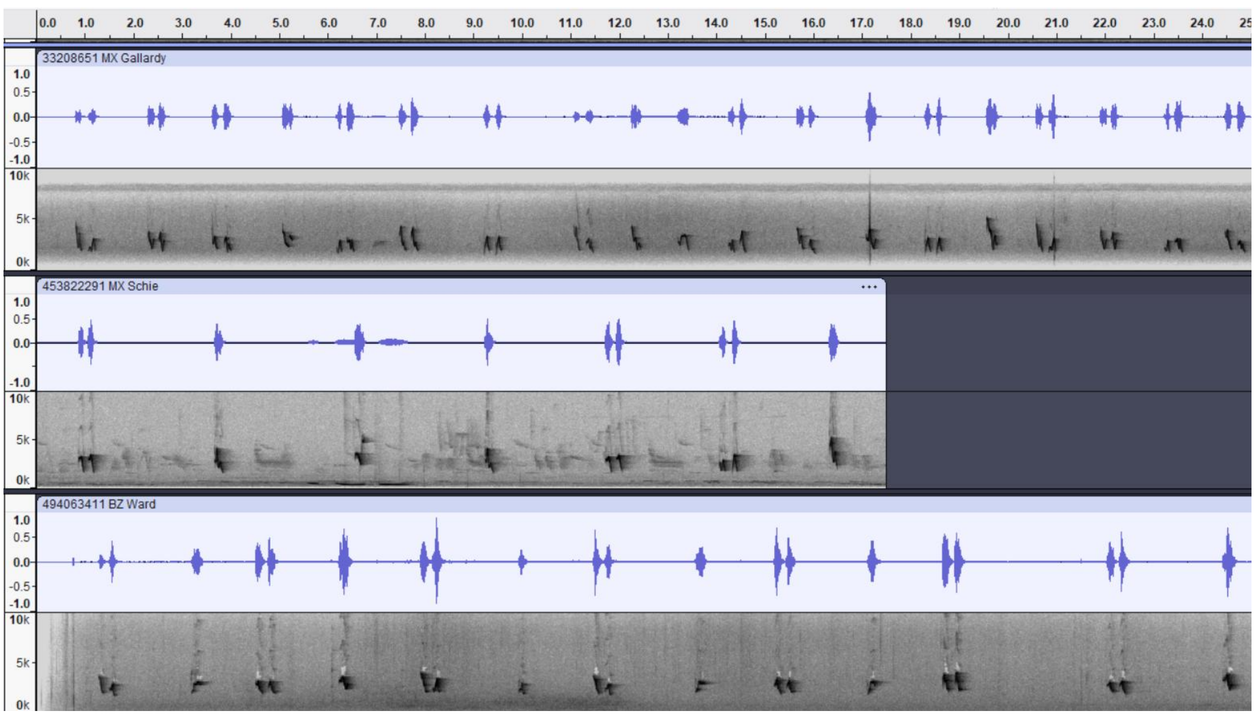
Undertail coverts of typical FMNH individuals of *caymanensis* (left) and *magister* (right).

