AOS Classification Committee – North and Middle America

Proposal Set 2024-B

18 December 2023, revised 11 January 2024

Change Japanese Bush-Warbler to Japanese Bush Warbler

Background:

AOS-NACC uses a hyphen in the English name for *Horornis diphone* (as Japanese Bush-Warbler), but birds using the group name "Bush Warbler" are spread across five genera and two families and do not form a monophyletic group. NACC guidelines indicate that hyphens should be used in group names only for monophyletic groups; therefore, the hyphen should be removed, changing the English name to Japanese Bush Warbler.

Below are the species named "Bush Warbler" in the Clements or IOC checklists; all members of each genus that includes at least one species with the group name "Bush Warbler" are listed.

Locustella **(Locustellidae)**

- Lanceolated Warbler (*Locustella lanceolata*)
- Bamboo Warbler (*Locustella alfredi*)
- River Warbler (*Locustella fluviatilis*)
- Savi's Warbler (*Locustella luscinioides*)
- **Brown Bush Warbler (*Locustella luteoventris*)**
- Common Grasshopper Warbler (*Locustella naevia*)
- **Long-billed Bush Warbler (Locustella major)**
- **Chinese Bush Warbler (*Locustella tacsanowskia*)**
- **Friendly Bush Warbler (*Locustella accentor*)**
- **Long-tailed Bush Warbler (*Locustella caudata*)**
- **Sulawesi Bush Warbler (*Locustella castanea*)**
- **Seram Bush Warbler (*Locustella musculus*)**
- **Taliabu Bush Warbler (*Locustella portenta*)**
- **Buru Bush Warbler (*Locustella disturbans*)**
- **Baikal Bush Warbler (*Locustella davidi*)**
- **West Himalayan Bush Warbler (*Locustella kashmirensis*)**
- **Spotted Bush Warbler (*Locustella thoracica*)**
- **Taiwan Bush Warbler (*Locustella alishanensis*)**
- **Russet Bush Warbler (*Locustella mandelli*)**
- **Dalat Bush Warbler (*Locustella idonea*)**
- **Sichuan Bush Warbler (*Locustella chengi*)**
- **Javan Bush Warbler (*Locustella montis*)**
- **Benguet Bush Warbler (*Locustella seebohmi*)**

***Elaphrornis* (Locustellidae)**

- **Sri Lanka Bush Warbler (*Elaphrornis palliseri*)**

***Urosphena* (Scotocercidae)** (note that the first two species sometimes placed in *Hemitesia*)

- Neumann's Warbler (*Urosphena neumanni*)
- **Pale-footed Bush Warbler (*Urosphena pallidipes*)**
- Timor Stubtail (*Urosphena subulata*)
- Bornean Stubtail (*Urosphena whiteheadi*)
- Asian Stubtail (*Urosphena squameiceps*)

Cettia (Scotocercidae)

- **Chestnut-crowned Bush Warbler (*Cettia major*)**
- **Gray-sided Bush Warbler (*Cettia brunnifrons*)**
- Chestnut-headed Tesia (*Cettia castaneocoronata*)
- Cetti's Warbler (*Cettia cetti*)

***Horornis* (**Scotocercidae**)**

- **Philippine Bush Warbler (*Horornis seebohmi*)**
- **Japanese Bush Warbler (*Horornis diphone*)**
- **Manchurian Bush Warbler (*Horornis canturians*)**
- **Palau Bush Warbler (*Horornis annae*)**
- **Tanimbar Bush Warbler (*Horornis carolinae*)**
- Shade Warbler (*Horornis parens*), IOC uses **Shade Bush Warbler**
- Odedi (*Horornis haddeni*), IOC uses **Bougainville Bush Warbler**
- **Fiji Bush Warbler (*Horornis ruficapilla*)**
- **Brownish-flanked Bush Warbler (*Horornis fortipes*),** IOC uses **Brown-flanked Bush Warbler**
- **Hume's Bush Warbler (*Horornis brunnescens*)**
- **Yellowish-bellied Bush Warbler (*Horornis acanthizoides*)**
- **Aberrant Bush Warbler (*Horornis flavolivaceus*)**

Recommendation:

I recommend that the hyphen be removed from the English name Japanese Bush-Warbler, changing it to Japanese Bush Warbler.

Submitted by: Marshall Iliff

Date of Proposal: 15 September 2023

Treat *Sula brewsteri* as a separate species from Brown Booby *S. leucogaster*

Background:
Note: *much of the background information below is from VanderWerf et al. (2023)*

The Brown Booby (*Sula leucogaster*) is a pantropical seabird found in the Pacific, Atlantic, and Indian Oceans that exhibits geographic morphological variation. Five subspecies have been described based on differences in color of the plumage, bill, and facial skin (Table 1; Nelson 1978, VanderWerf 2018a, Schreiber & Norton 2020). *Sula l. plotus* has the largest geographic range, from the Red Sea and Indian Ocean east to the central Pacific. In both sexes of *S. l. plotus*, the head is dark brown and the bill is yellow (females) or bluish-yellow (males). The nominate subspecies, *S. l. leucogaster*, occurs in the Atlantic and Caribbean and is similar to *plotus* but has a more pinkish bill. The form of Brown Booby occurring in the eastern Pacific, *S. l. brewsteri*, is the most distinctive morphologically and originally was described as a separate species called Brewster's Booby (*S. brewsteri*; Goss 1888). Male *S. l. brewsteri* have a geographically variable white head, a more grayish-blue bill, and a more greenish-blue gular pouch. In the Gulf of California and the western coast of Mexico south to the Revillagigedo Islands, male *S. l. brewsteri* have a white head and a pale brown upper neck. On some islands off Central America and South America, the white on the head of males is restricted to the forehead, and this form sometimes is considered a separate subspecies, *S. l. etesiaca*, but also has been grouped with *S. l. brewsteri* (Harrison 1983, Schreiber & Norton 2020). The form breeding on Clipperton Island is the palest, with the entire head and neck white in males, and is sometimes referred to as *S. l. nesiotes* (Heller and Snodgrass 1901, Pitman & Balance 2002, Schreiber & Norton 2020).

As noted above, Brewster's Booby originally was described as a species, *S. brewsteri*, by Goss (1888) based on type specimens from San Pedro Mártir Island, Mexico. In the description, Goss noted that characteristics of the species included the pale color of the head and neck, especially in the male, a dark brown iris with a narrow outer ring of grayish-white, and "unfeathered parts also differently colored." In 1944, *S. l. brewsteri* was lumped with other forms of the Brown Booby (Wetmore et al. 1944), who cited "Peters, checklist, 1, 1931" and Wetmore (1939) as justification for the lump. Wetmore (1939) stated that "while apparently uniform over large areas of the tropical oceans of the world there are three (barely possibly four) races of *Sula leucogaster* to be recognized…on the Pacific coast of the Americas… These differ from all other subspecies of the species." Wetmore (1939) discusses at length the variation among the forms in the eastern Pacific, which seems to support their distinction, and did not offer any explanation for why *S. l. brewsteri* should be lumped with other forms of the Brown Booby, yet he did so, and this, paradoxically, served as the basis for the lumping by Wetmore et al (1944).

Genetic population structure of Brown Boobies largely matches patterns of morphological variation (Steeves et al. 2003, Morris-Pocock et al. 2010, 2011). Mitochondrial haplotypes were not shared between the eastern and central Pacific or between the eastern Pacific and Caribbean (Steeves et al. 2003), and colonies grouped into four major, genetically differentiated populations; Caribbean, central Atlantic, Indo-central Pacific, and eastern Pacific (Morris-Pocock et al. 2011). The eastern Pacific population was found to be the most different genetically and was estimated to have diverged from all other populations approximately one million years ago (Morris-Pocock et al. 2011). These populations have diverged because of a combination of physical barriers (the Isthmus of Panama and the Eastern Pacific Basin) and a behavioral tendency in the Brown Booby to forage closer to shore than other booby species (Steeves et al. 2003).

Table 1. Distinguishing characteristics of Brown Booby subspecies. Copied from VanderWerf et al. (2023).

Character	*plotus*	*leucogaster*	*brewsteri*	*nesiotes*	*etesiaca*
Male head color	brown	brown	white head and upper neck	white head and entire neck	white forehead
Female head color	brown	brown	whitish forehead	whitish forehead	whitish forehead
Male bill color	bluish-yellow	bluish-yellow	grayish-blue	grayish-blue	grayish-blue
Female bill color	yellow	pinkish yellow	pinkish yellow	pinkish yellow	pinkish yellow
Ventral lesser wing coverts	white	white	white with brown bar	white with brown bar	?

New Information:

Three types of new information support recognizing Brewster's Booby as a separate species: 1) morphological data demonstrating that males and females of the subspecies differ in additional ways not previously recognized; 2) behavioral data on pairing patterns showing that interbreeding between *plotus* and *brewsteri* is rare despite increasing sympatry; 3) information on behavioral ecology demonstrating that the morphological differences between *plotus* and *brewsteri* act as a reproductive isolating mechanism that inhibits interbreeding. The information on behavioral ecology is not that new, but its relevance to taxonomy does not seem to have been considered previously.

1. Morphology. Descriptions of Brown Booby subspecies relied primarily on the appearance of males and did not consider the appearance of females. VanderWerf (2018) described differences between females of the subspecies that can be used to identify them in the field: female *S. l. brewsteri* have a pinker bill and paler forehead than female *S. l. plotus*. Females can be distinguished as reliably as males of these subspecies, although the characters used to identify females are less obvious. VanderWerf (2018) also showed that the underwing coverts in both sexes of *S. l. brewsteri* are less extensively white than those of *S. l. plotus*.

I have unpublished data showing that iris color and bill curvature also differ among Brown Booby subspecies, but I am still in the process of collecting and analyzing these data. I do not think this information about additional distinguishing characters is needed to assess the taxonomy of Brown Boobies, but it will be useful in their identification.

2. Pairing Patterns. The Eastern Pacific Basin is an enormous, island-free ocean area that for millennia has formed a physical barrier to dispersal and promoted geographic differentiation of many seabirds, including the Brown Booby (Avise et al. 2000, Steeves et al. 2003, Morris-Pocock et al. 2011). Recently, Brown Boobies have been overcoming the barrier posed by the Eastern Pacific Basin and have dispersed eastward and westward across the Pacific. VanderWerf et al. (2008) documented an increasing number of *S. l. brewsteri* present and breeding in the central Pacific, and Kohno and Mizutani (2011) documented the occurrence and breeding of *S. l. brewsteri* males on islands near Japan. Isla San Benedicto, in the Revillagigedo Islands off the west coast of Mexico, was recolonized by Brown Boobies following a volcanic eruption in 1952, and both *plotus* and *brewsteri* males are present and breeding on the island (Pitman and Ballance 2002, Morris-Pocock et al. 2011). VanderWerf et al. (2023) showed that the westward expansion of *brewsteri* has continued, resulting in even greater sympatry between the subspecies. The increasing sympatry of *S. l. brewsteri* and *S. l. plotus* could result in gene flow and erosion of differentiation between these forms, if they interbreed.

VanderWerf et al. (2023) also collected data on pairing patterns in locations where both forms were known to breed together. Quantitative data showed pairing by *S. l. brewsteri* and *S. l. plotus* was primarily assortative and interbreeding was rare (Table 2). At Moku Mana, Maui in 2021, there were fewer mixed pairs (zero), than expected by chance ($X^2 = 18.00$, df = 1, $p < 0.001$). On Palmyra, there also were fewer mixed pairs than expected by chance ($X^2 = 181.1$, df = 1, $p < 0.001$), although the sample size was small.

Anecdotal evidence also indicates that pairing was primarily assortative and interbreeding was rare. On Wake Island in 2021, J. Gilardi observed 301 *S. l. plotus* pairs, six *S. l. brewsteri* males, and one *S. l. brewsteri* female, which was paired with one of the male *S. l. brewsteri*. The other five male *S. l. brewsteri* on Wake that year did not attract a mate despite the presence of many unpaired *S. l. plotus* females. On Wake in 2022, J. Gilardi observed that the *brewsteri-brewsteri* pair remained together and raised another chick, but the other five *brewsteri* males were unpaired. On Wake in 2023, J. Gilardi observed seven male and four female *brewsteri*; all 4 *brewsteri* females were paired with *brewsteri* males, and the three single *brewsteri* males built nests but had no mate. On Moku Manu, Oahu, in May 2021, E. VanderWerf observed 93 *S. l. plotus* pairs and only one male and one female *S. l. brewsteri*, which were paired with each other and had a large chick. In September 2022, E. VanderWerf observed five *S. l. brewsteri* females on Moku Manu, all of which were unpaired. On Laysan, a nest with a male *brewsteri* and female *plotus* was reported in 1998 (VanderWerf et al. 2008), but re-examination of photos using identification criteria from VanderWerf (2018) revealed that the female was *S. l. brewsteri*, representing another instance in which a male and female *brewsteri* paired with each other amid large numbers of male and female *plotus*. The only instances of interbreeding occurred in locations where no female brewsteri were present. On Midway, J. Plissner observed a male *brewsteri* x female *plotus* pair that raised a chick in 2020, when no female *brewsteri* were present. At Nakanokamishima Island, Japan, one *brewsteri* male paired and raised offspring with a *plotus* female from 2012-2014, but a second *brewsteri* male was not able to attract a mate despite frequent courtship attempts with *plotus* females (Kohno and Mizutani 2015).

Moku Mana Islet off the north coast of Maui is a particularly interesting case. It was colonized by Brown Boobies recently, with the first nest documented in 2004 by J. Penniman. In 2021, the island held twice as many *S. l. brewsteri* pairs as *S. l. plotus* pairs, with no mixed pairs. This is the easternmost location in the Hawaiian Islands where Brown Boobies breed, and the colonies were formed by individuals dispersing from the east (*S. l. brewsteri*) and west (*S. l. plotus*), much like the situation on Isla San Benedicto (Pitman and Ballance 2002).

Table 2. Pairing patterns of Brown Boobies by subspecies, including only cases in which the identity of both parents was known. Copied from VanderWerf et al. (2023).

Location	Year	Male *plotus* + female *plotus*	Male *plotus* + female *brewsteri*	Male *brewsteri* + female *plotus*	Male *brewsteri* + female *brewsteri*
Palmyra Atoll †	2014	~200	1	0	8
Moku Mana	2021	6	0	0	12
Moku Manu	2021	93	0	0	1
Laysan	1998	~70	0	0	1
Midway ‡	2020	15	NA	1	NA
Wake Island	2023	301	0	0	4
Nakanokamishima ‡	2009	~900	NA	1	NA

† At Palmyra 30 nests were observed with at least one *brewsteri* parent, but some nests were attended by a single parent and the identity of the mate was unknown.

‡ At Midway and Nakanokamishima no female *brewsteri* were present so there was no chance of a mixed pair.

3. Reproductive Isolating Mechanisms. Mate choice and breeding biology of Brewster's Booby have been studied extensively in Mexico, and this literature is important for understanding the pairing patterns observed in the central Pacific. Most importantly, López-Rull et al. (2016) showed that male *S. l. brewsteri* with their head painted brown to look like male *S. l. plotus* were treated aggressively by their mate and that the level of aggression was higher at a colony closer to the zone of overlap between the forms. They concluded that female dislike of foreign males may function as a reproductive barrier in populations close to contact zones, where the risk of possibly maladaptive hybridization is highest. Montoya et al. (2018) showed that the carotenoid-based greenish-blue color of the gular pouch of males was energetically expensive to maintain, that its chroma peaked during courtship, and that it may serve as a reliable signal of individual quality. Michael et al. (2018) showed that color of the gular pouch in Brown Boobies in México was related to foraging range and location, with individuals in poor body condition constrained to low-cost, short-distance foraging trips closer to shore, where they were unable to obtain the pelagic diet necessary for production of the carotenoid-rich gular pouch ornament important in mate attraction. Cumulatively, this research indicates that the morphological differences between *S. l. brewsteri* and *S. l. plotus* act as an isolating mechanism that inhibits interbreeding.

The morphological and genetic differences between *S. l. brewsteri* and other forms of the Brown Booby meet the standards for species recognition under the typological (or morphological) and phylogenetic species concepts, respectively (Mayr 2000, Wheeler 2000). The behavioral evidence described in this study, increasing sympatry with primarily assortative mating and rare interbreeding, meets the standards of the biological species concept (Mayr 2000). Cumulatively, all three forms of evidence suggest that it would be appropriate to consider Brewster's Booby as a separate species again.

Occasional hybridization between *S. l. brewsteri* and *S. l. plotus* and the presence of some individuals of intermediate appearance do not constitute evidence that they are conspecific. Similar situations exist in two other pairs of booby species, specifically Blue-footed Booby (*S. nebouxii*) and Peruvian Booby (*S. variegata*), and Masked Booby (*S. dacylatra*) and Nazca Booby (*S. granti*). Blue-footed and Peruvian boobies are largely allopatric, but breeding colonies occur together on two islands off Peru, where mating is primarily assortative, with few instances of hybridization, resulting in genetic differentiation and only limited introgression (Figueroa 2004, Figueroa and Stucchi 2008, Taylor et al. 2012). Nazca Booby was considered a subspecies of Masked Booby but was split into a separate species based on morphological differences and assortative mating (Pitman and Jehl 1998, AOU 2000), which subsequently was supported by evidence of genetic differentiation (Friesen et al. 2002).

English name:

For the English common name, according to NACC guidelines for English names, when a split restores species status and a previously existing English name exists, that name would be resurrected. In this case the name would have been Brewster's Booby. However, given the recent decision by AOS to change all eponymous common bird names, the name Brewster's Booby is no longer an option. Below I have listed several possible alternative English common names, grouped by whether they are geographical or descriptive of the bird. I have offered some discussion of each name, including the pluses and minuses. My personal favorite is Cocos Booby and I recommend that as the new English common name for. *S. brewsteri*.

GEOGRAPHIC NAMES

Cocos Booby. The rationale for this name is similar to that of the Nazca Booby, which is named for a tectonic plate in the earth's crust that contains part of the range of that species. The Cocos Plate is located in the eastern Pacific and is adjacent to and north of the Nazca Plate. The Cocos Plate extends off the west coast of the Americas from Panama north to the Mexican state of Jalisco (Figure 1). The volcanoes and earthquakes in western Mexico and Central America are fueled by plate convergence and subduction of the Cocos Plate under the North American and Caribbean plates. The Cocos Plate is named for Cocos Island, which rides upon the plate and is the only part of the plate above sea level. Cocos Island is an important nesting site for *S. brewsteri*, though the colonies there are not among the largest of the species. One downside to this name is that the Cocos Plate encompasses only a small portion of the geographic range of *S. brewsteri*, though it contains a larger proportion of the range than the Nazca Plate contains of the Nazca Booby range. The parallel naming of Nazca Booby and Cocos Booby would provide a logical, geographical rationale for these two species that overlap considerably in range.

Mexican Booby. The name Mexican Booby would recognize that much of the range of *S. brewsteri* occurs in Mexico and Mexican Waters and that the type specimens were collected in Mexico. Two drawbacks to this name are that 1) two subspecies that would be included with *S.*

brewsteri (*S. b. nesiotes* and *S. b. etesiaca*) are not found in Mexico, and 2) increasingly less of the range of *S. brewsteri* will be in Mexico if the current range expansion continues across the Pacific. These same drawbacks also pertain to the name Cocos Booby. The name Mexican Booby would provide historical context for the likely origin for many of these dispersing birds.

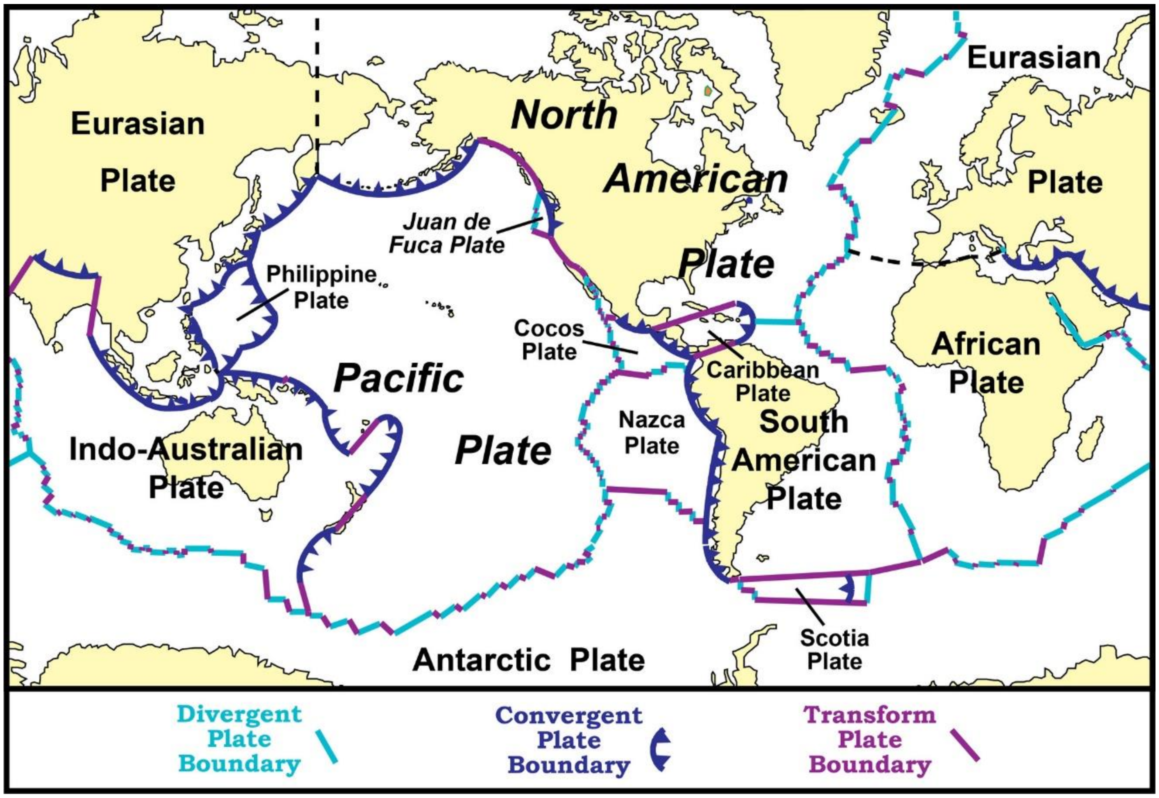


Figure 1. Map of the earth's tectonic plates, showing the location of the Cocos Plate. From National Park Service: https://www.nps.gov/subjects/geology/plate-tectonics-evidence-of-plate-motions.htm

Tropical Eastern Pacific Booby. The Tropical Eastern Pacific is a name applied to one of twelve marine realms that cover the coastal waters and continental shelves of the world's oceans as part of a global classification system called Marine Ecoregions of the World (MEOW), which was devised by an international team, including conservation organizations, academic institutions and intergovernmental organizations (Spalding et al. 2007). It extends along the Pacific Coast of the Americas, from the southern tip of the Baja California Peninsula in the north to northern Peru in the south. The range of *S. brewsteri* largely coincides with this geographic unit, though the species range does extend farther to the north and south. Among geographic names this would be the most geographically appropriate because it coincides most the with range of the species. The main downside to this name is that it is long and cumbersome, consisting of four words.

DESCRIPTIVE NAMES

White-headed Booby. The name White-headed Booby is based on the most distinctive character of the species, the white head of males, which was the character that seems to have contributed most to its description as a separate species. However, this name has two significant drawbacks that in my opinion disqualify it: 1) it would pertain only to males of the *brewsteri* and *nesiotes* forms, and not to males of *etesiaca*; and 2) it would not pertain to females of any form, and thus would perpetuate the neglect of female appearance that has occurred already.

Pale-headed Booby. Pale-headed Booby would be preferable to White-headed Booby because it would apply to females and males of all forms that would be included in *S. brewsteri*. The main downside is that it seems a little bland.

Recommendation:

I recommend that *S. l. brewsteri* be split from other forms of the Brown Booby into a separate species. This split has been mentioned previously (Schreiber and Norton 2020), and the additional evidence described in this proposal strengthens the rationale for the split. The scientific name for the re-split species would revert to *S. brewsteri*, as it was originally described by Goss (1888). *Sula brewsteri* should include all pale-headed subspecies that breed in the eastern Pacific, including *nesiotes* and *etesiaca* recognized by some authors (Schreiber and Norton 2020). If subspecific status continues to be recognized for these forms, they would become *S. brewsteri nesiotes* and *S. brewsteri etesiaca*, respectively. Although *etesiaca* males have a pale, not white, head, *etesiaca* females are similar to females in other forms of *brewsteri*, and genetically *etesiaca* clearly grouped with other populations in the eastern Pacific (Steeves et al. 2003, Morris-Pocock et al. 2010). No changes are needed in taxonomic status or nomenclature of the other Brown Booby subspecies, which are more similar to each other morphologically and genetically (Morris-Pocock et al. 2011). Thus, *S. l. plotus* and *S. l. leucogaster* would remain subspecies of the Brown Booby.

For the English name, I recommend Cocos Booby, for the reasons discussed above.

Literature Cited:

Avise, J. C., W. S. Nelson, B. W. Bowen, and D. Walker. 2000. Phylogeography of colonially nesting seabirds, with special reference to global matrilineal patterns in the sooty tern (*Sterna fuscata*). Molecular Ecology 9:1783-1792.

Del Hoyo, J., A. Elliott, and J. Sargatal. 1992. Handbook of birds of the world. Volume 1. Barcelona: Lynx Editions.

Figueroa, J. 2004. First record of breeding by the Nazca Booby *Sula granti* on Lobos de Afuera Islands, Peru. Marine Ornithology 32:117-118.

Figueroa, J., and M. Stucchi. 2008. Possible hybridization between the Peruvian Booby *Sula variegata* and the Blue-footed Booby *S. nebouxii* in Lobos de Afuera Islands, Peru. Marine Ornithology 36:75-76.

Friesen, V. L., D. J. Anderson, T. E. Steeves, H. Jones, and E. A. Schreiber. 2002. Molecular support for species status of the Nazca Booby (*Sula granti*). Auk 119:820–826.

Goss, N. S. 1888. New and rare birds found breeding on the San Pedro Martir Isle. Auk 5:240-244.

Heller, E. and Snodgrass, R.E. 1901. Descriptions of two new species and three new subspecies of birds from the Eastern Pacific, collected by the Hopkins-Stanford expedition to the Galapagos Islands. Condor:74-77.

Kohno, H., and A. Mizutani. 2011. The first record of Brewster's Brown Booby *Sula leucogaster brewsteri* for Japan. Journal of the Yamashina Institute for Ornithology 42:147–153.

Kohno, H., and A. Mizutani. 2015. First record of breeding behaviour of Brewster's Brown Booby *Sula leucogaster brewsteri* in Japan. Journal of the Yamashina Institute for Ornithology 46:108-118.

López-Rull, I., N. Lifshitz, C. M. Garcia, J. A. Graves, and R. Torres. 2016. Females of a polymorphic seabird dislike foreign-looking males. Animal Behaviour 113:31-38.

Michael, N.P., R. Torres, A. J. Welch, J. Adams, M. E. Bonillas-Monge, J. Felis, L. Lopez-Marquez, A. Martínez-Flores, and A. E. Wiley. 2018. Carotenoid-based skin ornaments reflect foraging propensity in a seabird, *Sula leucogaster*. Biology letters 14:20180398.

Montoya, B., C. Flores, and R. Torres. 2018. Repeatability of a dynamic sexual trait: Skin color variation in the Brown Booby (*Sula leucogaster*). The Auk: Ornithological Advances 135:622-636.

Morris-Pocock, J. A., D. J. Anderson, and V. L. Friesen. 2011. Mechanisms of global diversification in the Brown Booby (*Sula leucogaster*) revealed by uniting statistical phylogeographic and multilocus phylogenetic methods. Molecular Ecology 20:2835–2850.

Morris-Pocock, J. A., T. E. Steeves, F. A. Estela, D. J. Anderson, and V. L. Friesen. 2010. Comparative phylogeography of Brown (*Sula leucogaster*) and Red-footed Boobies (*S. sula*): the influence of physical barriers and habitat preference on gene flow in pelagic seabirds. Molecular Phylogenetic and Evolution 54:883–896.

Nelson, J. B. 1978. The Sulidae. Oxford University Press, London.

Pitman, R. L., and L. T. Ballance. 2002. The changing status of marine birds breeding at San Benedicto Island, Mexico. Wilson Bulletin 114: 11-19.

Pitman, R., and J. Jehl. 1998. Geographic variation and reassessment of species limits in the "Masked" boobies of the eastern Pacific Ocean. Wilson Bulletin 110:155–170.

Rauzon, M. J., D. Boyle, W. T. Everett, and J. Gilardi. 2008. The status of birds of Wake Atoll. Atoll Research Bulletin 561:1-41.

Schreiber, E. A., and R. L. Norton. 2020. Brown Booby (*Sula leucogaster*), version 1.0 In Birds of the World (S.M. Billerman, Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA: https://doi.org/10.2173/bow.brnboo.01

Spalding, M.D., H. E. Fox, G.R. Allen, N. Davidson, et al. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. Bioscience 57(7):573–583.

Steeves, T. E, D. J. Anderson, H. Mcnally, M. H. Kim, and V. L. Friesen. 2003. Phylogeography of *Sula*: the role of physical barriers to gene flow in the diversification of tropical seabirds. Journal of Avian Biology 34:217-223.

Steeves, T. E, D. J. Anderson, and V. L. Friesen. 2005. A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the Masked Booby (*Sula dactylatra*). Molecular Ecology 14:3877-3887.

Taylor, S. A., D. J. Anderson, C. B. Zavalaga, and V. L. Friesen. 2012. Evidence for strong assortative mating, limited gene flow, and strong differentiation across the Blue-footed/Peruvian booby hybrid zone in northern Peru. Journal of Avian Biology 43:311-324.

VanderWerf, E. A. 2018a. Geographic variation in the Brown Booby. Field identification of males and females by subspecies. Birding 50:48-54.

VanderWerf, E. A., B. L. Becker, J. Eijzenga, and H. Eijzenga. 2008. Nazca Booby *Sula Granti* and Brewster's Brown Booby *Sula leucogaster brewsteri* in the Hawaiian Islands and Johnston and Palmyra Atolls. Marine Ornithology 36:67–71.

VanderWerf, E. A., M. Frye, J. Gilardi, J. Penniman, M. Rauzon, H. D. Pratt, R. S. Steffy, and J. Plissner. 2023. Range expansion, pairing patterns, and taxonomic status of Brewster's Booby *Sula leucogaster brewsteri*. Pacific Science 77:1-12.

Wetmore, A. 1939. Birds from Clipperton Island collected on the presidential cruise of 1938. Smithsonian Miscellaneous Collections 98(22):1-6.

Wetmore, A., Friedmann, H., Lincoln, F.C., Miller, A.H., Peters, J.L., van Rossem, A.J., Van Tyne, J., and Zimmer, J.T. 1944. Nineteenth supplement to the American Ornithologists' Union Check-list of North American birds. Auk 61:441-464.

Wheeler, Q. D. 2000. The phylogenetic species concept (*sensu* Wheeler and Platnick). Pp. 55-60 in Species Concepts and Phylogenetic Theory: a Debate (Q.D. Wheeler and R. Meier, eds.). Columbia University Press, New York.

Submitted by: Dr. Eric A. VanderWerf, Director of Science, Pacific Rim Conservation, 3038 Oahu Avenue, Honolulu, HI 96822; eric@pacificrimconservation.org

Date of Proposal: 19 September 2023, revised 7 November 2023

Treat Common Redpoll *Acanthis flammea* and Hoary Redpoll *A. hornemanni* as a single species

Effect on NACC:

If approved, this proposal would merge the species *Acanthis flammea* and *Acanthis hornemanni* into a single species, *Acanthis flammea* Linneaus 1758, which has taxonomic priority over *A. hornemanni* Holboell 1843.