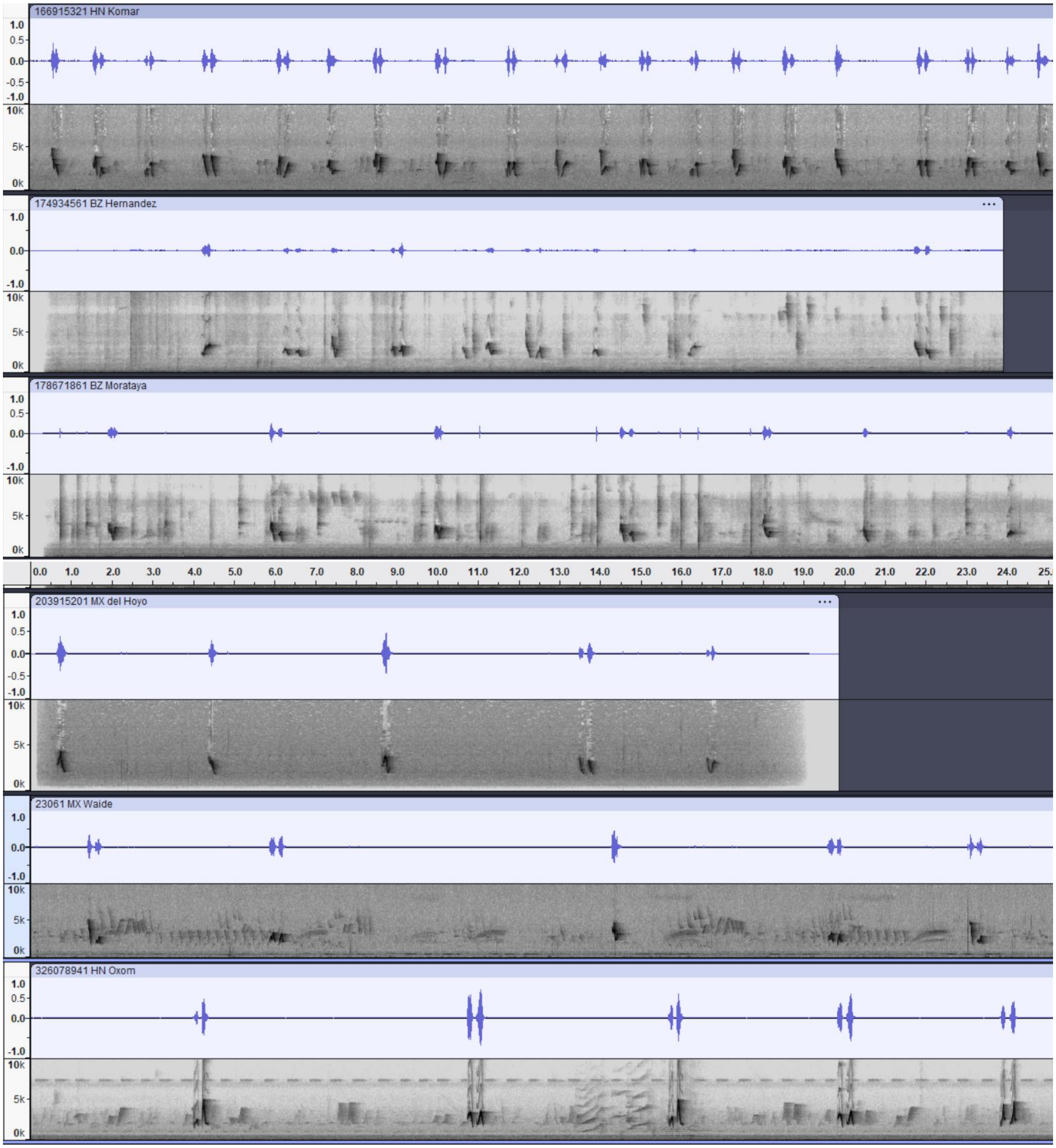
- The inner web of the outer rectrices in *caymanensis* has a prominent, contrasting pale yellowish edging when fresh, whereas that in *magister* is duller and less contrasting.

Obviously, with such drably plumaged birds, one would not expect many marked phenotypic differences. Those that do exist clearly call attention to the need to reevaluate the taxonomic status of *caymanensis*. Although no single character is entirely diagnostic in photos, in combination the two taxa are much more readily separable on phenotype than are, for example, the two recently split warbling-vireos.