Background:

Redpolls in the genus *Acanthis* are small-bodied, granivorous finches that are collectively distributed throughout the Holarctic. Species limits within the genus have been contentious; taxonomists have recognized from one to six species, among other alternative treatments (Coues 1862; Harris et al. 1965; Troy 1985; Herremans 1989; Seutin *et al.* 1992; Marthinsen *et al.* 2008). Currently, Clements et al. (2014) recognize three species within the genus, including two in North America: *A. flammea*, which typically has a longer, thinner bill and more streaking on the rump and crissum, and *A. hornemanni*, which typically has a shorter, more conical bill with less streaking on the rump and crissum. However, Troy (1985) documented substantial overlap in phenotypic variation among *A. flammea* and *A. hornemanni*, suggesting that phenotypic variation may be continuous rather than discrete. Previous molecular studies within the genus inferred ample genetic variation, but no evidence of population structure or monophyly among individuals classified as separate species by phenotype (restriction fragment length polymorphism (RFLPs), Marten and Johnson 1986; RFLPs, Seutin *et al.* 1995; mitochondrial control region, Ottvall et al. 2002; mitochondrial control region and ten microsatellites Marthinsen *et al.* 2008; 20,712 SNPs, Mason and Taylor 2015). The apparent lack of genetic differentiation suggests either substantial gene flow and weak reproductive isolation among currently recognized species or extremely recent divergence accompanied by incomplete lineage sorting that is amplified by large effective population sizes (Marthinsen *et al.* 2008; Mason and Taylor 2015). Additionally, patterns of assortative mating are largely anecdotal and mixed in the literature. Some studies allude to assortative mating by phenotype in Norway (Lifjeld & Bjerke 1996), whereas others document the presence of mixed pairs (Harris et al. 1965), and the presence of hybrid pairs has been debated (Molau 1985). Thus, species limits within *Acanthis* remain largely unresolved; however, recent molecular findings (Mason and Taylor 2015; Funk et al. 2021) have provided new insight into the evolutionary dynamics within *Acanthis*.

Mason and Taylor (2015) performed an array of population genetic analyses to further examine population structure, patterns of coalescence, and associations between phenotype and genotype among currently recognized species. The first PC axis of a genetic PCA analysis using the 20,712 ddRAD-Seq SNPs revealed weak differentiation among individuals of *A. flammea* and *A. hornemanni*, although this variation represents only 2.2% of the total variation. This pattern may be driven partially by isolation by distance and the sampling scheme of Mason and Taylor (2015), who included more *A. hornemanni* from the Old World and more *A. flammea* from the New World. STRUCTURE (Pritchard et al. 2000), a Bayesian population assignment program, placed all individual redpolls in a single population, regardless of phenotype and current classification. A similar pattern was observed by analyzing the 215,825 SNPs among the ten individuals with RNA-Seq libraries. Analyses within a multispecies coalescent framework based on 35 SNPs with no missing data favored a species delimitation model with a single species over the current taxonomy (Bayes factor = 36.80), which was also supported by data set of 200 randomly selected SNPs (BF = 15.22). Mason and Taylor (2015) also documented a pattern of isolation by distance, such that individuals were more closely related to geographically proximate individuals *regardless of their phenotype and current species status*. An Analysis of Molecular Variance (AMOVA) indicated that 98.11% of genetic variation is partitioned within species compared to 1.89% among species. Mason and Taylor (2015) also looked at correlations between continuous phenotypic variation and different components of genetic variation among the ten individuals that they collected from a single wintering flock. These analyses found no relationship between variation at anonymous SNPs and phenotypic variation; however, they revealed a strong correlation between phenotypic variation and multidimensional scaling scores of gene expression. In other words, anonymous, neutral SNPs did not correlate with phenotypic variation, while multigenic patterns of differential gene expression did correlate with phenotypic variation.

More recently, Funk et al. (2021) provide strong support that a chromosomal inversion—also known as a “supergene”—maintains phenotypic variation despite widespread geneflow between all currently named species. Here, we summarize their findings and discuss how this sheds new light on the nature of phenotypic variation and reproductive isolation in redpolls.

New information: Funk et al. (2021) generated whole-genome data from 73 individuals, many of which were included in Mason and Taylor (2015), including representatives of *A. flammea* (n = 26)*, A. hornemanni* (n = 33), and *A. cabaret* (n = 14), and used a whole-genome sequencing approach in combination with alignment to a high-quality reference Brown-capped Rosy Finch genome to assemble 25 million genome-spanning loci and assess genetic variation and differentiation (Figure 1). The geographic sampling also included individuals from Greenland and Iceland that were not included in the Mason and Taylor (2015) study. Funk et al. (2021) also examined the bill and plumage measurements in addition to RNA samples of multiple tissues from ten individuals in a single wintering flock, including three *A. hornemanni* and seven *A. flammea* that spanned a phenotypic continuum that were first analyzed in Mason and Taylor (2015). In Mason and Taylor (2015) individual RNA libraries from these ten individuals were aligned to a *de novo* transcriptome to quantify patterns of gene expression and identify 215,825 single nuclear polymorphisms (SNPs) among putative genes for the ten RNA-Seq libraries.

Funk et al (2021) repeated many of the analyses of Mason and Taylor (2015) but with a much higher-resolution, whole-genome dataset that was aligned to a high-quality reference genome (Figure 1A). The main advance provided by the whole-genome dataset was the discovery of an inversion polymorphism that is strongly associated with redpoll phenotypes and patterns of gene expression, explaining the pattern first described in Mason & Taylor (2015). Intuitively, this inversion contains genes with functional annotations that correspond to the phenotypic characters that are used to distinguish the currently recognized species of redpolls (Funk et al. 2021). Using an ABBA-BABA approach, Funk et al. (2021) demonstrated that *outside of the* *inversion there is widespread gene flow and little genomic differentiation across all currently recognized species of redpoll.* This result does not support a scenario of prolonged isolation and subsequent secondary contact.

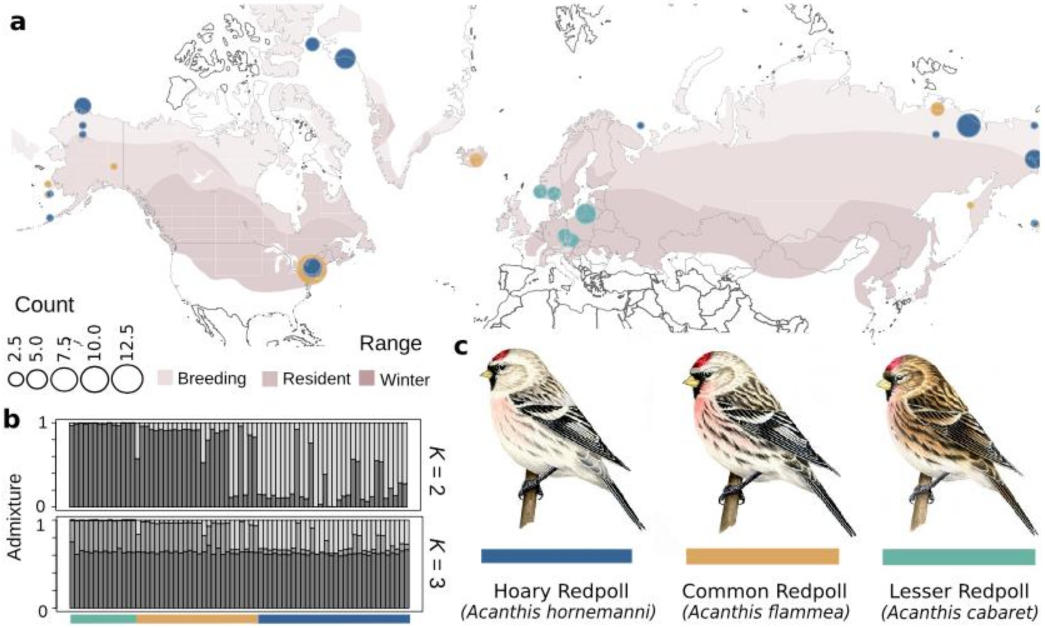


Figure 1: Geographic sampling from Funk et al. (2021) shown in panel a, while panel b shows the output of a population assignment program with K=2 cluster and K=3 clusters.

Outside of the inversion, Funk et al. (2021) observed a lack of genetic clustering by phenotype (Figure 2A) or geography (Figure 3) that is consistent with Mason and Taylor (2015) and other previous studies (e.g. Marthinsen (2008)). However, the recent findings are based on a much larger data set that includes orders of magnitude more loci that span the entire genome. Despite the strong association between the inversion and redpoll phenotypes, Funk et al. (2021) detected all possible genotype combinations at the inversion, suggesting that individuals with different inversion genotypes can still reproduce. *Together with the lack of differentiation outside of the inversion, these results suggest that the inversion does not act as a barrier to reproduction, and instead maintains variation within* Acanthis *as balanced*. Recently, Amouret et al. (2015) sampled mtDNA and nuclear markers of Icelandic redpolls (*A. f. islandica*) in addition to *A. hornemanni* and *A. cabaret* and similarly concluded that all redpolls likely comprise a single species.

Mason and Taylor (2015) also documented continuous phenotypic variation in their winter flock sample, in which plumage and bill characteristics spanned from those typical of *A. flammea* to those typical of *A. hornemanii*. This pattern that was likewise documented with a larger sample size and discussed by Troy (1985). Intriguingly, Mason and Taylor (2015) found that phenotypic variation within *Acanthis* was correlated with broad-scale patterns of gene expression. Funk et al. (2021) further associated these results with inversion genotypes, suggesting that gene expression is at least partly modulated by the chromosomal inversion (Figure 2B and 2C). Associations between phenotype and gene expression may be due to variation among *cis*-regulatory elements within the inversion, or interactions with either genomic elements outside of the inversion or the environment. Importantly, differential gene expression among currently recognized redpoll species does not imply that they have experienced prolonged reproductive isolation.

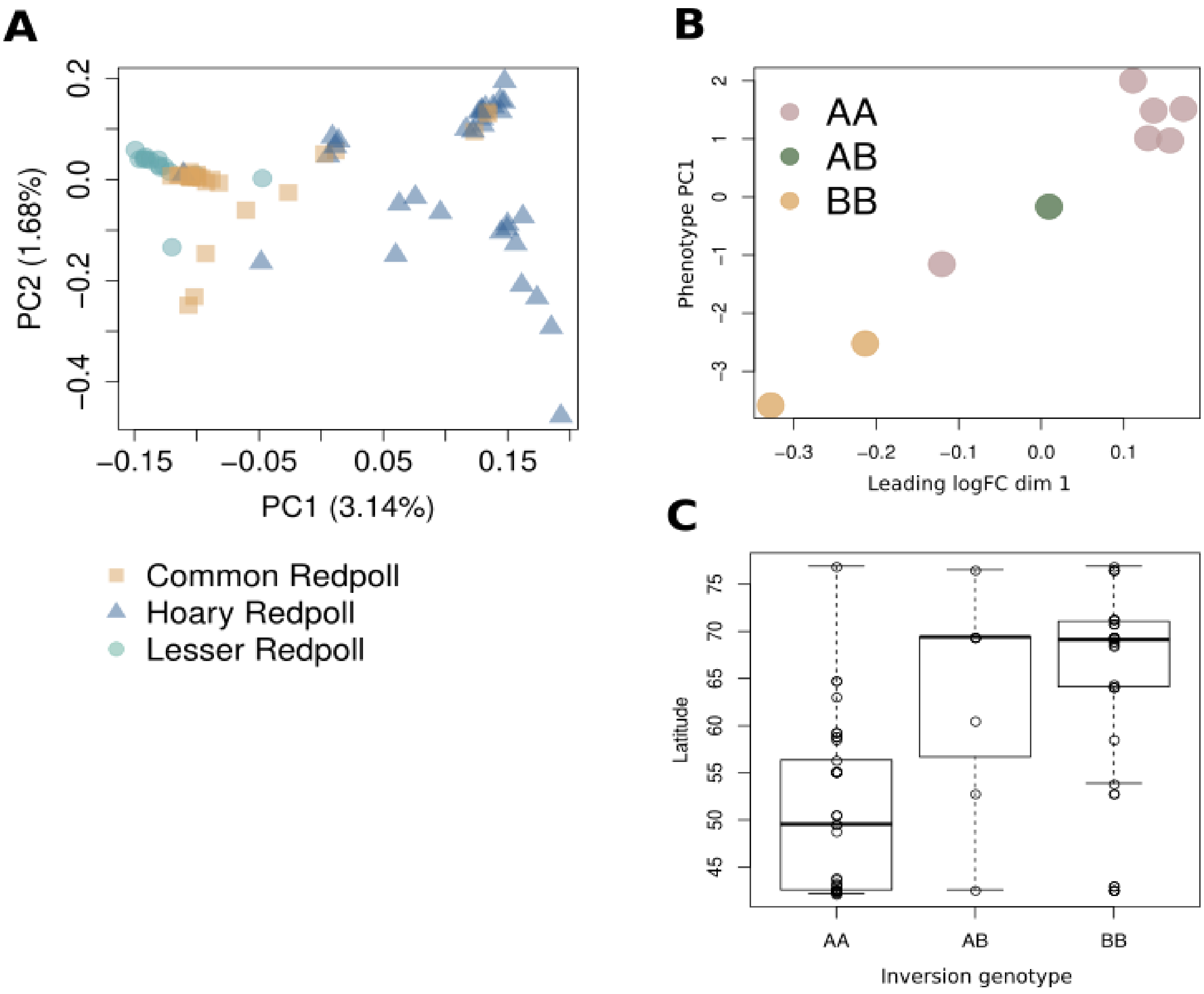


Figure 2. Redpoll population genomic and inversion analyses. A) Genomic PCA of 25 million single nucleotide polymorphisms demonstrating a lack of unique clustering based on current taxonomy, with Common Redpoll shown as yellow squares, Hoary Redpoll as blue triangles, and Lesser Redpolls as green circles. B) Correlation between phenotype PC1 score on the y-axis and dimension 1 of the leading log-fold change in gene expression, colored by individual inversion genotype indicating a relationship between phenotype, gene expression, and inversion genotype. AA individuals are homozygous for the “*flammea*” inversion allele, whereas BB individuals are homozygous for the “*hornemanni*” inversion allele. AB individuals are heterozygous and possess one allele of each type. C) Distribution of inversion genotypes by latitude demonstrating that AA genotypes (Common Redpoll-like) are distributed more southerly, and that BB genotypes (Hoary Redpoll-like) are distributed more northerly.

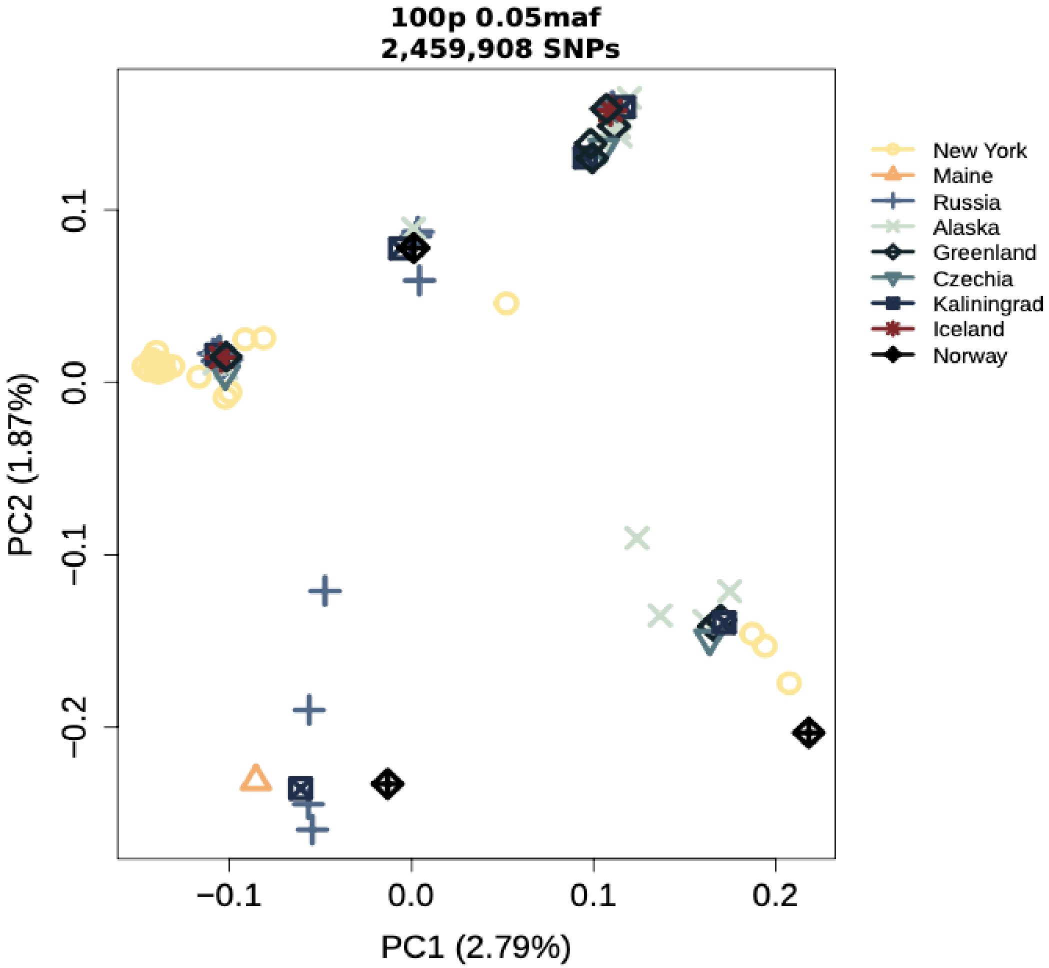


Figure 3: PCA conducted with over 2 million SNPs omitting Chromosome 1, which has a large chromosomal inversion associated with phenotypic differences. Note the lack of clustering among geographic regions.

Mason and Taylor (2015) found pervasive genomic homogeneity, continuous phenotypic variation, and overlapping suitable habitat among currently recognized species in the genus *Acanthis*. Whole genome evidence from Funk et al. (2021) supported the finding of genomic homogeneity spanning nearly the entire *Acanthis* genome. Funk et al. (2021) further linked variation in geography and phenotype to a large chromosomal inversion and suggested that *this inversion does not prevent reproduction, but instead maintains variation through a combination of environmental and sexual selection pressures*. Although the possibility persists that *A. hornemanni* and *A. flammea* may have diverged extremely recently (i.e., more recently than the last glacial maximum), there is no evidence that supports a scenario of prolonged reproductive isolation and assortative mating within the genus. Given these recent findings, we feel that the burden of proof now lies on those who would recognize multiple species within *Acanthis*. A more parsimonious explanation may be that *Acanthis* consists of a single, polymorphic evolutionary lineage that may be experiencing ongoing bouts of local adaptation, which has induced continuous, yet geographically heterogeneous, phenotypic variation among redpoll types. This phenotypic variation is maintained because the genes involved in phenotypic variation in *Acanthis* occur as a supergene that manifests as a large chromosomal inversion.

Response to comments from last submission:

In 2017, Mason and Taylor submitted a proposal to lump *Acanthis flammea* and *Acanthis hornemanni* into a single species. The proposal did not pass, receiving 5 YES votes and 5 NO votes with extensive commentary from NACC members regarding their rationale. The votes and comments from this proposal can be seen here:

https://americanornithology.org/about/committees/nacc/current-prior-proposals/2017-proposals/comments-2017-b/#2017-B-7

Here, we respond to some of the common criticisms of the case for lumping *flammea* and *hornemanni* into a single species.

Geographic and taxonomic sampling

A common criticism of the 2017 proposal centered on geographic sampling and the lack of samples from Greenland and Iceland. Funk et al. (2021) included samples from both of these localities, including *hornemanni* samples from Greenland and *flammea* samples from Iceland. The expanded geographic sampling resulted in similar inferences of widespread genomic homogeneity across all redpoll populations, with a few genomic regions (including the large chromosomal inversion on Chr1) differentiated as outliers. Furthermore, when all genomic loci were included in a PCA, little to no geographic structure was detected. Rather, there were discrete clusters formed that we suspect are the product of polymorphisms in structural variants, like the 55 MB inversion we detected on Chromosome 1. Thus, there is little to no genetic structure that corresponds to geography or existing subspecies when looking at whole genomes.

Lack of a field study to examine assortative mating

Another common criticism of the 2017 proposal was the lack of a field study regarding evidence for or against assortative mating between *flammea* and *hornemanni*. We still have not conducted an in-depth study of assortative mating in North America. However, the genomic data strongly suggest that hybridization and introgression is frequent across much of the genome—even in the large chromosomal inversion found on Chr 1. In our mind, these genomic data and analyses (i.e., ABBA-BABA; SLiM) tell us ‘what the birds are doing’ or more specifically, ‘what the birds have been doing demographically over the last million years’. In contrast, a behavioral study of assortative mating would tell us what some small portion of the global population(s) is doing in this current snapshot of time, and may vary spatially or temporally on contemporary time scales. The models presented in Funk et al. (2021) combined with the evidence of a large chromosomal inversion provide a plausible alternative to multiple species, in which even weak selection can generate locally abundant phenotypes or phenotypic gradients, such as seen in the whiter, larger-billed *hornemanni* in North America as one moves north. We understand that some people will want to see a field study regardless of what genomic data and analyses are presented, but continuing to recognize multiple species of redpolls with the information we have on hand would make them a dramatic outlier in terms of population structure, geographic overlap, and continuous phenotypic variation between currently recognized species.

Comparisons with other groups / data sets:

There are a few other lineages with pronounced phenotypic diversity despite widespread genome homogeneity that may be worth comparing to the *Acanthis* redpolls. First, Darwin's Finches are a famous adaptive radiation with very little genetic differentiation between currently recognized species. However, these species experience extremely strong selective pressures related to ecological differences among them. Selection forces imposed on Darwin's Finches are much stronger than any perceived ecological difference between currently recognized species of redpolls, which are broadly sympatric and are often seen feeding side-by-side in mixed flocks.

Another lineage with pronounced phenotypic diversity yet little genomic differentiation is the southern capuchino radiation in the genus *Sporophila*. However, in the southern capuchino lineage, phenotypes are discrete rather than continuous, and a recent study has uncovered strong assortative mating in at least one pair of species. Thus, both discrete phenotypic modularity and strong evidence for assortative mating present a much more compelling case for recognizing multiple species within the southern capuchino radiation compared to redpolls.

How to treat subspecies if we lump?

Another criticism raised of the 2017 proposal was that there was no discussion of how to treat subspecies if we were to lump the redpolls into a single species. We argue that the current subspecies can still be recognized as they represent phenotypic "clusters" within the broadly continuous distribution of phenotypic diversity among redpoll types. There are currently three subspecies of *A. flammea*, one of *A. cabaret*, and two of *A. hornemanni*. We suggest recognizing each of these subspecies (or species in the case of *A. cabaret*) as subspecies of a single species of redpoll.

Recommendation:

We recommend a YES vote to lump *Acanthis flammea* and *A. hornemanni* into a single species: *A. flammea*. This vote will also retain all currently recognized subspecies of redpoll.

Literature Cited:

Amouret, J., Steinauer, K., Hallgrimsson, G. T., & Pálsson, S. (2015). Evolutionary status of Icelandic Redpolls *Carduelis flammea islandica* (Aves, Passeriformes, Fringillidae). *Journal of Ornithology*. doi:10.1007/s10336-015-1208-3

Clements, J. F., Schulenberg, T. S., Iliff, M. J., Sullivan, B., Wood, C. L., & Roberson, D. (2014). *The Clements checklist of birds of the world: Version 6.8*. Retrieved from http://www.birds.cornell.edu/clementschecklist/downloadable-clements-checklist

Coues, E. (1862). A monograph of the genus *Aegiothus* with descriptions of new species. *Proc. Acad. Nat. Sci. Philadephia*, *13*, 373–390.

Funk, E. R., N. A. Mason, S. Pálsson, T. Albrecht, J. A. Johnson, and S. A. Taylor (2021). A supergene underlies linked variation in color and morphology in a Holarctic songbird. *Nature Communications* 12:6833.

Harris, M. P., Norman, F. J., & McColl, R. (1965). A mixed population of redpolls in northern Norway. *British Birds*, *58*, 288–294.

Herremans, M. (1989). Taxonomy and evolution in redpolls *Carduelis flammea–hornemanni*; a multivariate study of their biometry. *Ardea*, *78*, 441–458.

Lifjeld, J. T., & Bjerke, B. A. (1996). Evidence for assortative pairing by the *cabaret* and *flammea* subspecies of the common redpoll *Carduelis flammea* in SE Norway. *Fauna Norvegica Series C, Cinclus*, *19*, 1–8.

Marten, J. A., & Johnson, N. K. (1986). Genetic relationships of North American cardueline finches. *Condor*, *88*(4), 409–420.

Marthinsen, G., Wennerberg, L., & Lifjeld, J. T. (2008). Low support for separate species within the redpoll complex (*Carduelis flammea–hornemanni–cabaret*) from analyses of mtDNA and microsatellite markers. *Molecular Phylogenetics and Evolution*, *47*(3), 1005–1017. doi:10.1016/j.ympev.2008.03.027

Mason, N. A., & Taylor, S. A. (2015). Differentially expressed genes match bill morphology and plumage despite largely undifferentiated genomes in a Holarctic songbird. *Molecular Ecology*, doi:10.1111/mec.13140

Molau, M. (1985). Gråsiskkomplexet i Sverige. (The redpoll complex in Sweden). *Vår Fågelvärld*, *44*, 5–20.

Ottvall, R., Bensch, S., Walinder, G., & Lifjeld, J. T. (2002). No evidence of genetic differentiation between lesser redpolls *Carduelis flammea cabaret* and common redpolls *Carduelis f. flammea*. *Avian Science*, *2*(4), 237–244.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959.

Seutin, G., Boag, P. T., & Ratcliffe, L. M. (1992). Plumage variability in redpolls from Churchill, Manitoba. *Auk*, *109*, 771–771.

Seutin, G., Ratcliffe, L. M., & Boag, P. T. (1995). Mitochondrial DNA homogeneity in the phenotypically diverse redpoll finch complex (Aves: Carduelinae: Carduelis flammea-hornemanni). *Evolution*, 962–973.

Troy, D. M. (1985). A phenetic analysis of the redpolls *Carduelis flammea flammea* and *C. hornemanni exilipes*. *Auk*, *102*, 82–96.

Wagner, C. E., Keller, I., Wittwer, S., Selz, O. M., Mwaiko, S., Greuter, L., et al. (2013). Genome-wide RAD sequence data provide unprecedented resolution of species boundaries and relationships in the Lake Victoria cichlid adaptive radiation. *Molecular Ecology*, *22*(3), 787–798. doi:10.1111/mec.12023

Submitted by: Nicholas A. Mason, Erik Funk, and Scott A. Taylor

Date of proposal: 13 October 2023

Treat *Anas crecca* as two species: Green-winged Teal *A. carolinensis* and Common (or Eurasian) Teal *A. crecca*

Effect on NACC (and SACC):

This would change our treatment of the Green-winged Teal (*Anas crecca*), a Northern Hemisphere species, by splitting it into a largely New World species (*Anas carolinensis*; Green-winged Teal) and a largely Old World species (*Anas crecca*; Common Teal or Eurasian Teal). *Anas carolinensis* would be monotypic; *A. crecca* would include *A. c. crecca* and the sometimes-recognized Aleutian population *A. c. nimia*.

Background and new evidence:

We are revisiting this species limits issue in association with the effort to harmonize world lists, and treatment of *A. crecca* is a point of disagreement. As it turns out, this now fairly well-known group represents an interesting tale of species concepts, methodological limitations, and modes of speciation, each of which has influenced decisions on species limits.

AOU/AOS has treated *A. c. crecca* and *A. c. carolinensis* as a single biological species since 1973 (AOU 1973). The supporting citations, however, simply treated the forms as a single species and did not provide direct evidence (Delacour & Mayr 1945, Gabrielson & Lincoln 1959, Johnsgard 1965). This treatment followed Peters (1931), an early example of the application of the biological species concept to forms previously treated as full species. Later, justification for this treatment was given as “intergradation between the two groups occurs in the Aleutians.” (AOU 1983:74).

Sangster et al. (2001) reviewed phenotypic and genetic evidence and recommended splitting *crecca* and *carolinensis* into two biological species, which was later done (Sangster et al. 2002). They gave strong weight to the lack of a mitochondrial DNA sister relationship between *crecca* and *carolinensis*, and they gave little weight to the existence of hybrids—including considering the breeding ranges to be allopatric, apparently missing Hanna (1920), Gabrielson & Lincoln (1959), and Murie (1959). The mitochondrial relationship shown by Johnson & Sorenson (1999) seems to have been particularly compelling, with the South American *A. ‘flavirostris’* being sister to *carolinensis*, and *crecca* being sister to these two: i.e., (*crecca*(*carolinensis*,*flavirostris*)); more on this below. This was at about the time that systematists became aware of the unreliability of mtDNA to accurately track organismal lineage divergence at these shallower levels (e.g., Funk & Omland 2003), although over-reliance on that single-locus approach, termed ‘mtDNA myopia’ by Remsen (2010, 2015), still appears 20 years later. Quite a bit of research has been done on these teal since Sangster et al. (2001, 2002) determined that they should be split into two biological species.

Hybrids between *crecca* and *carolinensis* have long been known, and have been described from both eastern and western North America and western Europe (e.g., Cruickshank 1936, Poole 1940, Mayr & Short 1970, Vinicombe 1994, Gibson & Byrd 2007). But these are ducks, after all, in which hybridization is well known between species, so it is understandable that hybrids might be given less weight without more detailed knowledge of the frequency of their occurrence. But, as it happens, they are rather frequent.

Figure 3. *Anas crecca crecca* (left); two intergrades (middle two); *A. c. carolinensis* (right). Note the intermediacy of the breast bar and the extent of white scapular streak in the middle birds, as well as the coarseness of flank vermiculation and amount of white in facial outline.

(Gibson & Withrow 2015: fig. 3)

IOC has considered the two taxa to be separate species since version 1.0 (Gill & Wright 2006). Interestingly, HBW-BirdLife considered the two to be a single species both in the first HBW volume (del Hoyo et al. 1992) and again after application of the Tobias et al. (2010) species limits criteria in del Hoyo & Collar (2014). Application of these criteria brought new evidence to the subject, so it is worth relating that and the interpretation here:

“Race *carolinensis* sometimes considered a full species, and situation finely balanced. The male differs from nominate male in its vertical white breast-side line (2), lack of white horizontal scapular stripe (2), and lack of narrow buff supercilium (above broad green “eyestripe”) (1); various other very minor differences cannot be scored (plumage characters capped at three), differences in measurements do not exist, behavioural differences are matters of frequency rather than type[1616], and genetic evidence, while suggesting paraphyly involving *A. flavirostris*[868], indicates that hybridization[1861] is relatively widespread in Beringia[1368] (possible score for broad hybrid zone 1) leaving *carolinensis* extremely close to species status.” [Numbers refer to del Hoyo & Collar (2014) references.]