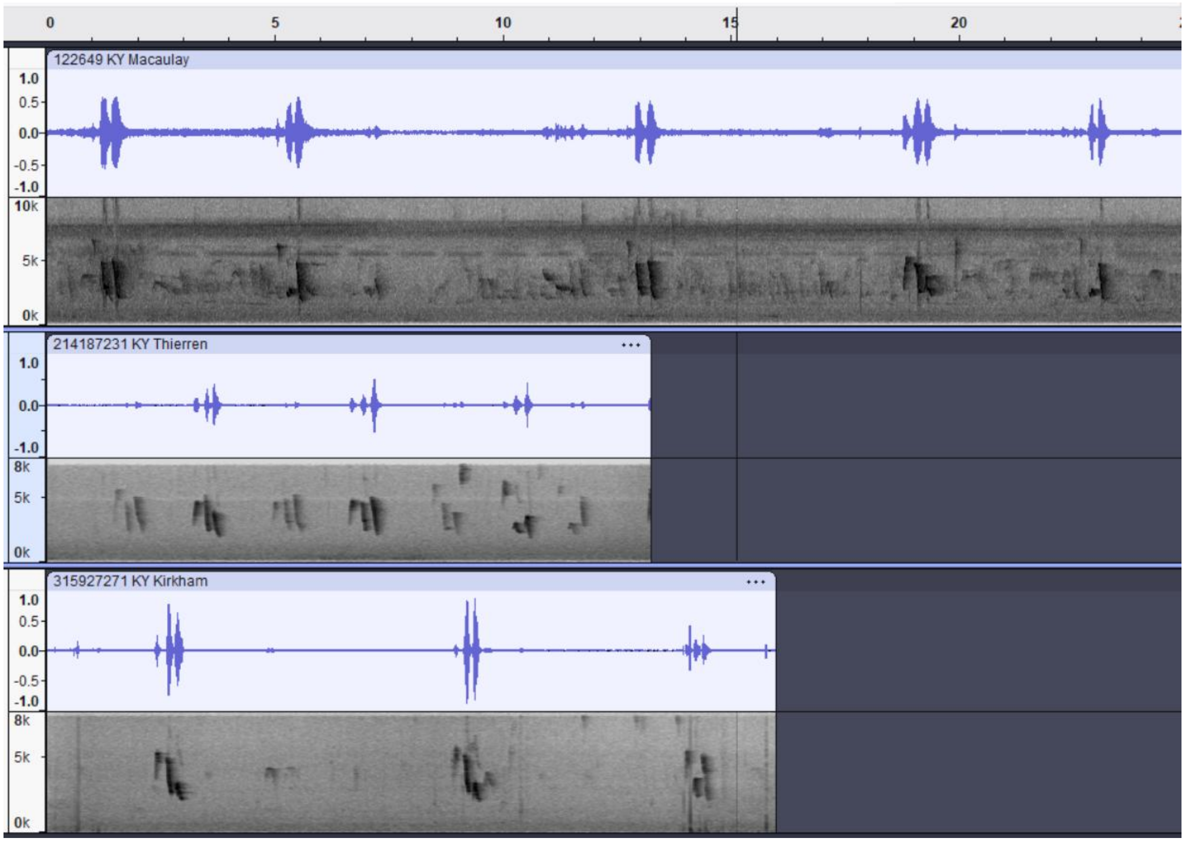
Vocalizations: Although Barlow's statement regarding lack of response by *caymanensis* to playback of song of the nominate was made anecdotally, it provides further impetus to reevaluate the situation. Fortunately, the songs of both taxa are now well-represented in public archives. In three days on Grand Cayman in May 2014, PCR encountered and sound-recorded many *caymanensis* (recordings now on ML), some of them singing nonstop, as vireos tend to do, and in some cases at least three birds could be heard singing at once. The usual song of *caymanensis* consists of three distinct, clear, simple notes, though often the first note is higher and very short and soft. Alternatively, the third note may be more modulated, or, less often, there may be only two notes (at least as captured by recording units), though these typically are mixed in with the more common three-note type. In contrast, the usual song of nominate *magister* is two-noted, sometimes single-noted, with mostly narrower-bandwidth but more complex notes. Most recordings of songs of these two taxa sound clearly different to the human ear; thus, Barlow's observation is unsurprising.

Below are waveforms and sonagrams for nine randomly selected ML recordings by different recordists of song of nominate *magister*:

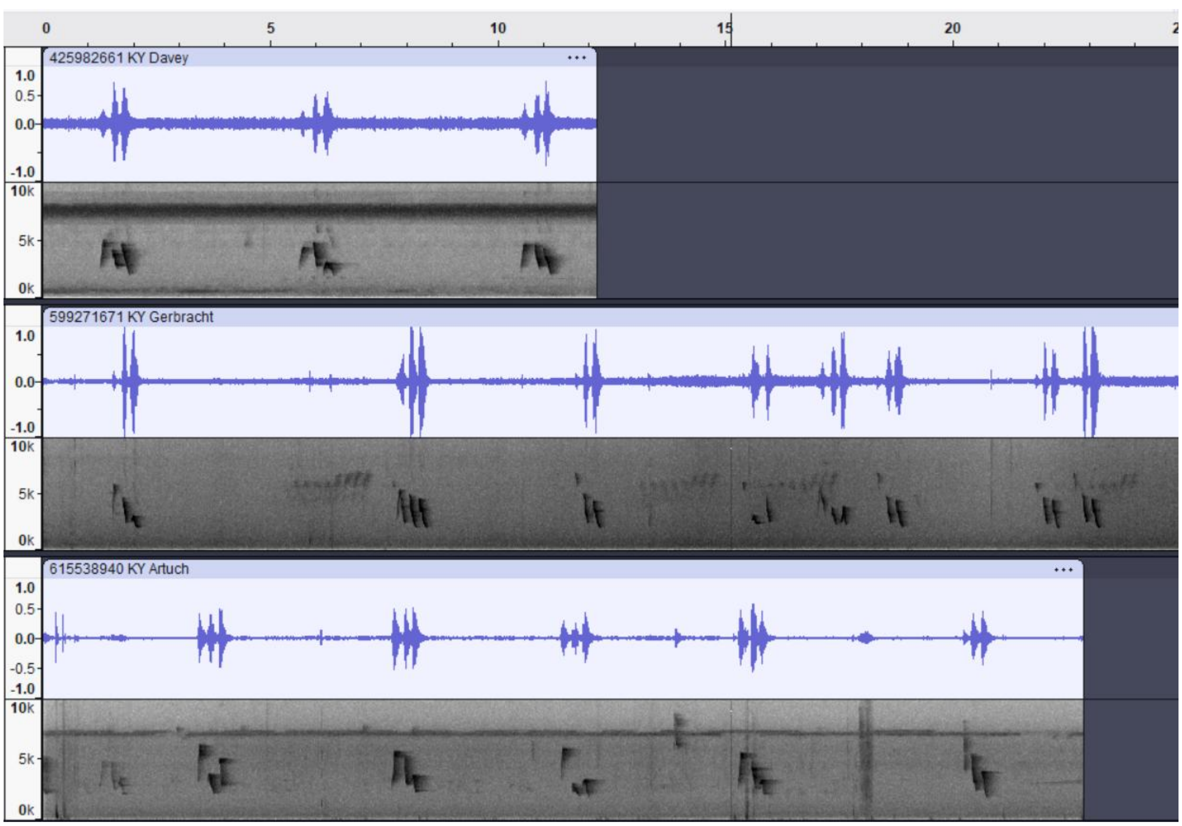




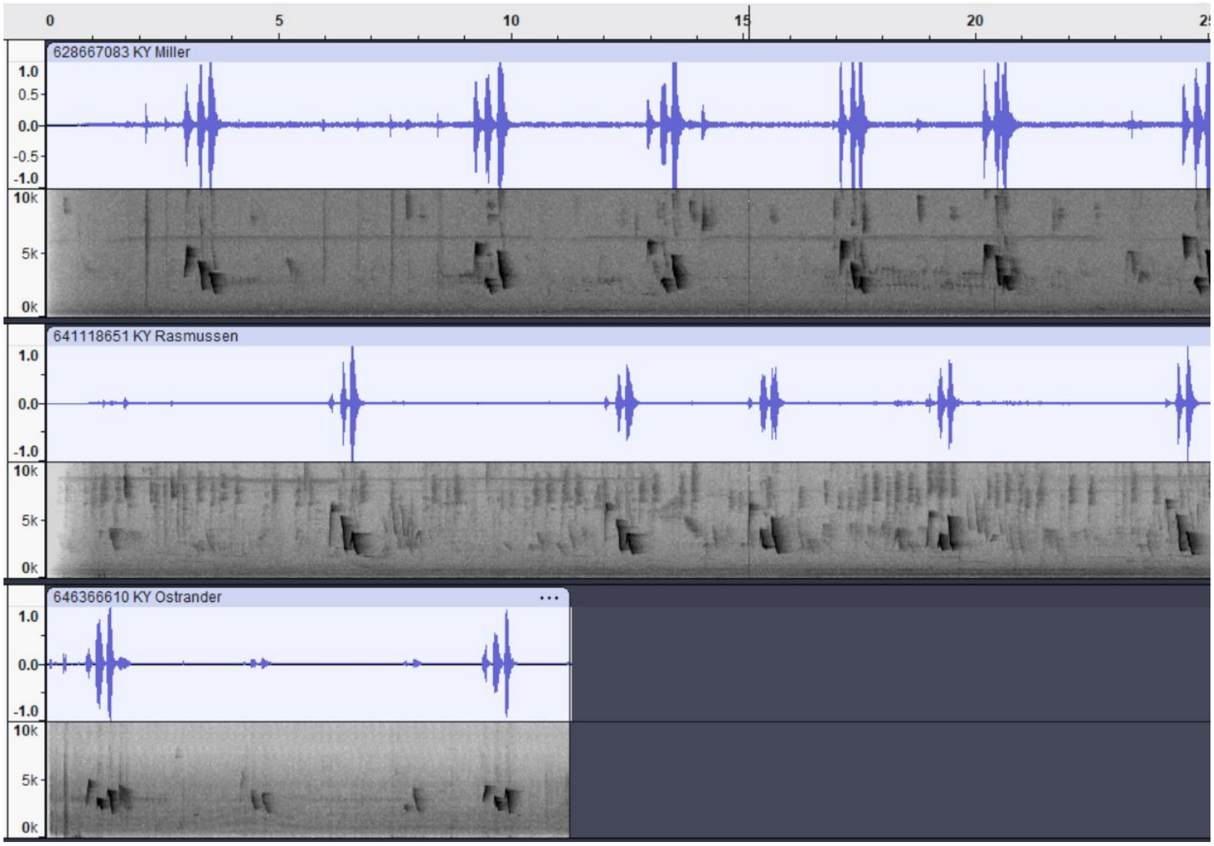
And here are waveforms and sonagrams for nine randomly selected ML recordings by different recordists of song of *caymanensis*:



122649 KY Macaulay
214187231 KY Thierren
315927271 KY Kirkham

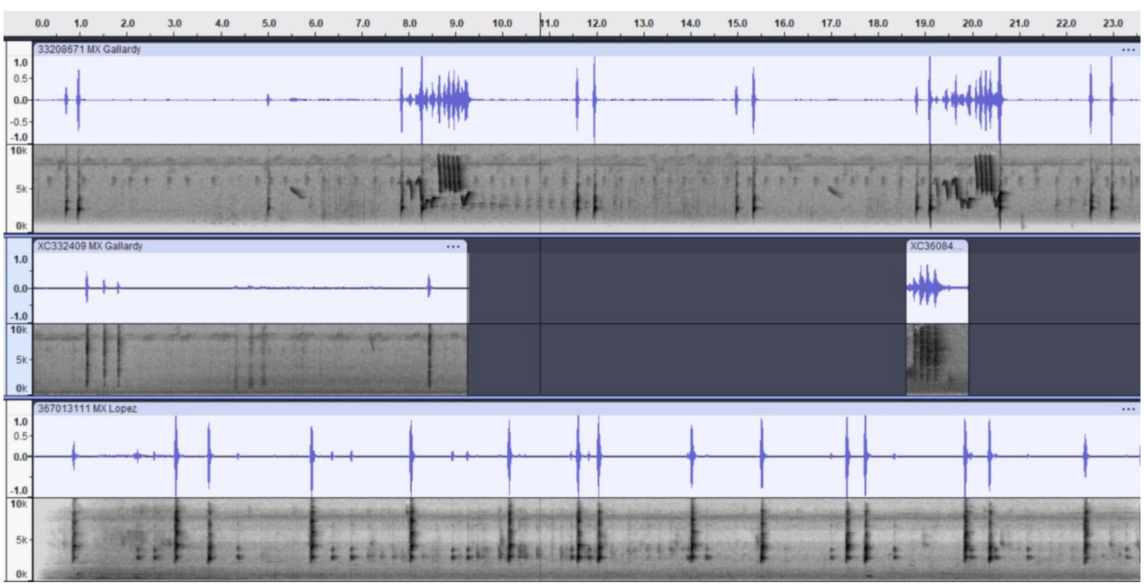


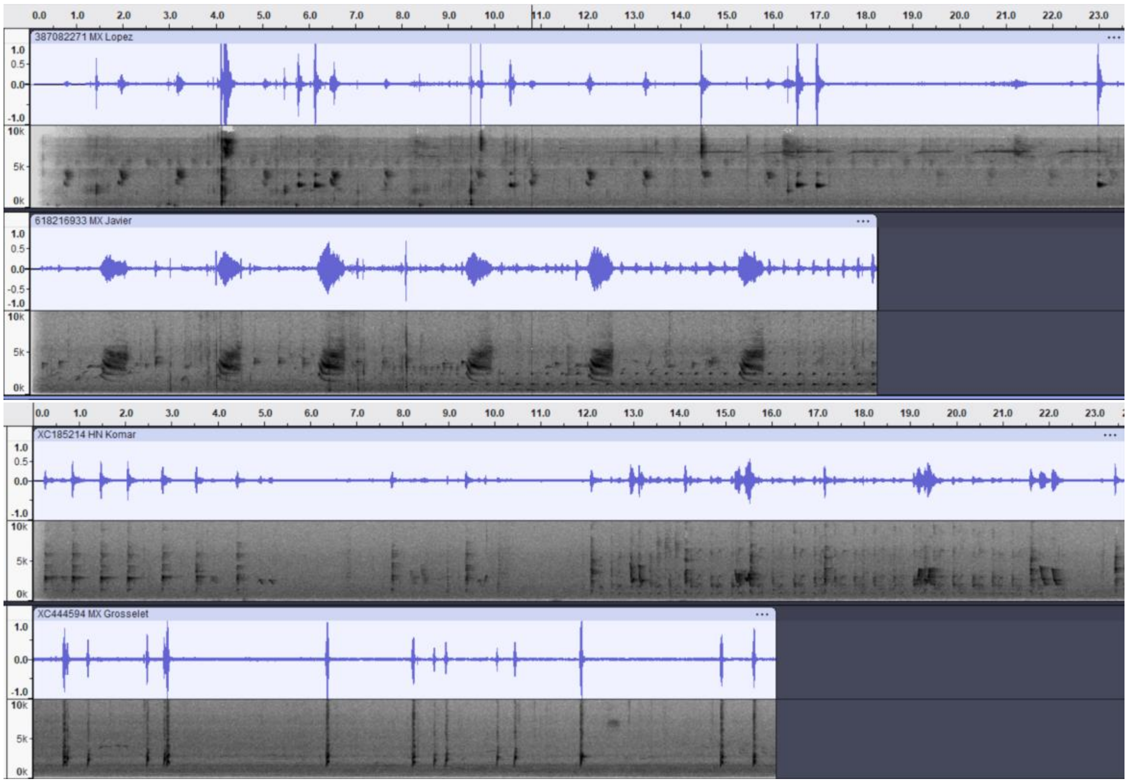
425982661 KY Davey
599271671 KY Gerbracht
615538940 KY Artuch



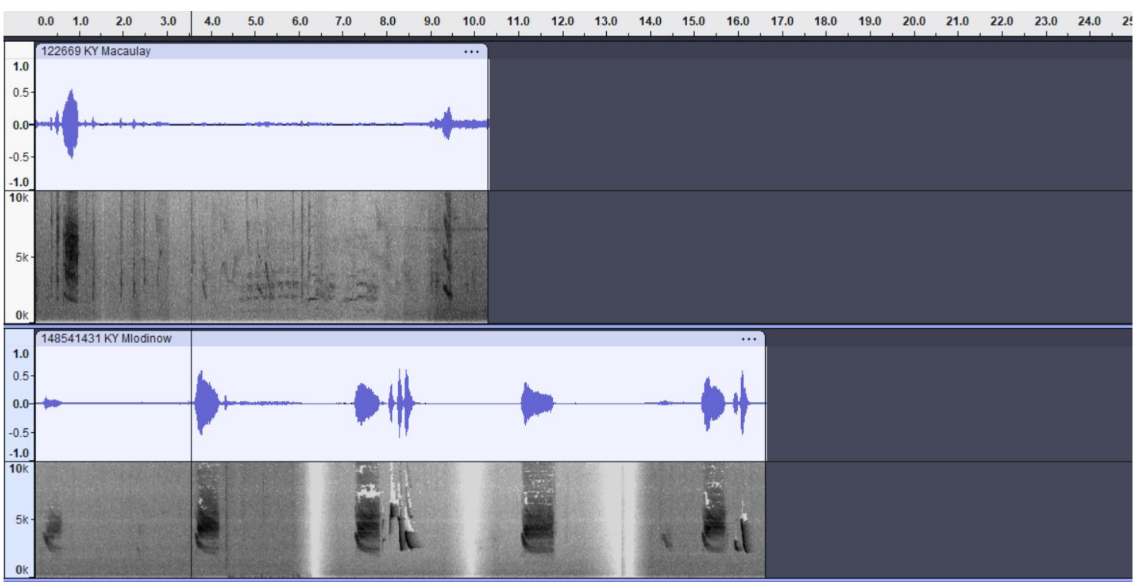
Note especially the 1-2-note song typical of nominate *magister* vs. the usually 3-note song of *caymanensis*. Reference to the numerous xc and ML recordings of both would affirm that they can usually be easily distinguished from the sonagrams alone.