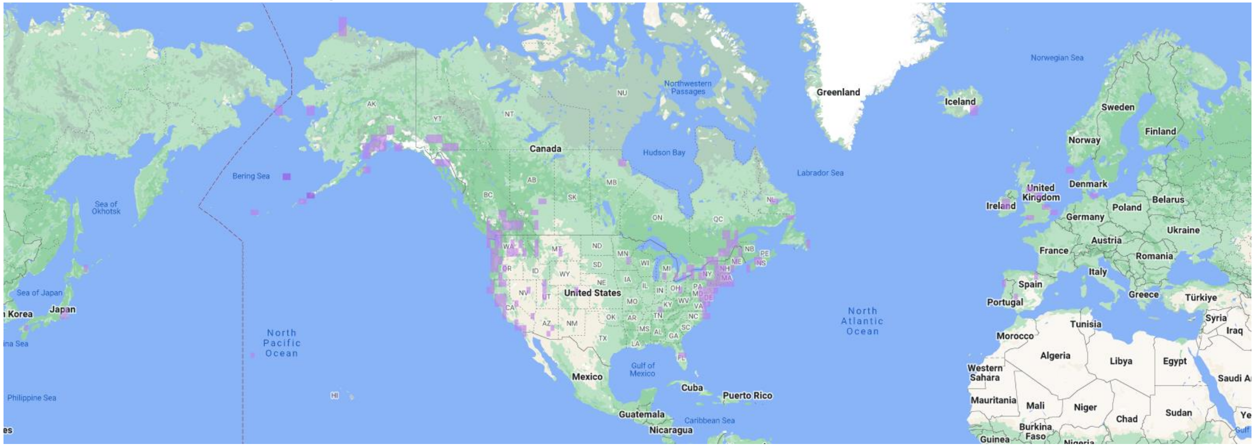
Given the evidence then available, that was a good outcome. But for some reason it was decided to try again with the Tobias et al. (2010) criteria, and a different outcome was achieved. From HBW-BirdLife (2020):

"Common Teal *A. crecca* (del Hoyo & Collar 2014) has been split into Common Teal *A. crecca* and Green-winged Teal *Anas carolinensis* (Handbook of the Birds of the World and BirdLife International 2020). This change follows a revision to the scoring of the males' vertical white breast-side line, due to its role as a signal in display. As such the revised scoring is as follows: male *A. carolinensis* differs from *A. crecca* male in its vertical white breast-side line, replicated on rear flank (3), lack of white horizontal scapular stripe (2), and lack of narrow buff supercilium (above broad green "eyestripe") (1); various other very minor differences cannot be scored (plumage characters capped at three), differences in measurements do not exist, behavioural differences are matters of frequency rather than type, and genetic evidence, while suggesting paraphyly involving *A. flavirostris*, indicates that hybridization is relatively widespread in Beringia (allow 1 for broad hybrid zone), indicating that *carolinensis* does warrant species status."

Thus, through a change in the scoring value of one plumage character (from 2 to 3) and rigid adherence to a methodological rubric, the two became full species. Diminishing the importance of hybridization is a well-recognized weakness of the Tobias et al. (2010) criteria (e.g., Winker 2010, Remsen 2015), but inadequate consideration of by now considerable evidence of levels of hybridization is surprising. I am not sure how widespread hybridization can be considered to warrant species status, but given the current state of knowledge this case seems to be one in which methodological constraints or limitations and corresponding decisions triggered a faulty decision under the BSC. One could argue that these constraints now include two facets: a strong preference for a cladistic view of mtDNA gene trees dictating species limits, and a rigid adherence to character scoring and related accounting preventing a full accounting of highly relevant data on hybridization rates. (As a reminder, the Tobias et al. [2010] criteria do not include hybrid zones in their divergence threshold calculations, but they do receive a score. Their "broad hybrid zone" is scored the lowest; i.e., is least indicative of species status; see their table 1. Hybridization frequency, which is the most important attribute of the phenomenon, is not considered.)

Hybridization, determined through male plumage, appears to be routine in the eastern Aleutians where the ranges of the two taxa come together, and intergrades also appear on other Bering Sea islands (Gibson & Byrd 2007:35; Gibson & Withrow 2015: fig. 3; DeCicco 2008; Lehman 2019). Co-occurrence of both taxa on the Chukchi and Seward peninsulas suggests hybridization might occur there as well (Kessel 1989, Konyukhov 2015). Palmer (1976) reviewed the occurrences of other intergrades in Colorado, California, and Japan. While the published literature provides ample evidence of hybridization, estimates of the frequency of individuals showing hybrid characteristics has become clearer. Reeber (2015) considered hybrids to not be very common, because they are detected with a frequency similar to the small numbers of males found on the wrong continent (citing Sibley 2011). Actually, that's a rather high ratio of hybrids to the rarer parental form (i.e., ~1:1). The expected value if reproductive isolation has essentially been achieved should be very low. Having it be approximately equal to the number of the rarer parental form seems quite high, because in a stable population it is indicative of a rate of hybridization roughly equivalent to the number of opportunities for it. This, and the occurrence of hybrids where the two taxa are in contact, suggests that any isolating mechanisms are providing fairly ineffective barriers.

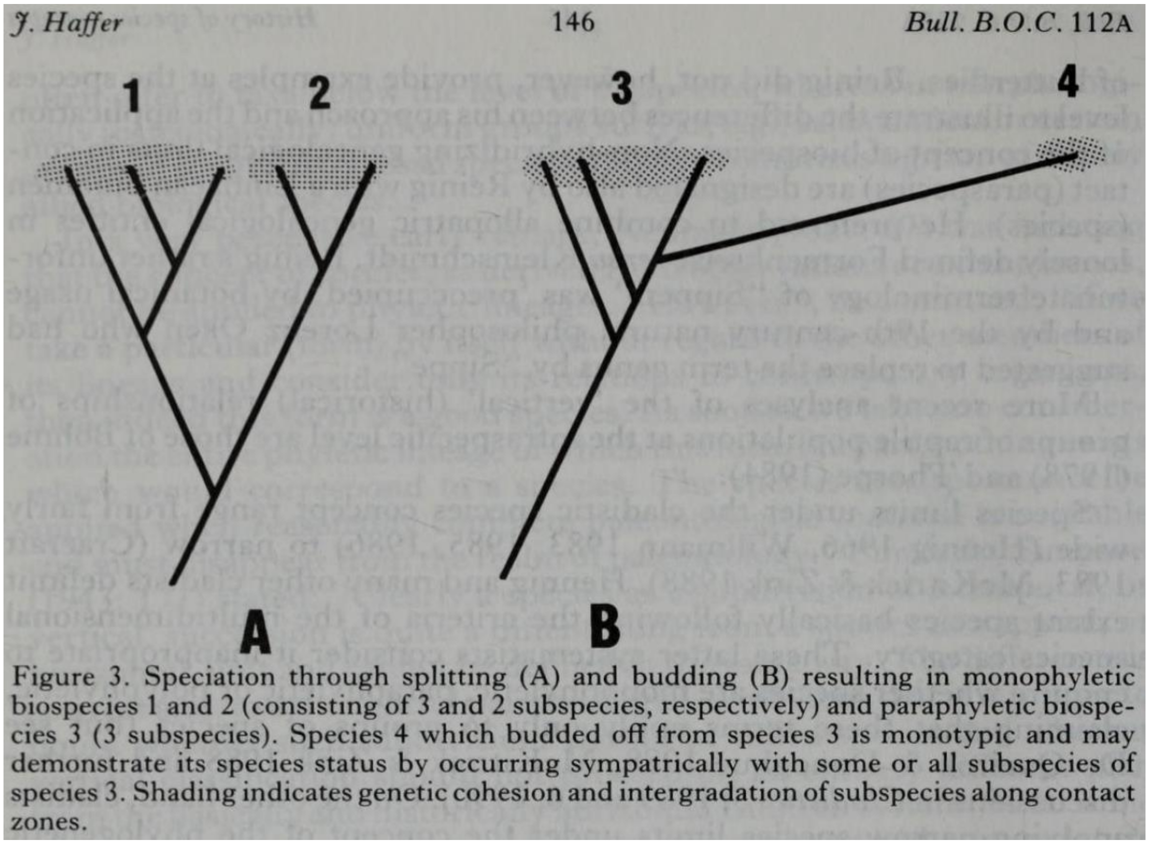
The seemingly high frequency of hybrids became jaw-droppingly obvious with the advent of eBird, where Green-winged Teal (Eurasian x American), *Anas crecca crecca x carolinensis* has its own page, with, at this time, 546 entries (with an abundance of photographs), showing concentrations in western and eastern North America and western Europe (see figure below; https://ebird.org/species/gnwtea1). Based on phenotype, it seems obvious that these taxa have not achieved essential reproductive isolation.



Green-winged Teal (Eurasian x American) *Anas crecca crecca* x *carolinensis*, global distribution of 546 records (https://ebird.org/species/gnwtea1).

Genetic information on relationships among *A. c. crecca* (including *nimia*), *A. c. carolinensis*, and *A. 'flavirostris'* has been accumulating for almost three decades. In terms of species limits, it is simply icing on the cake of phenotypic evidence for substantial hybridization. Beyond that, however, genetic and genomic data provide incomparable insights into the surprising variety of evolutionary processes and modes of speciation occurring in this small group.

Using mtDNA RFLPs, Zink et al. (1995) found relatively deep divergence between Russian and U.S. haplotypes, but also evidence that there was gene flow. Johnson & Sorenson (1999) found a deep mtDNA divergence between *crecca* and *carolinensis*, and also that the latter was sister not to *crecca* but rather to the South American *A. 'flavirostris'*, as noted above. At that time, an overcommitment to cladistic methodology in our discipline, in which paraphyletic mtDNA relationships for species are not allowed, often had a heavy influence (as in this case) on species delimitation. Haffer (1992) showed how this conceptual constraint could produce the wrong answer when considering biological species. Since then we have come to recognize that gene trees often disagree with species trees, and this is a case where it is good to revisit the undue weight that this was given in historic decisions to split these taxa (e.g., Sangster et al. 2001).



J. Haffer 146 *Bull. B.O.C.* 112A

Figure 3. Speciation through splitting (A) and budding (B) resulting in monophyletic biospecies 1 and 2 (consisting of 3 and 2 subspecies, respectively) and paraphyletic biospecies 3 (3 subspecies). Species 4 which budded off from species 3 is monotypic and may demonstrate its species status by occurring sympatrically with some or all subspecies of species 3. Shading indicates genetic cohesion and intergradation of subspecies along contact zones.

Haffer (1992: fig. 3).

Humphries & Winker (2011) confirmed substantial divergence in mtDNA sequence (ND2) between *crecca* and *carolinensis*, but they found no significant difference between them using 420 AFLP loci (presumed to be predominantly nuclear DNA). This indicates less divergence in the nuclear genome.

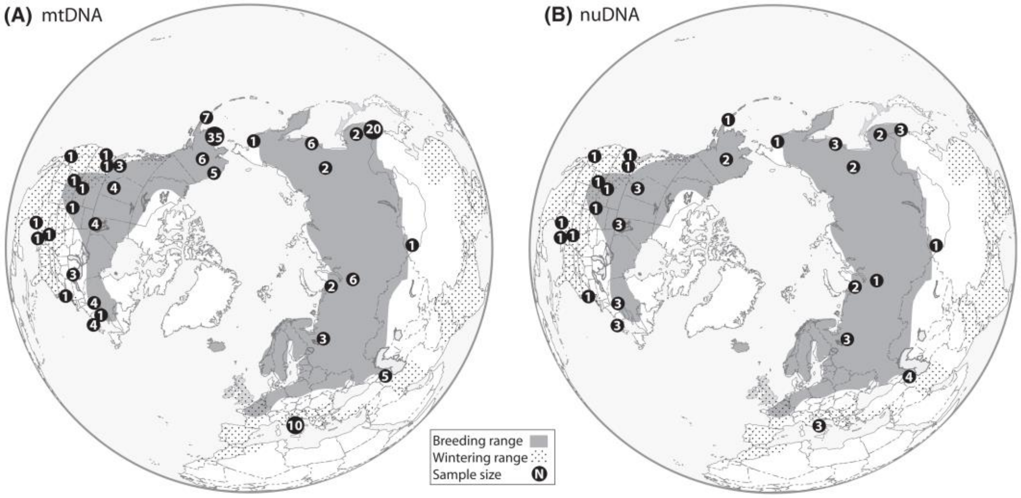


Fig. 1 Sampling localities of common and green-winged teal used for (A) mtDNA sequencing ($n = 144$) and (B) nuDNA sequencing ($n = 50$).

Peters et al. (2012: fig. 1).

Peters et al. (2012) considered these two continental populations in the context of the classic 'dumbbell' model of allopatric speciation, in which, at its extreme, populations are separated by a barrier that precludes gene flow (Mayr 1940, 1942; White 1978; Haffer 2007). If that barrier is insufficient and gene flow persists, divergence might be retarded and speciation could fail to go to completion. In such a case, i.e., when the 'handle' connecting the two populations in the dumbbell model is not broken (gene flow persists), then parapatric models apply (speciation with gene flow in a nonsympatric distribution; Gavrilets 2004). Using sequence data from mtDNA (control region) and eight nuclear introns, Peters et al. (2012) found that *crecca* and *carolinensis* did indeed fit a parapatric model of speciation, and that while they appear to have been diverging for ~2.6 My in mtDNA, gene flow has been sufficiently high to prevent completion of the speciation process under the BSC.

The natural history of these birds is of great interest here. They form breeding pairs on the wintering grounds (unlike most migratory birds), and males follow their mates back to her breeding grounds. This produces female-biased philopatry or male-biased dispersal. And, because mtDNA is maternally inherited, intercontinental phylogeographic mtDNA structure is very high and mtDNA gene flow is relatively low (~1/generation). In contrast, males disperse between continents at a much higher rate, and nuclear gene flow is moderate (~1-20 individuals/generation, with an asymmetric bias (appearing in this dataset) from *crecca* into *carolinensis* (Peters et al. 2012). Winker (2021) considered the situation between *crecca* and *carolinensis* to be an example of an evolutionary tryst, with divergence stalled for long periods short of speciation: almost-separate entities, but unbreakably joined by gene flow.

The most comprehensive study of these taxa thus far used 1,393 ultraconserved element (UCE) nuclear loci and complete mitogenomes to examine relationships in the whole complex (including the South American *A. flavirostris*/*andium*) and gene flow among the North American members (Spaulding et al. 2023). Although this study used small sample sizes, coalescent theory and an empirical study of sample size effects showed that key demographic parameters (in this case levels of gene flow, $N_e m$), are robustly estimated using these methods (Felsenstein 2005, McLaughlin & Winker 2020).

A note on the South American *A. 'flavirostris'* is warranted: SACC considers it to be two species, *Anas flavirostris* and *A. andium*, following passage of a proposal in 2008 in which differences in bill color largely drove the decision; see Remsen et al. (2023) and associated comments and links. The genetic situation there has yet to be fully resolved, but the taxa appear to be genetically differentiated (e.g., Spaulding et al. 2023). For the purposes of this proposal, it does not matter whether this South American lineage is treated as one species or two.

Spaulding et al. (2023) found gene flow rates ($N_e m$) of 10-11 individuals per generation between *crecca* and *carolinensis* (with evidence for cyclic contact likely related to glacial cycles), and 1-26 individuals per generation between *nimia* and *carolinensis* (the latter value reflects gene flow from *carolinensis* into *nimia* and is consistent with phenotypic evidence of eastern Aleutian intergrades). These levels of gene flow are similar to earlier estimates (Peters et al. 2012) and are well above levels deemed concordant with the 'essentially reproductively isolated' criterion of the biological species concept (reviewed by Winker 2021). Interestingly, divergence with gene flow was found in all pairwise comparisons in this study, and three geographic modes of divergence seem to be involved: parapatric (between *crecca* and *carolinensis*; Peters et al. 2012), heteropatric (between *crecca* and *nimia*; Winker et al. 2013), and (mostly) allopatric (between *carolinensis* and *'flavirostris'*; Spaulding et al. 2023). (Fun side note: Spaulding et al. (2023) hypothesized that the small levels of gene flow between *carolinensis* and '*flavirostris*' result from occasional re-colonizatioin of South America by wintering *carolinensis*, preventing strict allopatry from occurring.)

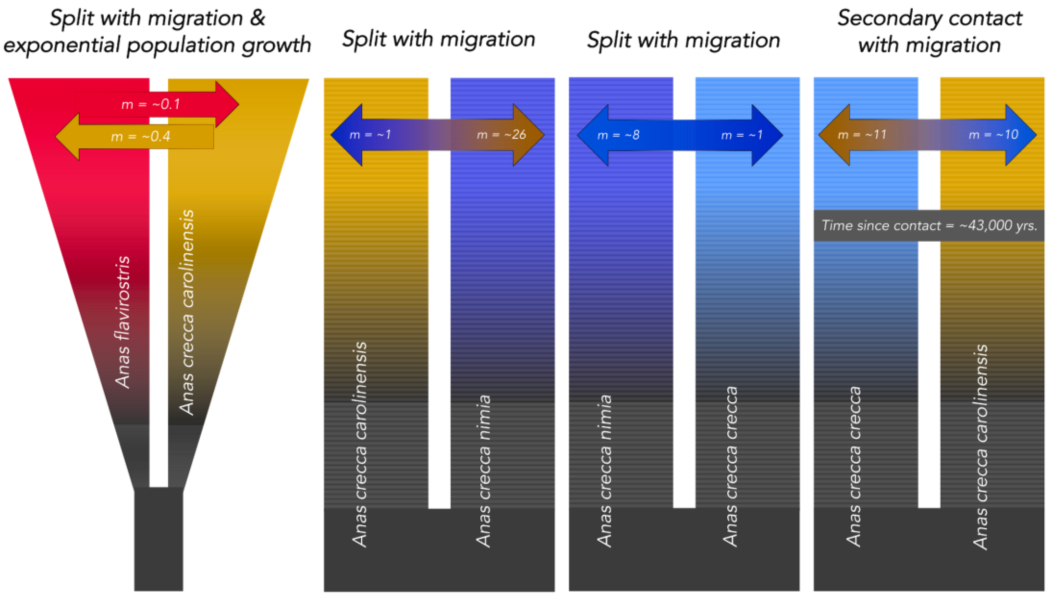


Fig. 5. Visual representations of the best-fit demographic model for each pairwise comparison using δaδi (Gutenkunst et al., 2009). Migration (gene flow) rate estimates (*m*) are in individuals per generation. All analyses indicated divergence with gene flow. Technically, all fit in parapatric speciation theory, but, geographically, allopatry and heteropatry are involved. Full biological estimates are given in Table 3. Color coding corresponds to Fig. 1.

Spaulding et al. (2023: fig. 5). Best-fit demographic models of pairwise population histories and corresponding estimates of gene flow using UCEs. These levels of gene flow are entirely commensurate with current views of species limits by NACC (Chesser et al. 2023).

Spaulding et al.'s (2023) results using whole mitogenomes corroborated prior evidence (Johnson & Sorenson 1999) of mtDNA paraphyly in the biological species of *crecca*+*carolinensis*: (*crecca*(*carolinensis,'flavirostris'*)). But, almost certainly because of ongoing or cyclic gene flow, the nuclear relationship is quite strongly ((*crecca,carolinensis*),*'flavirostris'*) (Spaulding et al. (2023:fig. 2, copied below). This situation thus seems to be a textbook example of Haffer's (1992:fig. 3, copied above) model of speciation through 'budding'. The currently favored hypothesis for this situation is that mtDNA accurately tracks the group's biogeographic history—i.e., after Eurasia and North America were occupied at the onset of the Pleistocene (~2.6 Mya) and mtDNA divergence between these populations was well established, ancestors of '*flavirostris*' colonized South America from North America and with considerable isolation this population became its own well-differentiated biological species and has continued to differentiate. But ongoing or intermittent gene flow between Northern Hemisphere populations has prevented speciation between *crecca* and *carolinensis* (Johnson & Sorenson 1999, Spaulding et al. 2023).

It must be remembered that these gene flow estimates are based on long-term effective population sizes (N_e), and that such population sizes are generally much lower than census size—especially among higher-latitude species during our current interglacial period. Although these values of gene flow provide key evidence about divergence in evolutionary time, they are unlikely to be accurate with respect to on-the-ground evidence of hybridization in today's populations. Spaulding et al. (2022) used gene flow as a proxy for levels of intercontinental movement in ducks as avian influenza vectors and scaled these 'evolutionary time' values to today's census sizes. For *A. crecca* (sensu lato), it was estimated that at present ~127 Eurasian-origin birds were likely to occur in North America per teal generation. Considering that this is a hybridization-based estimate, it seems noteworthy that it is roughly on par with the eBird records of hybrids illustrated above (e.g., at an order-of-magnitude level).

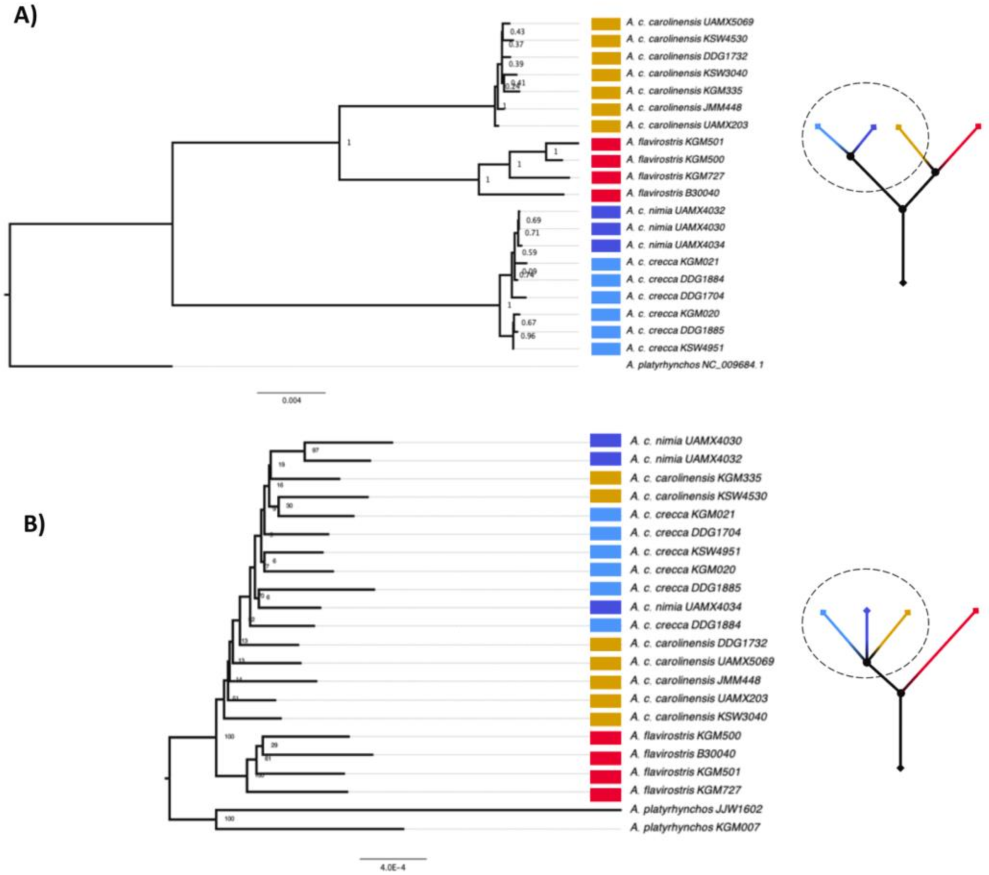


Fig. 2. Maximum likelihood phylogenies of mitogenomic and nuclear DNA sequences. Taxon colors correspond to Fig. 1. **A)** Phylogeny of complete mitogenomes with 100 bootstrap replicates using MEGA (node values: 0–1). **B)** Phylogeny of UCEs with 100 bootstrap replicates (node values: 1–100), reconstructed using a 95% complete data matrix using RAxML. Values on internal nodes differ due to different programs being used for phylogenetic reconstruction. Adjacent to each phylogeny is a sketch illustration highlighting the discordance between the topologies, with the relationship of the *A. crecca* subspecies (within the circle) relative to the sister taxon *A. flavirostris*. The mallard (*Anas platyrhynchos*) was used as an outgroup.

Spaulding et al. (2023: fig. 2). Note the similarity of the sketched tree at upper right with Haffer's (1992: fig. 3) model of speciation by 'budding'.

Peters et al. (2012) considered that female mate choice and migratory behavior probably both cause some limitation of gene flow between *crecca* and *carolinensis*, perhaps coupled with divergent selection. Sexual selection probably contributes to male plumage differences and to the frequency differences found in male displays (Laurie-Ahlberg & McKinney 1979). Migratory direction could also cause some divergent selection if it has a strong genetic component — although this seems less likely, because they migrate in flocks, their movements are temporally variable, and they lack pronounced winter site fidelity (Johnson 1995). It is not known whether there is assortative mating when the two groups come into contact. But that is not a particularly informative characteristic, given that it is commonly exhibited within species and that premating isolating mechanisms are frequently ineffective barriers upon secondary contact (especially relative to postmating mechanisms; Irwin 2020). As Winker (2021:10) observed, "...neither the presence nor the degree of assortative mating appears to be a reliable indicator of species limits, either in birds or in other taxa in which it has been studied." Peters et al. (2012:11) concluded that between these two taxa "…the strength of divergent selection and ⁄ or the number of traits undergoing such selection appear to fall short of that required for completion of speciation given the estimated levels of nuclear gene flow."

This case offers a good opportunity to consider how we can misread data to delineate biological species that do not meet the central BSC criterion of being essentially reproductively isolated. It shows how diagnosability, distinctiveness, and mtDNA relationships can be misleading and fail to properly delimit species under the BSC. Here, the presence of diagnostic adult male plumage traits and significant differences in male courtship displays, coupled with mtDNA evidence of divergence and lack of monophyly, drove decisions to split *A. crecca* and *A. carolinensis*. Although the presence of hybrids was recognized, the importance of hybridization was diminished. For example, Sangster et al. (2001) stated that "males showing a combination of characters of *crecca* and *carolinensis*…are not evidence of a lack of reproductive isolation." HBW-BirdLife (2020) and the Tobias et al. (2010) methodology also diminished evidence of hybridization (Winker 2010). When gene flow is evident, its extent is what is critical; reproductive isolation is not an all-or-none phenomenon. Isolating mechanisms are often incomplete, gene flow is common across step clines in birds, and this case in teal shows how effective this gene flow can be in preventing species-level divergence from occurring for long periods of time.

Taxonomy and nomenclature:

English names: If we were to support a split, we would likely revert to the names used before the two were lumped in 1973: Common Teal and Green-winged Teal (AOU 1957).

Recommendation:

Given considerable evidence from both male phenotype and diverse genetic markers of substantial levels of gene flow between *crecca* and *carolinensis*, these taxa are not biological species. Historic decisions under the BSC to split these taxa recognized divergence in male phenotype and mtDNA, but did not give evidence of hybridization sufficient weight. There are numerous issues yet to be resolved about evolutionary divergence among members of the *A. crecca-carolinensis-'flavirostris'* clade, but finding essential reproductive isolation between *crecca* and *carolinensis* is not one of them. I recommend voting "No" on this proposal.

Please vote yes (split into two species) or no (retain our current taxonomy, recognizing a single biological species with two subspecies).

Literature Cited:

American Ornithologists' Union (AOU). 1973. Thirty-second supplement to the American Ornithologists' Union's *Check-list of North American Birds*. Auk 90:411-419.

American Ornithologists' Union (AOU). 1957. *Check-list of North American Birds*, Fifth edition. American Ornithologists' Union, Baltimore, Maryland.

American Ornithologists' Union (AOU). 1983. *Check-list of North American Birds*, Sixth edition. American Ornithologists' Union, Lawrence, Kansas.

Chesser, R. T., S. M. Billerman, K. J. Burns, C. Cicero, J. L. Dunn, B. E. Hernández-Baños, R. A. Jiménez, A. W. Kratter, N. A. Mason, P. C. Rasmussen, J. V. Remsen, Jr., and K. Winker. 2023. Check-list of North American Birds (online). American Ornithological Society. https://checklist.americanornithology.org/taxa/

Cruickshank, A. D. 1936. Some observations of the European Teal. Auk 53:321-322.

Delacour, J., and E. Mayr. 1945. The family Anatidae. Wilson Bulletin 57:1-55.

DeCicco, L. 2008. Wildlife Observations at St. Paul Island, Alaska in 2008: U.S. Fish and Wildlife Service Report, AMNWR 08/20. 21 pp.

del Hoyo, J. A. Elliott, and J. Sargatal (eds.). 1992. *Handbook of the Birds of the World.* Vol. 1 Lynx Edicions, Barcelona.

del Hoyo, J.; Collar, N. J.; Christie, D. A.; Elliott, A.; Fishpool, L. D. C. 2014. *HBW and BirdLife International Illustrated Checklist of the Birds of the World*. Volume 1: Non-passerines. Lynx Edicions and BirdLife International, Barcelona, Spain and Cambridge, UK.

Felsenstein, J. 2005. Accuracy of coalescent likelihood estimates: do we need more sites, more sequences, or more loci? Molecular Biology and Evolution, 23(3), 691–700.

Funk, D. J., and K. E. Omland. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics 34:397-423.

Gabrielson, I.N. & Lincoln, F. C. 1959. *Birds of Alaska*. Stackpole Company, Harrisburg, Pennsylvania.

Gavrilets, S. 2004. *Fitness Landscapes and the Origin of Species*. Princeton Monographs in Population Biology No. 41.

Gibson, D. D., and G. V. Byrd. 2007. *Birds of the Aleutian Islands, Alaska.* Nuttall Ornithological Club and The American Ornithologists' Union, Cambridge, MA and Washington, D. C.

Gibson, D. D., and J. J. Withrow. 2015. Inventory of the species and subspecies of Alaska birds, second edition. Western Birds 46:94-185.

Gill, F., and M. Wright. 2006. Birds of the World, Recommended English Names – Version 1.0. Princeton, NJ, and London, UK: Princeton University Press.

Haffer, J. 1992. The history of species concepts and species limits in ornithology. Pp. 107-158 *in* Monk, J. F., ed., *Avian Systematics and Taxonomy*. Bull British Ornithological Club Centenary, Suppl. 112A.

Haffer, J. 2007. Ornithology, Evolution, and Philosophy: The Life and Science of Ernst Mayr 1904-–2005. Springer, Berlin.

Hanna, G. D. 1920. New and interesting records of Pribilof Island birds. Condor 22:173-175.

HBW and BirdLife Taxonomic Checklist v5 (HBW-BirdLife). 2020. http://datazone.birdlife.org/species/taxonomy (retrieved 27 Sep 2023). http://datazone.birdlife.org/species/factsheet/common-teal-anas-crecca/details

Humphries, E. M., and K. Winker. 2011. Discord reigns among nuclear, mitochondrial, and phenotypic estimates of divergence in nine lineages of trans-Beringian birds. Molecular Ecology 20:573-583.

Irwin, D. E. 2020. Assortative mating in hybrid zones is remarkably ineffective in promoting speciation. American Naturalist 195:E150-E167.

Johnsgard, P. A. 1965. *Handbook of Waterfowl Behavior.* Comstock Publishing Associates, Ithaca, NY.

Johnson, K. 1995. Green-winged Teal (*Anas crecca*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca.

Johnson, K., and M. D. Sorenson. 1999. Phylogeny and biogeography of dabbling ducks (genus *Anas*): a comparison of molecular and morphological evidence. Auk 116:195–208.

Kessel, B. 1989. *Birds of the Seward Peninsula, Alaska.* University of Alaska Press, Fairbanks, Alaska.

Konyukhov, N. B. 2015. [Rare and vagrant birds of the Chukchi Peninsula.] Russian Journal of Ornithology 24 (express issue 1172):2717-2720.

Laurie-Ahlberg, C. C., and F. McKinney. 1979. The nod-swim display of male Green-winged Teal (*Anas crecca*). Animal Behaviour 27:165–172.

Lehman, P. E. 2019. *The Birds of Gambell and St. Lawrence Island, Alaska.* Studies of Western Birds 4. Western Field Ornithologists, Camarillo, California.

Mayr, E. 1940. Speciation phenomena in birds. American Naturalist 74, 249-–278.

Mayr, E. 1942. *Systematics and the Origin of Species*. New York, Columbia University Press.

Mayr, E., and L. L. Short. 1970. Species taxa of North American birds. Publications of the Nuttall Ornithological Club 9:1-127.

McLaughlin, J. F., and K. Winker. 2020. An empirical examination of sample size effects on population demographic estimates in birds using single nucleotide polymorphism (SNP) data. PeerJ 8:e9939

Murie, O. J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. North American Fauna 61:i-xiii, 1-406.

Palmer, R. S. 1976. *Handbook of North American Birds*, Vol. 2. New haven and London, Yale University Press.

Peters, J. L. 1931. *Check-list of Birds of the World*, Vol. I. Harvard University Press, Cambridge.

Peters, J., K. McCracken, C. Pruett, S. Rohwer, S. Drovetski, Y. Zhuravlev, I. Kulikova, D. D. Gibson, and K. Winker. 2012. A parapatric propensity for breeding in teal (Anas crecca, sensu lato) precludes the completion of speciation. Molecular Ecology 21:4563-4577.

Poole, E. L. 1940. Recent records from Lake Ontelaunee, Pennsylvania. Auk 57:577-578.

Reeber, S. 2015. *Waterfowl of North America, Europe, and Asia: An Identification Guide.* Princeton University Press, Princeton and Oxford.

Remsen, J. V., Jr., J. I. Areta, E. Bonaccorso, S. Claramunt, G. Del-Rio, A. Jaramillo, D. F. Lane, M. B. Robbins, F. G. Stiles, and K. J. Zimmer. Version 28 Sep 2023. A classification of the bird species of South America. Museum of Natural Science, Louisiana State University. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm

Sangster, G., M. Collinson, A. J. Helbig, A. G. Knox, D. T. Parkin, and T. Prater. 2001. The taxonomic status of Green-winged Teal *Anas carolinensis*. British Birds 94:218–226.

Sangster, G., A. G. Knox, A. J. Helbig, and D. T. Parkin. 2002. Taxonomic recommendations for European birds. Ibis 144:153–159.

Sibley, D. 2011. Distinguishing Green-winged and Common Teal. https://www.sibleyguides.com/2011/03/distinguishing-green-winged-and-common-teal/ (retrieved 4 Oct 2023)

Spaulding, F. R., J. F. McLaughlin, T. C. Glenn, and K. Winker. 2022. Estimating movement rates between Eurasian and North American birds that are vectors of avian influenza (AI). Avian Diseases 66:155-164.

Spaulding, F. R., J. F. McLaughlin, K. G. McCracken, T. C. Glenn, and K. Winker. 2023. Population genomics indicate three different modes of divergence and speciation with gene flow in the green-winged teal duck complex. Molecular Phylogenetics and Evolution 182:000-000.

Tobias, J.A., N. Seddon, C. N. Spottiswoode, J. D. Pilgrim, L. D. C. Fishpool, and N. J. Collar. 2010. Quantitative criteria for species delimitation. Ibis 152:724–746.

Vinicombe, K. E. 1994. Common Teals showing mixed characters of Eurasian and North American races. British Birds 87:88-89.

White, M.J.D. 1978. *Modes of Speciation.* W. H. Freeman and Company, San Francisco.

Winker, K. 2010. Is it a species? Ibis 152:679-682.

Winker, K. 2021. An overview of speciation and species limits in birds. Ornithology 138: ukab006 1-27.

Winker, K., K. G. McCracken, D. D. Gibson, and J. L. Peters. 2013. Heteropatric speciation in a duck, *Anas crecca*. Molecular Ecology 22:5922-5935.

Zink, R. M., S. Rohwer, A. Andreev, and D. Dittmann. 1995. Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. Condor 97:639-649.

Submitted by: Kevin Winker

Date of Proposal: 26 October 2023

Treat *Colaptes mexicanoides* as a separate species from Northern Flicker *C. auratus*

Background:

The Northern Flicker *Colaptes auratus* complex has historically presented a taxonomic conundrum in North American ornithology, with its major morphological groups being ordered and reordered various times by multiple taxonomic authorities and authors over the latter half of the 20th century. Five major morphological groups have been recognized within this complex: the nominate *auratus* group or Yellow-shafted Flicker of the eastern US and Canada, the *chrysocaulosus* group or Cuban Flicker of Cuba and Grand Cayman Island, the *cafer* group or Red-shafted Flicker of the western US, Canada, and Mexico, the *chrysoides* or Gilded Flicker of the far southwestern US and Baja California, and the *mexicanoides* group or Guatemalan Flicker of Central American highlands east of the Isthmus of Tehuantepec. For the purpose of this proposal and to avoid confusion, these five *Colaptes* groups will be referred to simply by the epithets *auratus*, *chrysocaulosus*, *cafer*, *chrysoides*, and *mexicanoides*, and collectively will be referred to as the *Colaptes auratus* or Northern Flicker complex.

Prior to 1993, this complex was treated as two distinct species on the basis of morphological differences (Short 1965, 1967): the Red-shafted Flicker, exhibiting a red malar in males, a brown crown and gray facial plumage, consisting of *cafer*, *chrysoides* and *mexicanoides*; and the Yellow-shafted Flicker, exhibiting a black malar in males, a gray crown and brown facial plumage, consisting of *auratus* and *chrysocaulosus*. The discovery of widespread hybridization and introgression between *auratus* and *cafer* along the Great Plains (Moore 1987, 1993) then caused this complex to be re-lumped as a single species by the AOU. Around the same time, another study found a preferential desert ecology in *chrysoides* and a more limited amount of interbreeding in zones of overlap with *cafer*, which then led to *chrysoides* being split into its own species by the AOU in 1995. North American flicker taxonomy has remained unmodified from this arrangement thereafter.

Historically, less English scientific literature has existed on *mexicanoides*, and I posit this is a result of its distant range of distribution from most English-speaking ornithologists. The *mexicanoides* group was placed in the Red-shafted Flicker *C. cafer* when this taxon held species status, because of the red malar in males and reddish pigmentation concentrated at the shafts of flight feathers. However, the taxon differs from all other *C.s auratus* groups by a browner plumage, including an orange-brown nape and crown, in addition to slight differences in malar and breast color such as the presence of a bold orange malar in females (Howell and Webb 1995; del Hoyo et al. 2014; online images at Macaulay Library). Vocal behavior and sounds differ consistently from other *C. auratus* groups, but no studies had performed any in-depth analysis on vocalizations until 2020.

Isolating mechanisms: Genotype & Phylogeography

Manthey et al. (2017) found higher genetic divergence in *mexicanoides* compared to other *C. auratus* groups, including *chrysoides*. Manthey et al. extracted genomic DNA of fifteen individuals total within the *C. auratus* clade, and two samples of the South American *Colaptes rubiginosus* were used as an outgroup. To characterize phylogenetic relationships in this clade, they sequenced the full ND2 gene from mitochondrial DNA of each sample, and ran a RAD-seq method to obtain hundreds of single nucleotide polymorphisms (SNPs) among all but the samples of *chrysocaulosus* (Cuban Flicker).

In the TreeMix and SDVquartets phylogenetic analyses of the SNP data, *mexicanoides* appeared with the highest level of divergence and earliest offshoot from the *C. auratus* complex, prior to *chrysoides* (Figure 5 from Manthey 2017).

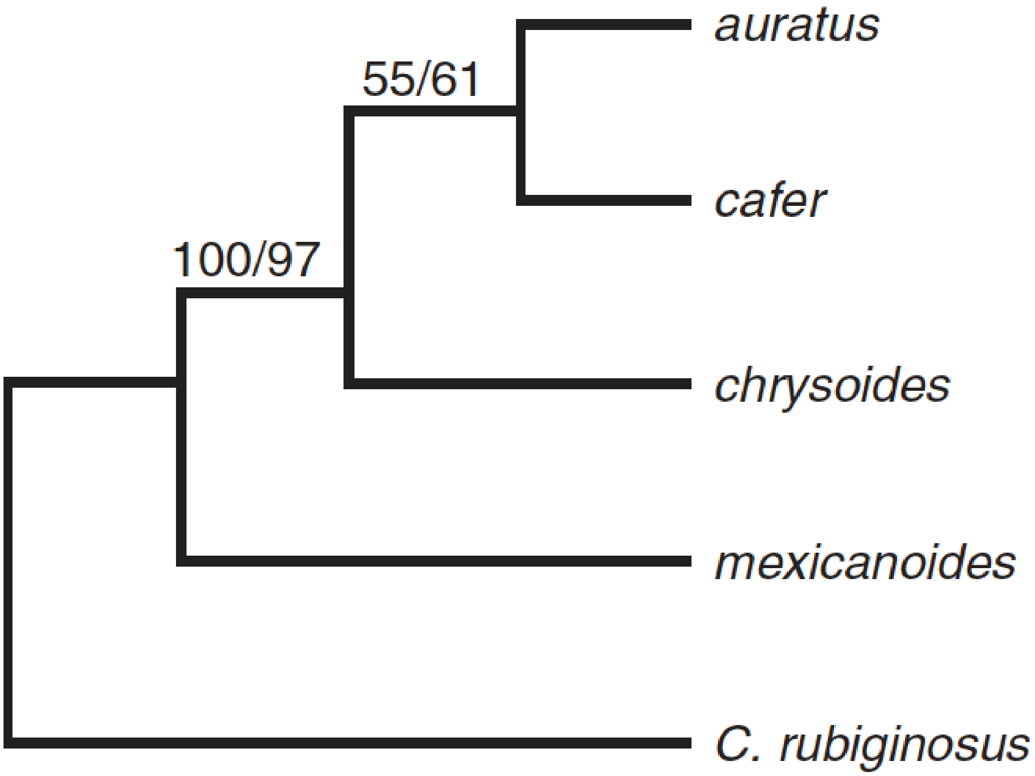


Fig 1. (Fig 5 from Manthey et al 2017). Phylogeny built with TreeMix and SDVquartets, where *C. rubiginosus* is the outgroup used for comparison.

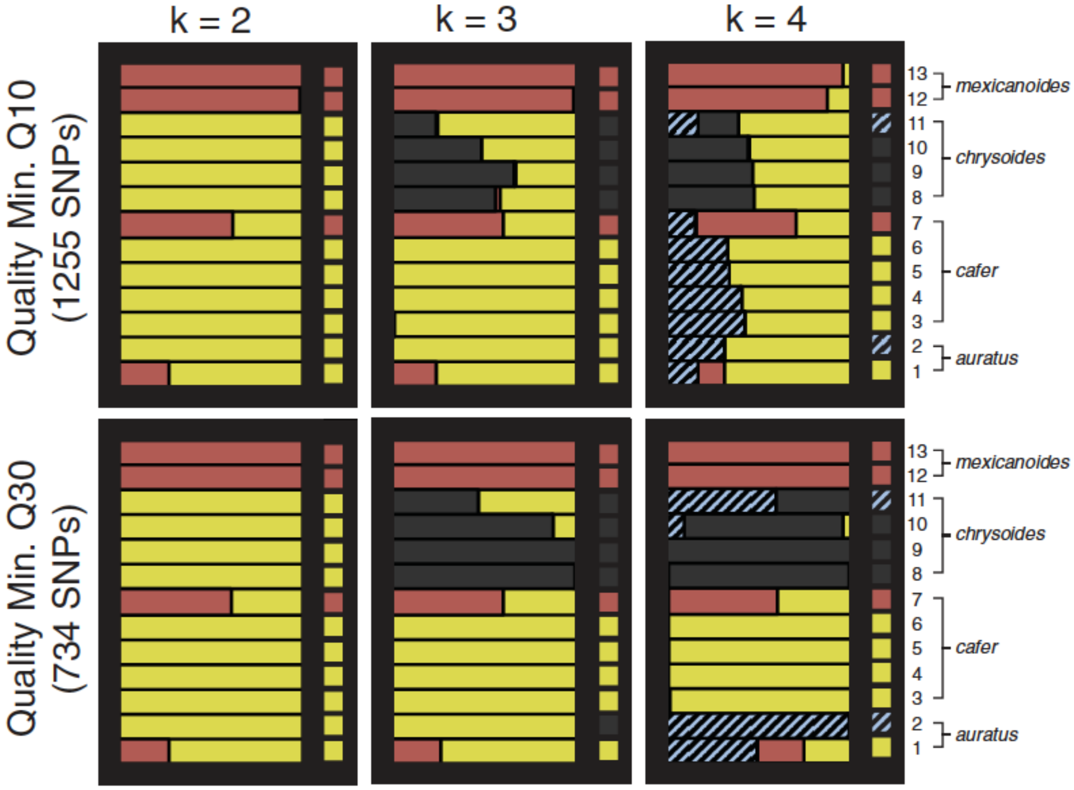


Fig 2. (Fig 4 from Manthey et al 2017). Tables representing probability of assignment to genetic cluster in rows, with each color representing a genetic cluster. The two rows of tables represent a different set of sampled SNPs, and each column of tables corresponds to how many genetic clusters were defined for that test, between k = 2, 3 or 4.

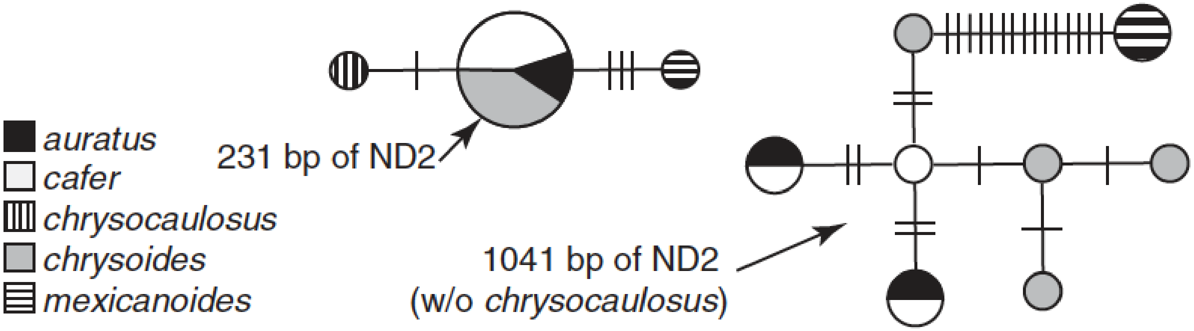


Fig 3. (Fig 2 from Manthey et al 2017). Median-joining haplotype networks of the mitochondrial ND2 gene, where haplotypes are connected by lines and bars represent mutational steps. In the dataset of 1041 base pairs, the two *mexicanoides* individuals are of the same haplotype and 15 mutational steps away from the nearest haplotype, while all other haplotypes are within 4 mutational steps from each other.

Manthey et al provided the first genetic analyses on both the *mexicanoides* and *chrysocaulosus* groups. Genetic samples in this study were limited to two individuals of *mexicanoides*, five individuals of *cafer*, four individuals of *chrysoides*, two individuals of *auratus* and two individuals of *chrysocaulosus*. These numbers, particularly of *mexicanoides*, are small sample sizes solely to create concrete inferences upon. Notwithstanding, results back up previous observations of *mexicanoides* as a distinctly diverged group. Known migration trends within the Northern Flicker in southern Mexico indicate a lack of dispersal across the lowlands in southern Mexico (eBird 2023; Howell 1995; Wiebe & Moore 2023), making the probability of gene flow existing across the Isthmus of Tehuantepec very low, following a pattern of divergence at this barrier among sister taxa that inhabit montane zones. The contact here is thus quite different from the situation of hybridization that exists between *C. cafer* and *C. auratus*, and between *C. cafer* and *C. chrysoides*.

New Information:

Isolating mechanisms: Vocal behavior

In 2020 Rabecca Lausch of the Northern Arizona University published a dissertation detailing analyses on vocalizations of the *Colaptes auratus* complex sampled over geographic space and with representatives from all five of the major groups. The long calls of each species were inspected, defined as those calls consisting of 20 to 80 "wikwikwikwikwik" notes, where each "wik" syllable represents a note; a vocalization known to be given immediately prior to pair-bonding and copulation in flickers, similar in function to the mate advertising songs given by oscines (Rosen 1982; Lausch 2020). From these vocalizations, quantitative parameters of total call duration, number of notes, note length, note frequency, and call pace (number of notes divided by total call duration) were recorded and assigned to two Canonical Discriminant Functions (DF1 and DF2). With these two Discriminant Functions she used an analysis of variance and pairwise comparisons using Tukey HSD post-hoc tests with a Holm-Bonferroni correction for multiple comparisons. Of *auratus*, *chrysocaulosus*, *cafer*, *chrysoides*, and *mexicanoides*, only *mexicanoides* showed calls that plotted outside confidence intervals for the five groups in both Discriminant Functions (Lausch 2020). In other words, the long call vocalizations of *mexicanoides* were consistently different in frequency, pacing, note length, and total duration resulting in a distinctly different sound, quantitatively and qualitatively, than other members of the *C. auratus* complex.

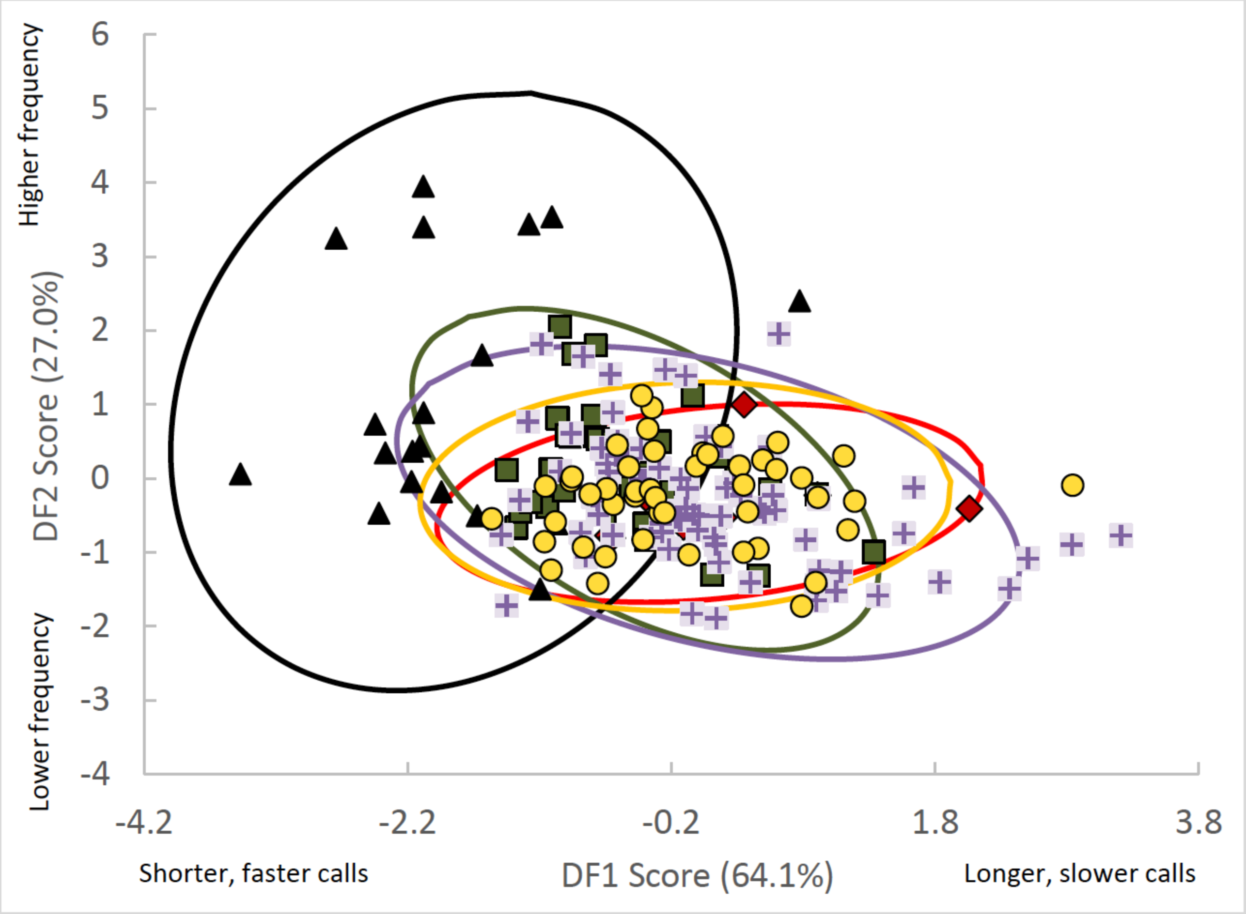


Fig 4. (Fig 3 from Lausch 2020). In this scatterplot, *C. mexicanoides* calls (n=20) represented by black triangles, average a lower DF1 score, meaning shorter and faster calls, and average a higher DF2 score, meaning higher frequency notes, than the other four flicker groups. *C. chrysoides* calls (n=39) are represented by green squares, *C. chrysocaulosus* calls (n=10) are represented by red diamonds, *C. cafer* calls (n=75) are represented by purple plus signs, and *C. auratus* calls (n=47) are represented by yellow circles. 95% confidence ellipses surround each sample group, of which there is considerable overlap between all five groups.

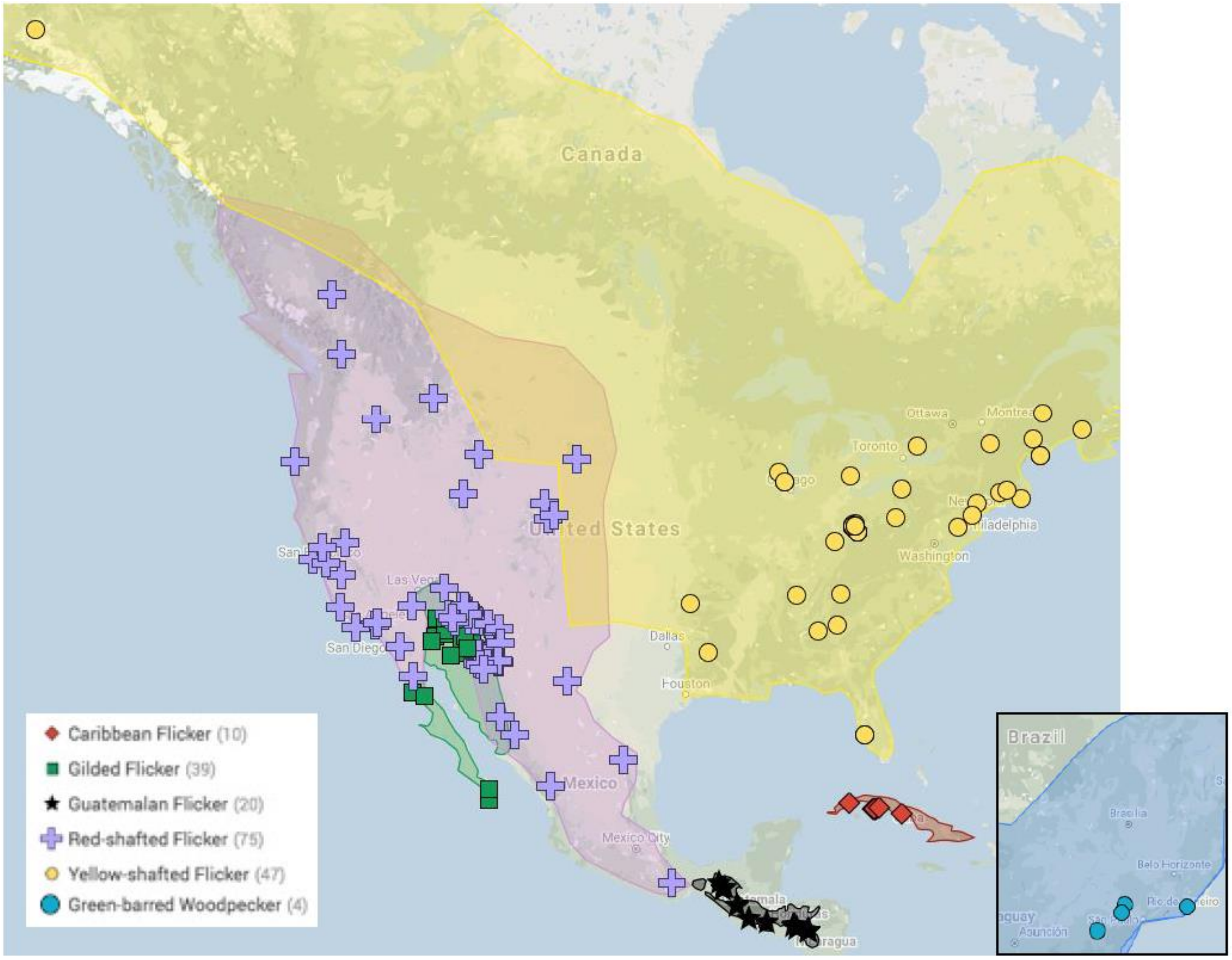


Fig 5. (Fig 1 from Lausch 2020). Map showing spread of sample locations for calls analyzed by Lausch, including an outgroup for the study (Green-barred Woodpecker *Colaptes melanochloros*).

In addition to this long call, the other notable vocal difference in *mexicanoides* is the apparent lack of a "kleer" call or equivalent in its repertoire, a call among the most common vocalizations in other *C. auratus* groups. Instead, *mexicanoides* seems to utilize its long call at a higher rate than other *C. auratus* groups, perhaps serving functions that the "kleer" call serves in other flickers. This was noted during observation of *mexicanoides* over many hours in Chiapas, Mexico in 2022 and 2023, and followed up with an inspection of all Guatemalan Flicker recordings in the Macaulay Library and xeno-canto on June 7, 2023, (in total, n=65). This analysis supported the lack of a "kleer" vocalization while yielding many variations of the long call vocalizations, "weak-weak-weak-weak-weak" interaction calls, and rattle or "churr" calls as referred to in Lausch (2020). Both databases are public and searchable, allowing for easily reproducible analyses of this nature (xeno-canto sound collection; Macaulay Library Media Collection 2015). In Piciformes woodpeckers, to which *Colaptes* flickers belong, vocalizations are known to be innate and not learned behavior, and thus, strongly indicative of evolutionary distance among taxa (Rosen 1982; Lausch 2020; de J. Zazueta-Algara 2022).

Recommendation:

As currently treated, the Northern Flicker *C. auratus* is a paraphyletic group, since genetic and vocal analyses support *mexicanoides* as basal to the rest of the *C. auratus* complex including *C. chrysoides*, which is currently treated as a separate species. Recognizing this paraphyly, there are two courses of action that could be taken in solving this issue. The first would be to re-lump *C. chrysoides* (Gilded Flicker) with *C. auratus*, treating the complex as it was prior to 1995 (AOU). The second option would be to split *C. mexicanoides* and treat this taxon as its own species.

Lumping *C. chrysoides* with *C. auratus* would acknowledge that differentiation in *C. chrysoides* is weak, and that widespread introgression exists between the two taxa in their zones of overlap. Recent analyses from Manthey 2017 and Lausch 2020 indicated that *C. chrysoides* lies closer to *C. auratus* than does *C. mexicanoides* in phylogeny, including no consistently diagnosable differences in vocalizations between *C. chrysoides* and *C. cafer*. Even earlier studies of allozymes and mitochondrial DNA found no diagnostic differentiation between *C. chrysoides* and *C. auratus/cafer* (Aguillon et al 2018; Fletcher and Moore 1992; Moore et al. 1991). Thus, the basis for its species status is essentially hinged upon its habitat preferences in conjunction with differences in morphology. Recent anecdotal observations of morphology indicate that hybridization exists in Arizona beyond zones originally identified in the study by Lester Short in 1965; however, no studies have provided a comprehensive overview of contact zones in Sonora and Baja California. The query that should be addressed is whether *C. chrysoides* is in active divergence or convergence in relation to *C. auratus*, and to do that, genetic sampling in overlap zones over a wide extent of its range would illuminate the extent of hybridization and consequently which of these two processes are in play. So, although evidence indicates that *C. chrysoides* is more recently diverged from the rest of the *C. auratus* clade than is *mexicanoides*, this information alone may not be sufficient to merit a lump without further genetic sampling to confirm a wide zone of introgression between *C. chrysoides* and *cafer*. Thus, at this time I do not endorse a vote on the taxonomic treatment of *C. chrysoides*.

A combination of genetic analysis (Manthey 2017), consistently diagnosable plumage differences, and highly differential vocal behavior including significantly differentiated courtship and mating vocalizations (Lausch 2020), indicate deep genetic divergence and a low likelihood of hybridization if presented the opportunity, between *C. mexicanoides* and other *C. auratus* groups. For these reasons, to recognize the taxon's distinctive biogeography, and finally, to solve the issue of paraphyly within the *C. auratus* complex, I recommend a YES vote for splitting *mexicanoides* from *C. auratus* (Northern Flicker).

As a separate species, I would recommend the English name Guatemalan Flicker be used for *Colaptes mexicanoides*, based on widespread usage of this name in literature and given that the distribution of this taxon centers on the Guatemalan Highlands.

Acknowledgements:

Thanks to Nathan Pieplow for his careful review and suggested structural changes of this proposal's drafts, without which this final version as presented would not be possible.

Literature Cited:

Aguillon, Stepfanie M., Campagna, L., Harrison, R.G., & Lovette, I. J. (2018). A flicker of hope: Genomic data distinguish Northern Flicker taxa despite low levels of divergence. *The Auk*, Volume 135, Issue 3, Pages 748–766, https://doi.org/10.1642/AUK-18-7.1

AOU (1995). Fortieth supplement to the American Ornithologists' Union *Check-list of North American Birds*. Auk 112:819-830.

AOU (2017). Proposals 2017-C.

Batista, R., Olsson, U., Andermann, T., Aleixo, A., Ribas, C. C., & Antonelli, A. (2020). Phylogenomics and biogeography of the world's thrushes (Aves, *Turdus*): new evidence for a more parsimonious evolutionary history. *Proc. R. Soc. B.*2872019240020192400. Accessed online at http://doi.org/10.1098/rspb.2019.2400

de J. Zazueta-Algara, J., Sosa-López, J. R., del Coro Arizmendi, M., & Navarro-Sigüenza, A. G. (2022). Structure and divergence of vocal traits in the Acorn Woodpecker (Melanerpes formicivorus). *The Wilson Journal of Ornithology*, *134*(1), 1-18.

del Hoyo, J., & Collar, N. J. (2014) HBW and BirdLife International Illustrated Checklist of the Birds of the World. Lynx Edicions and BirdLife International, Barcelona, Spain and Cambridge, UK.

Fletcher, S. D., and Moore, W.S. (1992). Further analysis of allozyme variation in the Northern Flicker, in comparison with mitochondrial DNA variation. *The Condor* 94: 988–991.

Howell, S. N. G., and Webb S. (1995). A Guide to the Birds of Mexico and Northern Central America. Oxford University Press.

Lausch, R. (2020). Vocalizations, Reproductive Isolating Mechanisms and Species Interactions in the North American Flickers. Northern Arizona University ProQuest Dissertations Publishing, 2020. 28256563. Accessed online at https://www.proquest.com/openview/d014956c1bb0f4a53def161542c459dc/1?pq-origsite=gscholar&cbl=44156

Manthey, J. D., M. Geiger, & R. G. Moyle. (2017). Relationships of morphological groups in the northern flicker superspecies complex (*Colaptes auratus* & *C. chrysoides*). Systematics & Biodiversity 15:183–191. Accessed online at https://www.tandfonline.com/doi/abs/10.1080/14772000.2016.1238020

Moore, W. S. (1987). Random mating in the Northern Flicker hybrid zone: implications for the evolution of bright and contrasting plumage patterns in birds. Evolution 41:539-546.

Moore, W. S., Graha, J.H., & Price, T.J. (1991). Mitochondrial DNA variation in the Northern Flicker (*Colaptes auratus*, Aves). *Molecular Biology and Evolution* 8: 327–344.

Moore, W. S., & Price, J. T. (1993). The nature of selection in the Northern Flicker hybrid zone and its implications for speciation theory. In Hybrid zones and the evolutionary process., edited by R. G. Harrison, 196-225. Oxford, UK: Oxford Univ. Press.

Short, L. L. (1965). Hybridization in the flickers (*Colaptes*) of North America. Bulletin of the American Museum of Natural History 129:307-428.

Short, L. L. (1967). Variation in Central American flickers. Wilson Bulletin 79:5-21.

Short, L. L. (1972). Systematics and behavior of the South American flickers (Aves, Colaptes). Bulletin of the AMNH 149:1-109.