Calls are much less frequently delivered by these vireos, or at least are rarely recorded. Below are call notes attributed to nominate *magister* that PCR found on ML and xc up to 26 Dec 2025:

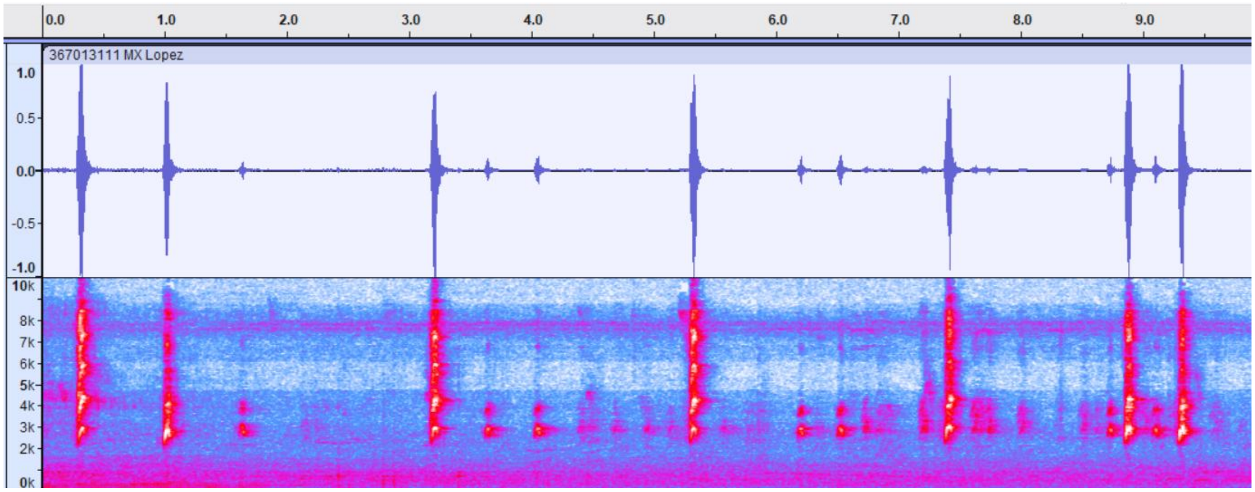




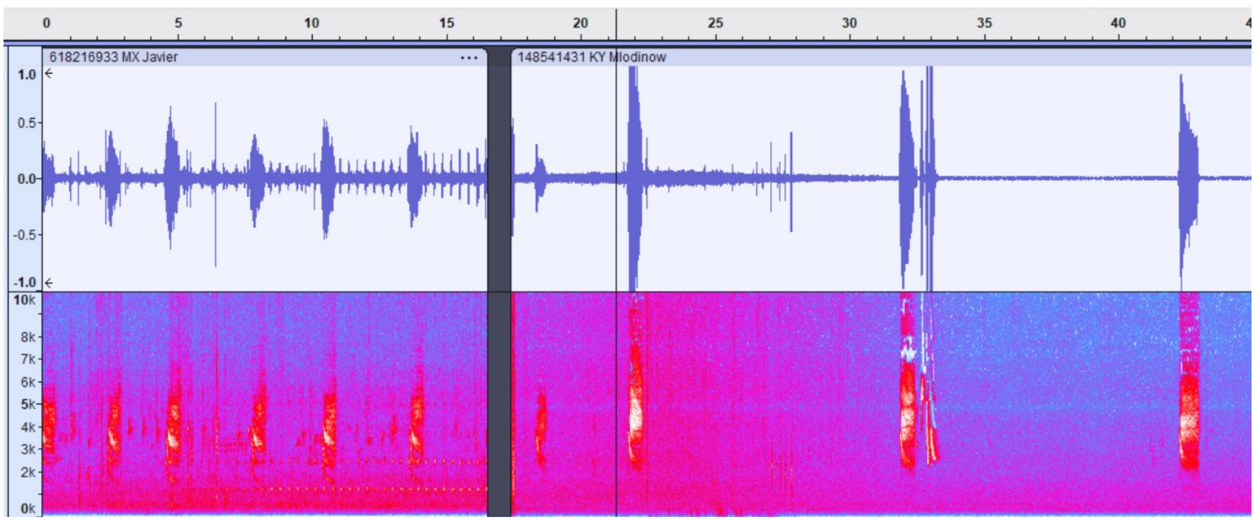
And below are the only two recordings of calls found on ML for *caymanensis* (none on xc):



It can be readily appreciated that the usual call of nominate *magister* is a short, sharp, metallic, slightly upturned *ptchick*! (PCR transliteration; a “bright nasal *piehk*, sometimes doubled” in Howell and Dyer 2023), enlarged below.