Wiebe, K. L., and W. S. Moore (2023). Northern Flicker (*Colaptes auratus*), version 2.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.norfli.02

Submitted by: David A. Tønnessen

Date of Proposal: 18 November 2023

Treat *Buteo elegans* as a separate species from Red-shouldered Hawk *B. lineatus*

Background:

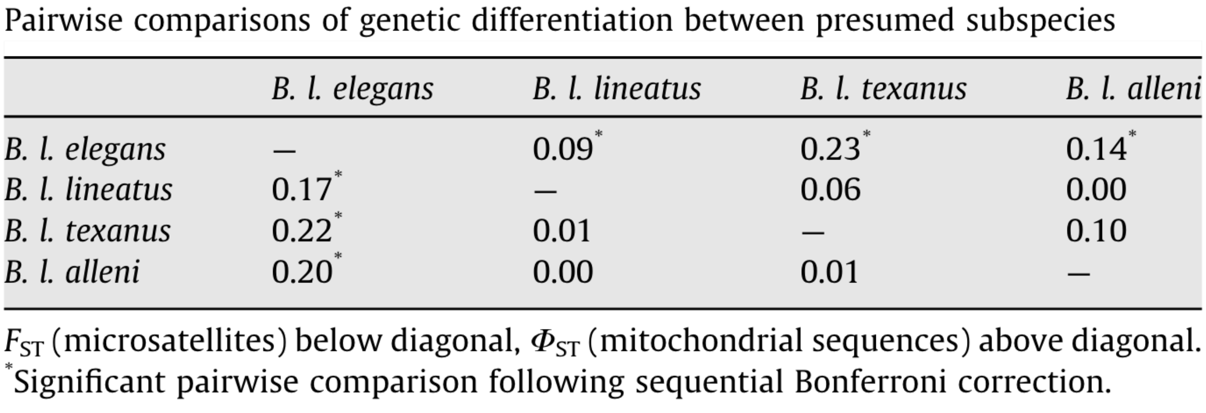
The Red-shouldered Hawk *Buteo lineatus* is a medium sized *Buteo* that inhabits forests throughout North America, from southern Quebec and Ontario south to the Florida Keys, from the east coast west to the start of the prairies, and the west coast from southern Oregon south through California to the Baja Peninsula (Fig. 1). The species is polytypic with 5 described subspecies; however, *B. l. alleni* (hereafter *alleni*) and *B. l. texanus* (hereafter *texanus*) are often treated as part of *B. l. lineatus* (hereafter *lineatus*). Plumage varies across the distribution, with the most extreme cases being a very pale type in peninsular Florida, (*B. l. extimus*; hereafter *extimus*) and a richly marked population on the west coast (*B. l. elegans*; hereafter *elegans*).

The Red-shouldered Hawk was first described as *Falco lineatus* (Gmelin 1788), after which several ornithologists described the variation throughout its distribution in different accounts, notably starting with *elegans* (Cassin 1855), which was first described as a distinct species. Other descriptions of new subspecies followed with *alleni* (Ridgway 1885), *texanus* (Bishop 1912), and arguably the most distinctive in definitive plumage, *extimus* (Bangs 1920).

New Information:

The first investigation into the genetic relationships between *Buteo lineatus* populations (Hull et al. 2008) involved *lineatus*, *elegans*, *alleni*, and *texanus*. Hull et al. sequenced 21 microsatellite loci and a 375 bp segment of domain 1 mitochondrial control region. From these loci, they found significant genetic differentiation between *elegans* and the other taxa in both the mitochondrial and nuclear data (Hull et al. 2008; Table 1).

Table 1. From Hull et al. 2008, table 2 showing pairwise comparisons in *F*st.



Pairwise comparisons of genetic differentiation between presumed subspecies

	B. l. elegans	*B. l. lineatus*	*B. l. texanus*	*B. l. alleni*
B. l. elegans	–	0.09^{*}	0.23^{*}	0.14^{*}
B. l. lineatus	0.17^{*}	–	0.06	0.00
B. l. texanus	0.22^{*}	0.01	–	0.10
B. l. alleni	0.20^{*}	0.00	0.01	–

F_{ST} (microsatellites) below diagonal, Φ_{ST} (mitochondrial sequences) above diagonal.
*Significant pairwise comparison following sequential Bonferroni correction.

Hull et al. (2008) concluded that at least two distinct evolutionary lineages exist in *B. lineatus*, the western *elegans* and the remaining eastern populations, and that the levels of divergence at both mitochondrial and microsatellite loci warrant species status under some definitions.

The second investigation into the genetic relationships among populations in *B. lineatus* (Barrowclough et al. 2019) involved all described subspecies, including *extimus*. In addition to including the Florida population, Barrowclough et al. stated that they chose to revisit the question from a population sampling approach rather than a subspecies-based approach (*sensu* Hull et al. 2008). Barrowclough sequenced the entire mitochondrial gene ND2 as well as two nuclear introns and found that no mitochondrial haplotypes were shared between *elegans* and eastern populations (Fig. 1). Importantly, Barrowclough et al. found a *F*st value of 0.65 between *elegans* and eastern populations at ND2, and less differentiation for the nuclear introns (Fig. 2), but with an *F*st of 0.22 at one of these. In addition, within-population sequence divergence at the loci of interest was extremely low for all populations (0.0003 for ND2 in northern California birds; Table 1 in Barrowclough et al. 2019).

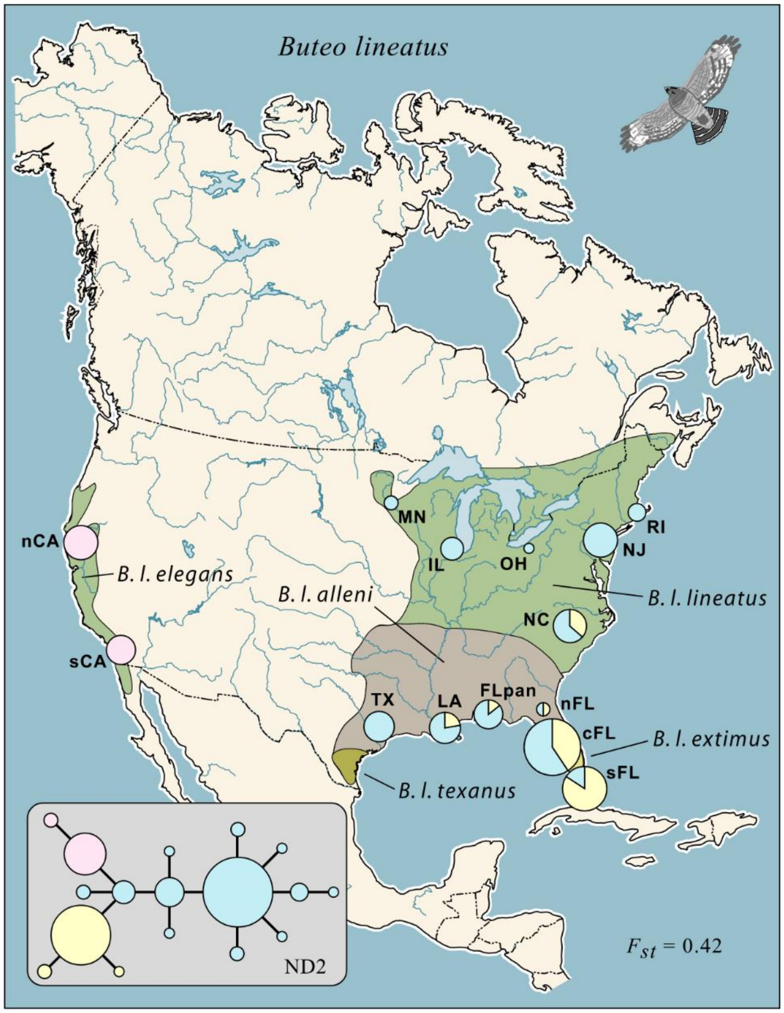


Figure 1. Network of observed ND2 haplotypes in *Buteo lineatus* and their geographic distribution; areas of haplotype pie diagrams are proportional to sample sizes. Approximate breeding distributions of five currently recognized subspecies are indicated. From Barrowclough et al. (2019).

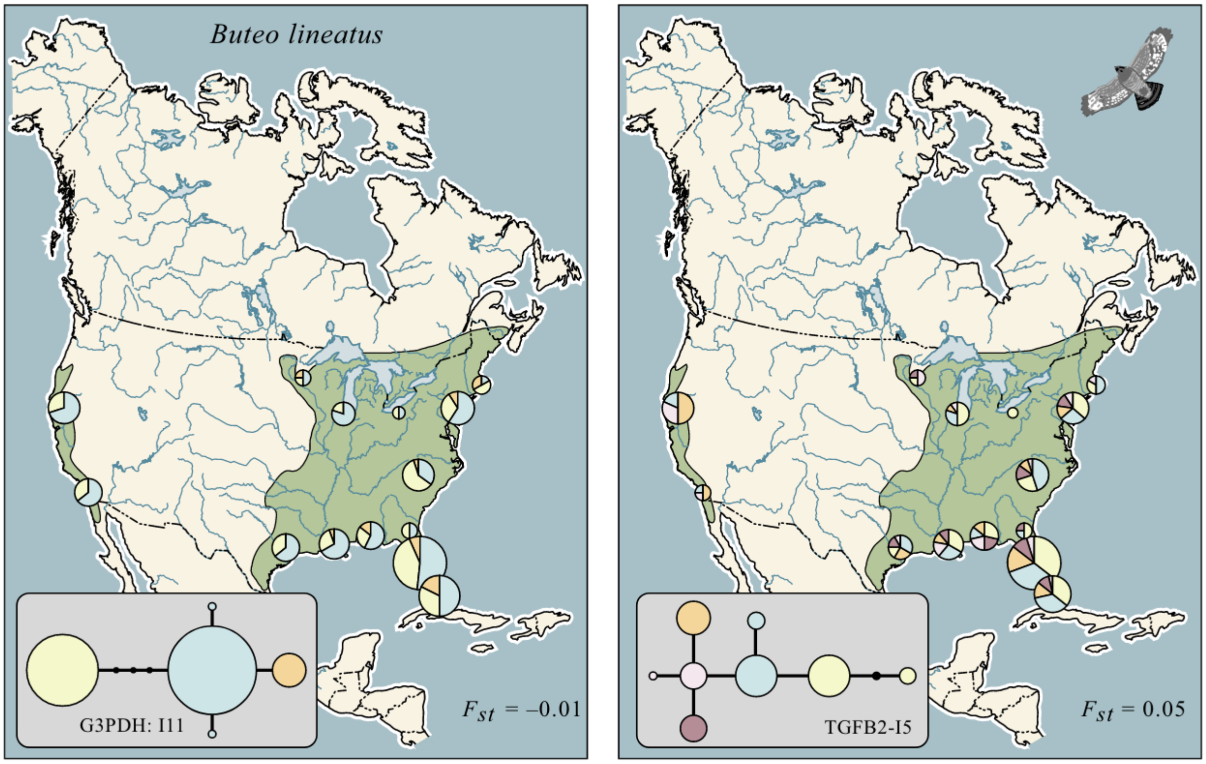


Figure 2. (a) Network and geographic distribution of observed G3PDH (intron-11) alleles in B. lineatus. (b) Network and geographic distribution of observed TGFB2 (intron-5) alleles. Areas of pie diagrams are proportional to sample sizes. From Barrowclough et al. (2019).

This complex presents a dilemma not unfamiliar in our attempt to understand species limits in birds. Allopatric populations have long vexed ornithologists, particularly in island systems, because of the weight given to the biological species concept for species determination in birds. In the absence of a perspective on how *elegans* would treat the rest of the *B. lineatus* complex at zones of contact, we are unfortunately unable to compare with similar *Buteo* species because I am unaware of other studies that have assessed mitochondrial divergence to support taxonomic revision. But, in other bird taxa, there seem to be many instances where taxa are treated at the species level, or even genus level, that have much lower *F*st values when comparing taxa. *F*st between American and Pacific Golden-Plovers at ND2 is much lower (*F*st = 0.21; Withrow and Winker 2014), and although we still lack a genome-wide perspective on differentiation in *B. lineatus*, it is interesting that the differentiation at ND2 between the eastern/western Red-shouldered Hawk is much higher than genome-wide *F*st for hummingbird species pairs in three different genera (*Archilocus* *F*st = 0.112; *Calypte*, *F*st = 0.323; *Selasphorus*, *F*st = 0.041 ; Henderson and Brelsford 2020), although mitochondrial *F*st is expected to be higher than nuclear *F*st. In addition, mean genome wide *F*st between *Zonotrichia* taxa is also much lower (*Z. leucophrys gambelii* and *Z. atricapilla*, *F*st = 0.273; *Z. l. pugetensis* and *Z. atricapilla*, *F*st = 0.303; McCallum et al. 2022). Although the latter two studies involve genome-wide perspectives, the level of differentiation at both the nuclear introns and the mitochondrial ND2 provide strong support that *elegans* has been isolated and without gene flow for an extensive amount of time, likely for as long as two glacial cycles, as stated in Barrowclough et al. (2019).

Barrowclough et al. (2019) concluded that under the phylogenetic species concept, *Buteo lineatus* includes three distinct evolutionary trajectories that are best treated as three species, *lineatus* (including *alleni* and *texanus*), *elegans*, and *extimus*.

Additional information supporting differences between *B. elegans* and *B. lineatus*

Plumage

Definitive plumage

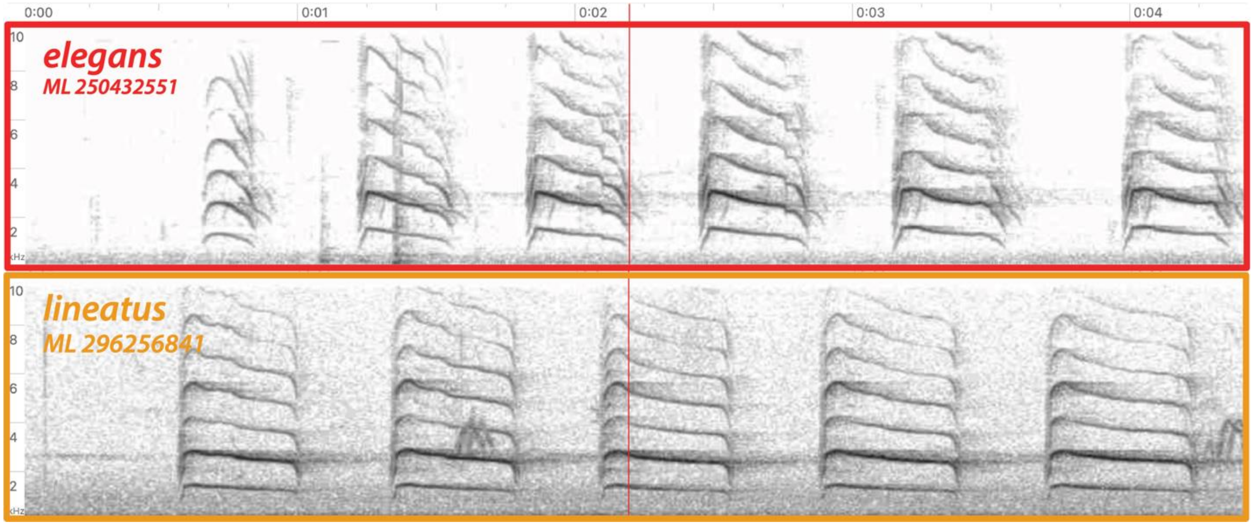
Although the difference between definitive plumage in *elegans* compared to *lineatus*, *alleni*, and *texanus* appears quite subtle, there are some obvious qualitative differences that deserve mention. Particularly, *elegans* has a much higher overall contrast to the dorsal coloration (https://macaulaylibrary.org/asset/543390681) when compared to other populations (https://macaulaylibrary.org/asset/288107931). In addition, *elegans* has a solid breast coloration that is not generally present in other populations (*elegans*: https://macaulaylibrary.org/asset/265570071; compare to the streaked and banded breast of *lineatus*: https://macaulaylibrary.org/asset/394770291, and *alleni*: https://macaulaylibrary.org/asset/422820271). In addition, the pale tips to the primaries are very white in *elegans* (https://macaulaylibrary.org/asset/142691771), differing from the more gray and subtle tone of *lineatus* (https://macaulaylibrary.org/asset/426567271), which appears to be an extension of the overall higher contrast in the black and white markings in *elegans*.

Juvenal plumage

There is a substantial difference in juvenal plumage between *elegans* and the rest of the complex. Juvenile *elegans* is generally more adult-like in appearance, and differs in ventral pattern in being much more heavily marked on average, with a heavily streaked bibbed, and with streaking, barring, and chevroned markings on the belly (https://macaulaylibrary.org/asset/610213776), in contrast to the overall paler appearance of the mostly streaked underside in other populations like *lineatus* (https://macaulaylibrary.org/asset/515312251). However, *extimus* averages fairly heavily marked below with markings similar in character to *elegans* (https://macaulaylibrary.org/asset/610284625). Another difference between *elegans* and other populations is the heavily marked and more rust-colored underwing of most individuals (https://macaulaylibrary.org/asset/205336121) compared to other populations, which have a lightly marked underwing that mostly matches the overall body coloration (https://macaulaylibrary.org/asset/366255081). Upperwing coloration also differs in *elegans*, with a more adult-like reddish coloration to the upperwing coverts (https://macaulaylibrary.org/asset/171432051) rather than the more subdued or absent rufous tones to the upperwing coverts in other populations (https://macaulaylibrary.org/asset/143570451). The remige coloration also differs between *elegans* and other populations, with a more contrasting adult-like appearance in *elegans* (https://macaulaylibrary.org/asset/171432071, https://macaulaylibrary.org/asset/610213776), compared to the muted coloration in other populations (https://macaulaylibrary.org/asset/33016101, https://macaulaylibrary.org/asset/608859397). Finally, the tail pattern is more adult-like in *elegans*, with generally 4 to 5 visible bands (https://macaulaylibrary.org/asset/77441391) compared with 6-7 in other populations (https://macaulaylibrary.org/asset/75778971).

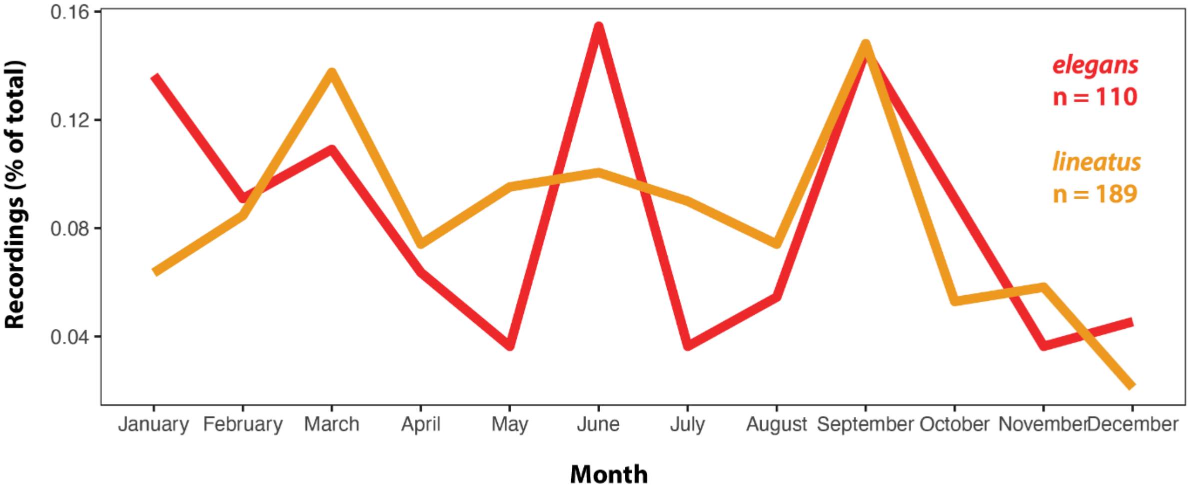
Morphometrics
Apart from *extimus*, *elegans* averages much smaller in wing chord than eastern populations, particularly for females (344.8 mm and 302.0 mm for *lineatus* and *elegans*, respectively; Dyrkstra et al. 2020). Mass also differs, with an average of 559 (409- 689) grams in *elegans* and 607 (486 – 774) grams in *lineatus* (Golden Gate Raptor Observatory unpublished data, Dykstra et al. 2020)

Vocalizations
The plumage and morphometric differences between *elegans* and the eastern populations suggest there may be other differences in phenotype, such as vocalizations. There are only 7 vocalization types that have been characterized in this species, and generally the most common is a broadcast call that advertises an individual's presence on a territory (Dykstra et al. 2020). Because of this, these calls may be a component of species recognition and warrant some consideration. Although not quantified, to my ear the typical kee-ah call between *elegans* and *lineatus* differ. I've included here two spectrograms, one from *elegans* and one from *lineatus*, to illustrate what I see as a general trend in vocalizations between the two. In character, *elegans* seems to call at a quicker pace with calls of shorter duration, while *lineatus* has a longer, slower-paced call. The spectrogram visually illustrates the difference in the length and pace of each call. Although there is a lot of within-taxon variation to these parameters, I believe the general trend holds true. Regardless, this deserves a close and thorough look in the future, but is generally suggestive of their genetic divergence.



Vocal Behavior

Although not quantified, many birders and ornithologists have suggested a difference in vocalization behavior between *elegans* and the rest of the complex. Specifically, many assert that eastern birds are essentially only vocal during the breeding season. In comparison, *elegans* is thought to be very vocal throughout the entire year. To investigate this, I recorded the number of recordings by month in the Macaulay Library for *elegans* and *lineatus* (which includes *alleni* and *texanus*) and plotted the results for each month (as a percentage of the total for that taxon) across the year for each group. Although this is admittedly a very imperfect approach to assessing any behavioral differences, the results suggest that there is not an obvious pattern in calling behavior in either taxon, except for a general reduction in calling behavior from October to February. This at least suggests there is no difference between these two taxa in this behavior, since given previous assumptions, *lineatus* should have most recordings in the period between early spring and mid-summer, rather than fitting the overall trend of *elegans* that spans most of the year. It is, however, important to note the difference in the number of recordings for each taxon and consider that sample sizes are quite low when spread across the year. In addition, I made no effort to sort through the calls to remove juvenile begging, which may be responsible for the peak in recordings in September. I also made no attempt to filter out any call type other than the typical broadcast call that is generally elicited to announce a bird's presence when on territory.



Recommendation:

I recommend voting yes to split the Red-shouldered Hawk into two species, the Red-bellied Hawk (*Buteo elegans*) and the Red-shouldered Hawk (*Buteo lineatus*), based primarily on the strong genetic divergence between the mitochondrial ND2 region as well as divergence at nuclear loci. Although Barrowclough et al. suggested that *extimus* should be considered a species based on the phylogenetic species concept, I recommend not to split *extimus* from *lineatus* for now. Although we are currently refining our understanding of how secondary contact and gene flow function in the process of speciation, complicating the reliance on the biological species concept alone, I suggest a conservative approach to assessing the status of *extimus*, waiting until whole genome work is conducted on the contact zone between *extimus* and *alleni* to better understand how hybridization functions between the two populations.

If the committee votes to split these taxa, I recommend the following English names:

Buteo lineatus – Red-shouldered Hawk. This would remove *elegans* from the species, retaining *lineatus*, *alleni*, *texanus*, and *extimus*.

Buteo elegans – Red-bellied Hawk. This name was used in the description of this taxon by Cassin (1855) and has appeared elsewhere in the literature (e.g., Dixon 1928, Hellmayr and Conover 1949). An additional option is California Hawk, since most of the distribution lies in the state of California as well as Baja California.

Effect on the AOS Checklist:

This split would add one species to the AOS *Check-List*.

References:

Barrowclough, G., J. G. Groth, W. M. Mauck, and M. E. Blair. 2019. Phylogeography and species limits in the red-shouldered hawk (*Buteo lineatus*): Characterization of the northern Florida suture zone in birds. Ecology and Evolution 00:1-14. https://doi.org/10.1002/ece3.5190

Dixon, J. B. 1928. Life history of the Red-bellied Hawk. The Condor. 228-236.

Dykstra, C. R., J. L. Hays, and S. T. Crocoll. 2020. Red-shouldered Hawk (*Buteo lineatus*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.reshaw.01

Hellmayr, C. E., and B. Conover. 1949. Catalogue of birds of the Americas, Part 1, Number 4. Field Museum Zoological Series, Volume 13.

Henderson, E. C., and A. Brelsford. 2020. Genomic differentiation across the speciation continuum in three hummingbird species pairs. BMC Evolutionary Biology 20:113. https://doi.org/10.1186/s12862-020-01674-9

Hull. J. M., B. N. Strobel, C. W. Boal, A. C. Hull, C. R. Dykstra, A. M. Irish, A. M. Fish, and H. B. Ernest. 2008. Comparative phylogeography and population genetics within *Buteo lineatus* reveals evidence of distinct evolutionary lineages. Molecular Phylogenetics and Evolution 49:988-996. doi:10.1016/j.ympev.2008.09.010

McCallum, Q., K. Askelson, F. Fogarty, L. Natola, E. Nikelski, A. Huang, and Darren Irwin. 2022. Extreme sex chromosome differentiation, likely driven by inversion, contrasts with mitochondrial paraphyly between species of crowned sparrows. BioRxiv.

Withrow, J. J., and K. Winker. 2014. Genetics of a high-latitude cryptic speciation event: American and Pacific Golden-Plovers. The Wilson Journal of Ornithology 126:429-442.

Submitted by: Bryce W. Robinson, Cornell Lab of Ornithology

Date of Proposal: 1 December 2023

Reconsider the generic treatment of *Calocitta, Psilorhinus,* and *Cyanocorax*

Background:

The avian family Corvidae includes a clade that consists of the genera *Calocitta* (2 species), *Psilorhinus* (1 species), and *Cyanocorax* (16 species). Ten of these species occur in the NACC area, including *P. morio* and both species of *Calocitta*. The magpie-jays (*Calocitta*) were already placed in a separate genus when Middle America was added to the 6th edition of the AOU Checklist in 1983. Historically (e.g., Ridgway 1904, Helllmayr 1934), the Brown Jay *Psilorhinus morio* was placed in a monotypic genus but then was merged into the genus *Cyanocorax* in the 6th edition; that treatment was maintained until 2010 when *Psilorhinus* was restored (Chesser et al. 2010; see NACC proposal 2009-A-4 for details and rationale). The first genetic studies of this group consistently recovered *Calocitta* and *Psilorhinus* as sisters, and those two genera as sister to *Cyanocorax* (Saunders and Edwards 2000, Bonaccorso and Peterson 2007), although these studies had limited sampling of *Cyanocorax* (from 3 to 6 species represented; also see Fernando et al. 2017).

Bonaccorso et al. (2010), however, sampled all species of *Cyanocorax*, *Calocitta*, and *Psilorhinus* for two mitochondrial genes and three nuclear loci. Their results (Figure 1) indicated that four species of *Cyanocorax* (*cyanomelas*, *cristatellus*, *violaceus*, and *caeruleus*), *Psilorhinus morio,* and the two species of *Calocitta* (*colliei* and *formosa*) formed a clade ("Clade A") sister to a clade consisting of all other species of *Cyanocorax* ("Clade B"). Thus, *Cyanocorax* is paraphyletic if *Psilorhinus* and *Calocitta* are considered separate genera. Within Clade A, the two species of *Calocitta* formed a clade sister to a clade consisting of *Psilorhinus morio* and the four species of *Cyanocorax*, but support for deeper relationships within the latter clade was not strong. Within Clade B, the relationships of *yncas* and *mystacalis* were unresolved but the other species of *Cyanocorax* formed two clades: "Group II", consisting of *cayanus*, *chrysops*, *cyanopogon*, *heilprini*, *affinis*, and *dickeyi*; and "*Cissilopha*", consisting of *melanocyaneus*, *yucatanicus*, *sanblasianus*, and *beechei*. After considering alternative taxonomic arrangements (e.g., placing all Clade A species in *Psilorhinus* or recognizing *Uroleuca* for the four species of *Cyanocorax* in Clade A), Bonaccorso et al. (2010) recommended recognizing only the single genus *Cyanocorax*, with *Psilorhinus* and *Calocitta* as synonyms. Both the Howard & Moore checklist (Dickinson and Christidis 2014) and HBW (del Hoyo and Collar 2016) adopted this recommendation and transferred *Psilorhinus morio* and the two species of *Calocitta* to *Cyanocorax*.

New Information:

McCullough et al. (2022) examined diversification within the Corvides (crows and jays, birds-of-paradise, vangas, etc.) to assess their historical biogeography. Their study combined a generic-level data set of thousands of ultraconserved elements (UCEs) and a species-level, 12-gene Sanger sequence matrix that resulted in a well-resolved supermatrix tree. We've pruned the portion of their tree that includes *Calocitta, Psilorhinus*, *Cyanocorax*, and related taxa (Figure 2). Their sampling included all 16 species of *Calocitta, Psilorhinus*, and *Cyanocorax* as well as "*C. luxuosus*" (NACC proposal 2023-B-9 to treat *C. luxuosus* as a separate species from *C. yncas* failed unanimously). The tree of McCullough et al. (2022) also shows that *Cyanocorax* is paraphyletic if *Psilorhinus* and *Calocitta* are considered separate genera.

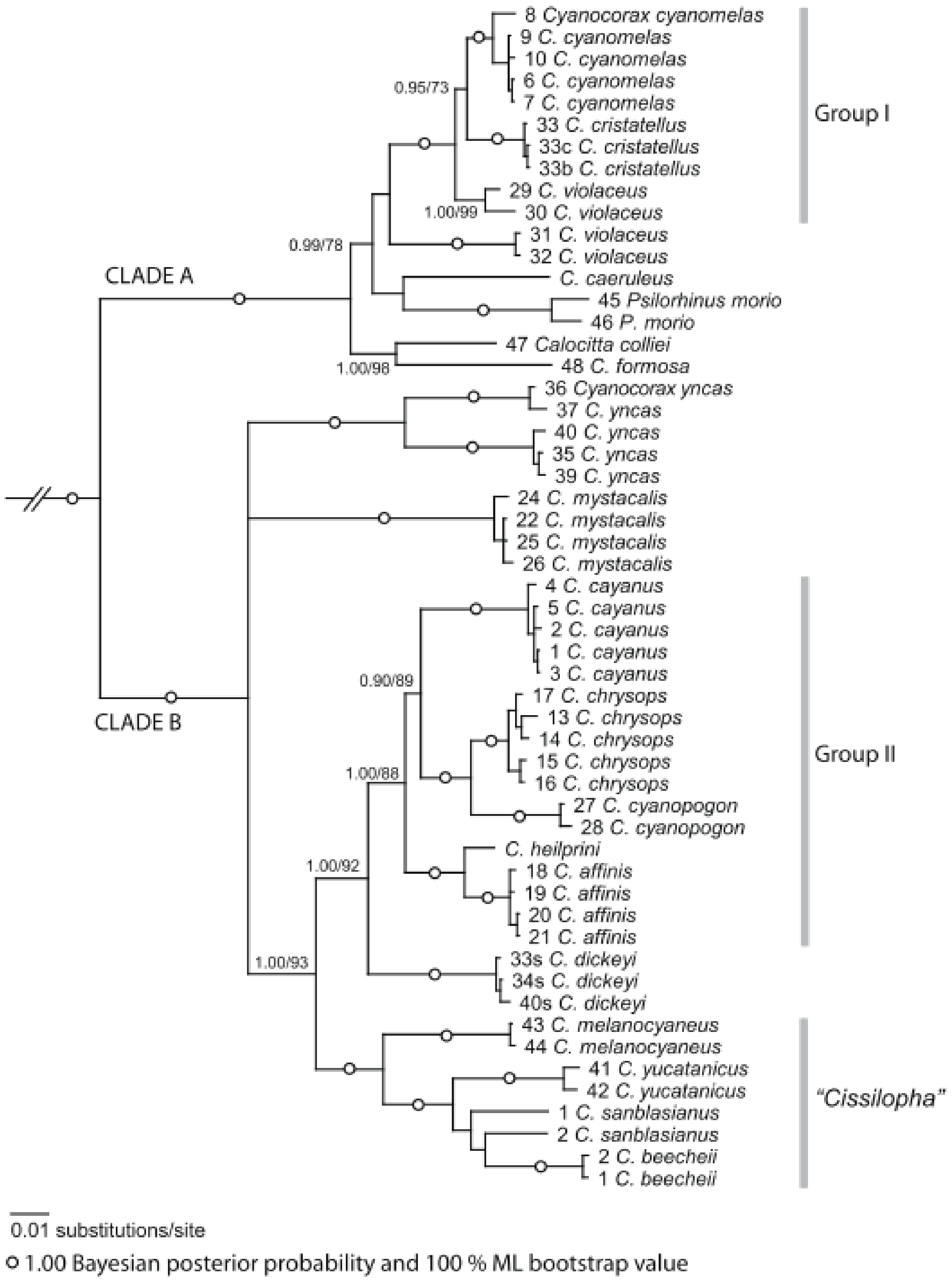


Figure 1. Bayesian tree from Bonaccorso et al. (2010) showing phylogenetic relationships among species of *Calocitta, Psilorhinus*, and *Cyanocorax*

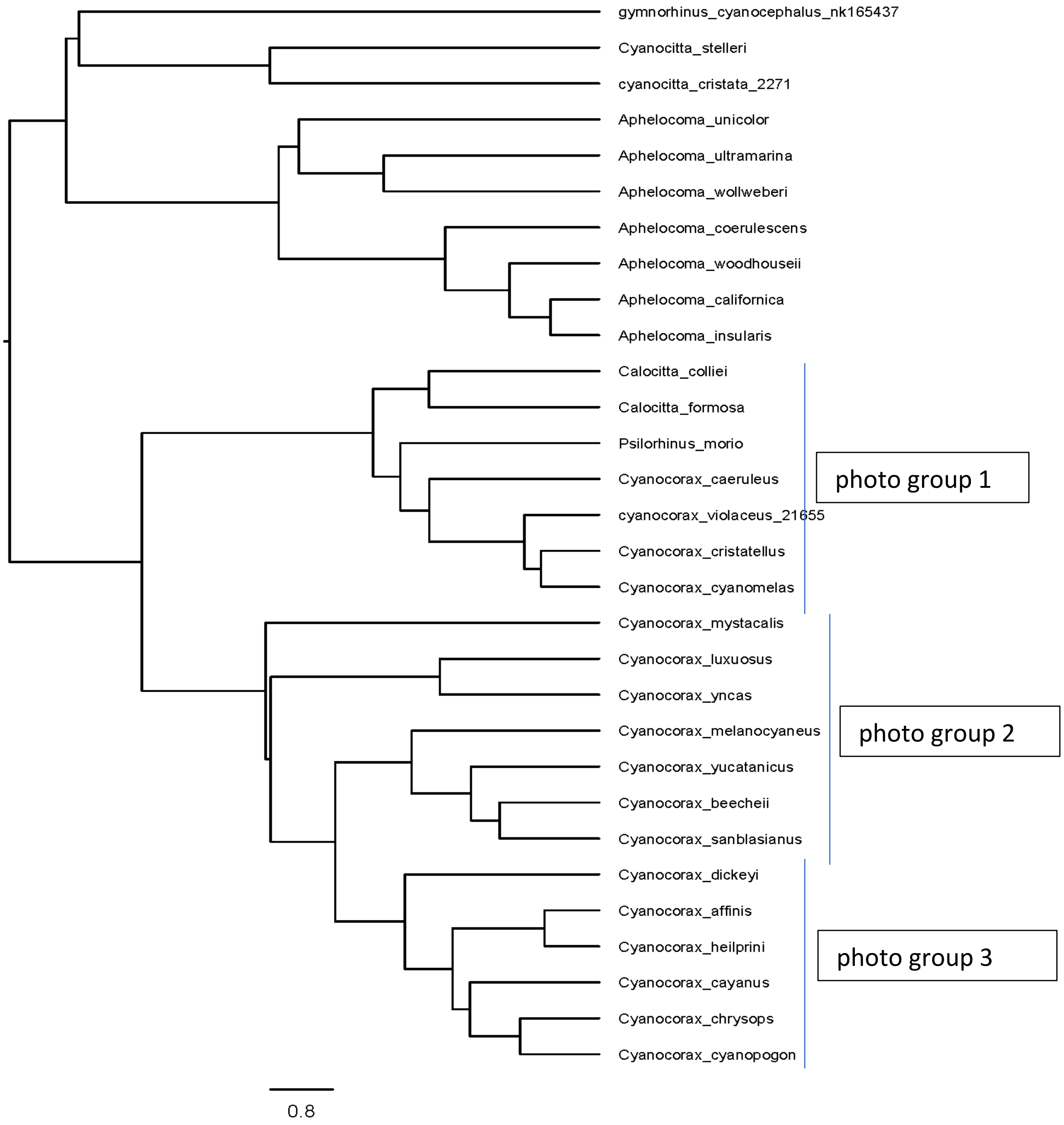


Figure 2. Relevant portion of tree from McCullough et al. (2022) containing species in the genera *Calocitta, Psilorhinus*, and *Cyanocorax.*

This issue has come before WGAC as a discrepancy among global bird lists because the IOC and eBird/Clements lists continue to recognize *Psilorhinus* and *Calocitta*, as does NACC, whereas the Birdlife-HBW and Howard & Moore lists recognize an expanded *Cyanocorax* that includes the three species formerly in these other genera.

There are three main options for resolving the paraphyly that would be consistent with the Bonaccorso and McCullough trees, as previously discussed by Bonaccorso et al. (2010):

(1) Transfer the four species of *Cyanocorax* that are sister to *Psilorhinus* to a separate genus, leaving all other species as is. *Uroleuca* Bonaparte, 1850, a genus recognized by Hellmayr for the type species *cristatellus*, appears to be available for these four species.
(2) Place these four species of *Cyanocorax*, the two species of *Calocitta*, and *Psilorhinus* in the same genus. *Psilorhinus* Ruppell, 1837, appears to have priority for this grouping.
(3) Transfer the species currently placed in *Calocitta* and *Psilorhinus* to *Cyanocorax*.

Relative branch lengths indicate that the branches leading to most related genera (e.g., *Aphelocoma*, *Cyanocitta*, *Gymnorhinus*, *Cyanolyca*, *Perisoreus*) in the McCullough tree are much deeper than those leading to the genera that would result from option 1, and somewhat deeper than those that would result from option 2. Moreover, if using branch lengths as a guide, option 1 would also seem to indicate that multiple genera, such as *Cissilopha*, should be recognized among the species remaining in *Cyanocorax*.

There's a great deal of phenotypic variation within *Cyanocorax*, *Calocitta*, and *Psilorhinus*, but it is difficult to partition the variation into phenotypic groups consistent with options 1 or 2. The photos below (Figures 3-5) show the 19 species in these genera in the sequence that they occur in the McCullough tree: the first group consists of the species of *Calocitta* and *Psilorhinus* and the four species of *Cyanocorax* from the top clade, the second group consists of the next seven species of *Cyanocorax*, and the third group consists of the next six species of *Cyanocorax*, which form a clade at the bottom of the tree. Thus, photo 1 in each group shows what would become *Calocitta*, *Psilorhinus*, and *Uroleuca* under option 1, or *Psilorhinus* under option 2, whereas photos 2 and 3 show the species that would remain in *Cyanocorax* under options 1 and 2.

The generic classification of Hellmayr (1934) is emblematic of the difficulty of phenotypically separating the *Cyanocorax* species into the groups identified by the genetic analyses. Hellmayr included nine species in *Cyanocorax*: three species from photo group 1, one species (*mystacalis*) from photo group 2, and all species (five at the time, because *dickeyi* was not yet described) from photo group 3. One species (*cristatellus*) from photo group 1 was placed in *Uroleuca*, one species (*yncas*, incl. *luxuosus*) from photo group 2 in *Xanthoura*, and four species from photo group 2 in *Cissilopha*.

Characters not available to Hellmayr and others working with specimens, such as eye color and vocalizations, may be somewhat better at matching the genetic data, but diagnostic characters are not readily apparent. For example, eye color is uniformly dark in photo group 1 and generally yellow in photo groups 2 and 3, but *yncas* and *yucatanicus* from group 2 have dark eyes, *heilprini* from group 3 has whitish eyes, and *cayanus* from group 3 has blue eyes.

Many of these species have large vocal repertoires, making comparisons difficult without more in-depth study, but some species can be clustered into groups showing similar features. Nevertheless, exact correspondence with genetic clades is not obvious. For example, typical of many species in photo group 3 is a short musical downslurred call; this applies to *affinis*, *heilprini*, *cayanus*, and *chrysops*, but the typical calls of *cyanopogon* and *dickeyi* are clipped metallic calls often given in a series. Likewise, most species in photo group 1 typically give calls that bear some resemblance to the calls of *Cyanocitta* jays, but this doesn't apply to the two species of *Calocitta*, whose vocalizations are highly variable, whereas *beecheii* of photo group 2 gives a very similar call. A typical call of some species in photo group 2 (e.g., *sanblasianus*) is a series of harsh notes, but others (e.g., *yucatanicus*, *mysticalis*) give clipped metallic calls similar to those of *cyanopogon* of photo group 3.

Figure 3. The first photo in these ventral views consists of *Calocitta colliei*, *C. formosa, Psilorhinus morio*, *Cyanocorax caeruleus, C. violaceus*, *C. cristatellus*, and *C. cyanomelas*. The second photo consists of the following species (or subspecies) of *Cyanocorax*: *mystacalis*, *luxuosus*, *yncas*, *melanocyaneus*, *yucutanicus*, *beecheii*, and *sanblasianus*. The third photo consists of the following species of *Cyanocorax*: *dickeyi*, *affinis*, *heilprini*, *cayanus*, *chrysops*, and *cyanopogon.* The size of each photo has been adjusted to better reflect the relative size of the species.

Figure 4. The first photo in these dorsal views consists of *Calocitta colliei*, *C. formosa, Psilorhinus morio*, *Cyanocorax caeruleus, C. violaceus*, *C. cristatellus*, and *C. cyanomelas*. The second photo consists of the following species (or subspecies) of *Cyanocorax*: *mystacalis*, *luxuosus*, *yncas*, *melanocyaneus*, *yucutanicus*, *beecheii*, and *sanblasianus*. The third photo consists of the following species of *Cyanocorax*: *dickeyi*, *affinis*, *heilprini*, *cayanus*, *chrysops*, and *cyanopogon.* The size of each photo has been adjusted to better reflect the relative size of the species.

Figure 5. The first photo in these lateral views consists of *Calocitta colliei*, *C. formosa, Psilorhinus morio*, *Cyanocorax caeruleus, C. violaceus*, *C. cristatellus*, and *C. cyanomelas*; the second photo of the following species (or subspecies) of *Cyanocorax*: *mystacalis*, *luxuosus*, *yncas*, *melanocyaneus*, *yucutanicus*, *beecheii*, and *sanblasianus*; and the third photo of the following species of *Cyanocorax*: *dickeyi*, *affinis*, *heilprini*, *cayanus*, *chrysops*, and *cyanopogon.* The size of each photo has been adjusted to better reflect the relative size of the species.

Recommendation:

We don't see much justification for separating four species of *Cyanocorax* into a separate genus (*Uroleuca*) and retaining *Calocitta* and *Psilorhinus*, as in option 1 above. Aside from the similarity of species of "*Uroleuca*" to some species remaining in *Cyanocorax* (especially *cristatellus*), this would create genera of very shallow depth in the phylogenetic tree. We also feel that it would be difficult phenotypically to justify adopting option 2 above, lumping *Calocitta*, *Psilorhinus*, and "*Uroleuca*" together, and separating this heterogeneous group of species from the remainder of *Cyanocorax*. Thus, we recommend option 3, i.e., to adopt a broad *Cyanocorax* that includes all taxa. This would also be in keeping with the change previously made by Howard & Moore and Birdlife-HBW, and with a recent WGAC vote to adopt the broad *Cyanocorax*.

Please vote on the following:

A. Make changes to the generic treatment of *Calocitta, Psilorhinus,* and *Cyanocorax*. YES or NO.

B. If voting YES on A, then vote for one of the following options:
  (1) Transfer the four species of *Cyanocorax* that are sister to *Psilorhinus* to a separate genus, leaving all other species as is. *Uroleuca* Bonaparte, 1850, a genus recognized by Hellmayr for the type species *cristatellus*, appears to be available for these four species.
  (2) Place these four species of *Cyanocorax*, the two species of *Calocitta*, and *Psilorhinus* in the same genus. *Psilorhinus* Ruppell, 1837, appears to have priority for this grouping.
  (3) Transfer the species currently placed in *Calocitta* and *Psilorhinus* to *Cyanocorax*.
  (4) Other (specify).

Literature Cited:

Bonaccorso, E. and A. T. Peterson. 2007. A multilocus phylogeny of New World jay genera. Molecular Phylogenetics and Evolution 42: 467-476.

Bonaccorso, E., A. T. Peterson, A. Navarro-Sigüenza and R. C. Fleischer, 2010. Molecular systematics and evolution of *Cyanocorax* jays. Molecular Phylogenetics and Evolution 54: 897-909.

Chesser, R. T., R. C. Banks, F. K. Barker, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen, J. D. Rising, D. F. Stotz, and K. Winker, Fifty-first supplement to the American Ornithologists' Union *Check-List of North American Birds.* Auk 127: 726–744.

del Hoyo, J., and N. J. Colla. 2016. HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 2: Passerines. Lynx Edicions and BirdLife International, Barcelona, Spain and Cambridge, UK.

Dickinson, E. C., and L. Christidis (eds.). 2014. The Howard and Moore Complete Checklist of the Birds of the World, Fourth Edition, Volume 2: Passerines. Aves Press, Eastbourne, UK.

Fernando, S. W., A. T. Peterson, and S. Li. 2017. Reconstructing the geographic origin of the New World jays. Neotropical Biodiversity 3: 80-92.

Hellmayr, C. E. 1934. Catalogue of birds of the Americas, Part 7. Zoological Series, Field Museum of Natural History, Volume 13.

McCullough, J. M., C. H. Oliveros, B. W Benz, R. Zenil-Ferguson, J. Cracraft, R. G Moyle, and M. J. Andersen. 2022. Wallacean and Melanesian islands promote higher rates of diversification within the global passerine radiation Corvides. Systematic Biology 71: 1423–1439.

Ridgway, R. 1904. The birds of North and Middle America, Part 3. Bulletin of the United States National Museum No. 50.

Saunders, M. A., and S. V. Edwards. 2000. Dynamics and phylogenetic implications of mtDNA control region sequences in New World Jays (Aves: Corvidae). Journal of Molecular Evolution 51: 97-109.

Submitted by: Terry Chesser and Carla Cicero

Date submitted: 4 December 2023, revised 11 January 2024

Treat Isthmian Wren *Cantorchilus elutus* as a subspecies of Cabanis's Wren *C. modestus*

Effect on AOS-CLC area:

If approved, this proposal would merge *Cantorchilus elutus* (Bangs 1902) and *Cantorchilus modestus* (Cabanis 1860) into a single species, *C. modestus*. This would result in one fewer species for the AOS-CLC area.

Description of the problem:

In 2016, a proposal (2016-C-13) to consider Isthmian Wren *Cantorchilus elutus* and Canebrake Wren *C. zeledoni* (Ridgway 1878) as species separate from Cabanis's Wren *C. modestus*, was unanimously approved by NACC. This three-species treatment of the species formerly known as Plain Wren was supported by deep mitochondrial divergence between the three taxa, differences in coloration and morphometrics, and purported differences in the song duet. The mitochondrial phylogeny has the topology (*modestus*(*elutus,zeledoni*)), with each clade being 6-8% divergent. All three are currently considered monotypic, but with two poorly differentiated subspecies occasionally recognized for *C. modestus*. Following the NACC decision, the three-species treatment was subsequently adopted by the eBird/Clements and IOC global checklists.

In the committee member comments on the 2016 NACC proposal to split *Cantorchilus modestus*, one member mentioned (correctly in my opinion) that the morphological evidence for considering *zeledoni* as a separate species is stronger than is the evidence for *elutus*, and HBW-BirdLife opted to instead retain *elutus* as a subspecies of *modestus*. The HBW-BirdLife taxonomic rationale for *elutus* is here:

> Frequently treated as conspecific with *C. zeledoni*. A recent study involving mtDNA, morphometrics and colorimetrics has proposed that subspecies *elutus* merits elevation to species rank (although morphological differences very small), citing as important supporting evidence significant differences in song duet pattern (Saucier, Sánchez & Carling 2015); however, this overlooks a finding that all *Cantorchilus* wrens sing the same duet pattern (Mann et al. 2009), and analysis of available recordings reveals no differences (Boesman 2016); therefore despite evidence suggesting *elutus* is more distant from nominate than nominate is from *C. zeledoni*, further and fuller evidence is required to substantiate the distinctiveness of *elutus*.

The 2016 NACC proposal and comments, which I recommend reading in addition to the present proposal, are here:
https://americanornithology.org/wp-content/uploads/2020/02/2016-C.pdf
https://americanornithology.org/about/committees/nacc/current-prior-proposals/2016-proposals/comments-2016-c/#2016-C-13
That proposal contains relevant figures for the respective distributions, phylogeny, coloration and morphometric differences for each taxon.

Kroodsma et al. (2020) noted that some authors (citing Hellmayr 1934 and three field guides) have considered *elutus* as a subspecies of *zeledoni*, maintaining only *modestus* as a separate species. This, however, appears to be in error, as Hellmayr (1934) considered both *zeledoni* and *elutus* as subspecies of *modestus*, and I suspect that this is the basis for the HBW-BirdLife statement that *elutus* is "Frequently treated as conspecific with *C. zeledoni*."

New information:

Very soon after the 2016 NACC proposal, Boesman (2016) wrote an 'ornithological note' on song differences in the *C. modestus* complex, which is available online here: https://static.birdsoftheworld.org/on294_plain_wren.pdf Here, he argued that the song differences reported by Saucier et al. (2015) were overstated, and that in fact the songs of *modestus* and *elutus* are qualitatively similar. Here is Boesman's explanation of the issue:

> Saucier et al. (2015) apparently only used evidence from a previous study by Mann et al. (2003), indicating that there are substantial differences in duetting structure. Mann et al. (2003) however only compared his own observations for *modestus* (??) and *zeledoni* with descriptions by Farabaugh (1983) of *elutus*. (Farabaugh (1983) is a PhD dissertation of which we were unable to find any details). In Saucier et al. (2015) it is said that *elutus* 'differs in the crucial introductory phrases', without explaining what those differences may be (absence thereof or comparable differences?).

Boesman (2016) noted that Saucier et al. (2015) also overlooked the findings of Mann et al. (2009), who found that song structure is conserved across the entire genus, and goes on to recommend that the song differences reported by Saucier et al. (2015) should be discounted entirely (which may be a bit drastic). The song structure in *Cantorchilus* is of the form 'IAB', where the 'I' phrase is given in isolation by the male and is a short and variable phrase. In a duet, the female response to the 'I' note with an 'A' phrase, and then the male joins in with the 'B' phrase with the AB form continuing through the duet, so that a duet is of the form 'IABABABAB…', etc. Although the Boesman (2016) note did not include catalog numbers for the recordings or any quantitative analyses (as is typical of these notes), he found that *modestus* and *elutus* both had quite variable I, A, and B phrases but that these overlapped considerably between the two taxa. In listening to recordings available online, I think I can hear slightly lower pitched and slower duets in *elutus* from Panama, but these differences are subtle and I certainly can't say with any confidence that I could identify one without knowing the locality. However, the recordings of *zeledoni* are fairly distinct, with both the I and A phrases containing rapidly rising or falling clear whistled notes that cover a large frequency range. I recommend listening to some of the available recordings to get a sense of these differences:

modestus:
https://media.ebird.org/catalog?view=list&taxonCode=plawre1&mediaType=audio&sort=rating_rank_desc
https://xeno-canto.org/species/Cantorchilus-modestus?dir=0&order=cnt&view=3&pg=2

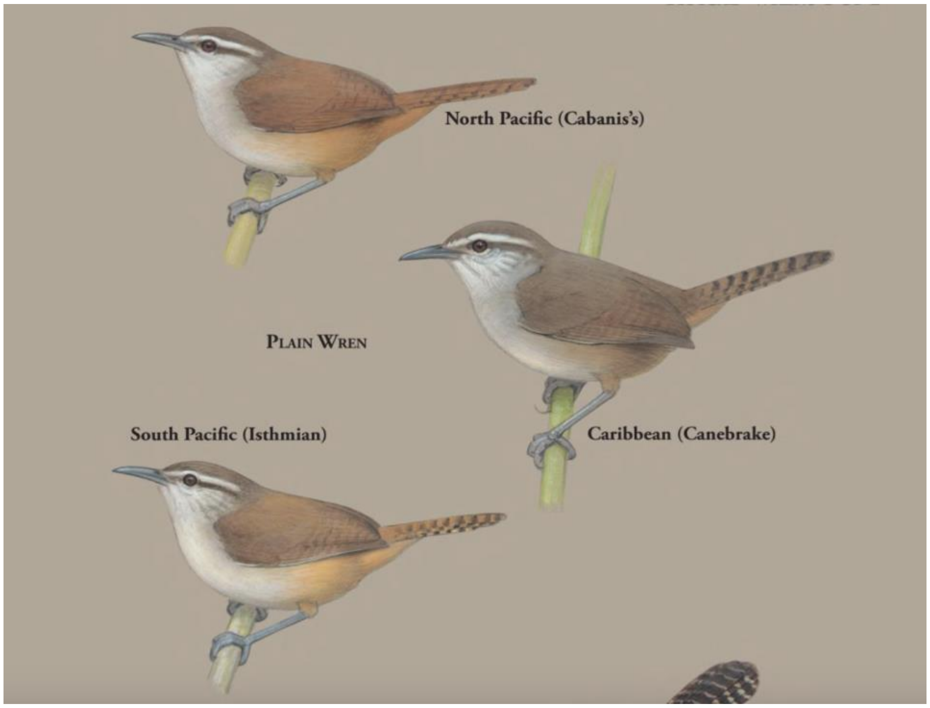
elutus:

https://media.ebird.org/catalog?view=list&taxonCode=istwre1&mediaType=audio&sort=rating_rank_desc
https://xeno-canto.org/species/Cantorchilus-elutus?view=3

zeledoni:
https://media.ebird.org/catalog?view=list&taxonCode=plawre3&mediaType=audio&sort=rating_rank_desc
https://xeno-canto.org/species/Cantorchilus-zeledoni?view=3

Freeman and Montgomery (2017) included *modestus* and *elutus* (but not *zeledoni*) in their song discrimination playback study and reported a discrimination score of zero (i.e., no discrimination in any of 12 playback trials). Their measure of acoustic divergence was also quite low (0.41), but they also reported that acoustic divergence was a poor predictor of song discrimination if acoustic divergence scores were below 3. The trials were not reciprocal (songs of *elutus* were played in territories of *modestus*, but not vice-versa), but in three other wren species where reciprocal playback trials were done, the primary and reciprocal discrimination scores were nearly identical.

Although Saucier et al. (2015) reported statistical differences in color measurements between all pairwise comparisons of the three taxa, only *zeledoni* clustered in a separate part of color space in the PCA (see Figure 4B in NACC proposal 2016-C-13). In fact, Saucier et al. (2015) noted that *modestus* and *elutus* “are remarkably similar in plumage despite significant morphometric differences and deep genetic divergences across a sharp phylogeographic break”. In comparison to the other two, *zeledoni* is considerably grayer overall, especially on the dorsum. Dyer and Howell (2023) nicely illustrate these plumage differences. See a screenshot of their plate below.



Hellmayr (1934) also made some relevant comments on plumage and morphometric differences in the complex. For *elutus* (in comparison to *modestus*) he noted that it is "of very doubtful validity, and I am just able to appreciate slight average differences in size and coloration". Regarding *zeledoni*: "Though well characterized by much larger feet and bill, much duller and less brownish upper parts with brownish instead of rufescent wings and tail, and much less fulvous flanks and under tail coverts, *T. m. zeledoni* is clearly conspecific with *T. modestus*, which it replaces in the Caribbean lowlands of Costa Rica and the adjacent districts of Nicaragua and Panama. Certain specimens of *T. m. modestus*, in one or several respects, exhibit an unmistakable tendency towards the characters of *T. m. zeledoni*, though intergradation, especially in dimensions, is far from being complete." This classification was made prior to the modern formulation of the BSC, but it does highlight the greater plumage differences of *zeledoni*.

Recommendation:

I recommend a **YES** on considering *elutus* to be a subspecies of *modestus* based on an apparent lack of vocal differences (but a formal analysis is sorely needed!), overall plumage similarity, and no studies of the dynamics in the hybrid zone. The split recommended by Saucier et al. (2015) now relies primarily on a sharp (and quite deep) mitochondrial genetic break but with few concordant morphological differences. Note that this taxonomic treatment will result in mitochondrial paraphyly, but that is based on just a single locus. The lack of playback response between *elutus* and *modestus* also supports these being conspecific, with the caveat that wrens are generally quite responsive to playback. However, Freeman and Montgomery (2017) conducted playback experiments on twelve other pairwise combinations in other wren taxa and found song discrimination (to varying degrees) in every one of those twelve cases, so *elutus* and *modestus* are clearly an outlier in this regard.

If *elutus* is treated as a subspecies of *modestus*, an English name proposal should be drafted to address the new name, as this will entail a new taxonomic circumscription. I tentatively recommend that Plain Wren be resurrected (despite *zeledoni* still being considered separate), the overall range roughly corresponds to that of the historical treatment of the complex, ranging from southern Mexico to central Panama and *C. zeledoni* comprises a relatively small portion of the range of the complex.

Literature Cited:

Boesman, P. 2016. Notes on the vocalizations of Plain Wren (*Thryothorus modestus*) and Canebrake Wren (*Thryothorus zeledoni*). HBW Alive Ornithological Note 294. In: Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/node/1251742 on 13 October 2016)

Dyer, D., and S.N.G. Howell. 2023. Birds of Costa Rica. Princeton University Press.

Hellmayr, C. E. 1934. Catalogue of Birds of the Americas and the Adjacent Islands, Part 7. Field Museum of Natural History Publication 330. Zoological Series 13.

Kroodsma, D. E., D. Brewer, and H. F. Greeney. 2020. Isthmian Wren (*Cantorchilus elutus*), version 1.0. In Birds of the World (S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S.

Schulenberg, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.istwre1.01

Mann, N. I., L. Marshall-Ball, and P. J. B. Slater. 2003. The complex song duet of the Plain Wren. The Condor 105:672682.

Mann, N.I., Dingess, K.A., Barker, F.K., Graves, J.A. & Slater, P.J.B. 2009. A comparative study of song form and duetting in Neotropical *Thryothorus* wrens. Behaviour 146(1): 1–43.

Saucier, J. R., C. Sánchez, & M. D. Carling. 2015. Patterns of genetic and morphological divergence reveal a species complex in the Plain Wren (*Cantorchilus modestus*). The Auk, 132: 795-807.

Submitted by: Oscar Johnson, The University of Texas at El Paso

Date of proposal: 5 December 2023

Treat Intermediate Egret *Ardea* (or *Casmerodius*) *intermedia* as two or three species

Background:

Most global lists (IOC, eBird/Clements, Howard & Moore) have traditionally considered *Ardea intermedia* to be a single species with three subspecies: *intermedia* of south and southeast Asia, breeding as far north as Korea and Japan and as far south as Indonesia; *brachyrhycha* of sub-Saharan Africa, and *plumifera* of Australia. The HBW-Birdlife list, however, recently elevated *brachyrhycha* and *plumifera* to species status, recognizing three species in this complex.

The Birdlife rationale, based on the 7-point system, was as follows:

> [*A. intermedia*] differs from *A. brachyrhyncha* and *A. plumifera* when breeding in having black vs yellow-and-pink bill (3), much yellower lores and facial area (2), and black vs reddish tops of legs (2)" and *A. plumifera* differs from *A. brachyrhyncha* "in its smaller size (effect size for tail −3.08, score 2) but longer bill (effect size 1.809, score 1) (3); head tucked into chest vs head and neck horizontal in snap-display (2); "glock" and "kroo" call in alarm vs apparently none (allow 3); confirmation needed on this vocal evidence, but given the interposition of *A. intermedia* and the morphometric disjunction of the taxa this uncertainty is provisionally overruled here.

Somewhat surprisingly, no genetic studies have included more than one representative of *A. intermedia*, so we don't know the relationships among subspecies, whether they are individually monophyletic, or even whether the three subspecies form a monophyletic group. Hruska et al. (2023), for example, only included a sample of *brachyrhyncha* from Africa. There have also been no formal vocal analyses, so the characters available for consideration are the soft part colors and morphometric differences and the anecdotal behavioral and vocal data in the Birdlife rationale.

New Information:

As part of an effort to consolidate global bird lists, the IOU's Working Group on Avian Checklists (WGAC) recently considered whether to separate *A. intermedia* into as many as three species. WGAC voted to recognize *A. brachyrhyncha* and *A. plumifera* as separate species from *A. intermedia*, This has already been adopted in the most recent Clements update and presumably will be adopted soon by the IOC list.

Members of WGAC voting in favor of the split emphasized the differences in soft part colors between breeding *A. intermedia* and breeding *A. brachyrhyncha* and *A. plumifera*, indicating that these were probably isolating mechanisms, and it was generally acknowledged, even by those voting against the splits, that the evidence for this change was more convincing than the evidence for separating *A. brachyrhyncha* and *A. plumifera*. The latter two were separated based on morphometric and shape differences (longer bill but shorter tarsus, wing, and tail for *plumifera*), apparently longer breeding plumes in *plumifera*, and the anecdotal display and vocal data. Also figuring into some of the comments was the idea that these differences exceed those between some other species of heron. Those voting to maintain the current single-species taxonomy, although open especially to the split of *intermedia* from the other subspecies, preferred to wait for firmer evidence.

Recommendation:

Although I voted against these splits, this is an Old World issue and I recommend that we adopt the new global taxonomy for this complex, following our standard policy. Most "Old World" representatives on the WGAC voted for the three-species arrangement. Again, the evidence for separating *intermedia* from the other subspecies is better than the evidence for separating *brachyrhyncha* from *plumifera*, but because the subspecies that has occurred in North America is *intermedia*, it makes little difference (except in the notes for the species account) as to whether we adopt the *brachyrhyncha-plumifera* split so long as we adopt the separation of *intermedia*. Just the same, and despite evidence that seems to fall short of our usual standards, I would recommend adopting the new global taxonomy recognizing three species.

English Names:

HBW-Birdlife retained the English name Intermediate Egret for *A. intermedia* and used Yellow-billed Egret for *A. brachyrhyncha* and Plumed Egret for *A. plumifera*. Clements, in keeping with our general policy of not retaining the name of the parent species as one of the daughter species, also uses Yellow-billed Egret for *A. brachyrhyncha* and Plumed Egret for *A. plumifera*, but has adopted Medium Egret for *intermedia*. This isn't a very exciting name, but it does have the advantage of retaining the notion of intermediate size without re-using the previous name. I recommend that we go with the Clements names unless the IOC list comes up with a better English name for *intermedia*.

Literature Cited:

Hruska, J. P., J. Holmes, C. Oliveros, S. Shakya, P. Lavretsky, K. G. McCracken, F. H. Sheldon, and R. G. Moyle (2023). Ultraconserved elements resolve the phylogeny and corroborate patterns of molecular rate variation in herons (Aves: Ardeidae). Ornithology 140: ukad005 doi.org/10.1093/ornithology/ukad005

Submitted by: Terry Chesser

Date of Proposal: 5 December 2023

Treat Cattle Egret *Bubulcus* (or *Ardea*) *ibis* as two species

Background:

Most global lists (e.g., eBird/Clements, IOC, Howard & Moore) have traditionally considered *Bubulcus ibis* to be a single species with two subspecies: *ibis* of southern Europe, Africa, Asia Minor as far east as Iran, and the Americas; and *coromandus* of South Asia and southeastern Asia south to Australia and New Zealand. These two subspecies are separated by a gap in distribution in Pakistan and Afghanistan. A third subspecies, *seychellarum* of the western Indian Ocean, is sometimes recognized (e.g., by Birdlife); otherwise, these populations are considered part of *ibis*.

The IOC list recently elevated *coromandus* to species status, recognizing two species in this complex. Their note on this change is as follows: "*Bubulcus coromandus* is split from *B. ibis* (Payne & Risley 1976; McAllan & Bruce 1989; Rasmussen & Anderton 2005). Status under discussion (Christidis & Boles 2008; Ahmed 2011; HBW)."