If this call type is given by *caymanensis*, it is not yet represented on ML or xc as far as we can determine, and the call types known for *caymanensis* are not very similar to any of those for *magister*. Although the more typical vireo snarls (ML618216933 of *magister* and ML148541431 of *caymanensis*) are at least broadly similar, the former is substantially lower pitched, with the fundamental frequency between 3-4 kHz for *magister* vs. 4-5.5 kHz in *caymanensis* (below, nominate *magister* is on the left, *caymanensis* on the right).



Genetics: Slager et al. (2014) found *Vireo magister magister* from Mexico to be a strongly supported sister to a clade formed by *Vireo olivaceus* from North America and *Vireo flavoviridis* from eastern Mexico. Genetic data do not appear to be available yet for *caymanensis*.

Biogeography: The biogeography of *Vireo magister s.l.* is anomalous, with no other species showing this pattern. Most other Grand Cayman taxa are shared with either Cuba or Jamaica, not with the Yucatan Peninsula. That said, there are no rules, and the Caymans Thick-billed Vireo *Vireo crassirostris alleni* Cory, 1886, also has an anomalous distribution that includes the Bahamas, some Cuban cays, and the Cayman Islands, but not mainland Cuba.

Summary: In summary, the Caymans race *caymanensis* differs strongly from nominate *magister* of the Yucatan region in size, and subtly in several shape and plumage features. It differs considerably in song, for a vireo (bear in mind that neither most people nor Merlin can consistently distinguish Philadelphia and Red-eyed vireo songs), and since these vociferous but plainly plumaged birds surely rely on song for territory holding and mate attraction, that must be relevant to species limits, as is known to be the case in warbling-vireos. No compelling rationale that takes into account the differences now evident has ever been published to our knowledge, and there is an indication of a lack of response to playback.

Effect of this proposal on the NACC area:

If successful, this would result in the addition of a species to the NACC area, and the addition of another endemic species to the avifauna of the Cayman Islands (a self-governing British Overseas Territory).

The photographs of the 1984 vagrant to Texas would seem to leave no room for doubt as to the identity of that individual as nominate *Vireo magister* (Morgan et al. 1985), although Phillips (1991) considered the identification doubtful (mainly because it was not specimen-based).

Recommendation:

We strongly recommend that *caymanensis* be considered a separate species. We recognize that some may prefer to await formal vocal analyses, well-documented playback experiments, and/or genetic data. However, no one has ever provided a rationale for their lumping, other than the spurious statements that *caymanensis* differs from *magister* only in being paler (Bangs 1916, Hellmayr 1935). We consider that the original lump was unjustified and that in this case the burden of proof should fall on demonstrating conspecificity. Furthermore, large numbers of photographs and sound recordings that were of course unavailable until recently clearly demonstrate a considerable number of differences that are inconsistent with conspecificity in this group of morphologically conservative and vocally oriented birds.

English names:

Should this proposal be successful, we consider that the name Yucatan Vireo, which is deeply embedded in the literature, highly familiar, and appropriate (especially with the exclusion of *caymanensis*) should be retained for this far more widely distributed species. The name Grand Cayman Vireo, in our opinion, as used by Ridgway (1904), would be appropriate for *caymanensis*. The race *alleni* of Thick-billed Vireo occurs on all three main Cayman Islands, whereas *caymanensis* has only been demonstrated to occur on Grand Cayman [contra Ridgway 1904, who incorporated Cory's (1889) previous errors on the occurrence of *caymanensis* on Little Cayman and Cayman Brac, as pointed out by Hellmayr (1935)].

Acknowledgments.---Thanks go to the staff of the Bird Division of the Field Museum of Natural History for facilitating examination of specimens and library materials for this proposal.

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Date of Proposal: 26 December 2025