The relevant passage from Payne and Risley (1976), who placed this species in *Egretta*, is here:

> Cattle Egrets of Africa (*E. i. ibis*) and India (*E. i. coromanda*) have very different breeding plumages and might better be regarded as two species or at least two allospecies of a superspecies. African birds have orangish-buff display feathers coloring the entire head, neck, and upper breast; long plumes of similar color cover the lower back and rump. Indian birds have pinkish-buff plumes and these are restricted to the crest, the upper breast, and the lower back; the neck and throat are white. The bill is shorter and stouter in *ibis*. The extent of feathering on the tarsus above the distal tarsometatarsal joint is greater in *ibis* (about 12 mm bare tarsus) than in *coromanda* (about 24 mm bare tarsus), but some overlap occurs between specimens of the two groups. Wing lengths differ on the average (Ali and Kipley, 1968; Mackworth-Praed and Grant, 1970) but the ranges of wing lengths overlap. The two forms are geographically separated from each other. Cattle Egrets of the Seychelle Islands have been regarded as intermediate between the Indian and African birds, but only one specimen in breeding plumage is known, and it has not been possible to test further the idea that Seychelle birds (described as a subspecies "*seychellarum*") are hybrid results of independent invasions and establishments on the islands from Africa and India (Benson and Penny, 1971). It is possible that the differences in breeding plumage would act as behavioral isolating mechanisms between the two forms of Cattle Egrets, and it would be of interest to complement the study of behavior of African birds (Blaker, 1969a) with a study of behavior of birds in India or Australia. Examination of skeletons in the present study showed no differences in the coded character states in the two forms, though the interorbital foramen was slightly more rounded anteriorly in the African specimens.

McAllan and Bruce (1989), referenced in the IOC note, is a working list of the birds of New South Wales, Australia. They presumably recognized *B. coromandus* as separate from *B. ibis*, whereas Christidis and Boles (2008) presumably treated them as conspecific in their list of Australian birds.

Volume 1 (Field Guide) of Rasmussen and Anderton (2005) stated that Western Cattle Egret *B. ibis* is "similar but stockier [than *B. coromandus*], in breeding plumage with orange-buff mainly on crown, breast, and mantle." In Volume 2 (Attributes and Status), they expand on this as follows:

> [Western Cattle Egret is] Like Eastern but smaller and stockier, with ***shorter bill, neck and legs*** (latter often paler yellowish, olive or grey, but never black), less bare facial skin and puffier 'jowls'. Breeding adult shows a shaggier, paler ***peach-colored crest*** only on top of head, finer, more hair-like peach breast-plumes, and brighter red legs. In flight, less leg extension than for Eastern….**Size** Length 330-380 [340-370 in *coromandus*]; head 90-100 [97-110 in *coromandus*]; tail 80-90 [81-93 in *coromandus*]; bare leg 168-180 [205-225 in *coromandus*]….
> **Habits** Much as for Eastern. **Voice** Calls noticeably higher-pitched, more nasal and less gravelly than Eastern's.

The Birdlife rationale for continuing to recognize only a single species was as follows:

> Race *coromandus* sometimes treated as a full species, with some authors [Rasmussen and Anderton 2005] mentioning different morphometrics, breeding plumage and calls; another [Ahmed 2011], however, indicated no difference in calls and that morphometric data yield only minor differences (effect size for longer tarsus 1.49, score 1; for shorter tail −0.94, score 1) (2), leaving the puffy, bright golden-orange head, neck and breast when breeding vs white on these parts except peachy-buffy crest and central breast plumes (3); thus, a total score of 5 retains this form at present as a well-marked subspecies, although further study may yield other points of divergence.

The only formal study of phenotypes appears to be that of Ahmed (2011), a paper published in Dutch Birding and directed towards identification of potential vagrant *coromandus* in the Western Palearctic. He concluded that

> the following features are useful in separating *ibis* and *coromandus*: ***1*** extent and coloration of adult summer plumage; ***2*** bill length; ***3*** tarsus length; ***4*** tail length; and ***5*** bill depth at both nostril and feathering (only in separation of 'Indian Ocean specimens' from *ibis* and *coromandus*). In addition, vocalisations are of use according to Rasmussen & Anderton (2005) but data on these were not collected and they require further work. Data to confirm the validity of the taxon '*seychellarum*' and its separation from *ibis* and *coromandus* are lacking.

However, although breeding plumage is readily diagnostic, the morphometric characters listed above, as noted in the Birdlife spiel as well as by Payne and Risley (1976) and Ahmed (2011), show a fair amount of overlap (see Table 1 and Fig. 3 from Ahmed 2011 below).

Ahmed (2011) also questioned the vocal differences discussed in Rasmussen and Anderton (2005), noting that Sangster (in litt.) could find no differences in vocalizations and that Kushlan and Hancock (2005) mentioned up to 11 call types. He suggested that the calls compared by Rasmussen and Anderton (2005) may not have been homologous. I'm not aware of any further discussion of the vocalizations.

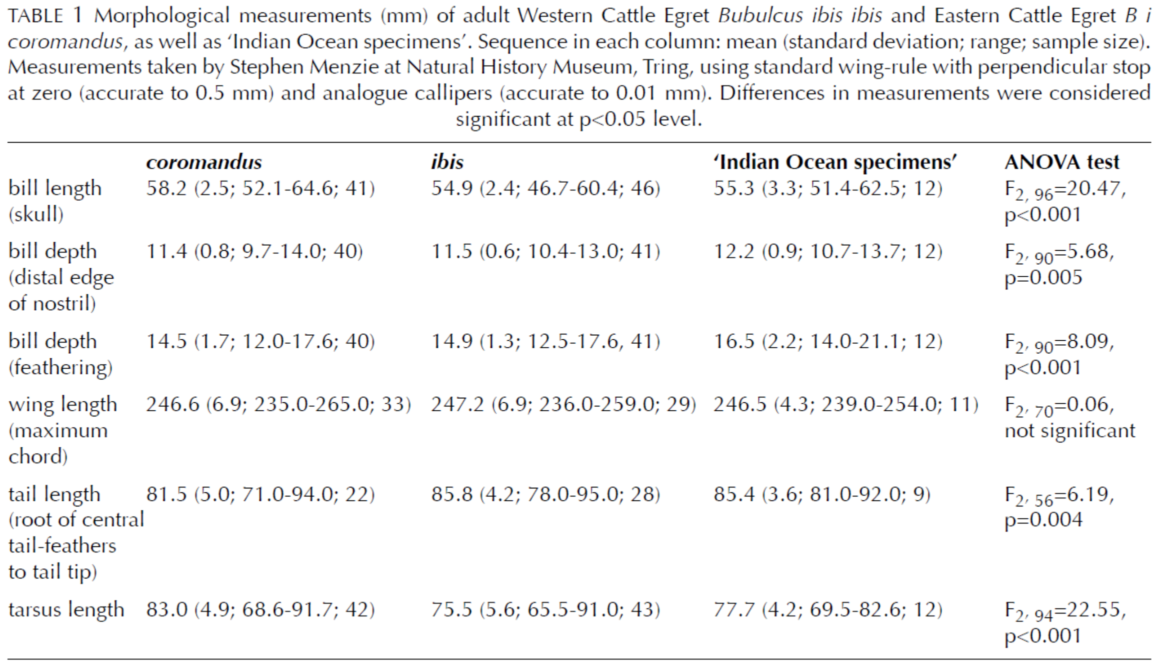


TABLE 1 Morphological measurements (mm) of adult Western Cattle Egret *Bubulcus ibis ibis* and Eastern Cattle Egret *B i coromandus*, as well as 'Indian Ocean specimens'. Sequence in each column: mean (standard deviation; range; sample size). Measurements taken by Stephen Menzie at Natural History Museum, Tring, using standard wing-rule with perpendicular stop at zero (accurate to 0.5 mm) and analogue callipers (accurate to 0.01 mm). Differences in measurements were considered significant at p<0.05 level.

	coromandus	***ibis***	**'Indian Ocean specimens'**	**ANOVA test**
bill length (skull)	58.2 (2.5; 52.1-64.6; 41)	54.9 (2.4; 46.7-60.4; 46)	55.3 (3.3; 51.4-62.5; 12)	$F_{2, 96}=20.47$, $p<0.001$
bill depth (distal edge of nostril)	11.4 (0.8; 9.7-14.0; 40)	11.5 (0.6; 10.4-13.0; 41)	12.2 (0.9; 10.7-13.7; 12)	$F_{2, 90}=5.68$, $p=0.005$
bill depth (feathering)	14.5 (1.7; 12.0-17.6; 40)	14.9 (1.3; 12.5-17.6, 41)	16.5 (2.2; 14.0-21.1; 12)	$F_{2, 90}=8.09$, $p<0.001$
wing length (maximum chord)	246.6 (6.9; 235.0-265.0; 33)	247.2 (6.9; 236.0-259.0; 29)	246.5 (4.3; 239.0-254.0; 11)	$F_{2, 70}=0.06$, not significant
tail length (root of central tail-feathers to tail tip)	81.5 (5.0; 71.0-94.0; 22)	85.8 (4.2; 78.0-95.0; 28)	85.4 (3.6; 81.0-92.0; 9)	$F_{2, 56}=6.19$, $p=0.004$
tarsus length	83.0 (4.9; 68.6-91.7; 42)	75.5 (5.6; 65.5-91.0; 43)	77.7 (4.2; 69.5-82.6; 12)	$F_{2, 94}=22.55$, $p<0.001$

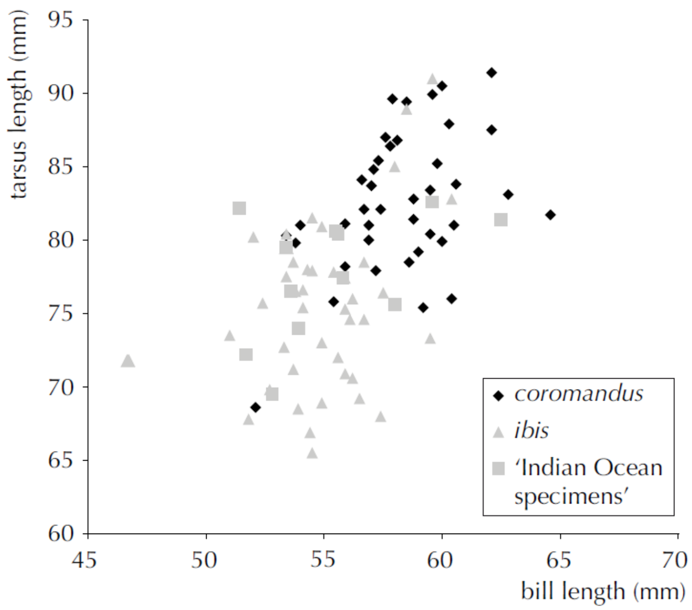


Fig. 3 from Ahmed (2011), plotting bill length versus tarsus length in the two subspecies of *B. ibis*, with Indian Ocean populations ("*seychellarum*") also separated.

Somewhat surprisingly, no genetic studies have included both subspecies of *B. ibis*. Hruska et al. (2023), for example, included only a sample of subspecies *ibis* from Louisiana.

New Information:

As part of an effort to consolidate global bird lists, the IOU's Working Group on Avian Checklists (WGAC) recently considered whether to separate *B. ibis* into two species. WGAC voted to recognize *B. coromandus* as a separate species from *B. ibis*. This change has already been adopted in the most recent Clements update and, as noted above, was previously adopted by the IOC list.

Members of WGAC who voted for the split emphasized the differences in breeding plumage, which involve not only the extent of the buff coloration but also the color and texture of the plumes. Also mentioned were differences in shape and proportions, although the morphometric data do show overlap. The lack of clinality in the plumage differences was also viewed as significant: breeding plumages of the westernmost individuals of *coromandus* and easternmost individuals of *ibis* were noted to be the same as those elsewhere in their respective ranges. Those voting against the split were not convinced that the differences between *coromandus* and *ibis* are more than subspecies-level distinctions, and preferred to wait for additional data bearing on species status.

Recommendation:

Although I voted against the split, this is primarily an Old World issue and I recommend that we adopt the new global taxonomy for this complex, following our standard policy. Most "Old World" representatives on the WGAC voted for the two-species arrangement. Despite evidence that may fall short of our usual standards, I would recommend adopting the new global taxonomy of recognizing *B. coromandus* as a species separate from *B. ibis*.

English Names:

Both the IOC and eBird/Clements lists are using Western Cattle Egret for *B. ibis* and Eastern Cattle Egret for *B. coromandus*. I would recommend that we also use these names, although our guidelines indicate that the group name should be Cattle-Egret, to indicate their status as sister species, rather than Cattle Egret.

References:

Ahmed, R. 2011. Subspecific identification and status of Cattle Egret. Dutch Birding 33: 294-304.

Christidis, L., and W. Boles. 2008. Systematics and Taxonomy of Australian Birds. CSIRO Publishing, Collingwood, Victoria, Australia.

Hruska, J. P., J. Holmes, C. Oliveros, S. Shakya, P. Lavretsky, K. G. McCracken, F. H. Sheldon, and R. G. Moyle. 2023. Ultraconserved elements resolve the phylogeny and corroborate patterns of molecular rate variation in herons (Aves: Ardeidae). Ornithology 140: ukad005 doi.org/10.1093/ornithology/ukad005

Kushlan, J. A., and J. A. Hancock. 2005. The Herons. Oxford University Press, Oxford, U.K.

McAllan, I. A. W., and M. D. Bruce. The Birds of New South Wales, a Working List. Biocon Research Group, Turramurra, NSW, Australia.

Payne, R. B., and C. J. Risley. 1976. Systematics and evolutionary relationships among the herons (Ardeidae). Miscellaneous Publications of Museum of Zoology 150:1‐115.

Rasmussen, P. C., and J. C. Anderton 2005. Birds of South Asia: The Ripley Guide. Smithsonian Institution Press/Lynx Edicions, Washington, DC.

Submitted by: Terry Chesser

Date of Proposal: 8 December 2023

Adjust the placement of the monotypic genus *Ectopistes* (Columbidae) in the linear sequence

Background:

The American Ornithological Society's Checklist (AOS; Chesser et al. 2023) has the following linear sequence of genera in the Columbidae:

Columba
Patagioenas
Streptopelia
Geopelia
Ectopistes
Columbina
Claravis
Paraclaravis
Starnoenas
Geotrygon
Leptotrygon
Leptotila
Zentrygon
Zenaida

The extinct species *Ectopistes migratorius* (Passenger Pigeon), the only representative of the genus *Ectopistes*, is currently placed between the genera *Geopelia* and *Columbina.* Several authors have previously speculated that the species was perhaps closely related to the New World genus *Zenaida* (Blockstein 2002, Goodwin 1983). Pereira et al. (2007) included *Ectopistes* in their phylogenetic studies of the Columbiformes using multiple mitochondrial and nuclear DNA markers, but were unable to clearly resolve its position in their trees, primarily due to large amounts of missing sequence data. The genus however, consistently grouped with a clade that included both Old and New World pigeons and doves (e.g., *Patagioenas*, *Columba*, *Streptopelia*, *Reinwardtoena*, *Turacoena*, and *Macropygia*; Figures 1-3), either as an unresolved polytomy (Bayesian consenus tree; posterior probability = 1.0), a basal clade to the remaining genera above (maximum likelihood; bootstrap value < 50%), or as a sister to the genus *Streptopelia* with low support (maximum parsimony; bootstrap value of 55%).

New Information:

Several recent studies have explored the phylogenetic relationships of genera in the Columbidae and several of these have included Passenger Pigeon (Johnson et al. 2010, Fulton 2012a, 2012b, Soares et al. 2016, Bruxaux 2018). These studies have consistently found a sister relationship with the genus *Patagioenas*, although with varying support. (Figure 4-7**;** Johnson et al. 2010, Fulton et al. 2012b, Soares et al. 2016, Bruxaux 2018).

Figure 1

Figure 2

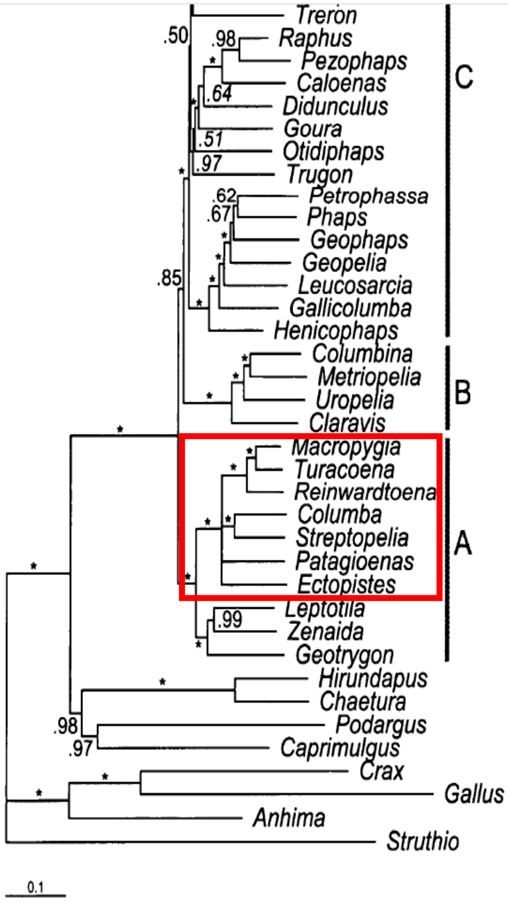


FIGURE 1. Bayesian consensus tree. Major clades within Columbiformes are indicated as A, B, and C. Numbers at nodes are posterior probabilities, which are indicated with an * when = 1.0. Scale bar represents expected number of substitutions per site.

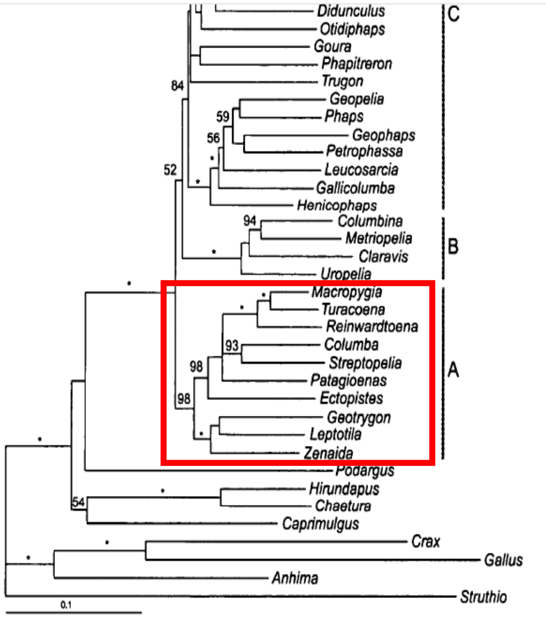
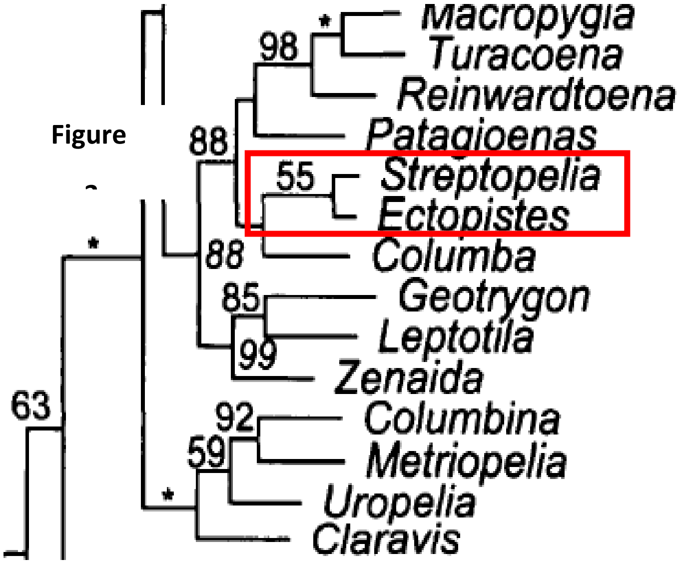


FIGURE 2. Maximum likelihood tree. Major clades within Columbiformes are indicated as A, B, and C. Numbers at nodes are bootstrap proportions and are indicated with an * when = 100 and not indicated when <50%. Scale bar represents expected number of substitutions per site.

Source: Pereira, S. L., Johnson, K. P., Clayton, D. H., & Baker, A. J. (2007). Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene. Systematic Biology, 56(4), 656-672.

Figure



100

FIGURE 3. Maximum parsimony tree. Major clades within Columbiformes are indicated as A, B, and C. Numbers at nodes are bootstrap proportions and are indicated with an * when = 100 and not indicated when <50%. Scale bar represents expected number of substitutions per site.

Johnson et al. (2010), using both mitochondrial (cytochrome b and ATPase8) and nuclear (beta-fibrinogen intron 7) markers, was the first study to document a sister relationship between *Ectopistes* and *Patagioenas*, although with poor support (parsimony bootstrap value of 52%; Figure 4). Subsequent studies (Fulton et al. 2012b, Soares et al. 2016, Bruxaux 2018). have also found a sister relationship between the two genera with more robust support (Figures 5-7).

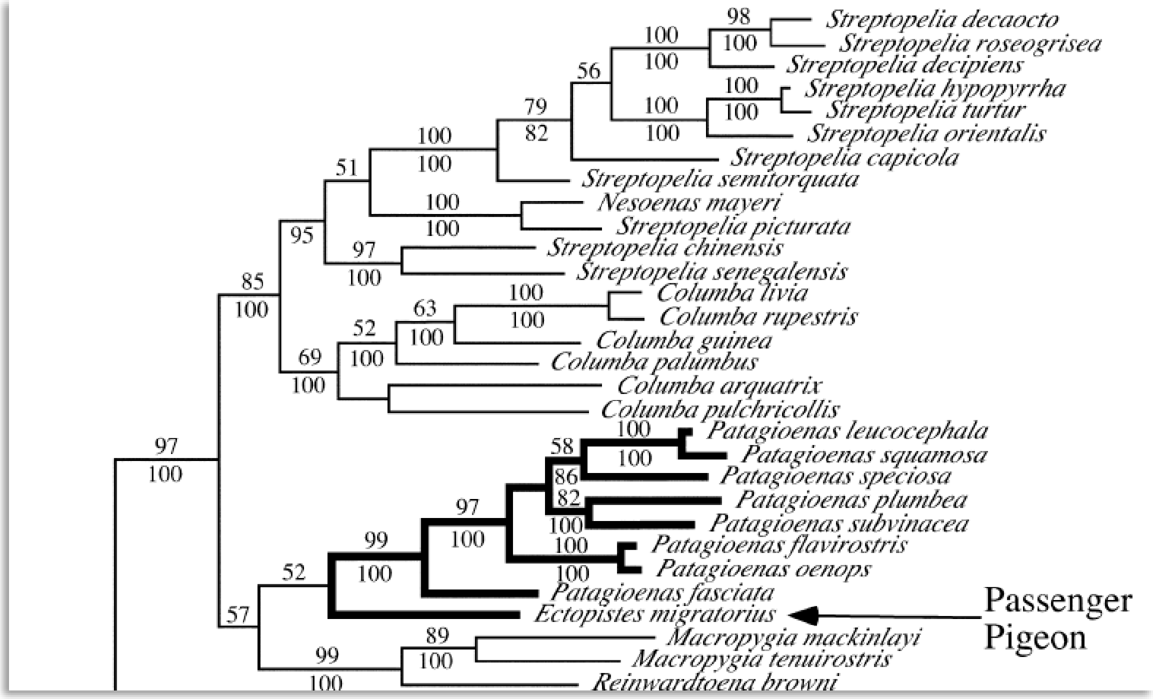


Figure 4. Johnson et al. (2010). The flight of the Passenger Pigeon: Phylogenetics and biogeographic history of an extinct species. Molecular Phylogenetics and Evolution, 57(1), 455-458.

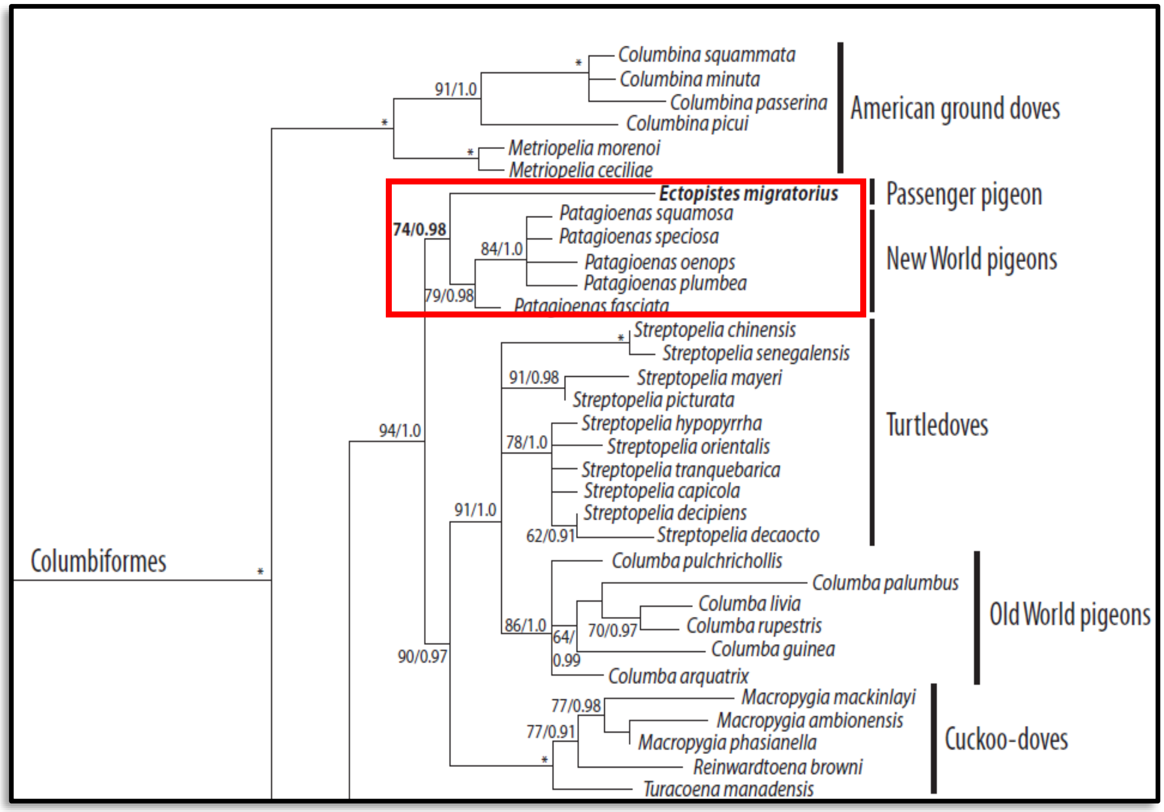


Figure 5. From Fulton et al. (2012b). Nuclear DNA from the extinct Passenger Pigeon (Ectopistes migratorius) confirms a single origin of New World pigeons. Annals of Anatomy-Anatomischer Anzeiger, 194(1), 52-57.

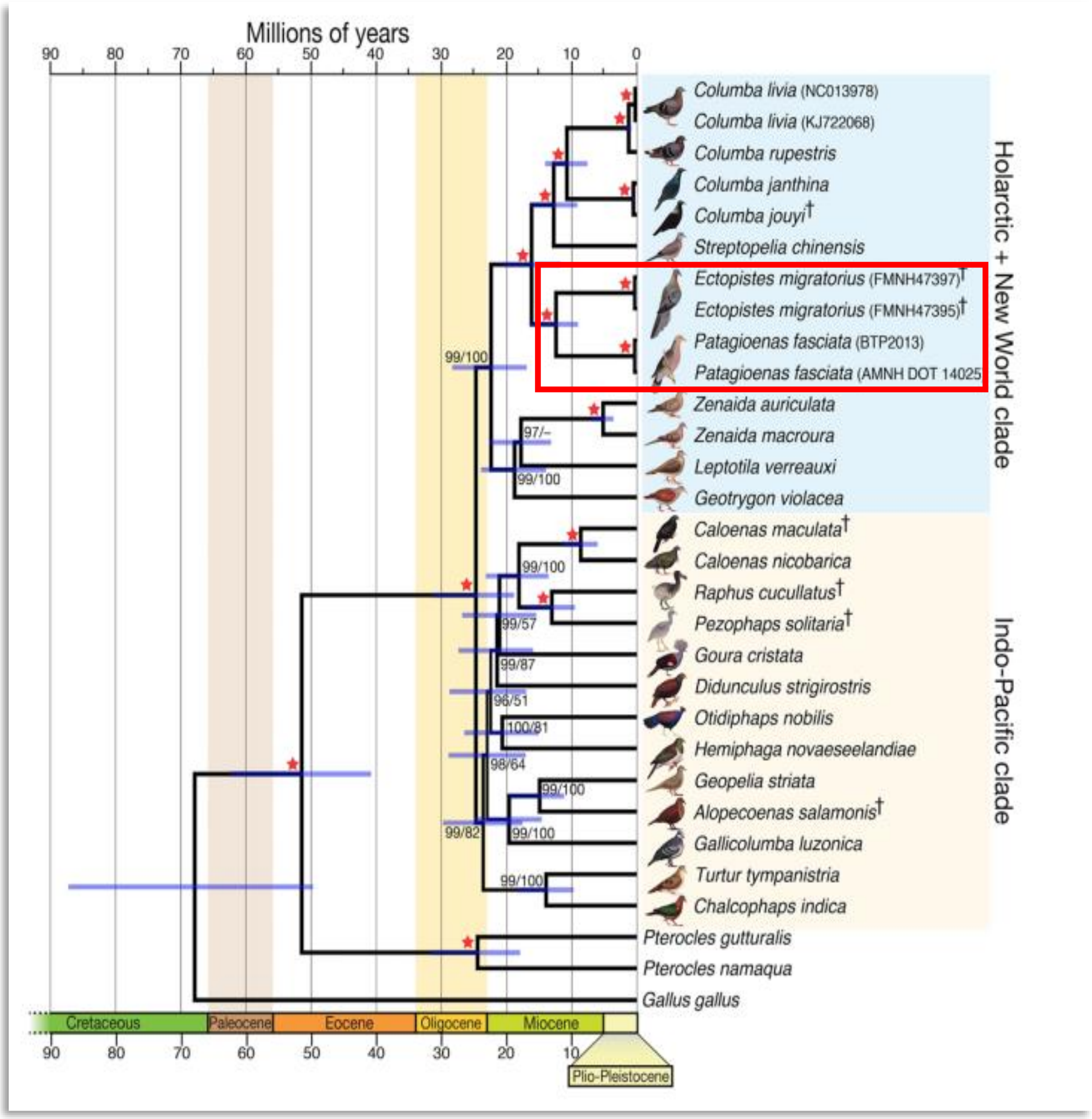


Figure 6. From Soares et al. (2016). Complete mitochondrial genomes of living and extinct pigeons revise the timing of the columbiform radiation. BMC Evolutionary Biology, 16(1), 1-9.

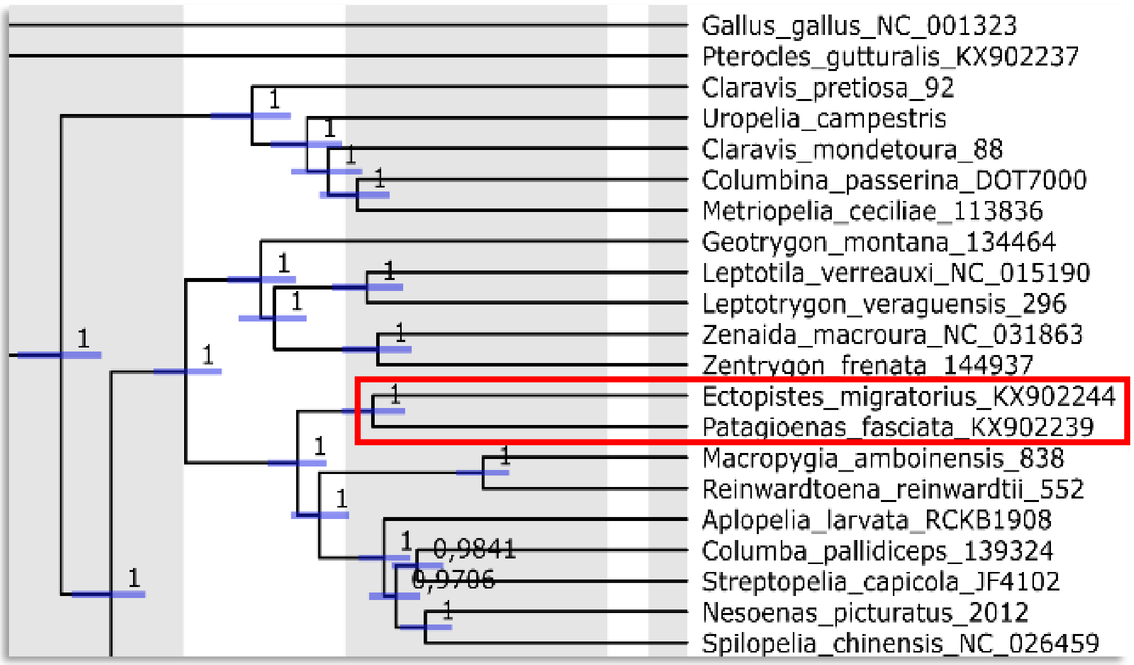


Figure 7. From Bruxaux, J. (2018). Phylogeny and evolution of pigeons and doves (Columbidae) at different space and time scales (Doctoral dissertation, Institut National des Sciences Appliquées (INSA), Toulouse, France).

Recommendation:

These multiple studies strongly support a sister relationship between *Ectopistes* and *Patagioenas.* Following the standardized rules used to generate the linear sequence of genera from phylogenies, it is recommended that the Passenger Pigeon (*Ectopistes migratorius*) be moved from its current position between the genera *Geopelia* and *Columbina* and newly placed between *Columba* and *Patagioenas* in the linear sequence of the Columbidae. Thus, the new sequence of genera would be:

Columba
Ectopistes
Patagioenas
Streptopelia
Geopelia
Columbina
Claravis
Paraclaravis
Starnoenas
Geotrygon
Leptotrygon
Leptotila
Zentrygon
Zenaida

As a final comment, note that the current position of several genera (e.g. *Starnoenas, Claravis, Paraclaravis, Columba, Columbina*, and others) appear to conflict with the recent phylogenetic data and additional changes will likely be needed to ultimately sort out a final linear sequence. However, at a minimum, the evidence appears to be solid to at least move *Ectopistes* above *Patagioenas*. This minor change should not be impacted by any future broad-scale adjustments.

Literature Cited:

Blockstein, D. E. (2002). Passenger pigeon: *Ectopistes migratorius*. Birds of North America, Incorporated.

Bruxaux, J. (2018). Phylogeny and evolution of pigeons and doves (Columbidae) at different space and time scales (Doctoral dissertation, INSA, Toulouse, France).

Chesser, R. T., S. M. Billerman, K. J. Burns, C. Cicero, J. L. Dunn, B. E. Hernández-Baños, R. A. Jiménez, A. W. Kratter, N. A. Mason, P. C. Rasmussen, J. V. Remsen, Jr., and K. Winker. 2023. Check-list of North American Birds (online). American Ornithological Society. https://checklist.americanornithology.org/taxa/

Fulton, T. L., Wagner, S. M., & Shapiro, B. (2012a). Case study: recovery of ancient nuclear DNA from toe pads of the extinct passenger pigeon. Ancient DNA: Methods and Protocols, 29-35.

Fulton, T. L., Wagner, S. M., Fisher, C., & Shapiro, B. (2012b). Nuclear DNA from the extinct Passenger Pigeon (*Ectopistes migratorius*) confirms a single origin of New World pigeons. Annals of Anatomy-Anatomischer Anzeiger, 194(1), 52-57.

Johnson, K. P., Clayton, D. H., Dumbacher, J. P., & Fleischer, R. C. (2010). The flight of the Passenger Pigeon: Phylogenetics and biogeographic history of an extinct species. Molecular Phylogenetics and Evolution, 57(1), 455-458.

Pereira, S. L., Johnson, K. P., Clayton, D. H., & Baker, A. J. (2007). Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene. Systematic Biology, 56(4), 656-672.

Soares, A. E., Novak, B. J., Haile, J., Heupink, T. H., Fjeldså, J., Gilbert, M. T. P., Poinar, H., Church, G. M., & Shapiro, B. (2016). Complete mitochondrial genomes of living and extinct pigeons revise the timing of the columbiform radiation. BMC Evolutionary Biology, 16(1), 1-9.

Submitted by: Howard E. Horne, Natural Communities Biologist, Thompson Engineering, Mobile, AL; *hhorne@thompsonengineering.com*

Date of Proposal: 11 December 2023

Transfer *Burhinus bistriatus* (Double-striped Thick-knee) to new genus *Hesperoburhinus*

Note: *This is a modified version of SACC proposal 976, which passed unanimously. The IOU's Working Group on Avian Checklists (WGAC) has also endorsed the new genus.*

Černý and Natale (2022) produced the most comprehensive phylogeny of the Charadriiformes to date. Their supermatrix approach included DNA sequence data (27 loci), 69 morphological characters, and 90% of all charadriiform species. They found that the thick-knee genus *Burhinus* is paraphyletic with respect to Old World *Esacus* (Fig. 1).

Based on those results, Černý et al. (2023) named a new genus, *Hesperoburhinus*, for the two New World *Burhinus* species, one of which (*Burhinus bistriatus*), occurs in the NACC area, and restricted *Burhinus* to Old World species. They further justified naming a new genus based on the great antiquity of the split between the lineages as postulated in their time-calibrated tree: 30+ mya. A set of plumage characters also supported the distinctiveness of *Burhinus*.

Their decription of *Hesperoburhinus* is as follows:

> Diagnosis: A clade of exclusively Neotropical thick-knees characterized by the following autapomorphies: (1) crown plumage coloration pattern comprised of three broad, longitudinal stripes, with black lateral stripes bordering a pale, grey median stripe that subdivides the entire pileum (Livezey, 2009: character states 551:b, 552:d, 553:b, 614:d; Figure 3A, cf. Figure 3B, 3C); (2) rectrices subterminally marked with a narrow transverse bar of white (Livezey, 2009: character state 914:c; Figure 3D, cf. Figure 3E, 3F). The genus can be further distinguished from other Burhinidae by superciliary stripes that extend caudally to the side of the neck (Livezey, 2009: character state 566:g; Figure 3G, cf. Figure 3H, 3I). Additionally, we have identified 55 single-nucleotide synapomorphies that unite the members of the genus and distinguish them from all other Burhinidae, as well as from outgroup species *Chionis albus*, *C. minor* and *Pluvianellus socialis*. These are, for COI: C54T, C69T, A81T, C105T, T111C, A126G, A147G, A220G, C222T, C231A, A252T, A255T, C316T, C372G, A375T, A402C, C453A, A486G, A552C, C567T, C576T, A630C, A642C, A669T; and for RAG1: G122A, T134C, G135A, A146G, T171C, T288C, T309C, G554A, T495C, T588C, A629G, T713C, A763G, C765T, C958T, G1137C, C1144T, A1371C, C1434T, A1548C, A1557G, C1677G, A1920T, A2025G, A2292G, T2343C, C2361T, T2434C, G2673A, G2793A, G2862A.
>
> Type species, by original designation: *Charadrius bistriatus* Wagler, 1829.
>
> Referred species: "*Oedicnenus*" (= *Oedicnemus*) *superciliaris* Tschudi, 1843.
>
> New combinations: *Hesperoburhinus bistriatus* (Wagler, 1829); *Hesperoburhinus superciliaris* (Tschudi, 1843).
>
> ZooBank LSID for genus: A9C859C6-090A-4734-AEEF-E91E5D105F82

Here is their tree:

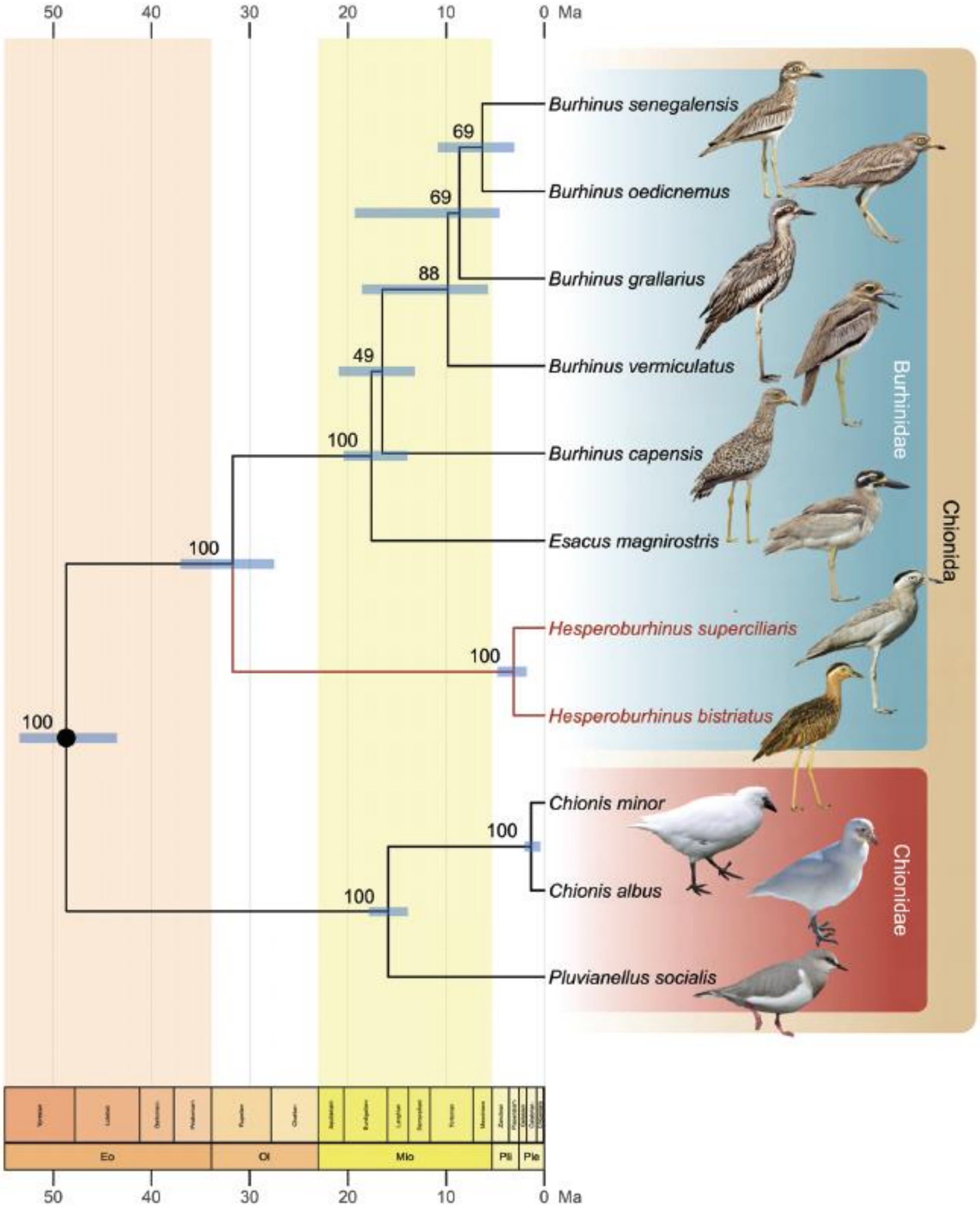


Figure 1. Time-scaled total-evidence phylogeny of thick-knees and their closest relatives, redrawn after Černý & Natale (2022). The genus *Hesperoburhinus* is highlighted with dark red branches and tip labels. Numbers above nodes indicate bootstrap support values; blue bars denote 95% node age confidence intervals derived from penalized-likelihood rate-smoothing of 1000 bootstrap pseudoreplicates. The black circle at the root denotes a fossil calibration associated with the corresponding node. Shaded tabs to the right of tip labels indicate suprageneric clades; background colours identify geochronological epochs. Abbreviations: Ma = million years ago; Eo = Eocene; Ol = Oligocene; Mio = Miocene; Pli = Pliocene; Ple = Pleistocene. Bird photo credits and licensing information from top to bottom: Frans Vandewalle (Flickr, CC BY-NC 2.0), Artemy Voikhansky (Wikimedia Commons, CC BY-SA 4.0), Cédric Larouche (Flickr, CC BY-NC-SA 2.0), Bernard Dupont (Flickr, CC BY-SA 2.0), Bernard Dupont (Flickr, CC BY-SA 2.0), John Harrison (Wikimedia Commons, CC BY-SA 4.0), Nick Athanas (Flickr, CC BY-NC-SA 2.0), Nick Athanas (Flickr, CC BY-NC-SA 2.0), "Nweider" (Wikimedia Commons, CC BY-SA 4.0), Murray Foubister (Flickr, CC BY-SA 2.0), Brendan Ryan (Flickr, CC BY-NC-SA 2.0).

Discussion:

I personally do not like combining genetic and morphological data – I prefer using the genetic data alone to construct the phylogeny and evaluating morphological differences separately. However, in Černý and Natale (2022; Figures 4 and 5 in the paper), analyses of the genetic data alone produced similar results. I favor a YES vote on this proposal even without the issue of paraphyly because the split between *Hesperoburhinus* is older than that between the sheathbills (Chionidae) and Magellanic Plover (Pluvianellidae) families and certainly much, much older than estimated divergence times in bird genera as a whole. Recognizing *Hesperoburhinus* emphasizes the comparatively slow morphological evolution in this group. Regardless of one's views on the use of lineage age for defining higher categories, the issue of paraphyly with *Esacus* requires a change. This solution is preferable to an expanded *Burhinus* that would merge extralimital *Esacus* into an expanded *Burhinus*, especially because we would be meddling with a genus that is not in the NACC area.

As an aside, Černý et al. also noted the problem of homonymy in an expanded *Burhinus* that would force a change in species names as a reason to maintain those two genera separately; see their paper for details. Looking at the support values in their tree, the minimal divergence between *Esacus* and *Burhinus* s.s. (shortest branch by far of any in the tree in Fig. 1 above), and the great similarity between the plumage and morphology of *Esacus* and *Burhinus* s.s., I would argue that the former should be merged into the latter, regardless of consequence to nomenclature. All analyses in Černý and Natale (2022), however, showed that *Burhinus* s.s was indeed monophyletic with respect to *Esacus*, so assigning generic limits are subjective. Nevertheless, retaining *Esacus* just to avoid the homonymy seems to me to be a classic case of "the tail wagging the dog." Regardless, it does not affect the recognition of *Hesperoburhinus* based on the rather amazing antiquity of that lineage (early Oligocene!), which rivals divergence times between many sister families, not just Chionidae and Pluvianellidae. To add some perspective, if the estimated divergence times are even close to being correct, that means that the New World and Old World lineages were already evolving separately when elephants still had not evolved trunks, when the huge pig-like entelodonts were part of the megafauna, when massive pelagornithids were present, when phorusracoid birds were apex predators in South America, and so on.

A YES vote would endorse *Hesperoburhinus* for *Burhinus bistriatus*. A NO vote means retaining *Burhinus* but implies merger of *Esacus* into *Burhinus* regardless of consequences to nomenclature.

Thanks to David Černý for corrections and input on the first version of this proposal.

Selected references:

Černý, D. and R. Natale. 2022. Comprehensive taxon sampling and vetted fossils help clarify the time tree of shorebirds (Aves, Charadriiformes). Molecular Phylogenetics and Evolution 177: 107620.

Černý, D., P. van Els, R. Natale, and S. M. S. Gregory. 2023. A new genus-group name for *Burhinus bistriatus* (Wagler, 1829) and *Burhinus superciliaris* (Tschudi, 1843). Avian Systematics 1: 31–43.

Submitted by: Van Remsen

Date of Proposal: June 2023, modified by Terry Chesser on 15 December 2023

Comments from SACC:

Comments from Stiles: "Definitely YES for recognizing *Hesperoburhinus*- the evidence seems very solid. The problem regarding *Esacus* as separate from *Burhinus* s.s. is for those working with Old World birds to resolve, and does not affect recognition of *Hesperoburhinus*."

Comments from Robbins: "I vote YES for erecting a new genus *Hesperoburhinus* for the two New World *Burhinus* species based on the Cerny & Natale results. As Gary points out, the *Esacus*-Old World *Burhinus* issue is beyond our committee's purview."

Comments from Areta: "YES. If the impressive age of the node uniting the South American taxa to other Burhinidae is to be trusted, and given the placement of *Esacus* (which might or might not be worth of recognition), I am fine with recognition of *Hesperoburhinus* for *superciliaris* and *bistriatus*. I tend to look with skepticism at "total evidence" trees, when the signal of the different characters has not been analysed separately."

Comments from Del-Rio: "YES because of the node date, but I would love to see phylogenetic trees with genomic data."

Comments from Claramunt: "YES. I think Černý et al. present sufficient arguments for separating the South American species into their own genus. The problem of the paraphyly of the traditional *Burhinus*, combined with nomenclatorial issues, and levels of divergence, results in a compelling case. Divergence times may be overestimated; my own (unpublished) estimates are around 22Ma, but still old for a genus. But solving the paraphyly plus the fact that *Hesperoburhinus* is perfectly diagnosable, are more important arguments. My only complaint is the name itself: it's too long. But we cannot do anything about it. My appeal to people coining new names: take into account that some of us actually use scientific names for oral communication."

Comments from Zimmer: "YES, for all of the reasons stated in the Proposal. As noted by Santiago, regardless of any questions over the apparent divergence times, this move solves the question of paraphyly of *Burhinus* with respect to *Esacus* no matter which course is ultimately adopted by Old World committees (maintain *Esacus* or merge it into an expanded Old World *Burhinus*), and *Hesperoburhinus* is readily diagnosable."

Comments from Lane: "YES"

Revise the taxonomy of the Sharp-shinned Hawk complex: Split mainland *Accipiter velox* from Caribbean *A. striatus*

Background:

Sharp-shinned Hawk (*Accipiter striatus*) is a widespread small raptor found throughout North America, Central America, the Caribbean, and parts of South America. Ten subspecies are recognized by most authorities and are usually divided into 3 main groups: northern *striatus*, white-breasted *chionogaster*, and rufous-thighed *erythronemius*. Across this broad distribution and these different subspecies, there is extensive variation in plumage, differences in ecology, and possibly differences in behavior (Bildstein et al. 2020). Given this variation, Sharp-shinned Hawk as it is currently recognized on the *Check-list* has at times been considered up to four distinct species, although it is more typically regarded as consisting of the three groups mentioned above. Three of the four main global checklists recognize a single species within the Sharp-shinned Hawk species complex, but the IOC Checklist currently recognizes four species: *A. striatus*, *A. chionogaster, A. ventralis,* and *A. erythronemius* (Gill et al. 2023), following the treatment of Ferguson-Lees and Christie (2005).

In the Caribbean, three subspecies of Sharp-shinned Hawk are recognized: *Accipiter striatus striatus* from Hispaniola, *A. s. fringilloides* from Cuba, and *A. s. venator* from Puerto Rico (Ferguson-Lees and Christie 2005, Dickinson and Remsen 2013, Clements et al. 2023, Gill et al. 2023). The taxa *striatus* and *fringilloides* have at times been lumped together, but Wetmore (1914) argued that they should be treated as distinct taxa on the basis of morphological differences. These three Caribbean taxa have long been treated as conspecific with, or as part of the same group as, the North American taxa, including *A. s. velox* of North America, *A. s. perobscurus* of Haida Gwaii, *A. s. suttoni* of northern and central Mexico, and *A. s. madrensis* of southern Mexico (Dickinson and Remsen 2013, Gill et al. 2023).

Morphologically, all of the Caribbean taxa are relatively small (Ferguson-Lees 2005), and have significantly lower hand-wing indices (HWI) than North American taxa, an important indicator of dispersal ability (higher HWI corresponds to greater dispersal ability; Catanach et al. 2021). In terms of adult plumage, all have distinctly rufous-brown cheeks, but the underparts vary; *venator* is the most heavily barred below and has distinctly rufous thighs, whereas *fringilloides* is the palest below, with faintly barred thighs, a white belly, and the sides of the upper breast barred with brown; nominate *striatus* is intermediate between the two. The tail of *venator* has sharply defined black bars, whereas the bars on the tail of both *fringilloides* and *striatus* are indistinct.

New Information

Catanach et al. (2021) studied the systematics of the Caribbean taxa of the Sharp-shinned Hawk complex using ultaconserved elements (UCEs), mtDNA sequence data, and SNPs. In the full UCE dataset, 5 Caribbean birds (Puerto Rico, *n* = 3; Hispaniola, *n* = 2) were included with 1 South American (*ventralis*), 1 North American (*velox*), and 1 Central American (*chionogaster*) sample in analyses; in the ND2 dataset, 14 Caribbean birds (Cuba, *n* = 2; Puerto Rico, *n* = 4;

Hispaniola, $n = 8$), 30 North American (*velox*), and 7 South American (*ventralis*) samples were included in analyses. In all genetic analyses (Fig. 1), the Caribbean taxa formed a highly supported monophyletic group that was sister to a clade of North American, South American, and Central American taxa. Within the Caribbean clade, individuals from each island formed monophyletic clades, with *venator* (Puerto Rico) sister to *striatus* (Hipaniola), and these two together in turn sister to *fringilloides* (Cuba). Using mitochondrial sequence data, the Caribbean clade was 1.83% divergent from North American birds, and 2.66% divergent from South American birds.

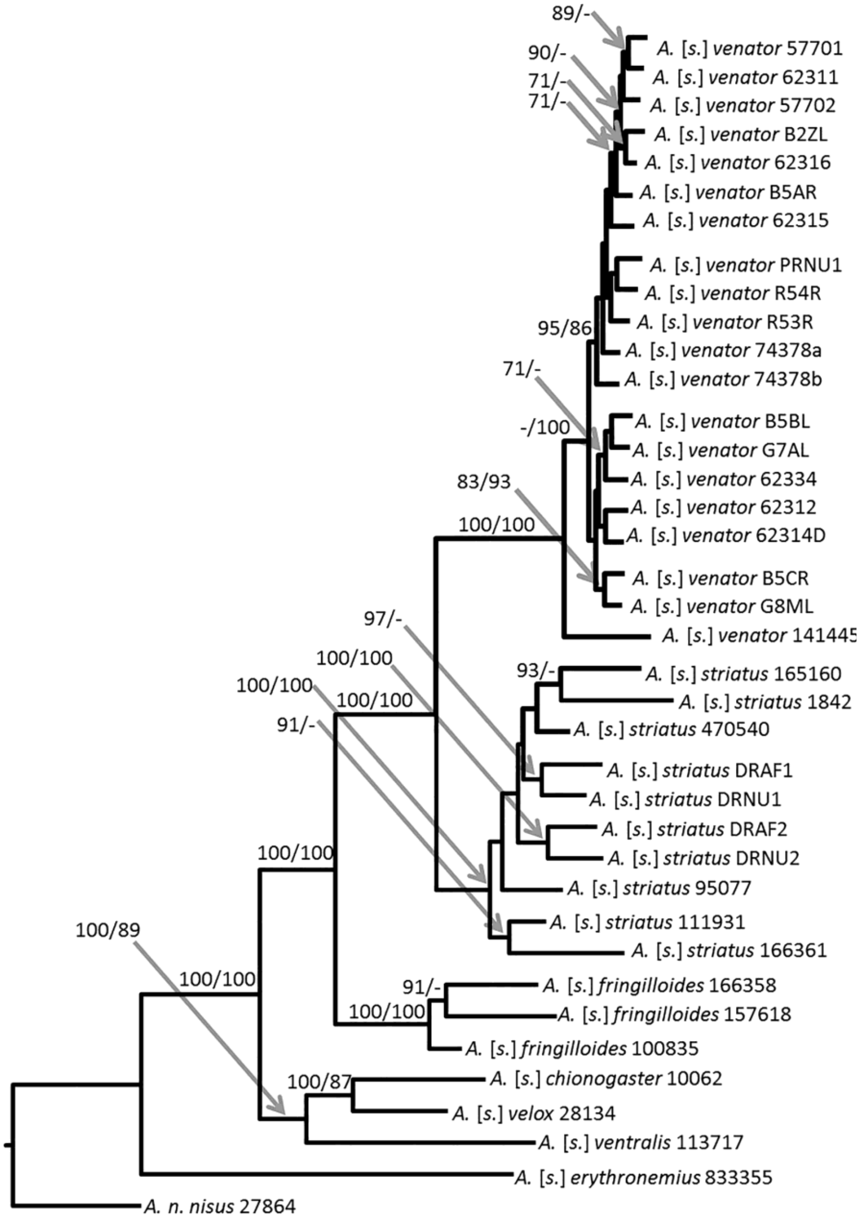


Figure 1. From Catanach et al. (2021), showing the maximum likelihood phylogeny based on the UCE dataset.

Puerto Rican *venator* was 0.68% divergent from *striatus*, and together these two taxa were 1.53% divergent from *fringilloides*. In a sparse non-negative matrix factorization (sNMF) analysis, which calculates admixture and identifies population structure, they found low admixture levels between the Caribbean populations and the mainland, as well as low levels of admixture between islands within the Caribbean.

The ecology and breeding biology of populations in the Caribbean do not appear to be much different from their North and South American counterparts (Delannoy and Cruz 1988, Ferguson-Lees and Christie 2005, Bildstein et al. 2020, Pacheco et al. 2023), although in Puerto Rico and Cuba, the breeding season was much earlier than in North America (Delannoy and Cruz 1988, Pacheco et al. 2023), and in Puerto Rico, the breeding season was much longer than in North America, with a much longer territory establishment/nest-building phase (~90 days versus ~30 days; Delannoy and Cruz 1988). In a study of the breeding biology of hawks in Cuba, Pacheco et al. (2023) did not observe any courtship or display flights as is typical of other populations, but they noted that their field work possibly began after courtship flights were finished; in Puerto Rico, display flights are well known, and it has been noted that these displays do not appear to be significantly different from those of North American populations (Delannoy and Cruz 1988). It should be noted, however, that descriptions of copulations from other populations all describe copulations taking place after a display flight (Delannoy and Cruz 1988, Bildstein et al. 2020), whereas in Cuba, all interactions that led to copulation took place in below the canopy.

Although the breeding biology appears to be very similar between the Caribbean taxa and those in North America, Catanach et al. (2021) did not find evidence for a recent history of gene flow between North American and Caribbean populations, with Caribbean populations each representing distinct monophyletic clades with unique mtDNA haplotpyes that were not shared with any other population (Fig. 2). While unlikely, there could be opportunities for North American Sharp-shinned Hawks to interbreed with Caribbean birds, as birds from North America do occasionally occur in the Caribbean (Wallace et al. 1996, Catanach et al. 2021), although migrant individuals from North America typically occupy lower elevation habitats than resident birds, which breed in higher elevation forests.

Recommendation

The Sharp-shinned Hawk complex is extremely variable in terms of plumage and is widely distributed from North to South America. As others have recognized in the past, these very distinctive taxa may represent distinct species (e.g., Sibley and Monroe 1990, Bierregaard 1994, Ferguson-Lees and Christie 2005, Gill et al. 2023). Catanach et al. (2021) analyzed UCE, SNP, and mtDNA and found that the Caribbean taxa (*striatus*, *venator*, and *fringilloides*) represented a monophyletic clade that was sister to a clade of mainland populations (North America, South America, and Central America, although the placement of *erythronemius* was not fully resolved); within the Caribbean, each of the three taxa were themselves monophyletic with low to moderate levels of divergence (0.68% between Hispaniola and Puerto Rico, and 1.53%

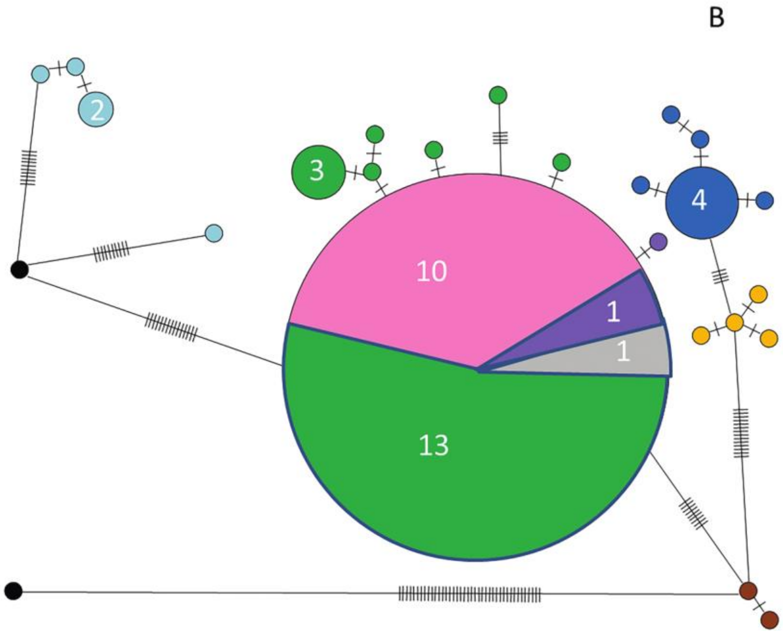


Figure 2. From Catanach et al. (2021), showing haplotype network of the ND2 sequence data, representing South American (light blue, black) samples, North American (green, pink, gray, purple) samples, and Caribbean (brown, yellow, dark blue) samples.

between Cuba and Hispaniola/Puerto Rico). Based on the low levels of admixture, indicating that there are not extensive or even moderate levels of gene flow between either migratory North American and resident Caribbean populations, or between any of the Caribbean populations, as well as diagnosable morphological differences, Catanach et al. (2021) recommended recognizing each of the three Caribbean taxa as distinct species. Although each of the three are diagnosable, I feel that there are similarities across the three taxa, and genetic divergence, especially between Puerto Rico and Hispaniola, is relatively low; further, divergence between Cuba and the other two islands are calculated from only 2 samples of *fringilloides*, which could bias estimates. For these reasons, I am recommending a YES vote to split the Caribbean populations as a single species with three subspecies from the mainland populations.

Effect on the NACC Region

Splitting the Caribbean populations of Sharp-shinned Hawk would result in one additional species on the AOS Check-list. Because the type locality of *striatus* is Hispaniola, the Caribbean Sharp-shinned Hawk would retain the name *Accipiter striatus*. The oldest available name for the mainland populations is *velox* (Wilson, 1812), which is the subspecies widely distributed across most of North America (type locality near Philadelphia).

If the committee votes to adopt this change, a separate proposal would be needed for English names.

References

Bildstein, K. L., K. D. Meyer, C. M. White, J. S. Marks, and G. M. Kirwan (2020) Sharp-shinned Hawk (*Accipiter striatus*), version 1.0. In Birds of the World (S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. http://doi.org/10.2173/bow.shsaw.01

Catanach, T. A., M. R. Halley, J. M. Allen, J. A. Johnson, R. Thorstrom, S. Palhano, C. Poor Thunder, J. C. Gallardo, and J. D. Weckstein (2021) Systematics and conservation of an endemic radiation of *Accipiter* hawks in the Caribbean islands. Ornithology 138: 1-23.

Delannoy, C., and A. Cruz (1988). Breeding biology of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*). Auk 105:649-662.

Ferguson-Lees, J., and D. Christie (2005) Raptors of the World. Helm Field Guides.

Gill, F., D. Donsker, and P. Rasmussen, Editors (2023) IOC World Bird List (v. 13.2). DOI 10.14344/IOC.ML.11.1

Pacheco, N. N., R. J. Lara, W. N. Méndez, J. C. L. Montero, N. C. Lobaina, and C. H. Peraza (2023). Primer registro de nidificación del Gavilancito Cubano (*Accipiter striatus fringilloides*) y nuevos datos sobre su biología reproductive y distribución. Journal of Caribbean Ornithology 36:135-146.

Sibley, C. G., and B. L. Monroe (1990) Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut.

Wallace, G. E., H. G. Alonso, M. K. McNicholl, D. R. Batista, R. O. Prieto, A. L. Sosa, B. S. Oria, E. A. H. Wallace (1996). Winter surveys of forest-dwelling Neotropical migrant and resident birds in three regions of Cuba. Condor 98(4):746-768.

Submitted by: Shawn M. Billerman, Cornell Lab of Ornithology

Date of Proposal: 16 December 2023